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ONTOGENETIC AND SEASONAL CHANGES IN WEBS AND WEBSITES OF A DESERT WIDOW SPIDER

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Abstract. Morphometric and nest position variables were used to examine the effects of spider growth and seasonality on webs and websites of the desert widow spider, *Latrodectus revivensis* Shulov (Theridiidae) in the Negev desert of Israel. The form of the web was similar over the full range of spider body sizes. All morphometric variables had strong positive correlations with spider size: larger spiders occupied larger nests in larger shrubs. However, nest characteristics were more highly correlated with spider size than were website characteristics. When the effect of spider size was removed by regression, more than 75% of the remaining variance consisted of correlated variation in three groups of variables relating to (1) website characteristics (48%), (2) nest characteristics (18%) and (3) capture web placement (12%). Most nest and website variables showed effects of seasonality that were independent of spider size, and may be related to the thermal regime in the nest. The results indicate that the relative quality of potential websites changes seasonally and with spider growth. We suggest that the costs of relocating a web outweigh the advantages of reaching a new website, with the result that spiders remain for some time in websites which have become less suitable.

The habitat requirements of many organisms change as they age, resulting in a shifts of their "ontogenetic niche" (Werner & Gilliam 1984). Ontogenetic changes in habitat may involve changes in living sites, in food requirements or in other factors which scale with body size. Such size-related changes in habitat requirements may have particularly important fitness consequences for sedentary animals for which the possibilities of moving to new sites may be limited (e.g., Shachak & Brand 1983).

Web-building spiders are relatively sedentary predators (Janetos 1986). In most species the web is primarily a prey-capture device whose location and structure reflect the local distribution of prey (Riechert & Luczak 1982; Janetos 1986; Riechert & Gillespie 1986). Thus, studies of website requirements have focused mainly on the effects of prey abundance (e.g., Turnbull 1964; Gillespie 1981; Olive 1980, 1982; Vollrath 1985). The changing requirements of developing spiders are also likely to affect web structure and website selection (Enders 1975; Vollrath 1987). However, these have not been examined systematically, and it is not known to what extent changes in web and website characteristics are due to growth, seasonal factors or other effects.

In this study, we use morphometric and nest position variables to characterize ontogenetic and seasonal changes in the webs and websites of the desert widow spider *Latrodectus revivensis* Shulov. Statistical analysis of these data allows us to separate the variation in web and website characters due to spider sex, size, season, and other factors. In addition, we examine the patterns of covariation among the morphometric variables and their relationships with spider size.

NATURAL HISTORY AND METHODS

Natural history.—*Latrodectus revivensi* (Theridiidae) is known only from the Negev desert of Israel (Levi & Amitai 1983). Females mature in spring or summer (March to August) an produce eggsacs throughout the summer and autumn (May to September; Levy and Amitai 1983 Incubation time is about one month. Some youn emerge in mid- to late summer and overwint as juveniles. In other instances, eggs remain

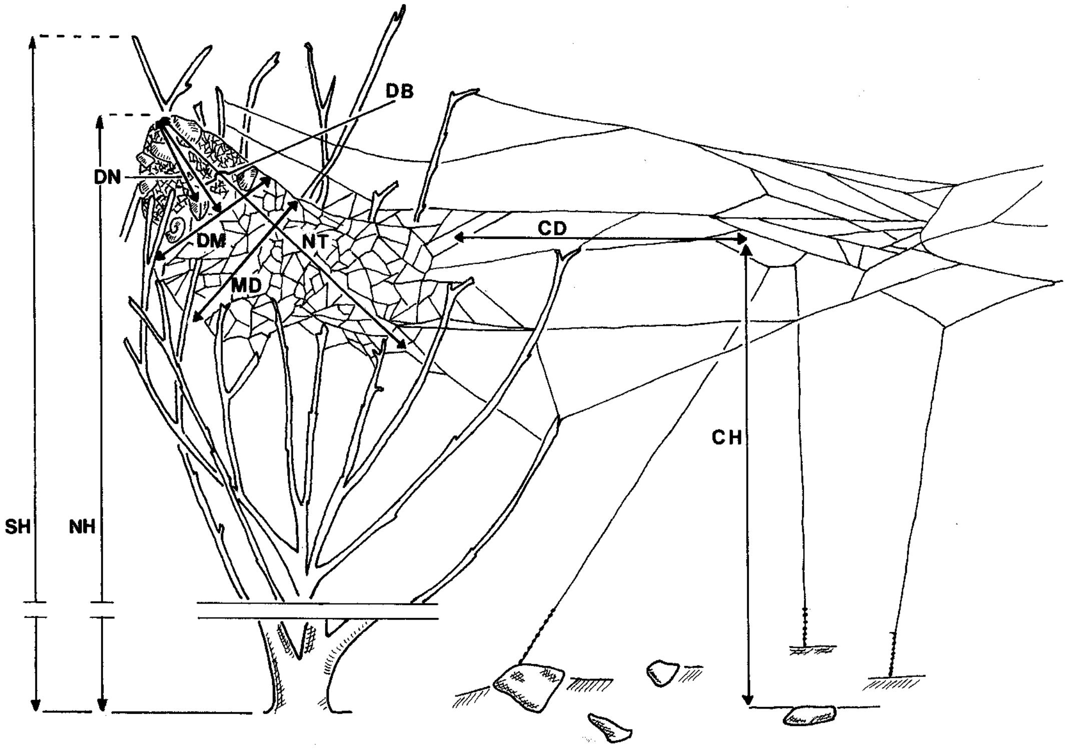

Figure 1.—Schematic drawing of the web of *L. revivensis,* showing (a) website and (b) nest variables measured in this study. NH = nest height, SH = shrub height, CD = distance from the nest to the capture web, CH = height of the capture web, NT = total nest length, DN = length of dense silk layer, DB = length of debris layer, DM = nest diameter at edge of debris layer, MD = maximum nest diameter.

the eggsac over the winter and the young emerge the following spring.

Webs of *L. revivensis* are durable and long-lasting structures which may persist for up to several months (Zilberberg 1988). The web consists of separate nest and prey-capture components (Shulov 1948; Szlep 1965; Fig. 1). The nest, built in a shrub, is connected by strong bridging threads of variable length (a few centimeters to over a meter) to a horizontal silk platform. The platform is usually placed over an area of bare ground beyond the edge of the shrub, and an array of sticky capture threads is suspended from the platform to the ground.

The nest of *L. revivensis* consists of a curved, silk cone (Fig. 1). The top of the cone is covered with a dense silk layer, while the lower section is a more open mesh. In addition, the nest top is covered with scattered debris which may include sand, pebbles, snail shells and feces, plant material, exuviae and remains of prey. The dense silk and debris layers are usually sparse or absent on new nests, but may completely obscure the upper half of an old nest.

The spiders are active at night and remain concealed in the nests during the day. Nocturnal activities include web repairs, renewal of the sticky, capture threads and prey capture. Web relocation also takes place at night.

Study area.—The study site was located on the rocky slopes of the Halukim Ridge, near Sede Boqer (30°50′N:34°46′E) in the central Negev region of Israel. The ridge runs north–south and is dissected laterally by dry watercourses producing a relief of about 50 m. The area is arid with highly variable winter rains (about 100 mm annually) and is sparsely vegetated with a permanent shrubland (Evenari et al. 1982). Nests of *L. revivensis* occurred in several shrub species, including *Zygophyllum dumosum, Artemesia herba-alba, Reaumuria negevensis, Noaea mucronata,* and *Hammada scoparia,* and sometimes in clumps of annuals (e.g., *Reboudia pinnata*) and grasses.

The study area was approximately 20 hectares of a north-facing slope of a small wadi. To reduce the effects of habitat heterogeneity, we limited our search for spiders to the lower portion of the slope, from the edge of the wadi bed to a rocky outcrop about 50 m up the slope (Shivta and colluvial formations; Olsvig-Whittaker et al. 1983).

Web and website measurements.—We located and individually flagged and mapped webs. Webs and websites were characterized with the following measurements (Fig. 1): height of the nest, height of the shrub, height of the capture platform and its distance from the nest, total nest length, length of the dense silk layer, the maximum length of the debris covering, nest diameter at the lower edge of the debris layer and maximum nest diameter. We also determined the compass orientation of the nest opening (nest aspect) and the quadrant of the shrub in which the nest was located (NE, NW, SE, SW). A total of 350 nests and 226 spiders were sampled in this manner between January and August 1987 and March and August 1988.

Spiders in occupied webs were sexed, classified as juvenile, subadult or adult, and measured for total body length and length of the tibia + patella of leg IV. For all statistical analyses, we used body length as a measure of spider size because of convenience of measurement in the field. Body length includes the expandable abdomen and may be influenced by spider condition (Anderson 1974), unlike the more rigid cuticle of the leg segments which does not change size during an instar (Miyashita 1968). However, body length was closely correlated with the length of the tibia + patella in *L. revivensis* ($r^2 = 0.92$, $n = 211$), suggesting that for *L. revivensis*, spider condition did not significantly affect the length of the abdomen.

Statistical analyses.—Comparisons between each pair of morphometric variables were made using standard regression (linear or polynomial) and correlation analyses. To remove heteroscedasticity, the dependent variable of each analysis was transformed using the Box-Cox family of power transformations with maximum-likelihood choice of parameters (Ruppert 1989; Krebs 1989).

Patterns of covariation among morphometric variables were examined by principal components analysis (PCA; Joliffe 1986). We calculated the variances and pairwise covariances of all variables. We used pairwise rather than listwise deletion of missing values; although the results of the two methods were nearly identical, listwise deletion greatly reduced the sample sizes for each covariance. PCA identifies a sequence of uncorrelated "components" (axes) which are linear combinations of the original variables. The first axis is chosen to "explain" as much as possible of the variance in the data, the second axis explains as much as possible of the remaining variance, and so on.

We applied PCA to a correlation matrix of the raw data and of the Box-Cox transformed data (Joliffe 1986). To determine the extent to which spider size alone was the basis of these correlations, we removed the effect of spider length by regression: each value was replaced by its residual deviation from a regression on spider length. Quadratic, rather than linear, regression was used in order to stabilize variances. We then applied PCA to the covariance matrix of the residuals. PCA of the covariance matrix of residuals is useful in this case, because the variables themselves had already been standardized to equal variance by the data transformations. Consequently, high variance of the residuals indicates a weak correlation with spider length.

RESULTS

Males and females.—Our measurements of male's webs were restricted to those of juveniles. Adult males often remained in their own juvenile webs ($n = 17$), built small nests lacking capture webs attached to nests of females ($n = 5$), shared nests of adult or juvenile females ($n = 26$ and 4, respectively) or occupied abandoned nests of females ($n = 4$).

Webs of juvenile males and females differed significantly in all morphometric variables except distance from the nest to the capture web. However, when we eliminated the difference in size between males and females by comparing only females of sizes equivalent to juvenile males (≤ 6.5 mm body length, Fig. 2), these differences disappeared. Therefore, web and website characteristics of juvenile males and females were treated as a single data set.

Effects of spider length.—The total body length of spiders in our sample ranged from 1.8–16.8 mm ($\bar{x} = 7.9$, SD = 3.8, $n = 246$ spider measurements; Fig. 2). In the following regression analyses, spider length is treated as an error-free independent variable (Snedecor & Cochran 1967), because the errors in measuring spider length were small and independent of spider length over

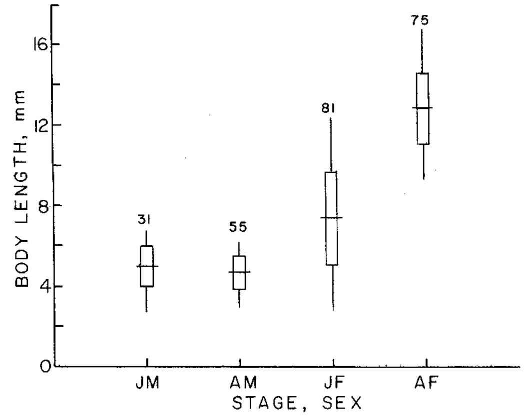

Figure 2.—Total body lengths (in mm) of *L. revivensis* used in the study: boxes show the means (center lines) and one standard deviation and vertical lines show ranges for juvenile and adult males (JM and AM, respectively) and for juvenile and adult females (JF and AF, respectively). Juvenile males were all subadults; juvenile females included all immature and subadult stages.

the range of sizes encountered ($r^2 = 0.04$, $P > 0.1$; based on 5 replicate measurements of each of 29 spiders). Pooling all measurements, the standard deviation of the measurement error was 0.23 mm (95% CI: 0.19–0.29 mm), which is much smaller than the standard deviation of spider length in our full data set (SD = 3.84 mm, n = 252 spiders).

Table 2.—Allometric regression equations for nest morphometric variables: $\ln y = a_0 + a_1 \ln x$, where x = nest total length. All regressions are significant at $P < 0.001$ (H_0: $a_1 = 0$).

Variable	n	r^2	a_0	a_1
Dense silk	290	0.67	0.21	0.70
Debris	291	0.79	−0.31	0.91
Nest diameter	287	0.84	−0.65	0.93
Maximum diameter	135	0.83	−0.78	1.01

Spider length explained a significant amount of the variation in all web and website variables (Table 1, $P < 0.001$ in all cases). The amount of variation explained by spider length was higher for variables that describe the nest itself (total nest length, lengths of dense silk and debris layers, and nest diameters) than for variables associated with nest placement in the shrub (shrub height and nest height) or with the capture web (height and distance from the nest).

Nest placement and allometry.—The height of the nest in a shrub was closely correlated with shrub height. Over the entire range of shrub heights of 15 to 122 cm, nest height was approximately ⅔ of shrub height (r^2 = 72.7%, n = 318). The allometric equation, **nest height = 0.69(shrub height)$^{0.98}$**, only slightly improved the amount of variance explained by shrub height (r^2 = 73.0%).

Variation in the length of the debris layer, nest diameter and maximum nest diameter can be described by allometric regressions on total nest length (Table 2). The length of dense silk increased linearly up to nest lengths of approximately 75 mm, but did not increase with further increase in nest length. Variation in this character was best described overall by the allometric equation, **dense silk length = 0.2(total nest length)$^{0.7}$** (r^2 = 0.67).

Table 1.—Regression equations for the effect of spider length on nest and website morphometric variables. The slopes of all of the regressions are significantly different from zero ($P < 0.001$). The equations are of the form: $y^\lambda = a_0 \pm a_1 x + a_2 x^2$, where x = spider length.

Variables	n	r^2	λ	a_0	a_1	a_2
WEBSITE						
Nest height	177	0.27	0.18	1.62	0.02	0.001
Shrub height	177	0.34	0.12	1.44	0.01	0.0001
Capture web distance	142	0.21	0.11	1.32	−0.004	0.0009
Capture web height	46	0.52	−0.06	0.89	−0.006	0.0001
NEST						
Nest length	175	0.85	0.47	1.74	0.88	−0.025
Dense silk length	172	0.66	0.19	1.2	0.13	−0.005
Debris length	173	0.76	0.27	1.27	0.23	−0.008
Nest diameter	171	0.90	0.14	1.14	0.07	−0.002
Maximum diameter	109	0.92	0.18	1.12	0.13	−0.004

Table 3.—Correlations among website and nest variables. Correlations based on the raw data are shown above the diagonal; below the diagonal are the correlations among residuals, after removing the effect of spider length by regression (see Methods: Statistical analyses). NH = nest height, SH = shrub height, CD = distance from nest to capture web, CH = capture web height, NT = total nest length, DN = length of dense silk layer, DB = length of debris layer, DM = nest diameter. * = nonsignificant correlations ($P > 0.05$).

	NH	SH	CD	CH	NT	DN	DB	DM
NH		0.85	0.64	0.43	0.55	0.32	0.47	0.48
SH	0.81		0.54	0.46	0.63	0.37	0.54	0.56
CD	0.63	0.49		0.31	0.41	0.19	0.42	0.41
CH	*	*	*		0.77	0.39	0.66	0.65
NT	0.25	0.23	*	0.42		0.71	0.87	0.91
DN	−0.14	*	−0.22	*	0.37		0.77	0.69
DB	*	*	*	0.27	0.46	0.57		0.87
DM	*	*	*	*	0.45	0.42	0.48	

Covariation of web and website variables.—All variables were significantly and positively correlated with each other (Table 3; $P < 0.01$, except for the height of the capture web against its distance from the nest, $0.02 < P < 0.05$). The residuals had fewer significant correlations and some negative correlations, indicating that many correlations in the original variables were due to the effect of spider length on all variables. As a result, PCA of web and website variables using the raw data was not very informative (Table 4). The first axis, which accounted for 63% of the variance, loaded evenly on all variables and simply reflects the positive correlation among the variables; the remaining axes could not be interpreted intuitively.

Clearer patterns were found in PCA of the residuals after removing the effects of spider length. Website variables (nest height, shrub height, and distance to the capture web) accounted for 48% of the residual variance (PCA axis 1, Table 4). The second axis, which loaded mainly on nest-concealment variables (dense silk and debris), accounted for 18% of the residual variance, and the third axis loaded mainly on capture web height (12% of the residual variance). Thus over 78% of the variance in web and website morphometric data may be summarized by four independent axes of variation: spider size and the three clusters of morphometric variables identified by the first three PCA axes.

Seasonal differences in nest and website characteristics.—Climatic conditions in the central Negev differ considerably in winter and summer. There is a "cold season" (November to April; mean monthly temperature 13.4° C, range of

Table 4.—Principal components analysis (PCA) of website and nest variables. The first two PCA axes are shown for the PCA based on the raw data (left side of table) and the first three PCA axes based on analysis of the residuals, after removing the effect of spider length (right side of table). The percent of the variance explained by each axis is shown. Variables are abbreviated as in Table 3.

	PCA axes based on				
	Data		Residuals		
Variable	1	2	1	2	3
% Variance explained	63	16	48	18	12
NH	0.12	0.20	0.32	0.03	−0.07
SH	0.12	0.15	0.27	0.03	−0.10
CD	0.09	0.19	0.28	−0.06	0.10
CH	0.12	−0.05	0.03	0.17	0.41
NT	0.15	−0.07	0.04	0.14	0.03
DN	0.11	−0.15	−0.05	0.25	−0.20
DB	0.14	−0.10	0.01	0.22	−0.05
DM	0.14	−0.08	0	0.10	−0.05

Table 5.—A comparison of spider website and nest variables in "hot" and "cool" seasons. Shown are means and standard deviations of all measurements and probabilities for t-tests performed on the raw data (P_{data}) and on the residuals, after removing the effect of spider length (P_{resid}). SL = spider length, MD = maximum nest diameter; all other abbreviations as in Table 3. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	Cool			Hot				
Variable	Mean	SD	N	Mean	SD	N	P_{data}	P_{resid}
SL (mm)	7.2	2.8	126	8.6	4.5	126	**	—
NH (cm)	20.2	9.7	139	29.1	13.0	180	***	***
SH (cm)	31.7	11.6	140	43.4	18.2	180	***	***
CD (cm)	13.4	7.9	95	28.3	19.9	71	***	***
CH (cm)	12.3	2.7	32	11.1	6.3	16	ns	ns
NT (mm)	55.2	22.4	118	65.8	37.3	178	**	ns
DN (mm)	25.4	10.0	114	19.8	9.2	177	***	***
DB (mm)	31.6	11.8	114	31.9	19.8	178	ns	***
DM (mm)	22.4	9.3	112	26.1	16.3	176	*	**
MD (mm)	29.7	10.9	34	41.1	22.2	101	**	***

means 9.8–18.0° C) and a "hot season" (May to October; mean monthly temperature 23.4° C, range 21.1–25.5° C).

There were statistically significant seasonal differences in most of the morphometric variables, both in the raw data and after removing the effect of spider length (Table 5). In the hot season, spiders were found in taller shrubs, built nests higher above the ground and built capture webs further from their nests. Nest diameter and maximum diameter were both greater in the hot season, but the dense silk layer was shorter in the hot season. Nests were longer in the hot season, but this appears to be the result of the seasonal difference in spider length (Table 5). The height of the capture web did not vary between seasons.

In the hot season, nests occurred more frequently on the east side of shrubs than on the west side ($\chi^2 = 8.85$, $P < 0.005$, $n = 76$ nests), but their distribution with respect to the N–S axis was random ($\chi^2 = 0.47$, $P > 0.1$). In the cold season the distribution of nests with respect to shrub quadrant was random ($\chi^2 = 0.728$, $P > 0.1$, $n = 125$). The orientation of the nest opening was not significantly different from random in both seasons (Rayleigh test; cold season: 106 nests; hot season: 68 nests), nor were there significant differences among webs of juveniles and adults in either season.

DISCUSSION

Scaling of nest and website components.—The form of the web is remarkably constant over the full range of spider sizes, from newly emerged young to adults. Webs of juvenile males did not differ from those of similar-sized juvenile females. Eggsac nests made by some females appeared to be wider and more barrel-shaped than nests made by subadult and juvenile females, possibly to accommodate the large, spherical sacs.

Nest diameter and the lengths of the layers of dense silk and debris all scaled allometrically with total nest length. For linear dimensions of the nest, isometry is the appropriate null model. However, nest dimensions also scale to body size, and the allometric equation ($y = ax^b$) is generally a good descriptor of body size relationships (Peters 1983). Allometric scaling may indicate that a functional relationship exists among the variables which depends on their geometry (LaBarbara 1989).

Both the dense silk layer and the debris provide protection for the spider from predators, whether mechanically or by crypsis (Konigswald et al. 1990). In the initial stages of nest construction, *L. revivensis* builds a thin silk cap, consisting of a few threads only (which will become the top of the nest), and then descends to the ground and carries up bits of debris which it attaches to the top of the cap. Thus, protection from visually-orienting predators is obtained quickly and with a minimal outlay of silk and activity, both of which are energetically expensive (Lubin 1973; Prestwich 1977). If the spider remains at that website, both debris and dense silk are added to the nest on successive nights.

Nests in the hot season had proportionately shorter lengths of dense silk relative to the debris layer. This may be related to the thermal regime within the nest. Temperatures during the day inside the dense-silk portion of the nest were consistently higher than in the lower, open mesh portion of the nest, due to the greater flow of cool air through the open mesh portion than through the dense silk (Lubin et al. unpubl.). By increasing the size of the debris layer without a concomitant increase in the dense silk, shade and protection are provided without reducing airflow through the nest.

Nests were generally placed ⅔ of the way up the shrub, but were located significantly higher in the hot season than in the cold season. The portion of the shrub above the nest can provide substantial shade and concealment from visual predators (Konigswald et al. 1990). In summer, spiders place their nests higher in shrubs (and in taller shrubs), perhaps in order to take better advantage of convective cooling. The placement of large nests in large shrubs is intuitively obvious, as small shrubs may provide insufficient support and cover for large nests. It is less clear why small nests are not found in large shrubs. Given the tendency for nests to be built ⅔ of the way up in shrubs, the upper branches of large shrubs may be unsuitable (e.g., too widely spaced) for suspending small nests.

Somewhat surprisingly, nest openings were random with respect to compass orientation both in summer and winter. In open habitats, a diurnal orb-weaver, *Micrathena gracilis* (Walckenaer), was shown to orient its web to reduce exposure to direct insolation (Biere & Uetz 1981). Similarly, the funnel openings of a desert agelenid, *Agelenopsis aperta* (Gertsch) tend to face north in summer (Riechert & Tracy 1975). Both species, however, were exposed regularly to direct solar radiation, the former while sitting on its web and the latter while basking and hunting. *Latrodectus revivensis* is mainly nocturnal and does not bask.

Sources of variation in web and website characteristics.—The sources of variation in web and website characteristics separate into three main components: (1) spider size, (2) seasonal effects and (3) residual variation. All morphometric variables had strong positive correlations with spider size: larger spiders occupied larger nests in larger shrubs. Nest-size variables were more tightly correlated with spider length than were website or capture web variables. Seasonal differences accounted for some variation in most web and website characters after removing the effect of spider length.

Nearly half of the variance not accounted for by spider length or by seasonal effects consists of correlated variation in website and capture web characteristics (residual PCA axis 1). An additional 18% was attributed to correlated variation in nest characteristics (axis 2). Distance to the capture web was a component of axis 1; thus, a larger shrub is associated with a greater distance to the capture web. However, the variation in the height of the capture web was also identified as a separate component of the PCA (axis 3). We conclude that the capture web and nest are relatively independent structures, and factors affecting capture web and nest placement may differ.

The residual variance in websites not accounted for by either spider size or seasonal effects may be due to imprecise site selection (see Janetos & Cole 1981), or to other factors that we did not measure. Such factors may include: variation in body condition, hunger and reproductive status of the spider, spatial and temporal variation in food supply. Riechert (1974) documented the importance of relatively short-lived phenomena (e.g., the presence of flowers and other insect attractants) in explaining the distribution of a desert web-building spider, *Agelenopsis aperta* (Agelenidae), and showed that such cues may influence the choice of a website (Riechert 1985). In orb-weaving spiders, which may relocate their webs frequently, site selection and movement have been correlated with the availability of web supports (Enders 1975; Hodge 1987a), the degree of disturbance to webs (Hodge 1987b) and food availability (Olive 1982; Vollrath 1985).

The residual variance in nest characteristics may reflect differences in site quality, for example, in the thermal regimes prevailing in different shrubs or the presence of suitable debris for nest concealment. The amounts of dense silk and debris might vary with immediate needs for crypsis against a heterogeneous background, or in response to the perceived risk of predation. In some orb-web spiders, variable development of stabilimenta (lines or zigzags of dense silk in the orb; Robinson & Robinson 1970) and of other web "decorations" (e.g., bits of debris) has been correlated with their degree of exposure to visual predators (Eberhard 1973; Lubin 1975, 1986).

These results suggest that the relative quality of different websites changes seasonally and with the spider's ontogeny. Changes in nest requirements can be accommodated by modification of the existing nest or the construction of a new nest at the same site, but changes in website requirements may necessitate moving to a new site. While nests are modified regularly and are therefore tightly correlated with spider size, the large variation observed in shrub and capture web characteristics suggests that the spiders remain for some time in websites that have become less suitable. Nonetheless, website relocation occurs several times in the spider's lifetime (Zilberberg 1988) and the choice of new websites is influenced by the spider's size and by the time of year. The decision to move to a new website may reflect a trade-off between the advantages of reaching a more suitable website and the costs of relocating, such as an increased risk of predation and the energetic costs of movement and web construction.

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