

INITIAL TESTS FOR PRIORITY EFFECTS AMONG SPIDERS THAT CO-OCCUR ON SAGEBRUSH SHRUBS

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ABSTRACT. Recent work in conservation biology and restoration ecology has highlighted the need for research on the process of community assembly and the effect of initial conditions on community development. Theory and limited experimental work in this area suggest that an initial “pioneer” colonist arriving in open habitat can strongly influence this process, resulting in a priority effect. We used a ubiquitous terrestrial animal group, spiders, to test for the existence of priority effects during colonization of individual sagebrush shrubs. In 1992, at a site in northern Utah, we applied three treatments to subsets of 60 cleared shrubs that represented available habitat to spiders. Two shrub treatments received different jumping spider pioneer colonists placed by hand (either *Metaphidippus aeneolus* (Curtis 1892) or *Phidippus johnsoni* (Peckham & Peckham 1883)), and a third shrub treatment received no placed spiders, serving as a reference. After 3–4 days of exposure to the same environmental conditions, including natural colonization by dispersing spiders, we collected a total of 285 spider assemblages that had developed on shrubs. We compared these assemblages by treatment type at both the species and guild levels, defining spider guilds based on differences in morphology and foraging technique (e.g., jumpers, trappers, ambushers, and pursuers).

The total number of spiders per shrub was not significantly different by treatment type ($P = 0.279$), and overall measures of species richness and abundance were similar. At the guild level of analysis, however, differences were observed. Total counts of trappers were 43–50% lower in treatments receiving a placed jumper pioneer. A log-linear model comparing treatments as a whole confirmed that jumper pioneers significantly reduced trapper numbers in subsequent assemblages compared to those from reference shrubs ($P = 0.019$), and significantly fewer trappers were collected from shrubs that had *Metaphidippus aeneolus* as a pioneer ($P = 0.034$). This evidence of short-term priority effects was found despite a conservative aspect of our test, in which the reference shrubs had some likelihood (35%) of receiving either of these jumper pioneers by chance from natural dispersal. It is not known whether these priority effects persist over longer time scales.

The observed results are consistent with predictions based on known spider behaviors of cannibalism and interguild predation. Outcomes of these spider-spider interactions relate to differences in foraging technique and body size. We suggest that a guild-level approach and the shrub-spider system we describe have promise for future research on priority effects and animal community assembly.

A major focus of research in animal ecology has been understanding how extant natural communities maintain their structures over time through such mechanisms as competition and predation (see reviews in Strong et al. 1984; Diamond & Case 1986; Kikkawa & Anderson 1986; Gee & Giller 1987; but also Dunson & Travis 1991). But contemporary problems in conservation biology and ecosystem restoration (Bradshaw 1987; Cairns 1988; Buckley 1989; Soule & Kohm 1989; Hansson 1992) have challenged us to expand

this program, both by considering how animal communities change over time (Pimm 1986, 1991; Giller & Gee 1987; Lawton 1987; Crawley 1989; Luken 1990) and by analyzing disturbed systems (Lewontin 1969; Sousa 1984; Pickett & White 1985; Harper 1987). In short, we are starting to pay more attention to the process of community development itself, exploring the sensitivity of ecological systems to different initial conditions and tracking community trajectories over time (Connor & Simberloff 1979; Fox 1987; Gilpin 1987; Drake 1990a, 1990b, 1991; Drake et al. 1993; Law & Morton 1993). The promise of this approach lies in the potential to describe particular “assembly rules” for natural commu-

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nities (M'Closkey 1978, 1985; Haefner 1981, 1988; Fox & Kirkland 1992; Fox & Brown 1993; Luh & Pimm 1993; Grover 1994) and relate them to problems in applied ecology. In a sense, this would fulfill Robert MacArthur's vision that ecological research would eventually yield a series of empirical rules in the form: "for organisms of type A, in environments of structure B, such and such relations will hold" (MacArthur 1972).

To some ecologists, these endeavors recall decades-old disputes concerning the existence of communities, the analysis of species co-occurrence data, and the description of species assembly rules (e.g., Wilson 1991, 1994, 1995; see responses by Palmer & White 1994; Fox & Brown 1995). Fox & Brown (1995) restate an important distinction between most earlier work and recent efforts in that guilds rather than species are often used to characterize assembly rules (M'Closkey 1978, 1985; Haefner 1981; Fox & Kirkland 1992; Fox & Brown 1993). Species are assigned to guilds based on ecological roles or functional similarities that not only simplify the number of variables but may also facilitate comparative studies and lead to broader utility. Although part of a continuum, we also note that manipulative studies of assembly rules are often concerned with short time scales between colonization events (days to years, see comments by Grover & Lawton 1994) and smaller spatial scales than biogeographic or animal succession studies (e.g., Morton et al. 1994; Shenbrot et al. 1994; Kelt et al. 1995).

A subset of assembly rule theory concerns the influence of an initial, "pioneer" colonist on subsequent community development (Drake 1990a). In replicated trials, if the identity of the pioneer changes the community trajectory and results in different community patterns at some later time, a "priority effect" is said to have occurred (Drake 1990a). In such cases, it is not only the community components that affect structure, but also the sequence of their interactions. One implication for applied ecology is that a "saving all the parts" strategy may be inadequate for ecosystem restoration if historical information is not considered (Drake 1990a; Luh & Pimm 1993). To date, studies of priority effects within animal communities have been performed under highly-controlled laboratory conditions with algae and protozoans (Dickerson & Robinson

1985; Gilpin et al. 1986; Robinson & Dickerson 1987; Robinson & Edgemon 1988; Drake 1991; Drake et al. 1993), and under field conditions with sessile invertebrates (Dean & Hurd 1980), dipterans (Kneidel 1983), ants (Cole 1983a, 1983b), odonates (Morin 1984), and frogs (Wilbur & Alford 1985).

Here, we report on the detection of short-term priority effects, in the field, among spiders (Arachnida, Araneae) that colonize shrub-steppe habitat in northern Utah. We believe this system has significant advantages for addressing assembly rule questions. Spiders are ubiquitous terrestrial animals and, as generalist predators, they have been model organisms for many ecological studies (Barnes 1953; Turnbull 1973; Foelix 1982; Spiller & Schoener 1988, 1990; Wise 1993). Spiders are also taxonomically diverse, locally abundant, and easy to manipulate. The shrub-steppe habitat type is globally widespread and individual shrubs represent habitat "islands" (*sensu* Price 1984) for many arid-land spiders (Fautin 1946; Chew 1961; Abraham 1983). Shrubs help spiders reduce some environmental stresses while providing substrates that facilitate prey capture (Hatley & MacMahon 1980; Riechert & Gillespie 1986). In northern Utah, Abraham (1980, 1983) reported that the spider faunae on big sagebrush shrubs (*Artemisia tridentata* Nutt.) shrubs are distinctive when compared to the local ground and herb stratum faunae. This observation, coupled with evidence that individual spiders remain on the same shrub for days to weeks (Wing 1984), suggests to us that, to some extent, individual shrubs define discrete spider assemblages and may be used as experimental units. Other studies with invertebrates have also adopted this perspective (see Price 1984).

The spider assemblages that develop in a given area are a consequence of dispersal processes (both ground and aerial mechanisms, see Turnbull 1973; Foelix 1982; Decae 1987; Greenstone 1990; Crawford et al. 1995) and interactions among colonists and their environment. In sagebrush shrub habitat in Utah, previous workers have studied the influences of substrate type, vegetation architecture, prey availability and dispersal mechanism on spider community structure (Hatley & MacMahon 1980; Robinson 1981, 1984; Abraham 1983; Wing 1984; Ehmann 1994a, 1994b). In

this study, we attempt to control or randomize these variables to detect priority effects among spiders that co-occur on sagebrush shrubs.

Spider assemblages can be described at both the species and guild levels of organization. Although the guild concept introduced by Root (1967) has been the subject of some confusion and debate (Hawkins & MacMahon 1989; Simberloff & Daylan 1991), it has value when organisms are grouped in biologically appropriate ways to study complex systems (MacMahon 1976; Hawkins & MacMahon 1989). This approach also has statistical utility, particularly when counts of individuals within species categories are low. In this study, we classified spider species into four *a priori* guilds based on behavioral observations of their foraging techniques and taxonomic characteristics at the family level, following Hatley & MacMahon (1980) and Wing (1984). "Jumpers" (including Oxyopidae and Salticidae of this study) are active, visually-oriented predators that leap onto their prey (Foelix 1982). "Trappers" (including Araneidae, Dictynidae, Linyphiidae, and Theridiidae) are sit-and-wait predators that rely on silk constructions to capture prey (Gertsch 1979). "Ambushers" (including Thomisidae) are sit-and-wait predators that require direct contact with prey for capture, and their first two pairs of legs are commonly elongated (Gertsch 1979; Wing 1984). "Pursuers" (including Anyphaenidae, Clubionidae, and Philodromidae) actively chase and overtake prey along the substrate using four pairs of subequal length legs (Kaston 1978).

The existence of priority effects among spiders on individual shrubs depends on the occurrence of significant spider-spider interactions, which must involve positive and/or negative components. Positive interactions are primarily known from studies of communal webs in tropical environments (Uetz 1986; Uetz & Hodge 1990); whereas, in temperate environments, four lines of evidence suggest that negative interactions predominate. First, cannibalism is widespread among spiders and it has been suggested that the major enemies of spiders are spiders themselves (Bristowe 1941; Foelix 1982; Wise 1993). Cannibalism not only provides a spider with a meal but eliminates a conspecific who is a potential competitor, a behavior that is expected to en-

hance lifetime fitness (see discussions in Elgar & Crespi 1992; Crowley & Hopper 1994). Second, spiders and their scorpion relatives are known to participate in intraguild predation, wherein different species of the same functional group feed upon each other (Schaefer 1972 as cited by Wise 1993; Polis & McCormick 1987; Polis et al. 1989; Hurd & Eisenburg 1990). Third, although many spider families remain unstudied (Wise 1993), there is experimental evidence for interspecific competition among two orb-web spiders (Araneidae) (Spiller 1984a, 1984b, 1986). Finally, non-random web spacing patterns observed for some arid-land spiders suggest that spiders are territorial (Riechert et al. 1973; Riechert 1981). In northern Utah, several workers have observed that cannibalism, intraguild predation, and interguild predation occur among shrub-dwelling spiders (Abraham 1980; Wing 1984; this study, see Discussion).

Our test for priority effects among shrub-dwelling spiders involved three experimental treatments applied to subsets of 60 shrubs (yielding a total of 285 samples) during the summer of 1992, and indicates that short-term priority effects occur at the guild level of organization. The results are consistent with known spider-spider interactions related to differences in foraging technique and body size.

METHODS

Spiders.—Previous sampling during two summers indicated that several jumping spiders among the 41 spider species identified on Mill Hollow shrubs were much more common than others, which suggested their use as experimental pioneer colonists. These spiders, *Metaphidippus aeneolus* (Curtis 1892) and *Phidippus johnsoni* (Peckham & Peckham 1883), represented 25% and 21% respectively of the spider fauna sampled from 769 census shrubs on the same plot during 1990–1991, and at least one of these species was present on 70% of the 325 census shrubs sampled in the year of this study (1992). Their abundance gave us a practical advantage in facilitating their collection for the experiment, but these species were also desirable because it is likely that they are common pioneer colonists at Mill Hollow. In addition, behavioral observations of jumping spiders, which are active and versatile hunters (Foelix 1982; Forster 1982), led

us to expect that they would be involved in the strongest spider-spider interactions that might result in priority effects. These spiders are also large enough (adult body lengths 7–12 mm) to be easily manipulated, marked, and released. Voucher specimens of this study have been deposited at the Field Museum, Chicago, Illinois.

Shrubs.—The site chosen for this research lies at the eastern edge of the Great Basin shrub-steppe ecosystem in Mill Hollow, Cache County, Utah (see Ehmann 1994a for details). A rectangular grid measuring 50 m × 120 m and containing approximately 1200 shrubs, was divided into 60 cells (each containing 10 m²). Within each grid cell, one shrub was selected as a sampling unit for collecting spider assemblages. The grid ensured that, on average, experimental shrubs would be at least 10 m apart, which we felt was large relative to observed spider movement distances (a jumper, *Phidippus johnsoni*, 2 m in one day (Ehmann, pers. obs.); an ambusher, *Misumena vatia* (Clerck 1757), 0.24–0.55 m/day (Morse 1981; Morse & Fritz 1982)). Our second criterion for shrub selection was shrub size, which we wanted to hold as constant as possible. In particular, we wanted to limit variation in canopy size, both to standardize the likelihood of aerial colonization and the amount of available substrate for spiders (Hartley & MacMahon 1980; Robinson 1981; Abraham 1983; Wing 1984). We measured candidate shrubs for maximum canopy width (MCW), canopy width perpendicular to maximum canopy width (PCW), and mean canopy height (MCH). We also required shrubs to have a single trunk at ground level (for equivalent ground colonization opportunities by spiders) not be in above-ground contact with any adjacent shrub, and be spaced at least two shrubs away from any other experimental shrub. In general, we sought shrubs that were approximately 50 cm in both width measurements and approximately 75 cm in average height. However, sagebrush has a variable growth form and we had the added complication of a small field site and a limited number of shrubs/grid cell to choose from. Consequently, some variation in shrub size persisted after final selection (Table 1), although all three measured variables formed normal distributions with no significant skew-

Table 1.—Summary of descriptive statistics for 60 sagebrush shrubs selected for this study (MCW = maximum canopy width, PCW = canopy width perpendicular to MCW, MCH = mean canopy height). All three variables are normally distributed.

	Shrub measurement (cm)		
	MCW	PCW	MCH
Mean	69.5	51.2	47.3
Standard deviation	13.5	10.5	7.6
Minimum	45.0	36.0	31.0
Maximum	100.0	90.0	72.0
Median	66.0	49.5	47.0
Skewness	0.76	1.21	0.62
Kurtosis	-0.34	1.95	1.00

ness or kurtosis ($P > 0.05$, two-sided t -tests, Sokal & Rohlf 1981).

Field trials.—To set up each field trial, a random subset of the 60 experimental shrubs was cleared of spiders using a variation on a beating-sheet technique (Southwood 1978). At the Mill Hollow site, striking a shrub (of the size detailed above) with an axe handle 30 times in approximately 15 sec yields, on average, 86% of the total number of spiders present on the shrub (Ehmann 1994a). To achieve a higher rate, consistent with the goals of this study, we added a second beating episode, at least 30 min following the first beating, to collect the residual spiders. A field trial with 10 shrubs verified a 100% collection rate using this double-beating method, and it was adopted for this study. Other concerns about induced leaf loss from shrubs, spider detection in the litter, and variation in spider abundance with sampling intensity were allayed with other preliminary tests (see Ehmann 1994a). Spiders collected from shrubs were removed from the grid cell.

Cleared shrubs were randomly assigned one of three experimental treatments: those that received a *Metaphidippus aeneolus* individual as a pioneer colonist (Treatment 1), those that received a *Phidippus johnsoni* individual (Treatment 2), and those that did not receive a placed spider ("reference shrubs", Treatment 3). Spiders used for release were typically late instar immatures collected from sagebrush shrubs adjacent to the field site. They were released onto cleared shrubs from a vial placed along the shrub trunk halfway between the canopy and the ground. After

treatment, 3–4 days were allowed for subsequent colonization by spiders and the developed assemblages were collected using the double-beating technique described earlier. Sampled shrubs are quickly recolonized (often within 24 h to average densities), and those without any spiders are uncommon (11% of 1094 shrubs sampled from 1990 to 1992). Although spider colonization is a continuous process, we were most interested in the assemblages that developed shortly after pioneer arrival. Collections were only performed in the absence of wind.

Seven experimental trials were performed from 19 July–18 September 1992, about one week apart. In the first six trials, 15 shrubs/treatment were used and in the seventh trial only five shrubs/treatment were used (due to a scheduling limitation), yielding a total of 285 sampled shrubs for the experiment. Data from one Treatment 2 shrub were lost.

Shrub selection.—To minimize the effect of remaining shrub size variation and other uncontrolled variables (e.g., prey density, microclimate), we randomized shrub selection and treatment assignment for each trial. This randomization assured good interspersion of treatments (Hurlbert 1984), but also meant that any shrub (of the 60 measured and set aside for this experiment) might be assigned to any of the three experimental treatments for a given trial, or remain unused. With more uniform shrubs, a strict repeated measures design would be appropriate, but we were limited to a small site with a small number of similar shrubs. Four considerations suggest that our imposition of treatments was acceptable and our observations from these shrubs were essentially independent. First, we detected no significant changes in physical shrub characteristics from one trial to the next due to sampling. We have previously referred to insignificant differences in leaf loss and spider abundance under different sampling regimes, and observed no other differences in shrub or site condition due to sampling. We did not measure chemical components of shrubs or chemicals that may have derived from spider activity, however, Wiens et al. (1991) reported no significant association of spider numbers with variation in sagebrush shrub chemicals. Second, all treatment shrubs were cleared of spiders before use, and at the end of each trial, all spider colonists were permanently re-

moved. Third, it seems highly unlikely that newly colonizing spiders would have any influential previous experience with the shrubs selected for a given trial, which were widely-spaced relative to on-site movements of the study organism. Fourth, in this prefatory work, we did not seek to predict particular spider assemblages on particular shrubs, but rather to compare average patterns among three treatments. Assignment of shrubs to treatments was equally random for each trial, “averaging out” uncontrolled differences. These details suggest to us that no significant carry-over effects occurred from one trial to the next, and that the treatments can be validly compared. We believe larger concerns would have arisen from steady use of atypical shrubs at our site, which could have resulted from a single randomization of treatment assignments and a repeated measures design.

Statistical analysis.—To compare treatments, we calculated species level comparisons of richness and abundance among treatments using the BASIC program SPDIVERS (Ludwig & Reynolds 1988) based on definitions by Hill (1973) and Alatalo (1981). We also compared the total number of spiders/shrub/treatment using contingency table analysis (Sokal & Rohlf 1981). Finally, counts of spiders in each guild by treatment type were compiled. These formed highly-skewed frequency distributions that resisted transformations for homoscedasticity and normality required for standard analysis of variance (ANOVA) tests. The limited number of categories for some guild counts reduced the value of contingency table analysis (except when the comparison between total spiders per shrub and treatment type was made), and non-parametric tests would have resulted in a substantial loss of information. For these reasons, we chose to analyze guild-level data using standard log-linear modeling techniques, which do not require ANOVA assumptions or large counts, and do not reduce information.

Log-linear models are a subset of generalized linear models which also include well-known ANOVA and linear regression techniques (McCullagh & Nelder 1983). To fit a log-linear model, it is first assumed that the data reflect independent observations (see earlier comments). Second, an underlying distribution (which does not have to be a normal distribution) is adopted for the model. Based

on goodness of fit tests using the guild counts per shrub by treatment, a Poisson distribution was accepted ($P > 0.05$).

The model was designed to predict the number of spiders within each guild among different shrub treatments over time. For each guild a two-way table was constructed with three levels (rows) for treatment and seven levels (columns) for time. Observed counts of spiders were assigned to the appropriate cells (15 counts/cell for six columns (one had 14), and 5 counts/cell for the seventh column). The full model asserts that counts within each cell can be expressed as a linear combination of date effects, treatment effects, and an interaction of date and treatment effects, and can be written as:

$$\log \mu_{ij} = \mu + \text{treatment}_i + \text{date}_j + (\text{treatment} \times \text{date})_{ij}$$

Four subsets of this model were also fit to the data: a null model which states that there is no effect by treatment, date, or treatment \times date interaction, a model that assumes only a date effect, a model that assumes only a treatment effect, and a model that assumes only treatment and date effects (no interaction). The GLM procedure in the S-PLUS statistical package (Statistical Sciences, Inc., Seattle, Washington) was used to fit these five models to the data in each of the four guild tables (date was used as a blocking factor and fit first). No significant treatment \times date interaction was detected ($P > 0.05$) and this term was removed from the full model. A 5% level of significance was selected for interpretation.

RESULTS

A total of 570 spiders was collected during the experiment (Table 2), representing a minimum of 26 species (95.8% of the spiders were identified to species level, 3.7% were identified to guild level, and 0.5% remained unidentified). Due to the short time frame considered in this experiment (to detect early priority effects), the average number of spiders per shrub was small (2 spiders/shrub, but note range of 0–14), but again, we sought mainly to compare groups of shrubs treated the same way, not single shrubs. At the species level, *Sassacus papenhoei* (Peckham & Peckham 1895) and *Hyposinga singaeformis* (Scheffer 1904) numbers were especially reduced on shrubs with placed jumpers. On shrubs with

placed *Phidippus johnsoni*, *Misumenops* sp. was more frequently collected and *Anyphaena pacifica* (Banks 1896) was less frequently collected relative to the two other treatments. All three treatments appear similar in terms of Hill's (1973) indices for overall species richness and species abundance (Table 2). The total number of spiders per shrub was independent of treatment type (Table 3, $X^2 = 12.096$, $df = 10$, $P = 0.279$).

At the guild level, inspection of the data reveals that shrub treatments with placed jumping spiders had 43–50% fewer trappers and 28–40% more pursuers relative to the reference treatment (Table 2). The log-linear model indicated two significant differences (Table 4). First, comparisons based on four different treatment combinations revealed that significantly fewer trappers were collected from shrubs that had *Metaphidippus aeneolus* as a pioneer compared to reference shrubs (Treatment 1 vs. Treatment 3, $P = 0.034$). Second, there were significantly fewer trappers collected from shrubs that had either jumper as a pioneer compared to reference shrubs (Treatments 1 and 2 combined vs. Treatment 3, $P = 0.019$). Tests with the model involving other guilds and comparisons were not significant at $P = 0.05$.

DISCUSSION

In a manipulative field experiment, *Metaphidippus aeneolus* pioneers significantly reduced trapper numbers in subsequent spider assemblages ($P = 0.034$), indicating that a priority effect occurred. *Phidippus johnsoni* pioneers did not yield a significant result, although the raw count data differs by only two trappers (Table 2). When treatments were combined for analysis, jumpers also significantly reduced trapper numbers ($P = 0.019$). This short-term response was detected despite some likelihood (35%) that cleared reference shrubs would have received one of these same jumper pioneers simply by chance (and a 66% chance of receiving any jumper species, based on 1992 census data). In this sense, our test was somewhat conservative. This detail may be balanced by the observation of only two significant results at the 0.05 level among 16 tests performed (4 comparisons \times 4 guilds). If a severe correction is made for these multiple comparisons (e.g., Bonferroni test), the results of the log-linear model are not signifi-

Table 2.—Counts of spiders collected from experimental shrubs (19 July–18 September 1992) arranged by guild and species identity for three treatments (*Metaphidippus aeneolus* = Treatment 1, *Phidippus johnsoni* = Treatment 2, reference = Treatment 3), accompanied by Hill's (1973) indices for species richness and diversity (N0 = species richness, N1 = number of abundant species, N2 = number of very abundant species).

Identity	Number of spiders		
	<i>M. aeneolus</i>	<i>P. johnsoni</i>	Reference
Jumpers			
<i>Metaphidippus aeneolus</i> (Curtis 1892)	54	32	24
<i>Oxyopes scalaris</i> (Hentz 1845)	6	6	2
<i>Habronattus hirsutus</i> (Peckham & Peckham 1888)	2	5	5
<i>Phidippus johnsoni</i> (Peckham & Peckham 1883)	29	44	31
<i>Phidippus</i> sp.	0	2	0
<i>Sassacus papenhoei</i> (Peckham & Peckham 1895)	26	35	48
<i>Synageles idahoanus</i> (Gertsch 1934)	4	2	6
<i>Tutelina similis</i> (Banks 1895)	4	5	3
Unidentified	3	2	2
Guild total	128	133	121
Trappers			
<i>Dictyna idahoana</i> (Chamberlin & Ivie 1933)	1	0	0
<i>Dipoena nigra</i> (Emerton 1882)	0	0	1
<i>Dipoena tibialis</i> Banks 1906	4	5	9
<i>Erigone</i> sp.	0	1	0
<i>Euryopsis</i> sp.	1	0	3
<i>Hyposinga singaeformis</i> (Scheffer 1904)	2	2	9
<i>Metepeira foxi</i> (Gertsch & Ivie 1936)	2	2	1
<i>Theridion neomexicanum</i> Banks 1901	3	3	1
Unidentified	1	3	4
Guild total	14	16	28
Ambushers			
<i>Coriarachne</i> sp.	1	0	0
<i>Misumena vatia</i> (Clerck 1757)	0	1	0
<i>Misumenops</i> sp.	1	7	2
<i>Xysticus gulosus</i> Keyserling 1880	5	1	5
<i>Xysticus montanensis</i> Keyserling 1887	1	0	0
<i>Xysticus</i> sp.	2	3	4
Unidentified	1	1	0
Guild total	11	13	11
Pursuers			
<i>Anyphaena pacifica</i> (Banks 1896)	8	1	6
<i>Chiracanthium inclusum</i> (Hentz 1847)	7	12	5
<i>Philodromus histrio</i> (Latreille 1819)	12	14	8
<i>Thanatus formicinus</i> (Clerck 1757)	2	4	3
<i>Tibellus oblongus</i> (Walckenaer 1802)	1	3	2
Unidentified	2	1	1
Guild total	32	35	25
Unidentified			
Total spiders collected ($n = 570$)	187	197	186
Total number of shrubs ($n = 284$)	95	94	95
Species richness (N0)	21	20	19
Number of abundant species (N1)	9.9	9.9	10.4
Number of very abundant species (N2)	6.5	7.1	7.2

Table 3.—Summary of contingency table analysis of total number of spiders per shrub. Frequencies represent the number of shrubs within each treatment. The three largest contributions to the chi-square value are marked (+). $\chi^2 = 12.096$, $df = 10$, $P = 0.279$.

Total spiders	Observed frequencies Shrub treatment			Expected frequencies Shrub treatment		
	<i>M. aeneolus</i>	<i>P. johnsoni</i>	Reference	<i>M. aeneolus</i>	<i>P. johnsoni</i>	Reference
0	19	13	20	17.39	17.21	17.39
1	30	25	28	27.76	27.47	27.76
2	20	28+	13+	20.41	20.19	20.41
3	11	13	21+	15.05	14.89	15.05
4	8	9	6	7.69	7.61	7.69
≥5	7	6	7	6.69	6.62	6.69
Total	95	94	95	95.00	94.00	95.00

icant. We note, however, that the log-linear model results are internally consistent, parallel other results from our study in a highly suggestive way, and match other published reports of spider-spider interactions.

We observed that when a jumping spider is placed onto a new shrub, the spider is usually very active and begins a nearly comprehensive exploration of the shrub branches and canopy (see also Wing 1984). Once these movements are performed, a pioneer may be familiar enough with its surroundings to detect quickly new arrivals. Salticids have extremely good eyesight for distances up to 40 cm (Foelix 1982), and may effectively survey the ~70 cm diameter shrubs used in this study. As trappers also perform some exploration of the shrub prior to web-site selection (Riechert & Gillespie 1986), their movements following colonization may be readily detected by active visual predators such as jumpers (even at night, see Forster 1982). Extended activity associated with web construction may further enhance their detection by jumpers, and the chemical properties of the silk itself may act as stimuli to other spiders (Tietjen &

Rovner 1982; Pollard et al. 1987). Completing a web before a jumper arrives may not eliminate this threat, as Jackson (1977) and Robinson & Valerio (1977) report that jumpers capture trappers on webs.

As noted earlier, spiders are often the major predators of other spiders. The outcome of an attack is usually a function of body size, with the smaller spider becoming the victim (Hallander 1970; Nentwig 1987; Dong & Polis 1992). As the smallest spiders at the site, trappers may be especially vulnerable to inter-guild predation. During this study, we observed *Metaphidippus aeneolus* attacks on a trapper (*Metepeira foxi* (Gerstch & Ivie 1936)); and Morse (1992) has described *Metaphidippus* predation on an ambusher (*Misumena*). *Phidippus johnsoni* is known to prey heavily on spiders, including trappers such as Theridiidae and Dictynidae (both present at Mill Hollow) (Jackson 1977). *P. johnsoni* usually attacks prey that measures 25–75% of its own body size (Jackson 1977), and nearly all Mill Hollow trappers lie within this range for late-instars and adults. We also observed immature *Phidippus johnsoni* capturing an am-

Table 4.—Summary of results from comparisons performed with a log-linear model to detect guild-level differences among three shrub treatments (Treatment 1 = *Metaphidippus aeneolus* pioneer; Treatment 2 = *Phidippus johnsoni* pioneer; Treatment 3 = reference).

Treatment comparison	Result	<i>t</i>	<i>df</i>	<i>P</i> -value
1 vs. 3	Fewer trappers if <i>M. aeneolus</i> is pioneer	-2.126	275	0.034
2 vs. 3	No significant differences			
1 and 2 vs. 3	Fewer trappers if a jumper is pioneer	-2.360	276	0.019
1 vs. 2	No significant differences			

busher (*Xysticus* sp.). Cutler et al. (1977) documented another jumper, *Oxyopes scalaris* (Hentz 1845), capturing members of five spider families, including trappers.

Pursuers were found in greater numbers in both jumping spider treatments relative to the reference treatment, though these differences were not statistically significant. These two groups are the most similar in adult body size, which may reduce stimuli for interguild predation and favor coexistence. Also, even if a jumper is approached by a pursuer, it may avoid capture by a single jump, a movement the pursuer cannot perform.

Intraguild predation was also observed among jumpers at our site, including cannibalism by *Metaphidippus aeneolus* and 11 attacks by immature *Phidippus johnsoni* on other immature spiders including four jumpers (conspecifics, *M. aeneolus*, *Sassacus papenhoei*, *Habronattus hirsutus* (Peckham & Peckham 1888)). Cutler (1991) has also reported predation by *Phidippus* on immature conspecifics. We also recorded adult *S. papenhoei* predation on immature *P. johnsoni*, an immature *S. papenhoei* preying on immature *M. aeneolus*, and an adult *Oxyopes scalaris* preying on immature *M. aeneolus*.

In all cases that we observed, the larger (attacking) spider consumed the smaller spider. Shrub spiders likely share similar environmental requirements, and given the demands of life in an arid climate, may be "enemies doomed to associate" (Diamond 1992). Other spiders may be some of the most available and reliably caught prey that they encounter on shrubs, and these interactions can be expected to directly influence spider assemblage structure.

Because *Metaphidippus aeneolus* and *Phidippus johnsoni* are members of the same guild, our tests have some relevance to recent discussions concerning the extent of species redundancy in nature (Walker 1992; Lawton & Brown 1993; Morin 1995). In our tests, only one statistically significant difference between these two species was detected. Because of the high species richness of spiders found among sagebrush shrubs and the high relative abundance of jumpers, we suggest that this system is well-suited for new experimentation on this question.

Finally, Moran & Hurd (1994) have described predator avoidance behavior by spi-

ders in response to introductions of mantids. Spider emigrations occurred rapidly after mantid introduction, especially among smaller size classes. Whether shrub spiders respond in a similar manner to other spiders is not known. Although we cannot exclude this mechanism, our present interpretations are based on widely-reported phenomena of cannibalism and interguild predation among spiders.

CONCLUSIONS

We have described a system and an experimental approach that we believe has value for work on assembly rule theory, in which community components can be manipulated and added to discrete habitat units in different temporal sequences. In preliminary experiments with two different jumper pioneer treatments, trapper numbers were reduced compared to a reference treatment, indicating that a priority effect occurred. Although we are unable to eliminate all ambiguity, we infer that spider-spider interactions can explain these outcomes, based on differences in foraging technique and body size. It is not known how long the observed priority effects persist or what the outcomes would be if trappers or other spiders were the pioneer colonists. We believe that additional work in this system, already underway, can test ideas concerning models of animal community assembly.

ACKNOWLEDGMENTS

This work was part of a dissertation completed by W.J. Ehmann at Utah State University in 1994 with support from the U.S.U. Ecology Center. We thank Adele Cutler, Richard Cutler, and Susan Durham for assisting with data analysis, Michael Garey and Janna Hewitt for assistance in the field, and Reilly Howell for stimulating discussions. Stan Miller, US Forest Service, kindly gave permission to use the Mill Hollow site.

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Manuscript received 19 January 1996, revised 15 June 1996.