Structure and organization of a winter community of cavity-inhabiting, web-building spiders (Pholocidae and Theridiidae) in a Chihuahuan Desert habitat

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Populations of Chihuahuan Desert spiders that construct webs in naturally occurring cavities were followed over a 20-week-period with modified pitfall traps. Of the three species studied, *Psilochorus imitatus* (Pholocidae) was the most abundant, followed in order by *Artema atlanta* (Pholocidae) and *Latrodectus hesperus* (Theridiidae). Canonical correlation analysis indicated a strong dependence of *L. hesperus* upon soil temperatures. A principal axis factor analysis explained 87 per cent of the variance in the spider-weather-habitat aspect system with five common factors. This model also gave a good fit to all monitored variables. This analysis demonstrated the importance of habitat aspect upon spider distributions, and allowed an examination of the partitioning of niche space by the three species. Experimental laboratory manipulations suggested that groups of *A. atlanta* can behaviorally dominate solitary *L. hesperus* females by restricting orb web construction, and suggested that patterns observed in the field may be shaped by interspecific competition.

Introduction

The rôle of spiders in desert ecosystems remains largely unexplored. Chew (1961) examined communities of desert spiders restricted to vegetation, while others, notably Muma (1975a, 1975b, 1980), have concentrated their investigations upon the ground-surface spider faunas. Although desert spiders are traditionally considered as being large and cursorial, these studies have shown that this is indeed not the case. Muma's studies are the only long-term studies of spider communities in the deserts of the south-western United States of America. His studies indicate that the most abundant ground spider was not cursorial, but rather a web-spinning pholocid, *Psilochorus imitatus*, and he suggested that this species, normally found in rodent burrows, was using pitfall traps as web-building sites. As such, modified pitfall traps could be used as trap nests (Fowler, 1980) to study populations of otherwise cryptic, ground-dwelling, web-building spiders in desert ecosystems.

We initiated our study in the Chihuahuan Desert of southern New Mexico to examine: (1) the temporal changes in spider populations; (2) the effects of habitat upon web-site selection, or colonization; and, (3) the interactions among the species of spiders. We limited our observations to three species, *P. imitatus*, *Artema atlanta* (Pholocidae), an immigrant species from tropical America (Comstock, 1940), and *Latrodectus hesperus* (Theridiidae), the common black-widow spider of this area.

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Methods

Our studies were conducted on the Jornada Validation site watershed on the New Mexico State University Ranch, 40 km north of Las Cruces, Dona Ana County, New Mexico. The site and its vegetation have been described in detail by Santos, DePree *et al*. (1978).

Spider populations were followed by weekly counts of individuals in 3·78 l (Number 10) tin cans set flush with the soil surface and covered with an elevated wooden plank. The spiders studied are normally restricted to naturally occurring cavities, usually abandoned rodent burrows. Thus, these pitfall traps functionally served as trap nests (Fowler, 1980). No collecting flasks or preservatives were employed, as the object of the study was to assess weekly changes in populations. Counts were easily conducted by removing the wooden plank and enumerating the spiders *in situ*. A total of 49 pitfall traps were monitored weekly. The traps were arranged in a 7 × 7 grid, with a 5 m spacing between grid intersections.

Weather data were obtained from a field weather station, located approximately 2 km from the study grid. Quantification of habitat aspect was performed by scoring each trap with respect to whether it was in a depression or not, by noting the mean percentage of cover afforded by annual plants (per m^2), and by noting the closest, here called dominant, or second closest, here called subdominant, plant near the pitfall trap. Plants scored by this method were: none; *Prosopsis glandulosa* (mesquite), *Ephedra trifurca* (Mormon tea), *Guterrezia sarothrae* (snakewood), *Yucca elata* (soap-tree yucca), *Opuntia* spp. (prickly-pear cactus), and *Bouteloua* spp. (a dominant grass). Other perennial plants were present, but none were present in the vicinity of the traps.

Canonical correlation analysis was performed to examine the interrelations between spider populations and micro-environmental parameters, using standard computer programs (Barr, Goodnight *et al*., 1979). A principal axis factor analysis was conducted on the complete data set, incorporating spider populations, weather, and habitat aspect, to examine the interrelations among all the variables. Due to a problem of scaling the variables, i.e. temperature, populations, etc. were all measured in different units, the correlation matrix was used instead of the variance-covariance matrix. Likewise, the factor analytic model was computed from standard computer programs (Barr, Goodnight *et al*., 1979).

To examine the potential competitive effects among members of the community, laboratory studies were undertaken. Solitary female *L. hesperus* were released into one corner of a glass terrarium, 40 cm × 25 cm × 32·5 cm, while in the opposite corner, *A. atlanta* were released in the following combinations: solitary males; solitary females; one male and one female; three males and one female; three males and three females; six males and three females; or six males and six females. In the morning, at mid-day, and in the late afternoon, the maximal extension of webbing produced by the *L. hesperus* female was measured with a meter stick from above, and the data were subjected to an analysis of variance. In addition, occasional observations were conducted to detect any notable behaviors in the test animals.

The three species exhibited disparate patterns of winter population trends (Fig. 1). *P. imitatus* was the most numerically abundant, peaking around 23 January 1979 (Fig. 1), while *A. atlanta* and *L. hesperus* populations peaked around 27 November 1978. Throughout the study period, populations of *L. hesperus* remained quite low, and no males were ever observed.

The results of the canonical correlation analysis, used to examine the effects of weather on spider populations, gave two significant canonical roots. These two roots explained 97 and 88 per cent of the variance, respectively (Table 1). The first pair of canonical variates (Table 2) indicated that the maximum soil temperatures were important factors explaining the abundance of *L. hesperus*. Maximum soil temperatures gave an inverse relationship with the pholocids. The second pair of canonical variates, lying orthogonal to the first pair, demonstrated the adverse effect of minimum soil temperatures, minimum air tempera-
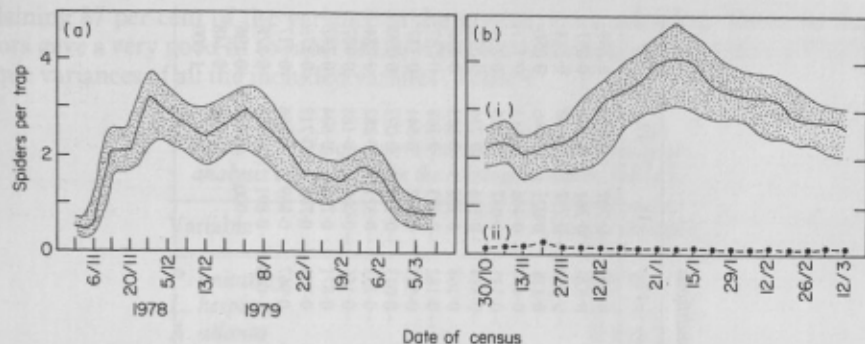
Figure 1. Weekly fluctuations of the populations of three web-building spiders in 'trap nests' on the Jornada Validation site, NM. Stipling depicts the 95% fiducial limits. (a) *Artema atlanta*; (b) (i) *Psilochorus imitatus* and (ii) *Latrodectus hesperus*.

tures, and time on *L. hesperus* populations, which were linked strongly to minimum soil temperatures at a depth of 45 cm.

The correlation matrix of the entire data set (Table 3) revealed strong correlations among many parameters. *L atrodectus hesperus* was inversely correlated with *A. atlanta*, while *P. imitatus* was not strongly linked to either. *P silochorus imitatus* was negatively correlated with weekly air and soil temperatures, a pattern paralleled by *A. atlanta* (Table 3).

By fitting a principal axis factor analytic model to the data, six common factors,

Table 1. *Successive statistical tests of the pairs of canonical roots of Table 2, relating spider populations to environmental conditions*

Pair of canonical roots	Canonical correlation	χ^2 value	Degrees of freedom	P
1	0·985	80·488	24	0·0001
2	0·941	35·077	14	0·0015
3	0·640	6·844	6	0·3352

Table 2. *Vector loadings associated with the first two pairs of canonical variates (Table 1)*

Canonical variates	Canonical root* I	Canonical root* II
Spiders		
Psilochorus imitatus	−529	−784
Lactrodectus hesperus	3689	·6951
Artema atlanta	−884	55
Environmental set		
Maximum air temperature	−201	−2348
Minimum air temperature	−1097	−399
45 cm Maximum soil temperature	2708	1004
45 cm Minimum soil temperature	923	4374
15 cm Maximum soil temperature	2533	2044
15 cm Minimum soil temperature	506	−4535
Week	−1562	−3059

*Decimal points have been eliminated

Table 3. *Correlation matrix of spider populations, plant characteristics, and meteorological conditions*

Variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
P. imitatus	1·000																			
L. hesperus	0·198	1·000																		
A. atlanta	0·285	-0·703	1·000																	
Week	-0·269	-0·843	-0·486	1·000																
Elevation	-0·399	0·107	-0·399	-0·100	1·000															
Annual cover	-0·092	-0·266	-0·240	0·228	-0·414	1·000														
Mesquite	0·017	-0·223	-0·397	0·089	-0·419	0·515	1·000													
Ephedra	-0·175	-0·034	-0·192	-0·004	-0·589	0·015	-0·015	1·000												
Gueterrezia	0·163	0·139	0·093	-0·171	-0·081	-0·263	0·025	-0·539	1·000											
Yucca elata	-0·560	0·063	-0·412	-0·085	-0·658	-0·140	-0·340	-0·224	-0·640	1·000										
Opuntia	-0·095	-0·126	-0·156	0·172	-0·275	-0·072	-0·504	0·015	0·391	-0·276	1·000									
Bouteloua	0·482	0·046	0·141	-0·168	-0·327	0·041	-0·076	-0·072	-0·084	-0·220	-0·563	1·000								
Bare ground	-0·017	-0·114	0·141	0·280	-0·267	0·201	0·217	0·201	-0·101	-0·145	-0·624	-0·521	1·000							
Maximum air temperature	-0·774	0·245	-0·655	-0·192	-0·501	-0·130	-0·132	0·591	-0·293	0·540	-0·094	-0·152	-0·343	1·000						
Minimum air temperature	-0·477	0·182	-0·582	-0·085	0·215	-0·115	-0·166	0·257	0·179	0·230	-0·125	-0·040	-0·095	-0·660	1·000					
45 cm Soil minimum temperature	-0·646	0·379	-0·842	-0·170	0·513	-0·111	-0·333	0·568	0·198	0·510	-0·005	-0·292	-0·173	0·861	0·740	1·000				
45 cm Soil maximum temperature	-0·690	0·320	-0·789	-0·118	0·474	-0·135	-0·314	0·537	0·168	0·490	-0·043	-0·233	-0·166	0·871	0·793	0·967	1·000			
15 cm Soil maximum temperature	-0·707	0·261	-0·737	0·021	0·446	-0·037	-0·136	0·522	0·392	0·470	-0·105	-0·321	-0·008	0·794	0·745	0·869	0·891	1·000		
15 cm Soil minimum temperature	-0·823	0·146	-0·630	0·046	0·413	0·015	-0·216	0·541	0·123	0·480	0·093	-0·282	-0·188	0·804	0·717	0·866	0·916	0·880	1·000	
Wind activity	-0·239	-0·057	-0·218	0·050	0·121	0·254	0·074	-0·337	0·175	-0·300	0·090	-0·084	-0·007	-0·242	-0·373	-0·217	-0·228	-0·196	-0·248	1·000

explaining 87 per cent of the variance in the system, were extracted. These six common factors gave a very good fit to most of the variables of the system, as evidenced by the low unique variances of all the included variates (Table 4).

Table 4.   *Unique variances associated with the factor analysis extracted from the correlation table (Table 3)*

Variable	Unique variance
P. imitatus	0·134
L. hesperus	0·053
A. atlanta	0·098
Week	0·188
Elevation	0·108
Annual cover	0·108
Mesquite	0·395
Ephedra	0·139
Gueterriza	0·093
Yucca elata	0·203
Opuntia	0·130
Bouteloua	0·033
Bare ground	0·163
Maximum air temperature	0·144
Minimum air temperature	0·176
45 cm Soil maximum temperature	0·053
45 cm Soil minimum temperature	0·051
15 cm Soil maximum temperature	0·070
15 cm Soil minimum temperature	0·076
Wind activity	0·141

An evaluation of some of the variate loadings of the vectors of the first three common factors (Fig. 2) allows us to interpret these factors in terms of niche dimensions. In the first common factor, populations of *P. imitatus* and *A. atlanta* were negatively associated with temperature, and to a lesser extent, with the presence of *Y. elata*. This factor may be interpreted as representing the weather, or seasonal dimension, of niche space. Factor II (Fig. 2) demonstrated a strong negative association between *L. hesperus* and time, as well as with populations of *A. atlanta*. This factor may be thought of as representing the temporal component of niche space. Factor III (Fig. 2) revealed patterns of spider associations with vegetation, and may be interpreted as representing the habitat aspect of niche space.

By plotting the positions of the three spider species in 'factor space' (Fig. 3), a clear discrimination of the species is present. This plot may be interpreted as specifying the niche of the species, or at least that portion of niche space discernible by our measurements. The plot of Factor I with Factor II produced a detectable ordination of the populations over time (Factor II), modified by the weather (Factor I). On this ordination, *L. hesperus* occupies a lower position than *P. imitatus*, which in turn occupies a lower position than *A. atlanta*. By including habitat aspect (Factor III) in the plot, *A. atlanta* and *P. imitatus* are seen to respond similarly to vegetation, and are widely separated from *L. hesperus*. *Latrodectus hesperus*, although not greatly separated from *P. imitatus* on the temporal axis, is greatly separated from the other two with respect to habitat aspect, reflecting differing colonization characteristics, and to weather, as *L. hesperus* is predominately active during the summer and fall, more so than the pholocids.

Laboratory studies on the interactions between *L. hesperus* and *A. atlanta* (Fig. 4, Table 5) indicated that groups of *A. atlanta* behaviorally subordinate the much larger solitary females of *L. hesperus*. Groups of *A. atlanta* significantly restricted the web-building
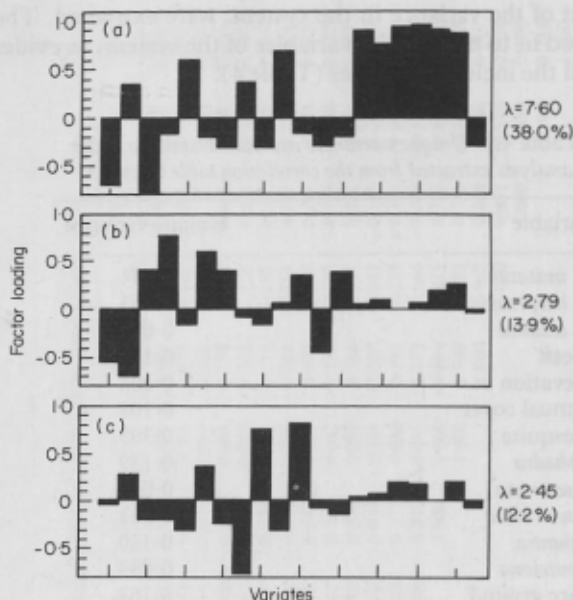
Figure 2. The variate loadings of the first three common factor vectors. Variate numbers are the same as those given in Table 3. Lambda is the eigenvalue, while the percentage of the variation explained by each factor is given in parenthesis. (a) $\lambda = 7 \cdot 60$ (38·0%); (b) $\lambda = 2 \cdot 79$ (13·9%); $\lambda = 2 \cdot 45$ (12·2%).

activity of *L. hesperus* females (Table 5, Fig. 4). In all cases, males contributed heavily to the subordination of *L. hesperus* females. Observations conducted during these tests revealed that males of *A. atlanta* cut the silk fibers of the *L. hesperus* webbing along the periphery using their chelicerae.

Discussion

The results of our studies are in close agreement with Muma's (1980) estimates of the populations of *P. imitatus* in various southern localities in New Mexico. Although *P.*
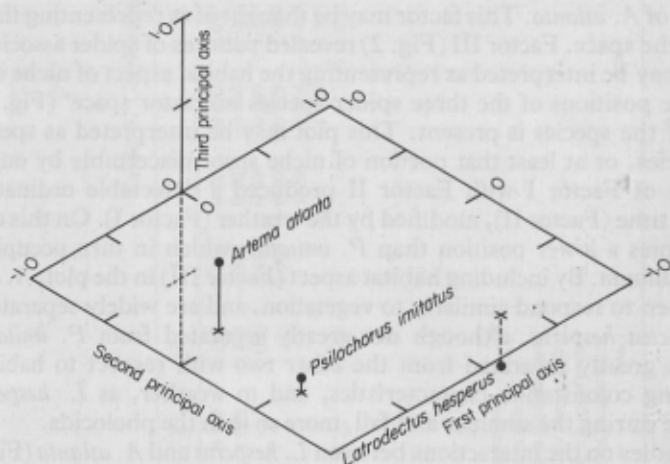
Figure 3. The ordination of the three spider species in factor space. See Fig. 2 for individual variate loadings.
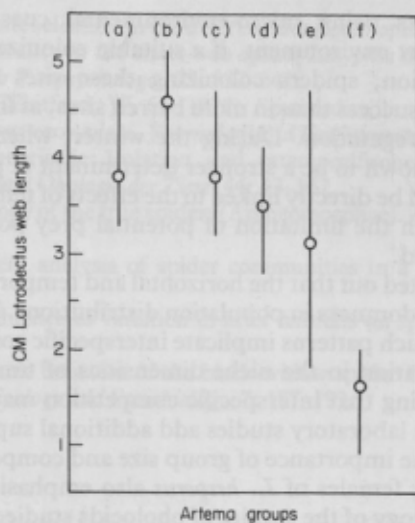
Figure 4. The effects of groupings of *A. atlanta* upon the web-building behavior of solitary female *L. hesperus*. Web length refers to the maximal length of the web from the corner of the terrarium which contained the *L. hesperus* female. Circles represent mean values, while bars represent the range of values found during the experiments. (a) 1 ♂ ; (b) 1 ♂ and 1 ♀ ; (c) 3 ♂ and 1 ♀ ; (d) 3 ♂ and 3 ♀ ; (e) 6 ♂ and 3 ♀ and (f) 6 ♂ and 6 ♀ .

imitatus is a dominant species in pitfall trap studies, under natural conditions *P. imitatus* is probably less dominant, and its populations are undoubtedly limited by the availability of web-building sites. Pitfall traps serve as new habitats for colonization, and the numbers present may be interpreted quite differently from the assumed random catches of cursorial species. For the species studied, catches are biased, as spiders actively sought out the pitfall traps for colonization, while catches of cursorial spiders are presumed to be stochastic. As pitfall traps are actively colonized by these web-building spiders, population estimates derived from these studies probably represent almost the entirety of the population, or, in other terms, reflect the carrying capacity of the habitat (Fowler, 1980). Long term prey supplementation experiments would have to be performed to validate this hypothesis.

A significant relationship was found between populations of species of web-building spiders and habitat aspect. Such relations have been previously reported for more mesic habitats (Duffey, 1966; Uetz, 1976, 1979). A desert funnel-web spider has also been

Table 5. *The effects of varying phlocid densities upon the laboratory activity of female* Lactrodectus hesperus *in glass aquaria*

Source of variation	d.f.	Sequential s.s.	Mean square	F value	Partial s.s.	F value
♀ *A. atlanta*	3	18224·37		89·17*	140·20	0·69
♂ *A. atlanta*	3	7176·60		35·11*	7176·60	35·11*
Model	6	25400·97	4233·49	62·14*		
Error	28	1907·60	68·13			
Total	34	27308·57				

R Square = 0·930

*P < 0·0001.

shown to colonize habitats using micro-environmental cues for web construction (Reichert, 1976). In a desert environment, if a suitable colonization site is available for web-builders near vegetation, spiders colonizing these sites should enjoy a greater probability of prey capture success than in more barren sites, as insect prey should tend to aggregate with respect to vegetation. During the winter, when our studies were conducted, temperature was shown to be a stronger determinant of populations than habitat aspect. These patterns could be directly linked to the effects of temperature on the spiders, or indirectly linked through the limitation of potential prey populations, although the latter aspect was not assessed.

Turnbull (1973) has pointed out that the horizontal and temporal stratification of spider species implies a lack of randomness in population distributions. Tretzel (1955) goes even further, and suggests that such patterns implicate interspecific competition. For the three species studied here, separation in the niche dimensions of time, weather, and habitat aspect were found, suggesting that interspecific competition may be important in structuring the community. The laboratory studies add additional support to the interspecific competition hypothesis. The importance of group size and composition demonstrated by *A. atlanta* in subordinating females of *L. hesperus* also emphasizes the effects of group living in the population biology of the species of pholocids studied.

The effective (anti-vertebrate) defense mechanisms of *L. hesperus* females (Vetter, 1980) were of little importance in responding to the group effects of *A. atlanta*. Continued restriction of the foraging area of *L. hesperus* females by groups of *A. atlanta* would, under field conditions, probably lead to web site abandonment, or possibly to their predation by pholocids. Undoubtedly, the size of the pholocid groups would greatly influence the final outcome, and further studies are needed to examine this aspect.

Interestingly, the cutting of the peripheral *L. hesperus* webbing by *A. atlanta* males resembles a component of the sexual behavior of sheet-web linyphiid spiders (Rovner, 1968). We are unfamiliar with any literature which suggests that a similar behavior may be used interspecifically.

This study has demonstrated that the structuring of desert cavity-dwelling, web-building spider communities is not stochastic. Moreover, we have inferred that community structure is the adaptive result of interspecific competition. This study has examined one of the many overlooked groups of animals in desert ecosystems, and points out the possibility of studying community structure with sesile, easily observed and manipulated, abundant animals.

References

Barr, A. J., Goodnight, J. H., Sall, J. P. & Helwig, J. T. (1979). SAS User's guide, 1979 edition. Raleigh, North Carolina: SAS Institute. 494 pp.

Chew, R. M. (1961). Ecology of the spiders of a desert community. *Journal of the New York Entomological Society*, **69**: 5–41.

Comstock, J. H. (1940). *The Spider Book*. Gertsch, W. J. (Ed.). New York: Doubleday & Doran. 729 pp.

Duffey, E. (1966). Spider ecology and habitat structure. *Senckenbergiana Biologie*, **47**: 45–49.

Fowler, H. G. (1980). Trap nests for studying desert web-building spiders (Araneae: Pholocidae). *Entomological News*, **91**: 136–138.

Muma, M. H. (1975a). Long term can trapping for population analysis of ground-surface, arid-land arachnida. *Florida Entomologist*, **63**: 257–270.

Muma, M. H. (1975b). Two vernal ground-surface arachnid populations in Tularosa Basin, New Mexico. *Southwestern Naturalist*, **20**: 55–67.

Muma, M. H. (1980). Comparison of ground-surface spider populations in Pinyon-juniper and arid-grassland associations in southwestern New Mexico. *Florida Entomologist*, **63**: 211–222.

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

Downer, J. S. (1968). Territorality in the sheet-web spider *Linyphia triangularis* (Clerck) (Araneae: Linyphiidae). *Zeitschrift für Tierpsychologie*, **25**: 232–242.

Santos, P. F., DePree, E. & Whitford, W. G. (1978). Spatial distribution of litter and microarthropods in a Chihuahuan Desert ecosystem. *Journal of Arid Environments*, **1**: 41–48.

Tretzel, E. (1955). Intragenerische Isolation und interspezifische Konkurrenz bei Spinnen. *Zeitschrift für Morphologie und Okologie der Tiere*, **44**: 43–162.

Turnbull, A. L. (1973). Ecology of the true spiders (Araneomorphae). *Annual Review of Entomology*, **18**: 305–348.

Uetz, G. W. (1976). Gradient analysis of spider communities in a streamside forest. *Oecologia (Berlin)*, **22**: 373–385.

Uetz, G. W. (1979). The influence of variation in litter habitats on spider communities. *Oecologia (Berlin)*, **40**: 29–42.

Vetter, R. S. (1980). Defensive behavior of the black-widow spider *Latrodectus hesperus* (Araneae: Theridiidae). *Behavioral Ecology and Sociobiology*, **7**: 187–193.