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SPIDER HABITAT SELECTION: AN EXPERIMENTAL FIELD TEST OF THE ROLE OF SUBSTRATE DIAMETER

Spider habitat selection is influenced by a variety of biotic and abiotic factors including the architectural attributes of the habitat (Duffey 1966; Turnbull 1973; Colebourn 1974; Greenquist & Rovner 1976; Riechert & Gillespie 1986; Uetz 1991). Architectural attributes include the size, shape, and spatial arrangement of substrate used by spiders. In the shrub-steppe ecosystem of northern Utah, four studies of spider architectural preferences have focussed on aspects of the latter factor, spatial arrangement of substrate. Substrate height was investigated by Abraham (1983) who sampled three different strata for spiders: the ground surface (0 cm high), herbaceous vegetation (< 25 cm high), and shrubs (37–73 cm high). She found that a pursuing guild of spiders dominated the ground stratum, an ambushing guild dominated the herb stratum, and jumping and trapping guilds dominated the shrub stratum. Substrate density was studied experimentally by Hatley & MacMahon (1980) who clipped branches from *in situ* sagebrush shrubs to create low density substrate and tied branches together to create high density substrate. In comparison to control shrubs, there were more spider species and foraging guilds in high density shrubs. Densities of ambushers and trappers were significantly higher in tied shrubs. Substrate orientation was studied by Robinson (1978, 1981). He constructed habitat modules made of chicken-wire cubes strung internally with several configurations of natural jute rope and placed them into a shrub-dominated habitat. Robinson (1981) reported that the most common jumping spider (*Pellenes hirsutus* (Peckham and Peckham)) preferred vertical substrate whereas the most common trapper (*Theridion petraeum* L. Koch) and an ambusher (*Xysticus montanensis* Keyserling) preferred horizontal substrate.

Here, I focus on an architectural attribute that has not been previously tested for spiders, substrate size. I hypothesize that narrow-diameter substrate may provide acceptable structure for web attachment points for some spiders and may be less conspicuous to potential prey. Wide-diameter substrate may improve the efficiency of movements by spiders that rely on swift running or precise jumps to capture prey (Foelix 1982) as found by Sinervo & Losos (1991) for lizards. Wide substrate may improve concealment of some sit-and-wait hunters (Wing 1984) and protect some spiders from their numerous predators (Wise 1993). It may also shield non-web-dwelling spiders from incident radiation and wind, factors known to influence arid-land spiders (Riechert & Tracy 1975).

I tested the null hypothesis that spider colonization is independent of substrate diameter using two sets of artificial habitat modules following Robinson (1978, 1981). Artificial modules have an advantage over natural vegetation in that all architectural variables can be experimentally controlled. The modules I used were strung in the same configuration with equivalent amounts of either narrow jute rope or wide jute rope. Both sets of modules were simultaneously exposed to field conditions for colonization by spiders. Counts of spiders from each treatment were then compared using a contingency table analysis that tested for independence between spider identity and substrate diameter.

The field site used for this study is in Mill Hollow, Cache County, Utah, 5.8 km northeast of Canyon Road along U. S. Highway 89. Located on U. S. Forest Service land at 41° 42′ 45″ N, 111° 42′ 45″ W, the site is part of a gently dipping terrace associated with Pleistocene Lake Bonneville at an elevation of 1707 m. It lies approximately 3 km south of the Green Canyon field site used by the four Utah studies discussed earlier, which has since been developed and was unavailable. Mill Hollow has a plant community similar to Green Canyon, consisting of big sagebrush shrubs (*Artemisia tridentata* Nutt. spp. *vaseyana*), bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Love), and bulbous bluegrass (*Poa bulbosa* L.). A 50 m × 120 m plot was established, bordered on all sides by at least 25 m of similar vegetation to minimize edge effects. The plot was divided into 60 grid cells, each 10 m square.

I constructed spider habitat modules from chicken-wire formed into cubes 30 cm on a side, following Robinson (1978, 1981) (Fig. 1). Fifteen

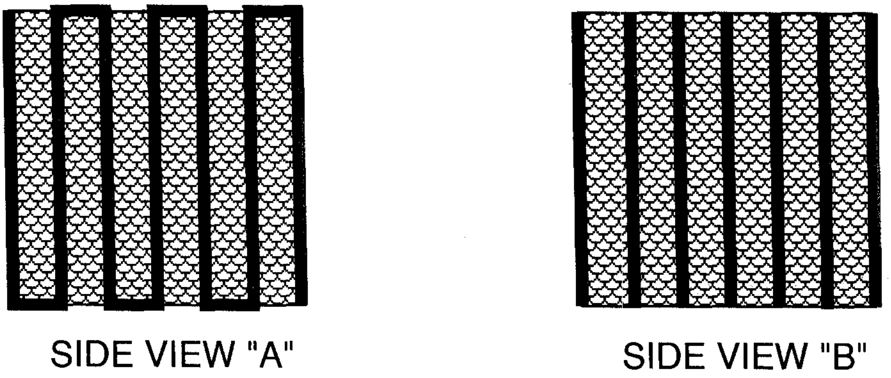

Figure 1.—Two side views of the module design used in this study (after Robinson 1978, 1981), showing the arrangement of seven strands of evenly spaced natural jute rope. Modules are cubes formed from chicken-wire and measure 30 cm on a side. One set of modules contained 2 mm diameter jute (narrow), whereas the other set contained 7 mm diameter jute (wide).

modules were strung internally with 2 mm diameter jute rope; another 15 were strung with 7 mm diameter jute. Based on my observations of vegetation at the field site and the morphologies of spiders collected from grass and sagebrush, I posited that these diameters would represent a sufficient contrast to elicit different responses by spiders. The slightly rough texture of jute (a natural fiber) corresponds better to natural vegetation than other possible experimental substrates (e. g., nylon or wooden dowels). All modules were strung to the same tension with the same amount of jute and in the same configuration, so that the only architectural parameter that varies between the two treatments is substrate diameter. The design used is only one of many possible configurations, but is field-tested and known to be acceptable habitat for at least 33 species of shrub-steppe spiders (Robinson 1978). The prevalence of vertical substrate may have favored colonization by jumping spiders in both module types (Robinson 1981).

Each habitat module was randomly assigned to one of 30 grid cells, and placed on the ground at the center of the cell for each trial. Modules were initially placed on 8 May 1991 and sampled for spiders eight times through 23 September 1991. I attempted to follow Robinson's (1981) recommendation for a 14-day sampling interval to maximize spider abundance on modules, but due to weather, sampling intervals in this study were slightly longer (range = 15–17 days). Modules were sampled using a beating-sheet technique (Southwood 1978) and visually inspected to assure complete collection of spider colonists.

Spiders were preserved in 70% propanol and identified to species level using a taxonomic key by Kaston (1978) and a reference collection of Utah spiders verified by W. J. Gertsch. Each specimen was also assigned to one of four spider guilds following Hatley & MacMahon (1980) and Wing (1984). These guilds are based on behavioral observations of foraging technique and closely correspond to taxonomic characteristics at the family level. Jumpers (Oxyopidae, Salticidae) actively track prey with advanced visual systems and pounce from large distances (Kaston 1978). Trappers (Araneidae, Dictynidae, Linyphiidae, Tetragnathidae, Theridiidae) are sit-and-wait predators that use silk constructions to capture prey (Turnbull 1973). Ambushers (Thomisidae) are sit-and-wait predators that do not use silk to hunt and rely on direct contact with their prey (Gertsch 1979; Wing 1984). Typically, their first two pairs of legs are longer than the other two pairs. Pursuers (Anyphaenidae, Clubionidae, Gnaphosidae, Lycosidae, Philodromidae) are active hunters that can chase and overtake prey along substrate using equally long legs (Turnbull 1973; Kaston 1978). For this experiment, I assumed that spider preference for substrate diameter was constant within each guild. The data were collected as counts of individual spiders within each guild for each module treatment.

A total of 119 spiders representing 26 species and all four guilds was collected during 3840 module-days (Table 1). All species collected, except *Dipoena nigra* (Emerton), were found by Robinson (1978) in modules at Green Canyon, and four of the eight most common species in each study correspond. Guild proportions also closely match those reported from Green Canyon

Table 1.—Spider species list from Mill Hollow modules, arranged by foraging guild. Numbers are indicated for both narrow and wide substrate treatments, and percentages are given for the proportion of total individuals collected ($n = 119$).

Identity	Narrow	Wide	Total (%)
Jumpers			
Habronattus hirsutus (G. and E. Peckham)	3	2	4.2
Metaphidippus aeneolus (Curtis)	3	0	2.5
Oxyopes scalaris (Hentz)	1	9	8.4
Phidippus johnsoni (Peckham and Peckham)	10	16	21.9
Sassacus papenhoei (Peckham and Peckham)	0	4	3.4
Sub-total	17	31	40.4
Trappers			
Argiope trifasciata (Forskal)	2	1	2.5
Dictyna completa Chamberlin & Gertsch	0	1	0.8
Dictyna idahoana (Chamberlin & Ivie)	0	1	0.8
Dipoena nigra (Emerton)	2	3	4.2
Dipoena tibialis Banks	2	4	5.0
Euryopis sp.	0	1	0.8
Hyposinga singaeformis (Scheffer)	7	3	8.4
Metepeira foxi (Gertsch & Ivie)	7	4	9.2
Micaria sp.	0	4	3.4
Theridion neomexicanum Banks	3	4	5.9
Theridion petraeum L. Koch	2	3	4.2
Unidentified	0	2	1.7
Sub-total	25	31	47.0
Ambushers			
Ebo sp.	0	1	0.8
Misumenops lepidus (Thorell)	1	0	0.8
Xysticus cuncator Thorell	0	1	0.8
Xysticus gulosus Keyserling	1	0	0.8
Xysticus montanensis Keyserling	0	1	0.8
Sub-total	2	3	4.2
Pursuers			
Anyphaena pacifica Banks	1	0	0.8
Chiracanthium inclusum (Hentz)	0	1	0.8
Schizocosa sp.	1	0	0.8
Thanatus formicinus (Clerck)	0	2	1.7
Tibellus oblongus (Walckenaer)	1	3	3.4
Unidentified	0	1	0.8
Sub-total	3	7	8.4
Total	47	72	100.0

shrubs by Abraham (1983), further suggesting that comparisons to Mill Hollow are valid.

Although the count data are sparse for many species, inspection suggests that some spider substrate preferences may exist. *Hyposinga singaeformis* (Scheffer) was more numerous on narrow substrate whereas *Oxyopes scalaris* (Hentz), *Phidippus johnsoni* (Peckham & Peckham), *Sassacus papenhoei* (Peckham & Peckham), and *Micaria* sp. appear to prefer wide substrate. At the guild level, jumpers and pursuers appear to have some preference for wide substrate, in accordance with the predictions of this study, but trapper and ambusher preferences appear less striking.

I performed a contingency table analysis to statistically test H_0: Module colonization by spider guilds is independent of substrate diameter (Table 2). Because some expected cell counts are low (< 5), I used the FORTRAN program CHITEST developed by Romesburg & Marshall (1985) for the analysis which employs a Monte

Table 2.—Number of spiders observed from modules compared to numbers expected under H_0: Module colonization by spider guilds is independent of substrate diameter. The calculated chi-square value for differences between corresponding cells is 1.333.

	Observed		Expected	
Guild	Narrow	Wide	Narrow	Wide
Jumpers	17	31	19	29
Trappers	25	31	22.1	33.9
Ambushers	2	3	2	3
Pursuers	3	7	3.9	6.1
Total	47	72	47	72

Carlo simulation routine that does not require large counts. The program tests for contingency between row and column factors by comparing differences in the observed and expected matrices from the experiment to a large number of simulated matrices. The simulations are based on fixed row and column totals provided by the experiment. I chose to run 10,000 simulations for my comparison, which estimates the true P-value to within 1% accuracy with 95% confidence (Romesburg & Marshall 1985). The P-value obtained by this technique represents the proportion of simulations that had differences in their matrices as great or greater than the differences in the experimental matrices.

In this test, the chi-square value calculated from the experimental data (Table 2) is 1.333. Simulated matrices yielded chi-square values between 0.003 and 18.797 with a mean of 3.030. Over 75% of the simulations had chi-square values as large or larger than the field data ($P = 0.7502$) and so the null hypothesis of no contingency cannot be rejected at a 0.05 significance level.

The lack of significant contingency between substrate diameter and guild identity at Mill Hollow, in conjunction with previous results from a similar site, suggests that substrate height, density, and orientation may be more important to shrub-steppe spider guilds during habitat selection. Future trials could present a larger contrast in substrate diameters to spiders and/or consider spider responses to different combinations of architectural factors (Robinson 1981). Additional work on determining the constancy of spider habitat preferences within individuals, species, or guilds would also be useful.

Architecture constitutes only part of each spider's niche (MacMahon et al. 1981), and its importance to individuals may be modified or eclipsed by other factors such as prey availability and temperature (Riechert 1985; Janetos 1986). Clearly, there is much work to be done to develop generalized models of spider habitat selection.

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William J. Ehmann: Department of Biology, Ecology Center, Utah State University; Logan, Utah 84322-5305 USA.

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