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SPIDER COMMUNITY COMPOSITION AND STRUCTURE IN A SHRUB-STEPPE

ECOSYSTEM: THE EFFECTS OF PREY AVAILABILITY

AND SHRUB ARCHITECTURE

by

Lori R. Spears

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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UTAH STATE UNIVERSITY
Logan, Utah

2012

ABSTRACT

Spider Community Composition and Structure in a Shrub-Steppe Ecosystem: The Effects

of Prey Availability and Shrub Architecture

by

Lori R. Spears, Doctor of Philosophy

Utah State University, 2012

Major Professor: James A. MacMahon
Department: Biology

Habitat structure is an important driver of many ecological patterns and processes, but few studies investigate whether habitat structure interacts with other environmental variables to affect community dynamics. The main objective of this study was to disentangle the relative importance of prey availability and shrub architecture on the distribution, abundance, and biodiversity of spiders of northern Utah, USA. We conducted field experiments which focused on: (1) describing the importance of these factors on spider community organization, (2) specifically evaluating whether prey availability mediates the relationship between shrub architecture and spider abundance and biodiversity, and (3) investigating spider and prey responses to manipulations of surrounding vegetation structures.

For the first two experiments, big sagebrush shrubs were randomly assigned to six experimental treatments: two levels of prey attractant (shrubs were either baited or not

baited) and three levels of foliage density (low, natural/control, or high). The purpose of manipulating both prey availability and shrub architecture was to delineate their significance to spiders. For the last experiment, changes in these factors were investigated at two different levels of spatial context (a single manipulated shrub surrounded by untreated shrubs vs. a manipulated shrub surrounded by a patch of similarly treated shrubs).

We found both prey availability and shrub architecture directly influenced patterns of spider abundance and species richness and that spider species diversity and community composition varied in response to shrub architecture alone. Preferences of some spiders for certain shrub types likely reflect differences in foraging strategies or the substrate required to support different types of webs. We also demonstrate that spider response to shrub architecture is the result of multiple processes (i.e., a combination of direct and indirect effects via prey availability) and that surrounding vegetation structures affect spider abundances on shrubs. In addition, prey composition varied among different shrub foliage density treatments, but only when surrounding vegetation structures were also manipulated. More generally, this study suggests that ecological responses to habitat structure are in part mediated by associated variables and the significance of shrub architecture varies depending on the organisms examined and the spatial scale to which they respond most strongly.

(130 pages)

PUBLIC ABSTRACT

Spider Community Composition and Structure in a Shrub-Steppe Ecosystem: The Effects

of Prey Availability and Shrub Architecture

by

Lori R. Spears, Doctor of Philosophy

Habitat structure is cited as an important factor influencing organisms, but few studies investigate whether habitat structure interacts with other environmental variables to affect community dynamics. The purpose of this study was to determine, using field experiments, the importance of prey availability and shrub architecture on a spider community in northern Utah, USA. We were also interested in determining whether surrounding shrub architectures influence spider and prey responses.

Our results suggest that spider distribution, abundance, and biodiversity are influenced by shrub architecture. Shrub architecture influenced spiders both directly and indirectly via associated changes in prey availability. Spiders were also directly influenced by prey availability. Further, spider and prey responses were affected by surrounding shrub architectures, but the type of prey present on shrubs of different foliage types varied only when surrounding shrub architectures were also manipulated. Therefore, the importance of shrub architecture depends on the spatial scale to which organisms respond most strongly.

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CHAPTER 1

INTRODUCTION

One of the most basic goals of ecology is to understand the importance of environmental factors on the distribution, abundance, and biodiversity of organisms (Hutchinson 1959; MacArthur 1965; Brown 1984; Putman 1994). Ecologists are also interested in investigating how, and to what degree, environmental factors interact with each other to influence organisms. The ubiquitous nature of ecological interactions, however, and the fact that ecological responses are often the combination of direct and indirect effects, makes it difficult to assess the relative contribution and importance of any one factor (Strauss 1991; Wootton 1994; Miller & Travis 1996; Peacor & Werner 2001; Krivtsov 2004). But if we are to understand and manage communities, we must disentangle the different ecological factors that shape their composition.

Habitat structure is an important driver of many ecological patterns and processes and has even been described as the "stage" of the "ecological theater" (*sensu* Hutchinson 1965; Byrne 2007). Habitat structure is defined as the physical composition, arrangement, and amount of objects in space and time and consists of at least three major axes: complexity, heterogeneity, and scale (McCoy & Bell 1991; Byrne 2007). Habitat complexity refers to the absolute abundance of individual components; for example, shrub complexity changes with the number of branches present per shrub. Habitat heterogeneity refers to the relative abundance of different structural elements; a habitat is more heterogeneous if, for instance, shrubs are surrounded and intermixed with other types of vegetation (McCoy & Bell 1991; Beck 1998; Downes et al. 1998; Hir & Hily

2005). Finally, the scale of examination refers to the size of area used to measure habitat heterogeneity and/or complexity. The concept of scale is important since ecological responses vary spatially and temporally and because different organisms perceive the environment in entirely different ways (Wiens 1989; Samu et al. 1999; Krawchuk & Taylor 2003; Tews et al. 2004).

One challenge facing ecologists is to tease apart the consequences of habitat structure from the myriad of other environmental influences (Bell et al. 1991; Srivastava 2006; Byrne 2007). Habitat structure may directly influence organisms by providing more microhabitats, but may also exert indirect influences by modifying environmental conditions, including resource availability (Larmuth 1979; McCoy & Bell 1991). For example, Bonte and Mertens (2003) found that the abundance of spiders positively corresponded with those of their prey and both groups of organisms were associated with several vegetation characteristics, such as vegetation height and percent coverage. Similarities in distribution may have been the result of greater habitat availability or of common and independently developed microhabitat preferences. Spiders may have also been associated with specific habitat types because of the presence of more prey. For spiders, the importance of both prey availability and habitat structure are well documented (see review in Wise 1993), but are not effectively disentangled.

Spiders are distributed worldwide, have evolved to conquer nearly all habitat types, and are common and important natural predators (Wise 1993; Foelix 2011), so it is understandable that much research has been devoted to them. They are routinely used in scientific studies that test predictions of optimal foraging theory (Morse 1979; Fritz &

Morse 1985; Harwood et al. 2003) or that seek to understand their effectiveness as biological control agents (Riechert & Lockley 1984; Nyffeler & Benz 1987; Riechert & Bishop 1990; Marc & Canard 1997; Riechert 1999; Samu 2003; Pluess et al. 2010). Spiders are generalist predators that feed heavily on insects from various taxa, but also regularly prey upon other arthropods, including spiders, and will occasionally feed on vertebrates (Bleckmann & Lotz 1987; Nyffeler et al. 1989; Nyffeler 1999, 2000; Timm & Losilla 2007).

Spiders often position themselves in the environment to maximize prey capture. They will place their webs near flowering plants or vertebrate fecal material, both of which may indicate greater prey availability (Riechert 1976). They are also known to aggregate in areas of high prey densities (Wise 1993; Harwood et al. 2003) or will relocate their webs when deprived of prey (Vollrath 1985). Some spiders build webs that take advantage of the color cues insects seek while foraging by adjusting the reflectance properties of their silk (Craig et al. 1996). Other spiders interfere with floral signals by creating a UV contrast that makes spider-occupied flowers more attractive to prey (Heiling et al. 2003, 2005).

Like most predators, spiders exhibit a wide range of foraging strategies which may have evolved as a mechanism to promote coexistence and reduce competition for valuable resources (Uetz 1992; Uetz et al. 1999; Foelix 2011). Some spiders are relatively stationary and build webs or sit camouflaged on stationary sites such as branches or flowers before ambushing their prey. Others are more active hunters that capture their prey in full pursuit. Spiders may also forage either individually or as part of

a coordinated group effort (Rypstra 1989; Craig 1991; Rypstra & Tirey 1991; Foelix 2011). For these reasons, researchers often explore spider hunting techniques as they relate to habitat use (Uetz et al. 1999; Harwood et al. 2003; Hore & Uniyal 2008). In addition, spiders are commonly used for addressing questions concerning habitat structure because, as predators, they are not directly reliant on a particular plant species as a food source (Colebourn 1974; Hatley & MacMahon 1980), but also because the building of a web requires specific substrates for attachment (Turnbull 1973; Riechert & Gillespie 1986; Uetz 1991).

The selection of a suitable foraging site is important for a spider's survival since structural features of the environment may be tied to the number and type of prey available, but also to thermal requirements for development and reproduction (Riechert & Tracy 1975; Riechert 1992). Habitat structure may also offer protection from predators (Gunnarsson 1996; Langellotto & Denno 2004). For spiders, habitat structure encompasses a variety of variables, including topographic features and other physical attributes of the environment (Barnes & Barnes 1954; Colebourn 1974; Ladle & Velander 2003; Goldsbrough et al. 2004; Oxbrough et al. 2006; Peres et al. 2007), vegetation physiognomy (see reviews in Uetz 1991 and Wise 1993), and even structures made by other organisms (Haddad & Dippenaar-Schoeman 2002), including spider webs (Rypstra & Binford 1995; Agnarsson 2003; Kerr 2005) and man-made structures (Uetz & Burgess 1979; Edwards & Edwards 1997).

This dissertation describes a field experiment conducted on a well-studied spider community in a shrub-steppe ecosystem of northern Utah, USA (Hatley & MacMahon

1980; Robinson 1981; Abraham 1983; Wing 1984; Ehmann & MacMahon 1996;

Heikkinen & MacMahon 2004; Cobbold & Supp, in press). Although prior studies

suggest that spiders respond primarily to habitat structure and secondarily to prey

availability (Rypstra 1983; Greenstone 1984; Bradley 1993; Halaj et al. 1998, 2000;

Nyffeler & Sunderland 2003; Langellotto & Denno 2004; Horváth et al. 2005; Chan et al.

2009), it remains largely unknown whether spiders respond directly to habitat structure

per se or to differences in prey availability caused by different structures, or some

combination thereof. In the second chapter of this dissertation, we examine the

importance of these factors and their interactions on spider community organization. The

third chapter specifically evaluates whether prey availability mediates the relationship

between shrub architecture and spider community organization. We use the same data set

as used in the previous chapter but, for this analysis, we use structural equation modeling,

a procedure well-suited for partitioning direct and indirect effects. In the fourth chapter,

we explore the effects of prey availability and shrub architecture and their interactions on

spider communities at two small spatial scales (i.e., a single treated shrub surrounded by

untreated shrubs vs. a treated shrub surrounded by a collection of similarly treated

shrubs). Previous studies in northern Utah examined spider response to shrub

architecture only at the scale of a single shrub and only Wing's study examined the

influence of prey availability. In the fifth and final chapter, we briefly summarize all of

the above information and present general conclusions from these studies. The goals of

this dissertation are to disentangle the relative importance of prey availability and shrub

architecture, to determine under what conditions these factors influence spider

community composition and structure, and to provide a conceptual framework to

stimulate future study of the factors driving spider community organization.

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CHAPTER 2

AN EXPERIMENTAL STUDY OF SPIDERS IN A SHRUB-STEPPE ECOSYSTEM:

THE EFFECTS OF PREY AVAILABILITY AND SHRUB ARCHITECTURE

ABSTRACT. Habitat structure is of great importance for the distribution and abundance of various organisms. Spiders are especially sensitive to structural features of their environment. Although spiders are influenced by habitat structure, it remains unclear whether spiders respond to architecture or to differences in prey availability associated with different architectures. Here, we investigated the effects of shrub architecture and prey availability on a spider community in a shrub-steppe environment in northern Utah, USA. Big sagebrush shrubs were randomly assigned to six experimental treatments: two levels of prey attractant (shrubs were either baited or not baited) and three levels of foliage density (low, natural/control, or high). We found that spider abundance and species richness were affected by both prey availability and shrub architecture, while variation in spider species diversity (Shannon-Wiener index) was governed by changes in shrub architecture alone. Spider species and family compositions were also associated with changes in shrub architecture, although guild composition was not. We discuss the implications and limitations of these findings and present suggestions for future research.

Ecologists have long been interested in patterns of community structure and the mechanisms that generate these patterns (Hutchinson 1959; Putman 1994). Community structure is the result of interactions among many factors, making it difficult to assess the relative contribution and importance of any one factor (Uetz 1991). Clearly, if we are to understand and manage communities, there is a need to disentangle the different ecological factors that shape their composition.

Habitat structure, defined as the physical composition and arrangement of objects in space and time, is one of several factors considered important in influencing the distribution and abundance of animals (McCoy & Bell 1991). Structurally complex habitats provide animals with a wider array of microhabitats (Brandt & Lubin 1998), more diverse ways of exploiting food resources (Brandt & Lubin 1998; Tews et al. 2004), amelioration of climatic extremes (Larmuth 1979), protection from predators (Gunnarsson 1996; Langellotto & Denno 2004) and, for some predators, more effective ways to locate and capture prey (Langellotto & Denno 2004). Habitat structure influences a variety of organisms, including birds (MacArthur & MacArthur 1961; Vander Wall & MacMahon 1984), lizards (Pianka 1966), some rodents (Rosenzweig & Winakur 1969; Parmenter & MacMahon 1983), and various invertebrates (Murdoch et al. 1972; Southwood et al. 1979; Lawton 1983; Parmenter et al. 1989), including spiders (Uetz 1991; Wise 1993).

Spiders are influenced by several structural attributes of the environment, including vegetation density, height, and orientation (Hatley & MacMahon 1980; Brown 1981; Abraham 1983; Rypstra & Carter 1995; Brierton et al. 2003), as well as

interactions among variables such as branch height and orientation (Heikkinen &

MacMahon 2004). Spiders may even distinguish between different branch types with

some spiders being more common on reproductive than on vegetative branches (de Souza

& Martins 2004; de Souza & Módena 2004).

Although spider communities differ with changes in habitat architecture, it

remains unclear whether spiders are responding to architecture *per se* or to differences in

prey availability caused by different architectures. While some studies suggest that prey

availability is important in understanding patterns of spider community structure

(Riechert 1974; Spiller 1992; Bogya et al. 2000; Horváth et al. 2005), others emphasize

that prey availability is of lesser importance and that spider communities are shaped

primarily by habitat structure (Rypstra 1983; Greenstone 1984; Bradley 1993; Halaj et al.

1998, 2000; Nyffeler & Sunderland 2003; Langellotto & Denno 2004; Chan et al. 2009).

These findings highlight the need to further evaluate the processes responsible for

structuring spider communities.

Our goal for this study was to investigate the relative importance of prey

availability and shrub architecture in determining the composition of a well-studied

spider community in a shrub-steppe environment in northern Utah, USA. Spiders are

model organisms for addressing ecological studies. They are ubiquitous, locally

abundant, taxonomically diverse, and amenable to experimental manipulations (Hatley &

MacMahon 1980; Uetz 1992; Wise 1993; Foelix 2011). Spiders are especially well-

suited for investigating the effect of shrub architecture on community organization

because, as carnivores, they are not directly reliant on a particular plant species as a food

source (Colebourn 1974; Hatley & MacMahon 1980) and, for web-builders, the building

of a web often requires specific substrates for attachment (Turnbull 1973; Riechert &

Gillespie 1986; Uetz 1991).

METHODS

Study site.—Our research expands upon earlier studies of spider communities in

the Great Basin shrub-steppe ecosystem of northern Utah (Hatley & MacMahon 1980;

Robinson 1981; Abraham 1983; Wing 1984; Ehmann 1994; Ehmann & MacMahon 1996;

Heikkinen & MacMahon 2004). This study was conducted at Hardware Ranch Wildlife

Management Area (41°61 N, 111°57 W). Hardware Ranch WMA is located in the

Wasatch-Cache National Forest, about 40 km southeast of Logan, Cache County, Utah

and is managed by the Utah Division of Wildlife Resources. The site is at an elevation of

1731 m and is dominated by big sagebrush (*Artemisia tridentata*) and low sage

(*Artemisia arbuscula*). Land is used primarily as winter range for big game.

Shrub selection.—To reduce the heterogeneity among individual shrubs, we

applied several criteria when selecting shrubs. Experimental shrubs (*A. tridentata*) had a

single trunk at ground level, were not in immediate contact with an adjacent shrub, and

were at least 10 m from another experimental shrub. We measured shrubs before and

after treatment for maximum canopy width, width perpendicular to maximum canopy

width, and canopy height (excluding the trunk beneath) (Ehmann 1994). Only shrubs

with all three canopy dimensions between 0.4 and 1 m were selected. Shrub volume was

determined by using the formula for an ellipsoid:

$$\text{Volume} = 4/3\pi abh$$

where a and b represent, respectively, the linear dimensions of the major and minor axes, and h represents height.

Study design and treatments.—We permanently marked shrubs selected for study with a numbered tag to facilitate location and data collection and then randomly assigned them to six experimental treatments, with 25 replicates per treatment. Experimental treatments consisted of factorial combinations of two levels of prey attractant and three levels of foliage density. Prey attractant treatments included shrubs that were either baited or not baited. The purpose of the bait was to increase the probability of prey visits and/or the length of each visit (Wing 1984). Baited shrubs contained four suspended containers: two (59 ml) containers filled with pig offal, one (22 ml) container filled with yellow banana-oil flavored honey, and one (22 ml) container filled with red-colored honey. Container lids were perforated to facilitate odor dispersion. As a control, identical but empty containers were suspended from shrubs not baited. We baited shrubs two weeks prior to sampling to maximize arthropod abundance on shrubs (Robinson 1981).

Shrub architecture was manipulated to either increase or decrease shrub foliage density (see Appendix B.1) (Hatley & MacMahon 1980). We increased foliage density by tightly binding all branches together with jute (hereafter referred to as "high") and decreased by clipping 50% of the shrub foliage ("low"). Shrubs not manipulated were used as controls ("natural"). Shrubs were manipulated in spring of 2007 and 2008. We calculated differences in shrub foliage density using photographs taken from a digital

camera (Nikon Coolpix L12) positioned approximately 1.5 m from the shrub. A white

cloth attached to a wooden frame (1.5 x 1.5 m) was positioned behind the shrub and

before and after treatment pictures were taken. Pictures were taken again at the end of the

first sampling season. The pictures were imported into Adobe Photoshop CS4. Here,

shadows surrounding the shrub were first removed using the 'color range' option.

Images were then transformed into a black and white image by means of the 'threshold'

option and the area occupied by the shrub was outlined using the magnetic 'lasso' tool.

The 'histogram' tool was then used to determine the ratio of white (background) vs. black

(vegetation) pixels. For each picture, this procedure was carried out twice and the

average was taken.

       Determination of sampling effort.—Before experimental manipulations, we

sampled fifty randomly chosen shrubs to obtain a preliminary survey of the spider

community. A species accumulation curve was then generated. Species accumulation

curves show the rate at which new species are found by plotting the cumulative number

of observed species as a function of the sampling effort required to observe them

(Colwell et al. 2004; Magurran 2004). As sampling efforts increase and as fewer new

species are found, the curve approaches an asymptote, indicating that a representative

sample was achieved given the collection method used. Here, we determined that a

sampling effort of 25 shrubs per treatment combination was sufficient to reach the

asymptote. Species accumulation curves were generated using the 'specaccum' function

in the vegan package of Program R (R Development Core Team 2011).

Sampling of arthropods.—We sampled shrubs during a five day sampling period once a month in June, July, August, and September of 2007 and 2008. September samples from both years and a few samples from the remaining collections were discarded because of bait disturbances. Sampling periods took place at intervals of no less than three weeks. Sampling began approximately two hours after sunrise, occurred only when there was an absence of high winds and precipitation, and did not occur when temperatures were below 10° C. We collected arthropods by using the beating technique (Ehmann & MacMahon 1996; Southwood & Henderson 2000). Each shrub was quickly surrounded at the base with a canvas sheet (1.5 x 1.5 m) and then beaten 15 times with an ax handle to dislodge specimens onto the beating sheet for collection. Specimens were collected with an aspirator and immediately preserved in vials containing 70% ethanol. After the arthropods from the first beating were collected, a second beating episode of the same duration followed. The double-beating method was used previously and resulted in a 100% collection rate (Ehmann & MacMahon 1996).

Since this sampling technique may emphasize sedentary prey while ignoring highly active prey, sticky traps were also used to monitor prey availability. A sheet of clear plexiglass (25 x 25 cm) was coated on both sides with Tanglefoot® trap coating (Tanglefoot Co., Grand Rapids, MI) and attached to two vertical stakes (Greenstone 1984; Brandt & Lubin 1998; Halaj et al. 2000). During July of 2007, we placed one trap next to each of five additional randomly chosen shrubs from each treatment type not sampled by the beating technique. Each trap was positioned 20 cm from a given shrub and cardinal direction of the trap was determined at random. After five days, the traps

were collected and taken to the laboratory (Wing 1984). The insects collected by these traps may not mirror suitable prey or the exact resource base available to spiders, but the traps do allow for the analysis of specimens active at a given time and place (Rypstra 1986).

We identified spiders to species and measured their body length (not including spinnerets) to the nearest 0.1 millimeter. We excluded immature spiders from analyses since their behavior and habitat may differ from adults, but also because some immature spiders were difficult to identify to species (Jiménez-Valverde & Lobo 2006; Sacket et al. 2008).

We further sorted spiders into *a priori* guilds, or groups of organisms that exploit the same resource in similar ways (Root 1967). These assignments are user-defined parameters widely used in community studies (Hawkins & MacMahon 1989). For spiders, guild membership is based on observations of foraging techniques that are often reinforced by morphological characteristics shared at the family level (Post & Riechert 1977). However, since there are no absolute guidelines, spider guild assignments vary widely (Uetz et al. 1999). In this study, two different approaches for the classification of spider foraging guilds were used. Following the classification proposed by Uetz et al. (1999), we grouped spider families into the following four guilds: 1) ambushers: Philodromidae and Thomisidae; 2) runners: Gnaphosidae and Lycosidae; 3) stalkers: Mimetidae, Oxyopidae, and Salticidae; and 4) trappers: Araneidae, Dictynidae, Linyphiidae, and Theridiidae. The second approach followed the classification commonly used for spiders on big sagebrush (Hatley & MacMahon 1980; Robinson

1981; Wing 1984; Ehmann 1994; Heikkinen & MacMahon 2004), where members from the family Philodromidae were analyzed as runners instead of ambushers. Relationships between spider hunting strategies and spatial characteristics of the vegetation have previously been described. In general, ambushers prefer dense foliage, stalkers and trappers prefer open foliage, and runners prefer a variety of foliage types (Hatley & MacMahon 1980; Uetz et al. 1999).

We identified potential prey items to the order level or below and assigned them to the following functional groups: detritivores, herbivores (including pollinators), and natural enemies (predators and parasites/parasitoids). Prey composition was examined to assess whether differences among treatments, if present, correspond to variations in spider community structure. Taxonomic classification followed Triplehorn and Johnson (2005) and functional group assignments were based on dietary information provided also by Triplehorn and Johnson (2005). Families containing members of multiple functional groups were categorized using the most commonly represented functional group within the family, while adult taxa that could not be readily assigned to a functional group were sorted based on feeding styles of the larval stage (Chust et al. 2004; Rango 2005). We did not collect ants (Hymenoptera: Formicidae) or aphids (Hemiptera: Aphididae) because their high abundances made collection of samples in a short period of time difficult. All specimens were deposited in the Department of Biology at Utah State University for reference.

Data analyses.—We compared mean shrub foliage density among treatments with a repeated measures one-way analysis of variance (ANOVA). Relevant pairwise

comparisons were made as needed and familywise Type I errors were controlled by applying the Tukey-Kramer method. An unstructured covariance matrix was selected to model repeated measures across the three measurements based on Akaike's Information Corrected Criterion (AIC_C). A two-way ANOVA, with foliage density and prey attractant treatments as factors, was used to analyze square-root transformed sticky trap data. ANOVAs were performed using the MIXED procedure in SAS/STAT software Version 9.2 in the SAS System for Windows (SAS Institute 2011).

We tested the effects of foliage density and prey attractant treatments on spider and prey abundance, as well as spider species diversity (H') and richness (S), using a general linear mixed model (LMM) with repeated measures. Spider diversity was determined using the Shannon-Wiener index (Magurran 2004) and spider and prey abundances were converted into densities (individuals per m^3) to account for differences in shrub volume. Experimental treatments were treated as fixed factors while shrubs were incorporated in the model as a random effect and treated as independent replications. An unstructured covariance matrix was used to model repeated measures across three months in each of two years. Response variables were ln-transformed ($x + 1$) to improve model performance. For main effects, pairwise mean comparisons were adjusted for familywise Type I errors using the Tukey-Kramer method. Pairwise comparisons for significant interaction terms were examined with stepdown Bonferroni adjustments. Analyses were carried out using the MIXED procedure in SAS/STAT software (SAS Institute 2011).

Experimental foliage treatments did not produce shrubs of equal density within each treatment group. Likewise, prey density varied among shrubs within a treatment group. Hence, because continuous variables typically are more informative than discrete levels, we also analyzed data using regression analyses (Cottingham et al. 2005). Spider density, diversity, and richness were regressed on continuous measures of foliage density and prey density using multiple linear regression and prey density was regressed on foliage density using simple linear regression. Since foliage densities were not measured consecutively across sampling periods, spider and prey densities were averaged for individual shrubs sampled during all sampling periods. Natural log-transformations were applied to averaged spider and prey densities to satisfy statistical assumptions. Regression analyses were performed using the REG procedure in SAS/STAT software (SAS Institute 2011).

To test the hypothesis that spider and prey community composition differed among experimental treatments, we used a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001, 2002). PERMANOVA differs from traditional multivariate analysis of variance (MANOVA) by relaxing the assumptions of a multivariate normal distribution. Computations were performed using the 'adonis' function in the vegan package of Program R (R Development Core Team 2011) and significance values were generated using 1000 permutations (Oksanen et al. 2010). We then used a similarity of percentages (SIMPER) analysis to determine which taxa contributed to overall differences in community composition. Taxa contributing $\geq 5\%$ to

the between-group dissimilarities were highlighted. SIMPER tests were carried out using

the program PRIMER v. 6 (Clarke & Gorley 2006).

We illustrated differences in compositional patterns with non-metric

multidimensional scaling (NMDS) plots using the 'metaMDS' function in the vegan

package of Program R (R Development Core Team 2011) (Oksanen et al. 2010). NMDS

arranges objects (i.e., sites) in multidimensional space so that points in close proximity

are more similar (e.g., in species composition) than those further apart. NMDS is

considered to be one of the most robust ordination techniques available because it is well

suited for non-normal data and does not assume linearity between species and

environmental gradients (McCune & Grace 2002).

Multivariate analyses were performed using pooled densities for shrubs sampled

during all sampling periods. Prior to analyses, data were square-root transformed to

reduce the influence of the most abundant taxa, then standardized by sample (i.e., shrub)

to minimize differences in total abundance (Gauch 1982). Distance matrices were

calculated using the Bray-Curtis dissimilarity index (Faith et al. 1987) and taxa

represented by less than 10 individuals were removed from the data set (McCune &

Grace 2002).

Significant differences in results refer to a statistical significance of $P \leq 0.05$.

Unless otherwise specified, data are presented as means ± standard errors.

RESULTS

Shrub manipulations.—Architectural treatments were designed to modify foliage densities. Shrub foliage densities were similar among treatment groups prior to experimental manipulations (ANOVA, $F_{(2,147)} = 0.5$, $P = 0.58$). Following manipulations, low and high foliage density shrubs were different from their initial foliage densities and foliage densities for each architectural treatment were different from the other two treatments, with differences persisting at the end of the sampling season (all $P < 0.001$). Low foliage density shrubs averaged a 13.5% loss of density (i.e., vegetation pixels), while high foliage density shrubs showed an 8.4% gain in density.

Prey density and community composition.—A total of 9929 potential prey were collected, representing 15 orders and more than 66 families (see Appendix A.1). Leafhoppers (Hemiptera: Cicadellidae), plant bugs (Hemiptera: Miridae), and leaf beetles (Coleoptera: Chrysomelidae) comprised over 77% of the non-Araneae arthropods collected.

Prey densities were influenced by the interaction between foliage density and prey attractant (LMM, $F_{(2,125)} = 3.5$, $P = 0.035$). With the exception of natural foliage density shrubs, baiting shrubs did not succeed in changing the prey base consistently among treatments. Low and high foliage density shrubs contained fewer prey items with the introduction of prey attractant, while natural foliage density shrubs contained more prey when shrubs were baited than when they were not, although none of these differences were significant (Fig. 2.1). In addition, the main effect of prey attractant was not statistically significant (LMM, $F_{(1,125)} = 0.02$, $P = 0.90$); although the main effect of

foliage density was highly significant (LMM, $F_{(2,125)} = 17.6$, $P < 0.001$). More prey items were collected in high foliage density shrubs than in natural or low foliage density shrubs and natural foliage density shrubs contained more prey than low foliage density shrubs. Prey densities were also influenced by the interaction between year and month of data collection (LMM, $F_{(2,127)} = 60.6$, $P < 0.001$). Prey densities declined from June to August of 2007, but were similar across months in 2008 (Fig. 2.2). A simple regression analysis also revealed a positive influence of foliage density on prey density (regression equation: $\ln(y) = 1.333 + 0.034(foliage\ density)$, $R^2 = 0.12$, $P < 0.001$). Lastly, sticky traps did not detect significant differences in prey densities among foliage density and prey attractant treatments (ANOVA, main effects and interaction, $P > 0.1$). Only one spider was collected from the sticky traps.

Prey community composition did not differ among foliage density and prey attractant treatments, neither at the level of orders nor by functional group (Table 2.1).

Spider density, diversity, and community composition.—A total of 6262 spiders were collected, of which 4518 (72%) individuals were immature. Of adult specimens, 31 species were collected (see Appendix A.2). Members from the family Salticidae were numerically dominant (48%), followed by Philodromidae (21%), Dictynidae (9%), Oxyopidae (8%), and Theridiidae (6%). Families Araneidae, Gnaphosidae, Linyphiidae, Lycosidae, Mimetidae, and Thomisidae were also collected, although in fewer numbers. The five most abundant species were *Pelegrina clemata* (Levi & Levi 1951) (Salticidae), *Philodromus histrio* (Latreille 1819) (Philodromidae), *Ebo pepinensis* Gertsch 1933 (Philodromidae), *Oxyopes scalaris* Hentz 1845

(Oxyopidae)*, and *Emblyna reticulata* (Gertsch & Ivie 1936) (Dictynidae), which together characterized 70% of the adult spiders collected.

Spider densities were influenced by foliage density treatment (LMM, $F_{(2,139)}$ = 22.1, $P < 0.001$). More spiders were collected in high foliage density shrubs than in natural or low foliage density shrubs and natural foliage density shrubs contained more spiders than low foliage density shrubs (Fig. 2.3). A multiple regression analysis showed that spider density was positively associated with both foliage density and prey density (P = 0.005 and < 0.001, respectively) (regression equation: ln(y) = -1.557 + 0.023(*foliage density*) + 0.502·ln(*prey density*), R^2 = 0.34), although the LMM main effect of prey attractant treatment on spider densities was not significant ($F_{(1,139)}$ = 1.0, P = 0.31), nor was the interaction between the two factors ($F_{(2,139)}$ = 1.7, P = 0.19). Spider density was also influenced by year and month of data collection (LMM, $F_{(2,138)}$ = 4.1, P = 0.018). Spider densities declined from June to August of 2007, but were static across months in 2008 (Fig. 2.4).

Spider species diversity differed by month of collection (LMM, $F_{(2,114)}$ = 8.0, $P <$ 0.001) and by foliage density treatment (LMM, $F_{(2,108)}$ = 3.1, P = 0.048). Spiders reached their highest diversity in June (mean Shannon index ± SE: 0.90 ± 0.03), followed by July (0.77 ± 0.03) and August (0.77 ± 0.03). Spiders were also more diverse on high and natural foliage density shrubs (0.86 ± 0.01 and 0.82 ± 0.07, respectively) than on low foliage density shrubs (0.75 ± 0.02). A multiple regression analysis showed that spider diversity was positively associated with foliage density ($P < 0.001$), but was not related

to prey density ($P = 0.24$) (regression equation: $y = -0.471 + 0.01(foliage\ density)$, $R^2 = 0.13$).

Spider species richness was influenced by year and month of collection (LMM, $F_{(2,140)} = 4.9$, $P = 0.009$), as well as foliage density treatment ($F_{(2,139)} = 15.4$, $P < 0.001$). More species were collected during June (mean number of species ± SE: 6.62 ± 0.09) than July (6.20 ± 0.07) and August (6.14 ± 0.06), with species richness being higher in June 2007 (6.90 ± 0.12) than in June 2008 (6.35 ± 0.11). More species were also collected on natural and high foliage density shrubs (6.63 ± 0.10 and 6.42 ± 0.10, respectively) than on low foliage density shrubs (5.93 ± 0.09). A multiple regression analysis revealed that spider species richness was positively related to both foliage density and prey density ($P = 0.012$ and 0.001, respectively) (regression equation: $y = -1.244 + 0.02(foliage\ density) + 0.262 \cdot \ln(prey\ density)$, $R^2 = 0.17$).

Spider species composition varied with foliage density (Table 2.2; Fig. 2.5a). A SIMPER analysis indicated that natural and high foliage density shrubs were more similar to each other in species composition than either were to low foliage density shrubs (Table 2.3). Low foliage density shrubs differed from natural and high foliage density shrubs by having higher relative abundances of *P. clemata* (Salticidae) and *Metepeira foxi* Gertsch & Ivie 1936 (Araneidae) and lower relative abundances of *P. histrio* (Philodromidae), *E. pepinensis* (Philodromidae), *O. scalaris* (Oxyopidae), and *Dipoena nigra* (Emerton 1882) (Theridiidae).

Family composition also varied with foliage density (Table 2.2; Fig. 2.5b). A SIMPER analysis showed that natural and high foliage density shrubs were more similar

to each other in family composition than either were to low foliage density shrubs (Table 2.4). Low foliage density shrubs differed from natural and high foliage density shrubs by having higher relative abundances of jumping spiders (Salticidae) and orb-weavers (Araneidae) and lower relative abundances of Oxyopidae, Philodromidae, and Theridiidae. Dictynids were more abundant on natural foliage density shrubs.

Experimental treatments had no effect on spider guild composition, regardless of classification used (Table 2.2; Fig. 2.5c). In general, the distribution of spider guilds was similar across treatments.

DISCUSSION

Habitat structure is cited as an important factor in the distribution and abundance of various organisms (see reviews in McCoy & Bell 1991). Results presented here demonstrate that spider density and species richness and diversity (H') are influenced by changes in shrub architecture. High foliage density shrubs supported more spiders and more species than structurally less complex habitats (i.e., low and natural foliage density shrubs). Our results are generally consistent with other studies involving structural influences of vegetation on spiders (Uetz 1991; Wise 1993). This pattern of greater abundance and diversity on more dense and structurally complex habitats often is attributed to the availability of more microhabitats or as a way to partition resources and reduce interspecific competition (Turnbull 1973; Uetz 1991).

Spider species and family compositions were also influenced by changes in shrub architecture; however, variations in community composition appear to have been caused

by changes in relative abundances, rather than differences in taxonomic composition. For example, although *P. clemata* (Salticidae) was the most frequently captured spider on all shrub types, their relative abundances were higher on low foliage density shrubs. Open substrates may collect a higher proportion of jumping spiders since dense branching can obstruct their vision and impede their ability to capture prey (Hatley & MacMahon 1980). Since jumping spiders are active hunters that leap onto prey, more compact branching may further interfere with their ability to jump (Stratton et al. 1979; Stevenson & Dindal 1982). Structurally simple environments also supported relatively more orb-weaving spiders. Wide gaps between shrub branches are considered structurally more suitable for the building of large orb webs than shrubs with more dense architectures (Hatley & MacMahon 1980; Uetz & Hartsock 1987; Marc & Canard 1997; Balfour & Rypstra 1998; Tsai et al. 2006) and may also be associated with larger species of web builders (Hatley & MacMahon 1980).

Structurally diverse environments, on the other hand, may be chosen by species that attack their prey within close proximity. For example, although thomisids were largely underrepresented in this study, they are thought to prefer more concealed locations for prey capture (Gertsch 1979; Hatley & MacMahon 1980; Uetz 1991). Space-web builders (Dictynidae and Theridiidae) are also thought to require more complex substrates since they tend to build three-dimensional webs that occupy spaces between branches (Stratton et al. 1979; Marc & Canard 1997; Amalin et al. 2001). Our results suggest that some space-web builders have different habitat associations. Theridiids were relatively more abundant on high foliage density shrubs, while dictynids were more

abundant on either natural or low foliage density shrubs. In this study, theridiids were smaller than dictynids (mean body length ± SE: 2.89 ± 0.04 mm vs. 3.3 ± 0.06 mm, respectively). Small web builders could have favored high foliage density shrubs because such architectures may provide either more refuges than open substrates or more attachment sites for webs (Gunnarsson 1992, 1996). Likewise, some researchers suggest that complex architectures are better at supporting small species since small-bodied individuals are able to utilize more of a plant's structure than large individuals (Morse et al. 1985; Lawton 1986). We plan to conduct further tests to reveal whether spider size distributions are influenced by changes in shrub architecture.

Despite notable differences in spider species and family composition, guild composition did not vary by foliage type. These results contradict previous studies suggesting that habitat structure influences the distribution of spider guilds found on big sagebrush (Hatley & MacMahon 1980; Robinson 1981; Abraham 1983; Wing 1984; Ehmann 1994; Heikkinen & MacMahon 2004) and elsewhere (Uetz et al. 1999; Brierton et al. 2003; Hore & Uniyal 2008). Discrepancies between research findings may have been due to underlying differences in field site characteristics. Previous studies in northern Utah were mostly conducted at sites more than 200 m below our study area (Hatley & MacMahon 1980; Robinson 1981; Abraham 1983; Wing 1984). Since spider composition is known to vary with elevation (Uetz 1976; Bowden & Buddle 2010; Cardosa et al. 2011), it is possible that factors associated with elevation, such as temperature or vegetation structure, contributed to changes in relative abundances of species or families across field sites that then translated into major differences in guild

structure. For example, Abraham (1983) found a higher proportion of some families (Theridiidae and Thomisidae), but a lower proportion of others (Dictynidae, Oxyopidae, and Salticidae), relative to our study site. Patterns of guild abundance and distribution may also have been influenced by cattle during part of this study, as some spiders are known to be particularly sensitive to livestock grazing and trampling (Gibson et al. 1992; Bonte et al. 2000; Warui et al. 2005; Kovac & Mackay 2009).

The lack of guild response may also suggest that individual species have specific ecological requirements that cannot always be captured using a guild approach (Churchill 1998). For spiders, guild membership is usually taxonomically based since spider hunting strategies are thought to emerge at the family level (Post & Riechert 1977). However, many suggest that these generalizations are not entirely applicable to all species and that guild membership should reflect natural histories, rather than taxonomic relatedness (Hawkins & MacMahon 1989; Uetz et al. 1999). In addition, since foraging strategies are not entirely fixed, some species may align with more than one guild (Peckarsky 1982; Gillespie & Caraco 1987).

Although the use of guilds in this study revealed little about the relationship between spider hunting strategies and shrub architecture, the concept is still useful for examining competitive interactions and niche relations in ecological studies or when comparing communities that vary in space and time (Hatley & MacMahon 1980; Hawkins & MacMahon 1989). Guild classifications are also helpful when describing biological communities that are complex (i.e., species richness) or that are not well

known taxonomically (Adams 1985; Hawkins & MacMahon 1989; Simberloff & Dayan 1991).

Results from this study suggest that prey availability is also important in determining spider abundance and species richness. Spiders may have responded to higher prey densities by either increasing prey consumption, thereby influencing rates of survival, development, and/or fecundity, or by simply migrating from areas of low prey availability to areas of high prey availability (Riechert 1974; Riechert & Lockley 1984; Marc et al. 1999; Bogya et al. 2000; Harwood et al. 2001). Positive relationships could also reflect shared microhabitat preferences or physiological constraints (Cherrett 1964; Riechert 1974; Bonte & Mertens 2003; Horváth et al. 2005), especially considering that prey availability was also positively associated with shrub foliage density. Therefore, until we can investigate such factors further, our results should be interpreted with care. Since some spiders are known to ignore prey significantly smaller or larger than themselves (Nentwig & Wissel 1986; Bartos 2004) and are capable of assessing nutritional quality of prey (Toft 1999; Mayntz et al. 2005), it is also possible that true resource availability was never captured and the importance of prey availability was exaggerated. We further recommend that future studies incorporate observations of actual prey consumption to better understand prey importance for spiders. It is also not known whether spiders exerted negative effects on prey populations, either by suppressing their densities, by targeting specific prey types, and/or by causing changes in prey behavior (Sunderland 1999; Cronin et al. 2004; Reader et al. 2006). We were unable to assess these interactions given that our measure of prey availability was based

only on available prey, not prey taken by spiders. Additional studies are, therefore, needed to properly evaluate the direction of causality between spiders and their prey. This could include examining prey populations in the absence of spiders or by comparing prey populations in areas with differing densities of spiders.

Spiders are an important group of predators in nearly every ecosystem (Wise 1993). Their ability to suppress insect populations has been widely documented in various habitats (Nyffeler & Benz 1987; Riechert & Bishop 1990; Riechert 1999; Sigsgaard et al. 2001; Sanders et al. 2008). Single species are considered less efficient at regulating pest populations since they will eat almost anything that is of appropriate size (Riechert & Lockley 1984; Murdoch et al. 1985; but see Hoefler et al. 2006). Diverse spider assemblages, however, are considered a significant part of the natural enemy complex since spiders of different foraging strategies, despite their overlapping diets, collectively increase the number and type of prey consumed (Marc & Canard 1997; Riechert & Lawrence 1997; Riechert et al. 1999; Pluess et al. 2010). Therefore, given that habitat structure is associated with spider diversity, preserving appropriate environmental structures holds considerable potential for enhancing the success of spiders as important agents in biological control (Samu 2003).

Finally, shifts in spider community structure associated with changes in habitat structure may translate into differences in ecosystem functioning (McIntyre et al. 2001). By suppressing species in lower trophic levels, spiders may influence ecosystem properties and functions by indirectly varying the quantity and quality of plant material entering the system (Wise 2004; Sanders et al. 2008; Castro & Wise 2009; Schmitz 2009;

Schmitz et al. 2010). In addition, variability in spider foraging strategies may differentially impact plant community structure and ecosystem function. For example, Schmitz (2008) demonstrated that an ambushing spider altered its prey behavior such that the prey, a grasshopper, sought a competitively dominant herb for refuge and food resources instead of preferred grasses and herbs. By invoking competitive release, spiders helped to promote plant diversity, although primary productivity and nitrogen mineralization were negatively impacted. An active hunting spider, however, was not capable of altering grasshopper feeding behaviors, but was able to suppress grasshopper densities, thereby enhancing productivity and nitrogen mineralization. Despite these results, it is not clear what type of influence multiple spider species characteristic of structurally complex environments would have on ecosystem functioning (Sih et al. 1998; Sokol-Hessner & Schmitz 2002).

Our results demonstrate that shrub architecture and prey availability, considered together, are better predictors of spider density and species richness than either variable considered independently. In addition, shrub architecture was a major factor governing spider diversity (H') and community composition. However, since prey densities were also influenced by changes in shrub architecture, the effect of shrub architecture on spider communities may instead be operating indirectly via effects on prey availability, rather than directly. While not addressed here, future studies should explicitly evaluate the role of prey availability in mediating the relationship between shrub architecture and spider communities.

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Table 2.1.—*F* and *P* values from PERMANOVA analysis of prey order and functional group composition. PERMANOVA analyses are based on Bray-Curtis dissimilarities.

	df	Order		Functional group	
		F value	*P* value	*F* value	*P* value
Foliage density treatment (FDT)	2	0.957	0.495	0.529	0.687
Prey attractant treatment (PAT)	1	0.371	0.857	0.616	0.522
FDT × PAT	2	1.199	0.268	1.148	0.318

Table 2.2.—*F* and *P* values from PERMANOVA analysis of spider species, family, and guild composition. For guild composition, values preceding a slash indicate results following the classification proposed by Uetz et al. (1999), whereas values following a slash indicate results when guild assignments followed the classification used for spiders on big sagebrush. PERMANOVA analyses are based on Bray-Curtis dissimilarities.

		Species		Family		Guild	
	df	*F* value	*P* value	*F* value	*P* value	*F* value	*P* value
Foliage density treatment (FDT)	2	2.778	0.004	2.772	0.003	1.619 / 1.579	0.245 / 0.176
Prey attractant treatment (PAT)	1	1.037	0.316	1.124	0.354	1.559 / 1.511	0.317 / 0.264
FDT × PAT	2	0.680	0.677	1.568	0.163	2.016 / 1.681	0.144 / 0.190

Table 2.3.—Summary results of a similarity of percentages (SIMPER) analysis of spider species composition among shrubs of different foliage density treatments (i.e., low, natural, or high). Results indicate average abundance and % contribution to Bray-Curtis dissimilarities.

Pairwise comparison	Species	Low	Natural	High	Contribution (%)	Cumulative (%)
Low vs. Natural (average dissimilarity = 65.46%)	P. clemata	25.98	25.46	-	15.08	15.08
	P. histrio	11.82	13.22	-	11.71	26.79
	M. foxi	9.59	4.30	-	8.60	35.39
	E. reticulata	6.99	8.36	-	8.01	43.40
	O. scalaris	5.87	8.91	-	7.69	51.09
	E. pepinensis	5.62	8.91	-	6.98	58.07
	D. nigra	4.36	5.63	-	6.44	64.51
	E. piratica	5.07	4.60	-	5.73	70.24
Low vs. High (average dissimilarity = 69.29%)	P. clemata	25.98	-	18.62	14.91	14.91
	P. histrio	11.82	-	13.92	11.17	26.08
	M. foxi	9.59	-	6.31	9.12	35.20
	E. pepinensis	5.62	-	13.16	8.74	43.94
	O. scalaris	5.87	-	8.55	7.41	51.35
	D. nigra	4.36	-	7.01	6.91	58.26
	E. reticulata	6.99	-	5.22	6.56	64.82
	H. americanus	4.00	-	5.99	6.06	70.88
Natural vs. High (average dissimilarity = 57.48%)	P. clemata	-	25.46	18.62	12.31	12.31
	P. histrio	-	13.22	13.92	11.60	23.91
	E. pepinensis	-	8.91	13.16	9.27	33.18
	O. scalaris	-	8.91	8.55	8.21	41.39
	E. reticulata	-	8.36	5.22	7.43	48.82
	M. foxi	-	4.30	6.31	7.05	55.87
	D. nigra	-	5.63	7.01	6.83	62.70
	H. americanus	-	3.20	5.99	6.53	69.23

Table 2.4.—Summary results of a similarity of percentages (SIMPER) analysis of spider family composition among shrubs of different foliage density treatments (i.e., low, natural, or high). Results indicate average abundance and % contribution to Bray-Curtis dissimilarities.

Pairwise comparison	Family	Low	Natural	High	Contribution (%)	Cumulative (%)
Low vs. Natural (average dissimilarity = 49.35%)	Salticidae	34.02	33.01	-	19.97	19.97
	Philodromidae	21.19	23.88	-	17.79	37.76
	Dictynidae	12.20	13.36	-	14.88	52.64
	Araneidae	10.16	5.46	-	12.37	65.01
	Oxyopidae	6.43	10.19	-	11.29	76.30
	Theridiidae	7.06	7.78	-	10.82	87.12
	Thomisidae	5.46	3.47	-	7.42	94.54
	Gnaphosidae	3.49	2.85	-	5.46	100.00
Low vs. High (average dissimilarity = 50.96%)	Salticidae	34.02	-	29.12	20.10	20.10
	Philodromidae	21.19	-	28.11	17.46	37.56
	Dictynidae	12.20	-	9.03	13.13	50.69
	Araneidae	10.16	-	6.82	13.03	63.72
	Theridiidae	7.06	-	10.56	12.44	76.16
	Oxyopidae	6.43	-	9.84	11.17	87.33
	Thomisidae	5.46	-	2.38	6.55	93.88
	Gnaphosidae	3.49	-	4.15	6.12	100.00
Natural vs. High (average dissimilarity = 38.97%)	Philodromidae	-	23.88	28.11	17.47	17.47
	Salticidae	-	33.01	29.12	16.06	33.53
	Dictynidae	-	13.36	9.03	14.12	47.65
	Oxyopidae	-	10.19	9.84	13.55	61.20
	Theridiidae	-	7.78	10.56	13.31	74.51
	Araneidae	-	5.46	6.82	11.63	86.14
	Gnaphosidae	-	2.85	4.15	7.49	93.63
	Thomisidae	-	3.47	2.38	6.37	100.00
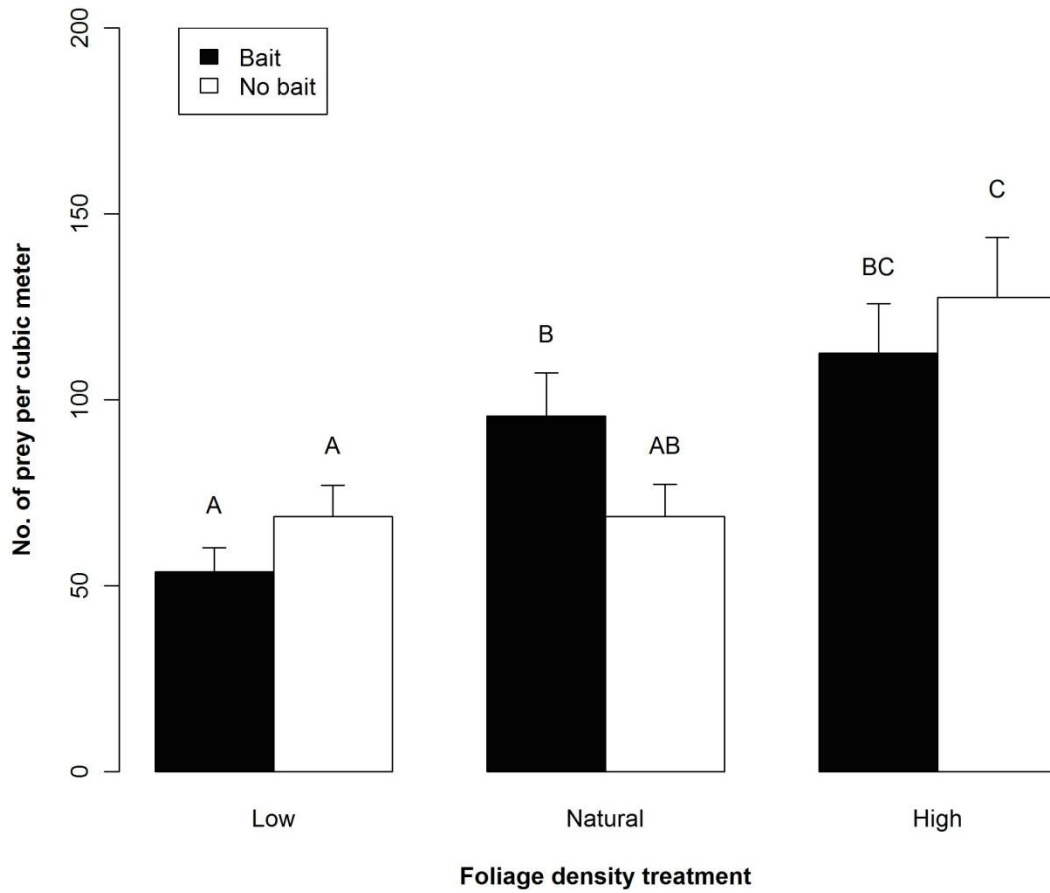
Figure 2.1.—Prey densities sorted by two different prey attractant and three different foliage density treatments. Graphs show means with standard errors. Different letters indicate a significant difference at $P < 0.05$. Means and standard errors were back-transformed from ln-transformed estimates.
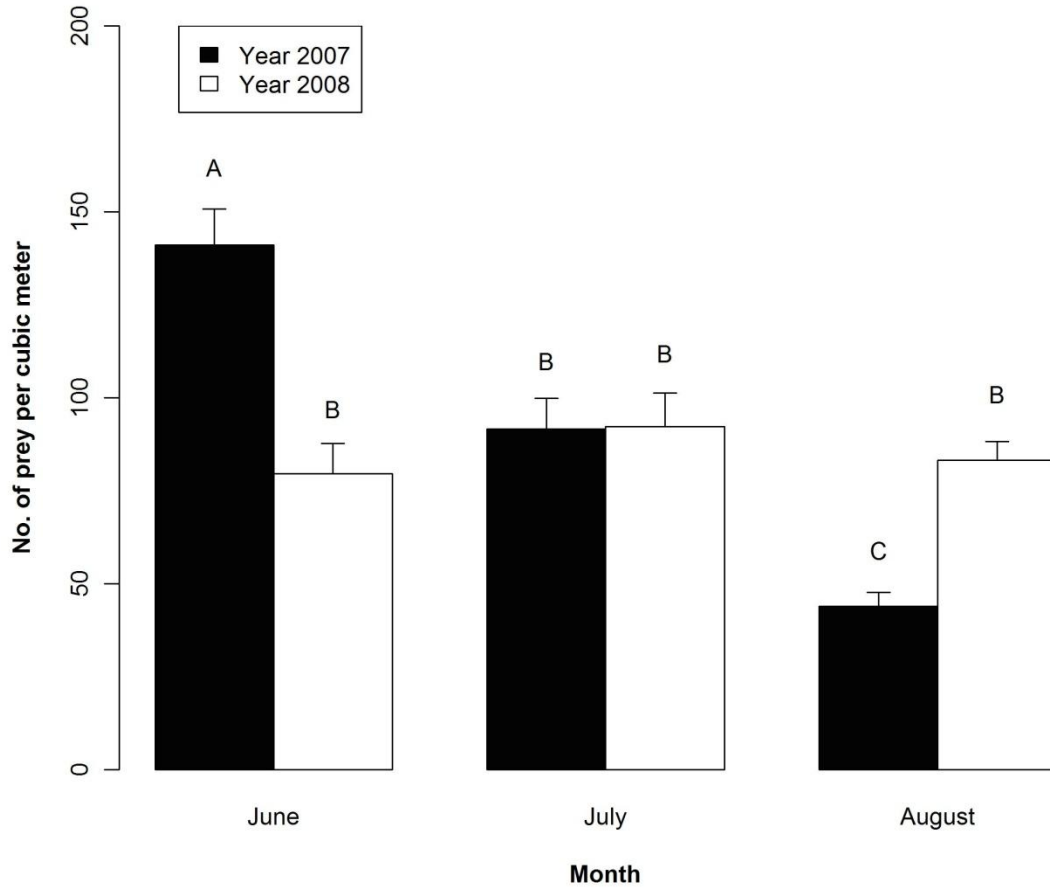
Figure 2.2.—Prey densities sorted by year and month of collection. Graphs show means with standard errors. Different letters indicate a significant difference at $P < 0.05$. Means and standard errors were back-transformed from ln-transformed estimates.
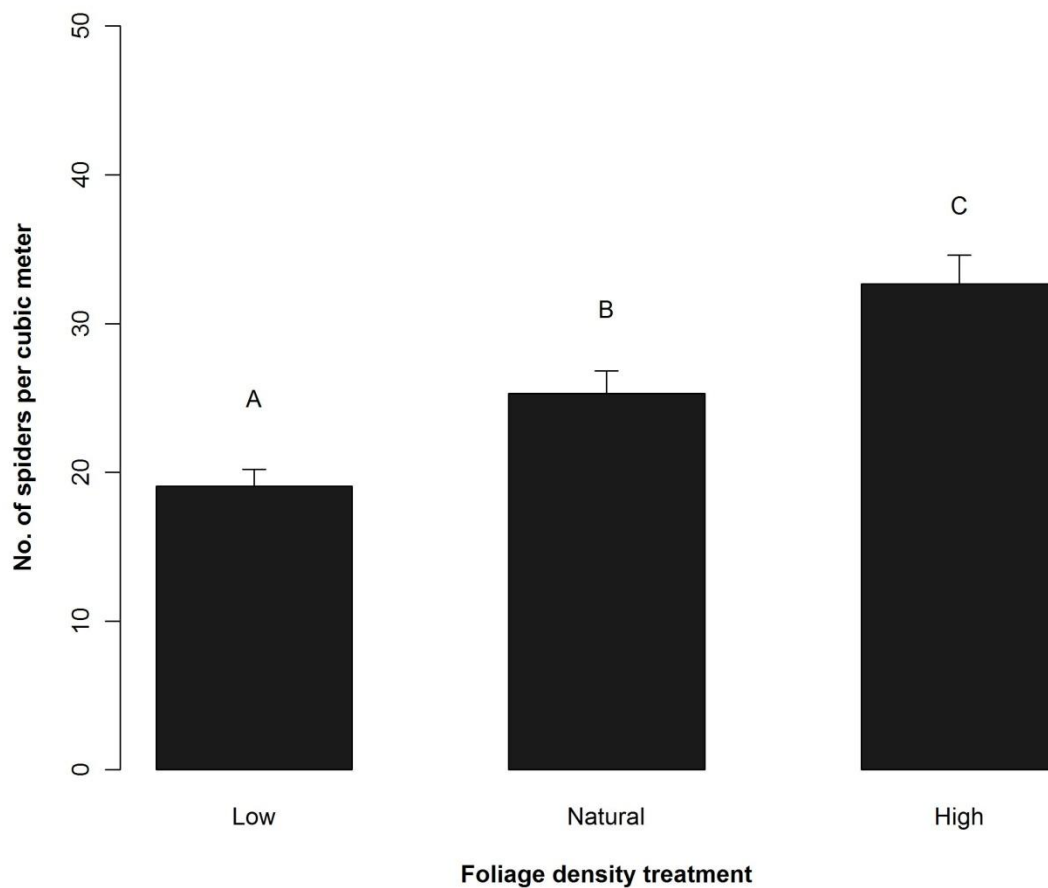
Figure 2.3.—Spider densities sorted by three different foliage density treatments. Graphs show means with standard errors. Different letters indicate a significant difference at $P < 0.05$. Means and standard errors were back-transformed from ln-transformed estimates.
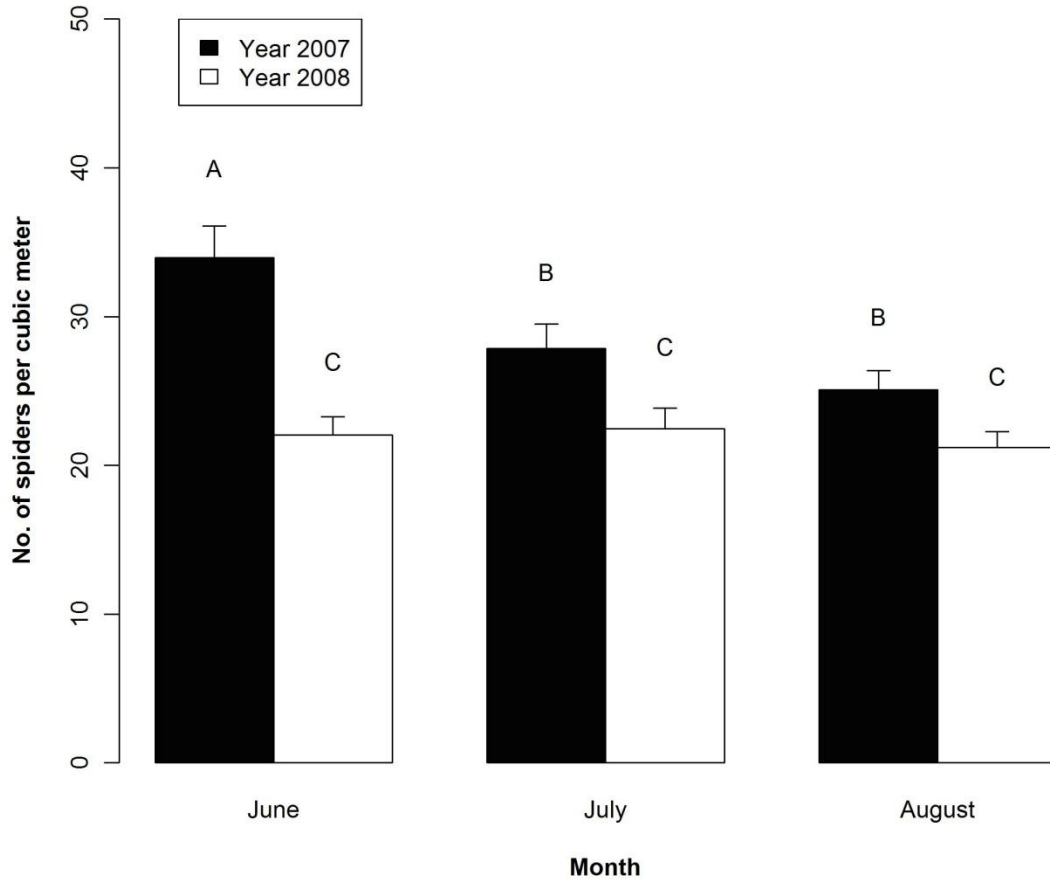
Figure 2.4.—Spider densities sorted by year and month of collection. Graphs show means with standard errors. Different letters indicate a significant difference at $P < 0.05$. Means and standard errors were back-transformed from ln-transformed estimates.
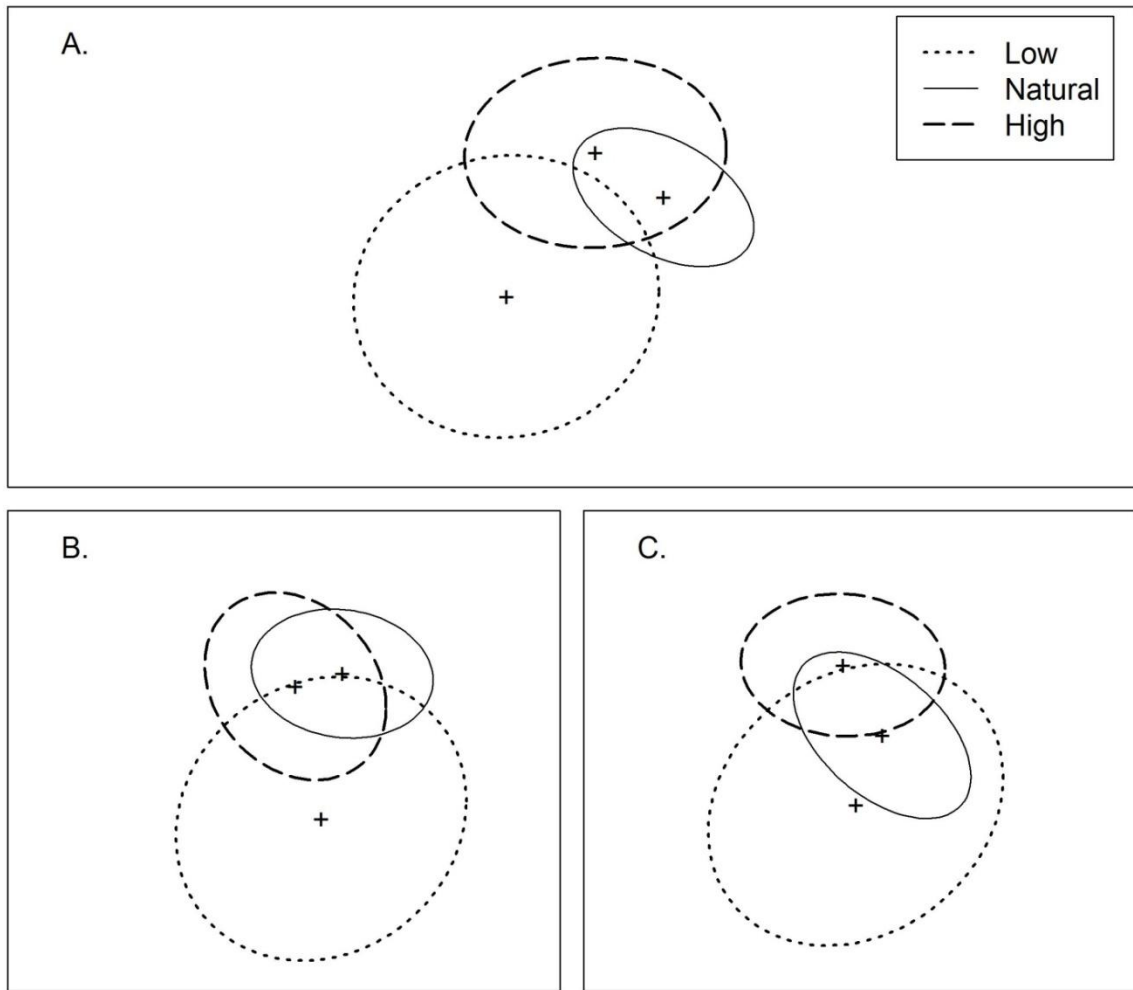
Figure 2.5.—Non-metric multidimensional scaling (NMDS) plots representing variation in A) spider species composition, B) spider family composition, and C) spider guild composition, where guild composition followed the classification proposed by Uetz et al. (1999). Foliage density (low, natural, and high) is plotted as centroids (+ symbols) and 95% confidence ellipses of the mean sample score. Confidence ellipses are for visualization only; actual significance tests were obtained from PERMANOVA analyses (see Table 2.2 for significance values). Final stress for a two-dimensional (2D) solution was 21.66 for the species ordination, 21.48 for the family ordination, and 11.25 for the guild ordination.

CHAPTER 3

PREY AVAILABILITY MEDIATES SPIDER RESPONSE TO SHRUB

ARCHITECTURE: A STRUCTURAL EQUATION MODELING APPROACH

Abstract Habitat structure is associated with the abundance and diversity of various

organisms. Spiders are especially sensitive to plant architecture even though they are not

directly reliant on a particular plant species as a food source. It remains unclear,

however, whether spiders respond directly to plant architecture or indirectly via

differences in prey availability caused by different structures, or some combination

thereof. Here, we explicitly evaluate the relative role of prey availability in mediating the

relationship between shrub architecture and spider communities in a shrub-steppe

environment in northern Utah, USA by using structural equation modeling, a procedure

well-suited for partitioning direct and indirect effects. Our results suggest that both direct

and indirect pathways are involved in the relationship between shrub architecture and

spider density and species diversity (H'), while spider species richness (S) was affected

only indirectly.

Introduction

Understanding the patterns and processes that control natural communities is a fundamental goal in ecology. Patterns of species abundance and diversity, in particular, have intrigued ecologists for decades (Hutchinson 1959; MacArthur 1965; Brown 1984). Some of the factors thought to influence animal species abundance and diversity include measures of productivity (Rosenzweig and Abramsky 1993), latitudinal gradients (Pianka 1966), size of geographical area (Connor and McCoy 1979), degree and length of isolation (MacArthur and Wilson 1967), and regional and evolutionary history (Ricklefs and Schluter 1993). More recently, the influence of habitat structure on community dynamics has received considerable theoretical and empirical support (Lawton 1983; McCoy and Bell 1991; Tews et al. 2004). Habitat structure in the form of heterogeneity and/or complexity (*sensu* McCoy and Bell 1991) is positively associated with the abundance and diversity of various organisms and is generally thought to provide more microhabitats and/or niche space than relatively uniform environments (McCoy and Bell 1991; Langellotto and Denno 2004; Tews et al. 2004).

Although habitat structure is an important driver of many ecological patterns and processes, few studies investigate how habitat structure interacts with other environmental variables to affect community dynamics (Srivastava 2006; Byrne 2007). Likewise, there has been little information concerning the extent to which ecological responses to habitat structure are mediated by associated variables. Indirect effects are not immediately obvious and are difficult to distinguish from direct effects; however, their influences are thought to have considerable impacts on community dynamics

(Strauss 1991; Wootton 1994; Miller and Travis 1996; Peacor and Werner 2001; Krivtsov 2004). Habitat structure may indirectly influence organisms by modifying either environmental conditions or resource availability (Larmuth 1979; Byrne 2007). For example, habitat heterogeneity and/or complexity may affect prey availability, and thereby the organization and structure of predator communities.

As predators, spiders are model organisms for addressing the roles of habitat structure on community dynamics and the possible intervening influences of prey availability on this relationship since they are not directly reliant on a particular plant species as a food source (Hatley and MacMahon 1980). Further, the importance of both prey availability and habitat structure are well documented (Wise 1993), but are not effectively disentangled. Although prior studies suggest that spiders respond primarily to habitat structure and secondarily to prey availability (Rypstra 1983; Greenstone 1984; Halaj et al. 1998, 2000; Nyffeler and Sunderland 2003; Langellotto and Denno 2004; Horváth et al. 2005; Chan et al. 2009), it remains largely unknown whether prey availability mediates the relationship between habitat structure and spider communities.

We previously investigated the importance of prey availability and shrub architecture on spider communities in northern Utah and found that both factors were associated with spider abundance and species richness, while spider species diversity (H') varied with changes in shrub architecture, but not with prey availability (Chapter 2). However, given the analyses used, it was unclear whether spiders were responding directly to habitat structure *per se* or to differences in prey availability caused by different structures, or some combination thereof. Our intention here is to expand upon that study

and prior studies by using structural equation modeling, a multivariate statistical

procedure designed specifically to understand relationships through intervening variables

(Grace 2006).

Materials and methods

Study site

Our research expands upon earlier studies of spider communities in the Great

Basin shrub-steppe ecosystem of northern Utah (Hatley and MacMahon 1980; Robinson

1981; Abraham 1983; Wing 1984; Ehmann 1994; Ehmann and MacMahon 1996;

Heikkinen and MacMahon 2004; Cobbold and Supp, in press). This study was conducted

at Hardware Ranch Wildlife Management Area (41°61 N, 111°57 W). Hardware Ranch

WMA is located in the Wasatch-Cache National Forest, about 40 km southeast of Logan,

Cache County, Utah, and is managed by the Utah Division of Wildlife Resources. The

site is at an elevation of 1731 m and is dominated by big sagebrush (*Artemisia tridentata*)

and low sage (*Artemisia arbuscula*). Land is used primarily as winter range for big

game.

Shrub selection

To reduce the heterogeneity among individual shrubs, several criteria were

applied when selecting shrubs. Experimental shrubs (*A. tridentata*) had a single trunk at

ground level, were not in immediate contact with an adjacent shrub, and were at least 10

m from another experimental shrub. Shrubs were measured before and after treatment for

maximum canopy width, width perpendicular to maximum canopy width, and canopy

height (excluding the trunk beneath) (Ehmann 1994). Only shrubs with all three canopy

dimensions between 0.4 and 1 m were selected. Shrub volume was determined by using

the formula for an ellipsoid:

$$Volume = 4/3\pi abh$$

where a and b represent, respectively, the linear dimensions of the major and minor axes,

and h represents height.

Study design and treatments

Selected shrubs were randomly assigned to six experimental treatments, with 25

replicates per treatment. Experimental treatments consisted of factorial combinations of

two levels of prey attractant and three levels of foliage density. Prey attractant treatments

included shrubs that were either baited or not baited. The purpose of the bait was to

increase the probability of prey visits and/or the length of each visit (Wing 1984). Baited

shrubs contained four suspended containers: two (59 ml) containers filled with pig offal,

one (22 ml) container filled with yellow banana-oil flavored honey, and one (22 ml)

container filled with red-colored honey. Container lids were perforated to facilitate odor

dispersion. As a control, identical but empty containers were suspended from shrubs not

baited. Shrubs were baited two weeks prior to sampling to maximize arthropod

abundance on shrubs (Robinson 1981).

Shrub architecture was manipulated to either increase or decrease shrub foliage

density (Hatley and MacMahon 1980). Foliage density was increased by tightly binding

all branches together with jute (hereafter referred to as "high") and decreased by clipping

50% of the shrub foliage ("low"). Shrubs not manipulated were used as controls

("natural"). Differences in shrub foliage density were calculated using photographs taken from a digital camera (Nikon Coolpix L12) positioned approximately 1.5 m from the shrub. A white cloth attached to a wooden frame (1.5 x 1.5 m) was positioned behind the shrub and before and after treatment pictures were taken. The pictures were imported into Adobe Photoshop CS4. Here, shadows surrounding the shrub were first removed using the 'color range' option. Images were then transformed into a black and white image by means of the 'threshold' option and the area occupied by the shrub was outlined using the magnetic 'lasso' tool. The 'histogram' tool was then used to determine the ratio of white (background) vs. black (vegetation) pixels. For each picture, this procedure was carried out twice and the average was taken.

Sampling of arthropods

Shrubs were sampled during a five day sampling period once a month in June, July, and August of 2007 and 2008. A few shrubs were discarded because of bait disturbances. Sampling periods took place at intervals of no less than three weeks. Sampling began approximately two hours after sunrise, occurred only when there was an absence of high winds and precipitation, and did not occur when temperatures were below 10° C. Each shrub was quickly surrounded at the base with a canvas sheet (1.5 x 1.5 m) and then beaten 15 times with an ax handle to dislodge specimens onto the beating sheet for collection. Specimens were collected with an aspirator and immediately preserved in vials containing 70% ethanol. After the arthropods from the first beating were collected, a second beating episode of the same duration followed. The double-

beating method was used previously and resulted in a 100% collection rate (Ehmann and MacMahon 1996).

Spiders were identified to species and their body length (not including spinnerets) was measured to the nearest 0.1 millimeter. Immature specimens were excluded from analyses since their behavior and habitat may differ from adults, but also because some immature spiders were difficult to identify to species (Jiménez-Valverde and Lobo 2006; Sackett et al. 2008). Remaining arthropods were sorted and counted. Ants (Hymenoptera: Formicidae) and aphids (Hemiptera: Aphididae) were not collected because their high abundances made collection of samples in a short period of time difficult. All specimens were deposited in the Department of Biology at Utah State University for reference.

Data analyses

Structural equation modeling was used to measure the direct and indirect effects of shrub architecture, and to evaluate the relative importance of prey availability in spider community organization. Structural equation models (SEMs) differ from traditional multivariate regression models by allowing response variables to influence other variables in the model (Menéndez et al. 2007; Grace et al. 2009). Therefore, SEMs are especially well-suited for evaluating hypotheses that partition direct and indirect effects (Grace et al. 2010).

To test the hypothesis that prey availability mediates the relationship between shrub architecture and spider community organization, three SEMs were created and used to derive parameter estimates. The first model examined the direct and indirect effects of

shrub foliage density on spider abundance, while the second and third models examined

the direct and indirect effects of shrub foliage density on spider species richness and

diversity (Fig. 3.1a and b). Diversity was determined using the Shannon-Wiener index

(Magurran 2004). Spider abundance was incorporated in the last two models to

determine whether the relationship between shrub foliage density and spider richness or

diversity is explained by an associated change in spider abundance or if there is a unique

and direct influence of shrub foliage density on these variables. SEMs were analyzed

using AMOS v. 18 (Arbuckle 2009). A critical ratio test, available in AMOS, was used

to test the significance of individual pathways. Single-headed arrows in a SEM describe

hypothesized causal relationships with arrows pointing to response variables. In addition,

path coefficients are associated with pathways between variables and indicate either the

effect of x on y in absolute terms (unstandardized form) or the relative strength of

predictors (standardized form). Here, we present both standardized and unstandardized

coefficients.

Experimental foliage treatments did not produce shrubs of equal density within

each treatment group. Likewise, prey abundance varied among shrubs within a treatment

group. Hence, because continuous variables typically are more informative than

categorical treatments, the effects of actual measures of foliage density and prey

abundance on response variables were used during analyses (Cottingham et al. 2005). In

addition, prior to all analyses, spider and prey abundances were converted into densities

(individuals per m^3) to account for differences in shrub volume. Since foliage densities

were not measured consecutively across sampling periods, spider and prey densities were

averaged for individual shrubs sampled during all sampling periods. To satisfy statistical assumptions, ln-transformations (x + 1) were applied to spider and prey densities.

SEM results were compared to regression results to illustrate differences in the two approaches. Regression analyses were performed using the REG procedure in SAS/STAT software Version 9.2 in the SAS system for Windows (SAS Institute, Inc. 2007). Significant differences in results refer to a statistical significance of $P \leq 0.05$.

Results

A total of 1744 adult spiders representing 31 species from 11 families and 9929 potential prey representing 15 orders from more than 66 families were collected (see Appendices A.1 and A.2).

Spider density was positively associated with both shrub architecture and prey availability (multiple regression, P = 0.004 and < 0.001, respectively) (Table 3.1). The SEM confirmed that spider density was influenced by shrub architecture and prey availability and further suggested that shrub architecture had a direct effect on spider density and an indirect effect through its relationship with prey availability (Table 3.2 and 3.3; Fig. 3.2). The direct effect of shrub architecture had less explanatory power than the direct effect of prey availability; however, when considering the total effect of shrub architecture (i.e., the sum of direct and indirect pathways), spider density was more similarly affected by shrub architecture and prey availability.

Spider species richness was not associated with shrub architecture (multiple regression, P = 0.61), marginally related to prey availability (P = 0.05), and positively associated with spider density (P < 0.01) (Table 3.1). Shrub architecture did not have a

direct effect on spider richness, but did exert indirect effects mediated largely through accompanied changes in spider density (Table 3.4 and 3.5; Fig. 3.3). Prey availability influenced species richness indirectly through variations in spider density and was marginally directly related. The nonsignificant negative direct effect of prey availability on species richness was offset by a stronger positive indirect effect so that the total effect was positive. Overall, shrub architecture exhibited slightly more predictive power than prey availability, although spider species richness was influenced mostly by spider density.

Spider species diversity (H') was positively associated with shrub architecture and spider density (multiple regression, $P = 0.01$ and < 0.01, respectively), but was not associated with prey availability ($P = 0.11$) (Table 3.1). Results from the SEM showed that shrub architecture affected spider diversity directly, as well as indirectly through variations in mostly spider density (Table 3.6 and 3.7; Fig. 3.4). Despite this, the direct effect of shrub architecture had higher explanatory power than any single indirect effect. Prey availability did not exert direct effects on spider diversity, but did influence spider diversity via spider density. However, the indirect effect of prey availability was offset by the weak direct effect so that the total effect of prey availability was less pronounced. Spider species diversity was influenced mostly by spider density.

Discussion

Numerous studies have demonstrated that spiders are particularly sensitive to structural features of their environment (Uetz 1991; Wise 1993). Although a great deal of research has been conducted regarding the effects of habitat structure, little attempt has

been made to disentangle these effects from others (Gibson et al. 1992; Srivastava 2006; Jiménez-Valverde and Lobo 2007). Results from this study support the view that relationships between shrub architecture and spider community structure are mediated in part by prey availability. Both direct and indirect pathways were involved in the relationship between shrub architecture and spider density and diversity, whereas species richness was influenced only indirectly.

Shrub architecture may have directly affected spider density by providing more resources (e.g., shelter, nesting sites, web attachment sites, sites for foraging) and/or by mediating interactions (e.g., predation and competition) to allow more individuals to coexist (Lawton 1983; Wise 1993; Byrne 2007). Likewise, shrub architecture may have directly contributed to spider species diversity by providing more microhabitats. Habitat specificity appears to be an important attribute of spider diversity (Uetz 1991; Wise 1993). However, shrub architecture seems to have mostly influenced the number of individuals observed for each species rather than enabling the coexistence of more species since shrub architecture did not have a direct effect on species richness. The absence of a direct effect of shrub architecture on species richness could imply that the number of spider species present on a shrub in this system depends more on, for example, the regional species pool or dispersal patterns of individual species (Ricklefs 1987; Lawton 1999; Bonte et al. 2003) than on shrub architecture itself.

Prey availability also had a positive direct effect on spider density. Spiders may have responded to increased prey availability by either increasing prey consumption, thereby influencing rates of survival, development and/or fecundity, or by simply

migrating to areas of high prey availability (Riechert 1974; Riechert and Lockley 1984; Marc et al. 1999; Bogya et al. 2000; Harwood et al. 2001). The positive relationship between prey availability and spider density could also reflect shared microhabitat preferences or physiological constraints (Riechert 1974; Bonte and Mertens 2003; Horváth et al. 2005), especially since prey availability was also positively associated with changes in shrub architecture.

Prey availability also indirectly affected species richness and diversity via spider density. Furthermore, spider species diversity was not directly associated with prey availability, but spider species richness appeared to be and decreased as prey availability increased. This may be due, in part, to competitive exclusion, whereby competitor species suppress other species at high prey densities. Similarly, species that track variations in prey availability better than others may have exerted negative influences on other colonists. Given the above information, future studies should continue to investigate how and under what conditions prey influence spider communities.

Although our measure of available prey describes well the prey types that are active at the same time and place (Rypstra 1986), it may not represent true resource availability for spiders. For example, although some spiders are able to consume prey larger than themselves (Nentwig 1985; Schmalhofer 2001), others may only take prey items their own size or smaller (Nentwig and Wissel 1986; Bartos 2004). Spiders may also exhibit selective feeding that maximizes nutritional intake (Greenstone 1979; Toft 1999; Mayntz et al. 2005). In addition, spiders may have exerted negative effects on prey populations, either by suppressing their densities, by targeting specific prey types, and/or

by causing changes in prey behavior (Sunderland 1999; Cronin et al. 2004; Reader et al. 2006). Therefore, we recommend future studies take greater care in accounting for prey preferences of spiders and more carefully investigate the direction of causality between spiders and their prey.

Despite our findings discussed above, spider species richness and diversity were most influenced by spider density and affected to a lesser degree by shrub architecture and prey availability. Similar observations have been reported elsewhere (Gonçalves-Souza et al. 2011). Although we controlled for abundance during this study, others may not have and, as a consequence, either exaggerated or undermined the importance of habitat structure. It is therefore necessary that researchers consider the impact of abundance on species richness and diversity relationships.

Low R^2 values indicate that additional factors not examined here were also involved in structuring the arthropod community. For example, microclimate conditions are especially important to living organisms because of their effects on biological processes and, therefore, may have contributed to spider response either directly and/or indirectly through changes in prey availability. Microclimate may also have acted as an intermediary variable since structurally complex habitats offer a variety of microhabitat types that differ in physical conditions (Riechert and Tracy 1975; Bell et al. 2001; Byrne 2007; Hore and Uniyal 2010).

In conclusion, our study supports the hypothesis that variation in prey availability, linked to changes in shrub architecture, at least partly describes patterns of spider density and species richness and diversity. Using structural equation modeling, we found that

indirect effects account for a substantial amount of variation in spider community

organization, but direct pathways were also present. These conclusions would not have

been easily recognized if only traditional techniques (e.g., analysis of variance or

regression methods) were used. Such approaches are incapable of evaluating mediating

causes (Grace and Bollen 2005; Grace 2006; Grace et al. 2009). Therefore, if two or

more ecological factors are thought to be related, structural equation modeling may

provide a more effective way to separate their effects.

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Table 3.1 Multiple regression models.

Independent variable (s)	Dependent variable	Regression equation	R^2
Foliage density (fd) and prey density (pd)	Spider density	$\ln(y) = -1.557 + 0.023(fd) + 0.502 \cdot \ln(pd)$	0.34
Spider density (sd), foliage density (fd), and prey density (pd)	Spider species richness	$y = -0.094 + 0.739 \cdot \ln(sd) + 0.003(fd) - 0.109 \cdot \ln(pd)$	0.66
Spider density (sd), foliage density (fd), and prey density (pd)	Spider species diversity (H')	$y = -0.277 + 0.153 \cdot \ln(sd) + 0.007(fd) - 0.044 \cdot \ln(pd)$	0.31

Table 3.2 Results of the structural equation model relating shrub architecture and prey availability to spider density.

Pathway	Regression weight	C.R.-value	P-value
Shrub architecture → Prey availability	0.034	4.225	< 0.001
Prey availability → Spider density	0.502	6.201	< 0.001
Shrub architecture → Spider density	0.023	2.899	0.004

Table 3.3 Pathways and inferred processes relating shrub architecture and prey availability to spider density. Indirect pathway strength is calculated as the product of coefficients along that pathway, while total effects represent the sum of direct and indirect effects (adapted from Grace et al. 2009). Pathway strength is based on standardized values.

Pathway	Process	Strength of association
Shrub architecture → Spider density	Effect of shrub foliage density on spider density independent of influences mediated through prey density	0.22
Shrub architecture → Prey availability → Spider density	Effect of shrub foliage density on spider density mediated through prey density	0.17
Total net effect of shrub architecture on spider density	Sum of direct and indirect pathways relating shrub foliage density to spider density	0.39
Prey availability → Spider density	Effect of prey density on spider density yet unrelated to shrub foliage density	0.47
Shrub architecture → Prey availability	Effect of shrub foliage density on prey density	0.35

Table 3.4 Results of the structural equation model relating shrub architecture, prey availability, and spider density to spider species richness.

Pathway	Regression weight	C.R.-value	P-value
Shrub architecture → Prey availability	0.034	4.225	< 0.001
Shrub architecture → Spider density	0.023	2.899	0.004
Prey availability → Spider density	0.502	6.201	< 0.001
Spider density → Species richness	0.739	13.853	< 0.001
Prey availability → Species richness	- 0.108	- 1.948	0.051
Shrub architecture → Species richness	0.003	0.521	0.602

Table 3.5 Pathways and inferred processes relating shrub architecture, prey availability, and spider density to spider species richness. Indirect pathway strength is calculated as the product of coefficients along that pathway, while total effects represent the sum of direct and indirect effects (adapted from Grace et al. 2009). Pathway strength is based on standardized values. Pathways linking shrub architecture (direct or indirect) and prey availability to spider density or shrub architecture to prey availability are listed in Table 3.3.

Pathway	Process	Strength of association
Shrub architecture → Species richness	Effect of shrub foliage density on species richness independent of influences mediated through prey density and/or spider density	0.03
Shrub architecture → Spider density → Species richness	Effect of shrub foliage density on species richness mediated through spider density	0.19
Shrub architecture → Prey availability → Species richness	Effect of shrub foliage density on species richness mediated though prey density	- 0.04
Shrub architecture → Prey availability → Spider density → Species richness	Effect of shrub foliage density on species richness mediated through prey density and spider density	0.14
Total net effect of shrub architecture on species richness	Sum of direct and indirect pathways relating shrub foliage density to species richness	0.32
Prey availability→ Species richness	Effect of prey density on species richness independent of influences mediated though spider density	- 0.12
Prey availability → Spider density → Species richness	Effect of prey density on species richness mediated through spider density	0.41
Total net effect of prey availability on species richness	Sum of direct and indirect pathways relating prey density to species richness	0.29
Spider density → Species richness	Effect of spider density on species richness	0.87

Table 3.6 Results of the structural equation model relating shrub architecture, prey availability, and spider density to spider species diversity.

Pathway	Regression weight	C.R.-value	P-value
Shrub architecture → Prey availability	0.034	4.225	< 0.001
Shrub architecture → Spider density	0.023	2.899	0.004
Prey availability → Spider density	0.502	6.201	< 0.001
Spider density → Species diversity	0.153	5.849	< 0.001
Prey availability → Species diversity	- 0.044	- 1.625	0.104
Shrub architecture → Species diversity	0.007	2.724	0.006

Table 3.7 Pathways and inferred processes relating shrub architecture, prey availability, and spider density to spider species diversity. Indirect pathway strength is calculated as the product of coefficients along that pathway, while total effects represent the sum of direct and indirect effects (adapted from Grace et al. 2009). Pathway strength is based on standardized values. Pathways linking shrub architecture (direct and indirect) and prey availability to spider density or shrub architecture to prey availability are listed in Table 3.3.

Pathway	Process	Strength of association
Shrub architecture → Spider diversity	Effect of shrub foliage density on species diversity independent of influences mediated through prey density and/or spider density	0.22
Shrub architecture → Spider density → Species diversity	Effect of shrub foliage density on species diversity mediated through spider density	0.12
Shrub architecture → Prey availability → Species diversity	Effect of shrub foliage density on species diversity mediated though prey density	- 0.05
Shrub architecture → Prey availability → Spider density → Species diversity	Effect of shrub foliage density on species diversity mediated through prey density and spider density	0.09
Total net effect of shrub architecture on species diversity	Sum of direct and indirect pathways relating shrub foliage density to species diversity	0.38
Prey availability → Species diversity	Effect of prey density on species diversity independent of influences mediated though spider density	- 0.14
Prey availability → Spider density → Species diversity	Effect of prey density on species diversity mediated through spider density	0.25
Total net effect of prey availability on species diversity	Sum of direct and indirect pathways relating prey density to species diversity	0.11
Spider density → Species diversity	Effect of spider density on species diversity	0.53
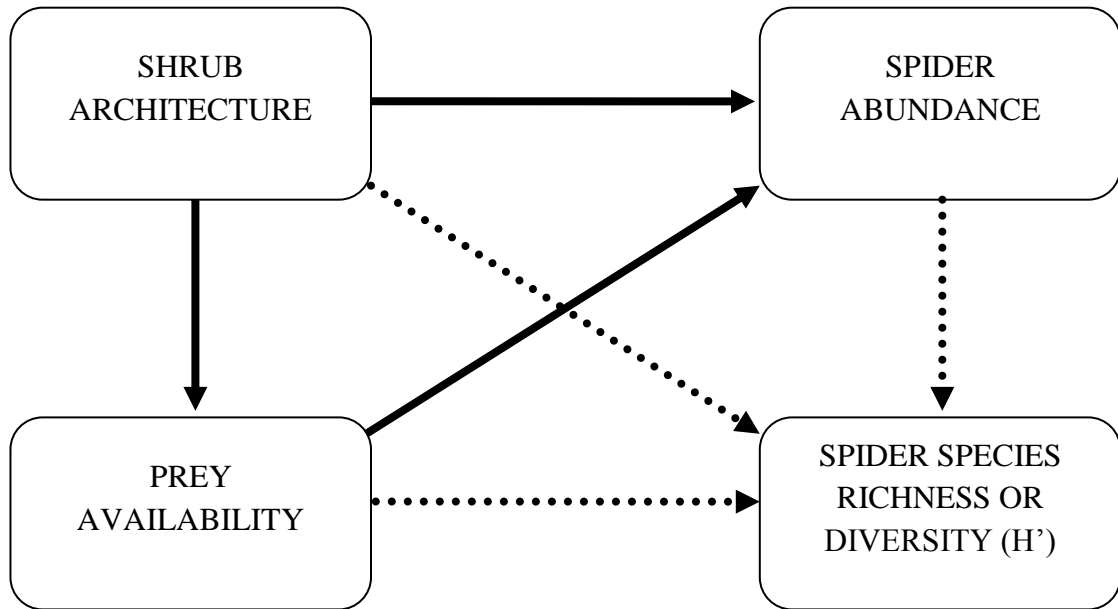
Fig. 3.1 Conceptual model predicting A) the influence of shrub architecture and prey availability on spider abundance (as indicated by the solid arrows) and B) shrub architecture, prey availability, and spider abundance on spider species richness and diversity (all arrows). Single-headed arrows describe hypothesized causal relationships with arrows pointing to response variables.
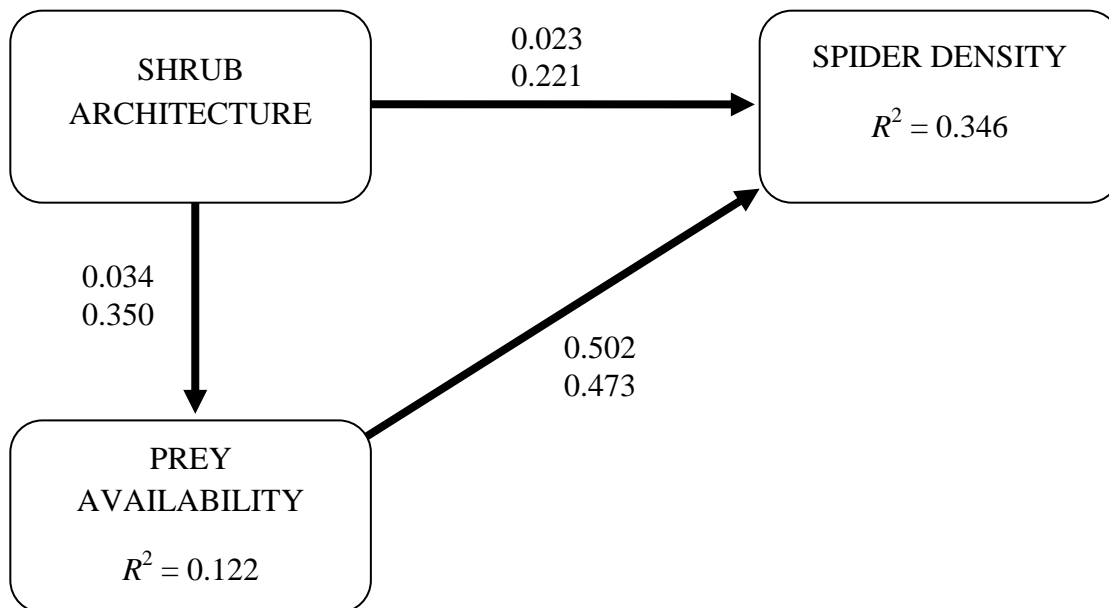
Fig. 3.2 Structural equation model representing the influence of shrub architecture and prey availability on spider density. Two coefficients appear on each path. Top path coefficients are unstandardized, whereas bottom coefficients are standardized. All pathways were significant ($P < 0.01$).
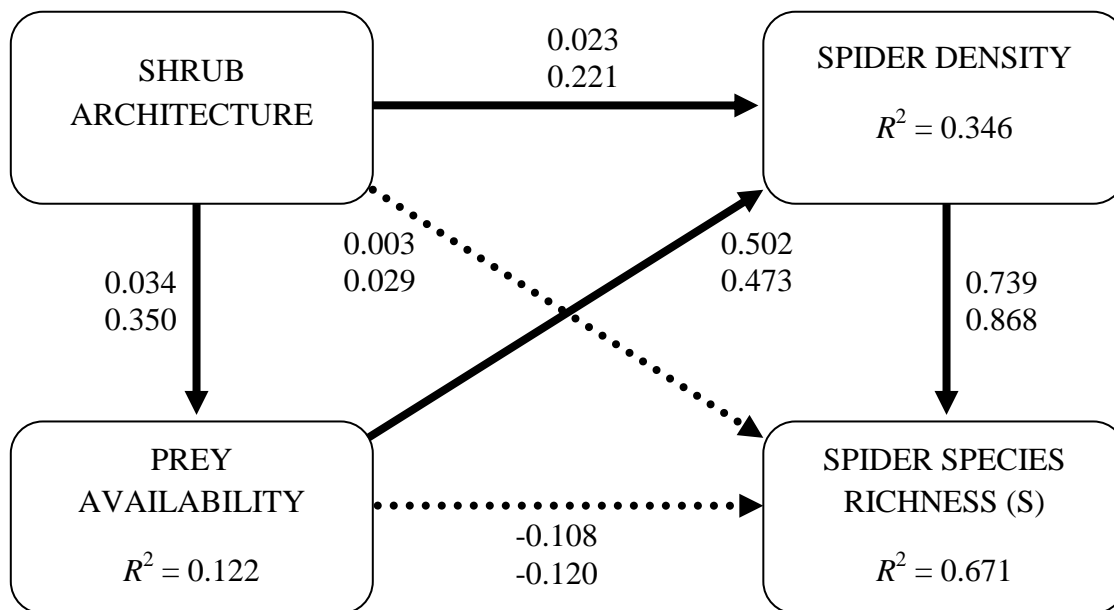
Fig. 3.3 Structural equation model representing the influence of shrub architecture, prey availability, and spider density on spider species richness. Two coefficients appear on each path. Top path coefficients are unstandardized, whereas bottom coefficients are standardized. Dotted pathways from shrub architecture to species richness and from prey availability to species richness represent nonsignificant or marginal relationships ($P = 0.60$ and 0.05, respectively). All other pathways were significant ($P < 0.05$).
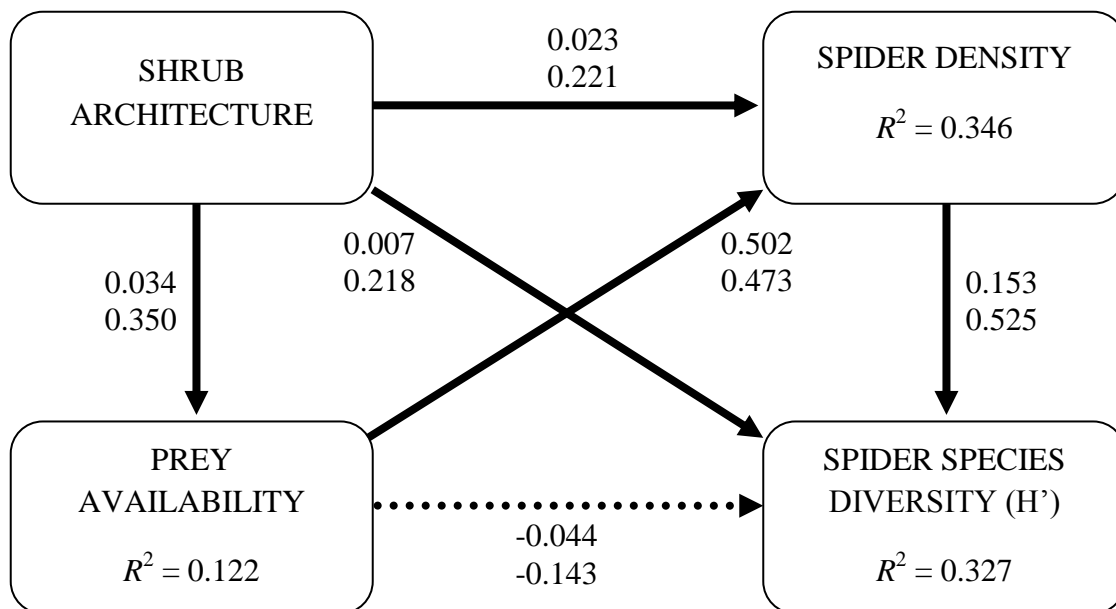
Fig. 3.4 Structural equation model representing the influence of shrub architecture, prey availability, and spider density on spider species diversity. Two coefficients appear on each path. Top path coefficients are unstandardized, whereas bottom coefficients are standardized. The dotted pathway from prey availability to species diversity represents a nonsignificant relationship ($P = 0.104$). All other pathways were significant ($P \leq 0.01$).

CHAPTER 4

EFFECTS OF SHRUB ARCHITECTURE AND SURROUNDING VEGETATION

STRUCTURE ON SPIDERS AND THEIR PREY

ABSTRACT. It has been suggested that habitat structure strongly influences many types of organisms, but its importance depends on the organisms being examined and the spatial scale to which they respond most strongly. In this study, we examined the effects of prey availability, shrub architecture, and surrounding vegetation structure on an arthropod community in northern Utah. Big sagebrush shrubs were assigned to six experimental treatments: two levels of prey attractant (shrubs were either baited or not baited) and three levels of foliage density (low, natural/control, or high). We also examined arthropod responses to changes in these factors under two different levels of spatial context (a single manipulated shrub surrounded by untreated shrubs vs. a manipulated shrub surrounded by a patch of shrubs treated in the same fashion). Our results suggest that surrounding vegetation structures play significant roles in determining arthropod abundances and distributions on shrubs, but its importance varies among organisms that differ in mobility.

Both experimental and observational studies show that the distribution and abundance of organisms is often positively associated with habitats of high structural complexity and/or heterogeneity (*sensu* McCoy & Bell 1991; see reviews in Bell et al. 1991; Langellotto & Denno 2004; Tews et al. 2004). But despite its significance, the relative importance of habitat structure depends on the organisms studied, and varies especially if community members differ in their trophic strategies and ability and tendency to move across the landscape (Krawchuk & Taylor 2003; Stoner & Joern 2004; Hewitt et al. 2005).

Although spiders are not directly reliant on a particular plant species as a food source (Colebourn 1974; Hatley & MacMahon 1980), they are strongly affected by changes in plant architecture. For example, spiders respond to variations in foliage density, height, and orientation (Hatley & MacMahon 1980; Brown 1981; Abraham 1983; Rypstra & Carter 1995; Brierton et al. 2003; Heikkinen & MacMahon 2004), as well as artificial vegetation of different architectural configurations (Robinson 1981), foliage densities (de Souza & Martins 2005), shapes (Cobbold & Supp, in press), and substrate diameters (Ehmann 1994a).

Insects are also influenced by changes in habitat structural features (Murdoch et al. 1972; Lawton 1983), including vegetation composition (Axmacher et al. 2009), density (Garono & Kooser 2001), and patch size and isolation (Krawchuk & Taylor 2003), but their response might reflect habitat conditions over a greater range of spatial scales (Krawchuk & Taylor 2003). For example, while a single shrub of a given

architectural type may be preferred by a spider, a highly mobile insect may perceive the same shrub as just an island surrounded by a sea of other islands.

The goal of this study was to determine if variation in shrub architecture at different spatial scales influences spiders and their prey. The effect of shrub architecture on spiders has been well-documented in Utah (Hatley & MacMahon 1980; Abraham 1983; Wing 1984), but these studies examined spider response to shrub architecture only at the scale of a single shrub and only Wing's study and our studies from Chapters 2 and 3 examined prey responses.

METHODS

Study site.—We conducted this study at Hardware Ranch Wildlife Management Area (41°61 N, 111°57 W), which is located in the Wasatch-Cache National Forest, about 40 km southeast of Logan, Cache County, Utah and is managed by the Utah Division of Wildlife Resources. The site is at an elevation of 1731 m and is dominated by big sagebrush (*Artemisia tridentata*) and low sage (*Artemisia arbuscula*). Land is used primarily as winter range for big game.

Shrub selection.—To reduce the heterogeneity among individual shrubs, we applied several criteria when selecting shrubs. Experimental shrubs (*A. tridentata*) had a single trunk at ground level, were not in immediate contact with an adjacent shrub, and were at least 10 m from another experimental shrub. We measured shrubs before and after treatment for maximum canopy width, width perpendicular to maximum canopy width, and canopy height (excluding the trunk beneath) (Ehmann 1994b). Only shrubs

with all three canopy dimensions between 0.4 and 1 m were used. Shrub volume was

determined by using the formula for an ellipsoid:

$$\text{Volume} = 4/3\pi abh$$

where a and b represent, respectively, the linear dimensions of the major and minor axes,

and h represents height.

Study design and treatments.—Big sagebrush shrubs were randomly assigned to

six experimental treatments consisting of factorial combinations of two levels of prey

attractant and three levels of foliage density. Prey attractant treatments included shrubs

that were either baited or not baited. The purpose of the bait was to increase the

probability of prey visits and/or the length of each visit (Wing 1984). Baited shrubs

contained four suspended containers: two (59 ml) containers filled with pig offal, one (22

ml) container filled with yellow banana-oil flavored honey, and one (22 ml) container

filled with red-colored honey. Container lids were perforated to facilitate odor

dispersion. As a control, identical but empty containers were suspended from shrubs not

baited. We baited shrubs two weeks prior to sampling to maximize arthropod abundance

on shrubs (Robinson 1981).

Shrub architecture was manipulated to either increase or decrease foliage density

(Hatley & MacMahon 1980). We increased foliage density by tightly binding all shrub

branches together with jute (hereafter referred to as "high") and decreased by clipping

50% of the shrub foliage ("low"). Shrubs not manipulated were used as controls

("natural").

Shrubs were further randomly assigned to one of two different levels of spatial context: 1) a single manipulated shrub surrounded by a patch of untreated shrubs (hereafter referred to as "single") and 2) a manipulated shrub surrounded by a patch of similarly treated shrubs ("patch"). While selecting patches, we ensured that the number of shrubs in each patch, the area of each patch, and the distribution of the shrubs within the patches were similar. In general, each patch contained 15 shrubs in a 2.5 m radius, but arthropods were only collected from the shrub at the center of each patch. Patch area was chosen using average daily distances traveled by some wandering spiders (Samu & Sárospataki 1995; Framenau 2005), although spiders are capable of traveling much larger distances (Turnbull 1973).

Sampling of arthropods.—Experimental shrubs were sampled in July of 2008. Single shrubs consisted of 25 replicates per treatment combination, whereas patch shrubs consisted of 5 replicates. Sampling began approximately 2 hours after sunrise, occurred only when there was an absence of high winds and precipitation, and did not occur when temperatures were below 10° C. Each shrub was quickly surrounded at the base with a canvas sheet (1.5 x 1.5 m) and then beaten 15 times with an ax handle to dislodge specimens onto the beating sheet for collection. Specimens were collected with an aspirator and immediately preserved in vials containing 70% ethanol. After the arthropods from the first beating were collected, a second beating episode of the same duration followed. The double-beating method was used previously and resulted in a 100% collection rate (Ehmann & MacMahon 1996).

Spiders were identified to species, but immature spiders were excluded from analyses since they may differ from adults in behavior and habitat and because some immature spiders were difficult to identify to species (Jiménez-Valverde & Lobo 2006; Sacket et al. 2008). Adult spiders were further sorted into *a priori* guilds, or groups of organisms that exploit the same resource in similar ways (Root 1967). These assignments are user-defined parameters widely used in community studies (Hawkins & MacMahon 1989). For spiders, guild membership is based on observations of foraging techniques that are often reinforced by morphological characteristics shared at the family level (Post & Riechert 1977). However, since there are no absolute guidelines, spider guild assignments vary widely (Uetz et al. 1999). Following the classification proposed by Uetz et al. (1999), we grouped spider families into the following four guilds: 1) ambushers: Philodromidae and Thomisidae; 2) runners: Gnaphosidae; 3) stalkers: Oxyopidae and Salticidae; and 4) trappers: Araneidae, Dictynidae, Linyphiidae, and Theridiidae.

Prey items were identified to the order level. Taxonomic classification followed Triplehorn and Johnson (2005). Ants (Hymenoptera: Formicidae) and aphids (Hemiptera: Aphididae) were not collected because their high abundances made collection of samples in a short period of time difficult. All specimens were deposited in the Department of Biology at Utah State University for reference.

Data analyses.—We tested the effect of experimental treatments on spider and prey abundances, as well as spider species richness (S), using a general linear mixed model (LMM). Spider and prey abundances were converted into densities (individuals

per m^3) to account for differences in shrub volume. Experimental treatments were treated as fixed factors while shrubs were incorporated in the model as a random effect. Spider and prey densities were square-root transformed to improve model performance, whereas spider species richness was ln-transformed ($x + 1$). The above analyses were performed using the GLIMMIX procedure in SAS/STAT software Version 9.3 in the SAS System for Windows (SAS Institute 2011).

To determine whether spider and prey community composition differs among treatments, we used a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001, 2002). Computations were performed using the 'adonis' function in the vegan package of Program R (R Development Core Team 2011) and significance values were generated using 1000 permutations (Oksanen et al. 2010). We then used a similarity of percentages (SIMPER) analysis to determine the taxa that contributed most to overall differences in composition. SIMPER analyses were carried out using PRIMER v. 6 (Clarke & Gorley 2006). Prior to multivariate analyses, data were square-root transformed to reduce the influence of the most abundant taxa, then standardized by sample (i.e., shrub) to minimize differences in total abundance (Gauch 1982). Distance matrices were calculated using the Bray-Curtis dissimilarity index (Faith et al. 1987).

RESULTS

Prey density and community composition.—A total of 2644 potential prey, representing 13 orders were collected (see Appendix A.3). The most abundant orders were Hemiptera (81%), Coleoptera (5%), and Acari (3%).

Prey densities were influenced by the interaction between foliage density and context (LMM, $F_{(2, 146)} = 9.9$, $P < 0.001$) and were marginally unrelated to prey attractant ($F_{(1, 146)} = 3.6$, $P = 0.06$). High foliage density shrubs contained more prey than natural or low foliage density shrubs, but differences were much more pronounced on patch shrubs (Fig. 4.1). Although not statistically significant at $P \leq 0.05$, more prey items were also collected on baited shrubs than on shrubs not baited (mean prey items $\pm$ SE: 254.08 $\pm$ 30.22 and 181.0 $\pm$ 26.03, respectively).

Prey community composition differed by context, as well as by the interaction between foliage density and prey attractant treatments (Table 4.1). A SIMPER analysis revealed that differences between single shrubs and patch shrubs resulted largely from a greater abundance of Hemiptera on patch shrubs. Hemiptera were also largely responsible for differences among shrubs of different foliage density and prey attractant treatments. Hemiptera were most abundant on baited high foliage density shrubs, but least abundant on baited natural foliage density shrubs.

Spider density, species richness, and community composition.—A total of 391 adult spiders were collected, representing 22 species (see Appendix A.4). Members from the family Salticidae were numerically dominant (63%), followed by Dictynidae (12%), Philodromidae (12%), Oxyopidae (5%), and Theridiidae (3%). Families Araneidae, Gnaphosidae, Linyphiidae, and Thomisidae were also collected, although in fewer numbers. The five most abundant species were *Pelegrina clemata* (Levi & Levi 1951) (Salticidae), *Emblyna reticulata* (Gertsch & Ivie 1936) (Dictynidae), *Ebo pepinensis* Gertsch 1933 (Philodromidae), *Oxyopes scalaris* Hentz 1845 (Oxyopidae), and *Emblyna*

piratica (Ivie 1947) (Dictynidae), which together characterized nearly 82% of adult

spiders.

Spider densities were influenced by foliage density (LMM, $F_{(2, 146)} = 6.5$, $P =$

0.002) and by context ($F_{(1, 146)} = 18.0$, $P < 0.001$). More spiders were collected on high

(mean number of spiders ± SE: 43.24 ± 7.40) than on natural (20.27 ± 5.20) or low

foliage density shrubs (15.71 ± 4.60), and more than twice as many spiders were

collected on patch shrubs than on single shrubs (40.24 ± 7.47 and 13.57 ± 2.09,

respectively). Although the interaction between foliage density and context was not

statistically significant at $P \leq 0.05$ ($F_{(2, 146)} = 2.7$, $P = 0.07$), more spiders were collected

on high foliage density shrubs surrounded by other high foliage density shrubs (Fig. 4.2).

Spider species richness varied only by context ($F_{(1,146)} = 10.4$, $P = 0.002$). More

species were collected on patch shrubs (mean number of species ± SE: 1.86 ± 0.18) than

on single shrubs (1.3 ± 0.07).

Spider species composition varied with context and foliage density (Table 4.2). A

SIMPER analysis revealed that differences between single shrubs and patch shrubs

resulted largely from a greater abundance of *P. clemata* on patch shrubs, while *E.*

pepinensis and *E. reticulata* were more abundant on single shrubs. *P. clemata* were also

largely responsible for differences among shrubs of different foliage density treatments

and were more abundant on natural or low foliage density shrubs than on high foliage

density shrubs. *E. pepinensis* were more abundant on high foliage density shrubs,

whereas *E. reticulata* were more abundant on natural or high foliage density shrubs.

Spider guild composition, on the other hand, was marginally, but nonsignificantly related to shrub context (Table 4.2). Stalkers were relatively more abundant on patch shrubs, but ambushers, trappers, and runners were more abundant on single shrubs.

DISCUSSION

Our findings contribute to the growing body of literature suggesting that habitat structure, including surrounding structures, are important for determining the distribution and abundance of spiders and other arthropods (Lawton 1983; Uetz 1991; Wise 1993). We found that spiders and their prey were more abundant on high foliage density shrubs, especially when these shrubs were surrounded by shrubs of similar architectures. These observations may have resulted from colonization of organisms from adjacent shrubs since structurally diverse environments are thought to provide organisms with a wider array of microhabitats and/or niche space (McCoy & Bell 1991; Brandt & Lubin 1998), as well as more diverse ways of exploiting food resources (Brandt & Lubin 1998; Langellotto & Denno 2004; Tews et al. 2004). Surrounding vegetation and its importance has been considered in other studies (e.g., Webb et al. 1984; Kareiva 1985; Grez & Prado 2000) and seems especially influential if such habitats are accessible and provide supplemental resources or opportunities.

A greater abundance of spiders on high foliage density shrubs surrounded by similarly treated shrubs could also have been driven by higher abundances of prey. Spiders may have tracked variations in prey resources by spending more time on shrubs containing more prey and/or by migrating from shrubs of low prey availability to shrubs

with high prey availability (Riechert 1974; Riechert & Lockley 1984). Spiders may leave

a shrub if the prey capture yield in that shrub drops below the average rate of yield over

all shrubs in which the spider has been foraging (Charnov 1976; Holt 1987). Spiders may

also have responded by increasing their reproductive rates, but because of the short

duration of this study, we assume that this was not the case.

Our data also support the idea that responses by organisms are sensitive to

differences in spatial scale and context (Churchill & Arthur 1999; Samu et al. 1999;

Whitehouse et al. 2002; Chust et al. 2004; De Mas et al. 2009). For example, prey

community composition was not related to shrub foliage density at the scale of a single

shrub (Chapter 2), but was influenced when surrounding shrub architectures were also

manipulated. Hemiptera, in particular, were associated with differences in shrub context

and were more abundant on patch shrubs. Since Hemiptera were also more abundant on

baited high foliage density shrubs, we suspect that patch shrubs intensified the effects of

foliage density and/or prey attractant, although the three-way interaction among factors

was not significant, nor were the main effects of foliage density or prey attractant

treatments. Prey communities may have responded more to variation in shrub

architecture at broader spatial scales than at finer spatial scales since they may be more

readily able to move between shrubs (Stoner & Joern 2004).

Some spiders (i.e., *P. clemata* and, more generally, spiders of the stalker foraging

guild) appear also to have been more abundant on patch shrubs. We suspect that *P.

clemata*, which belongs to the stalker guild, were influenced by surrounding vegetation

structure because they are more mobile than other species (e.g., web-building spiders

such as *M. foxi*) and may, therefore, be more willing to exploit shrubs in close proximity.

P. clemata were also relatively more abundant on natural and low foliage density shrubs.

Salticids are commonly thought to seek out more open substrates since dense branching

obstructs their vision and interferes with their ability to jump (Stratton et al. 1979; Hatley

& MacMahon 1980; Stevenson & Dindal 1982).

This study's observations, together with results taken from Chapters 2 and 3 and

from other studies in the area (e.g., Hatley & MacMahon 1980; Robinson 1981; Abraham

1983; Wing 1984; Heikkinen & MacMahon 2004), confirm that habitat structure is an

important factor in determining spider community structure. We recommend that

researchers continue to investigate spider responses to habitat structure and prey

availability across different spatial scales and contexts to obtain a more detailed

description of what factors, operating under what conditions, influence spider community

composition and structure.

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Table 4.1.—*F* and *P* values from PERMANOVA analysis of prey community composition. PERMANOVA analyses are based on Bray-Curtis dissimilarities.

	df	*F* value	*P* value
Context	1	2.460	0.031
Foliage density treatment (FDT)	2	0.801	0.643
Prey attractant treatment (PAT)	1	0.277	0.915
Context $\times$ FDT	2	0.897	0.519
Context $\times$ PAT	1	0.425	0.816
FDT $\times$ PAT	2	2.129	0.026
Context $\times$ FDT $\times$ PAT	2	1.069	0.370

Table 4.2.—*F* and *P* values from PERMANOVA analysis of spider species and guild composition. PERMANOVA analyses are based on Bray-Curtis dissimilarities.

	df	Spider species		Spider guild	
		F value	*P* value	*F* value	*P* value
Context	1	2.579	0.016	2.922	0.054
Foliage density treatment (FDT)	2	2.104	0.019	0.634	0.628
Prey attractant treatment (PAT)	1	1.325	0.210	0.261	0.780
Context × FDT	2	0.796	0.656	0.629	0.623
Context × PAT	1	1.265	0.251	0.917	0.393
FDT × PAT	2	1.562	0.104	0.636	0.636
Context × FDT × PAT	2	0.528	0.906	0.416	0.792

Figure 4.1.—Prey densities from shrubs sampled in 2008 and sorted by two different spatial contexts and three different foliage density treatments. Graphs show means with standard errors. Means and standard errors were back-transformed from square-root transformed estimates.
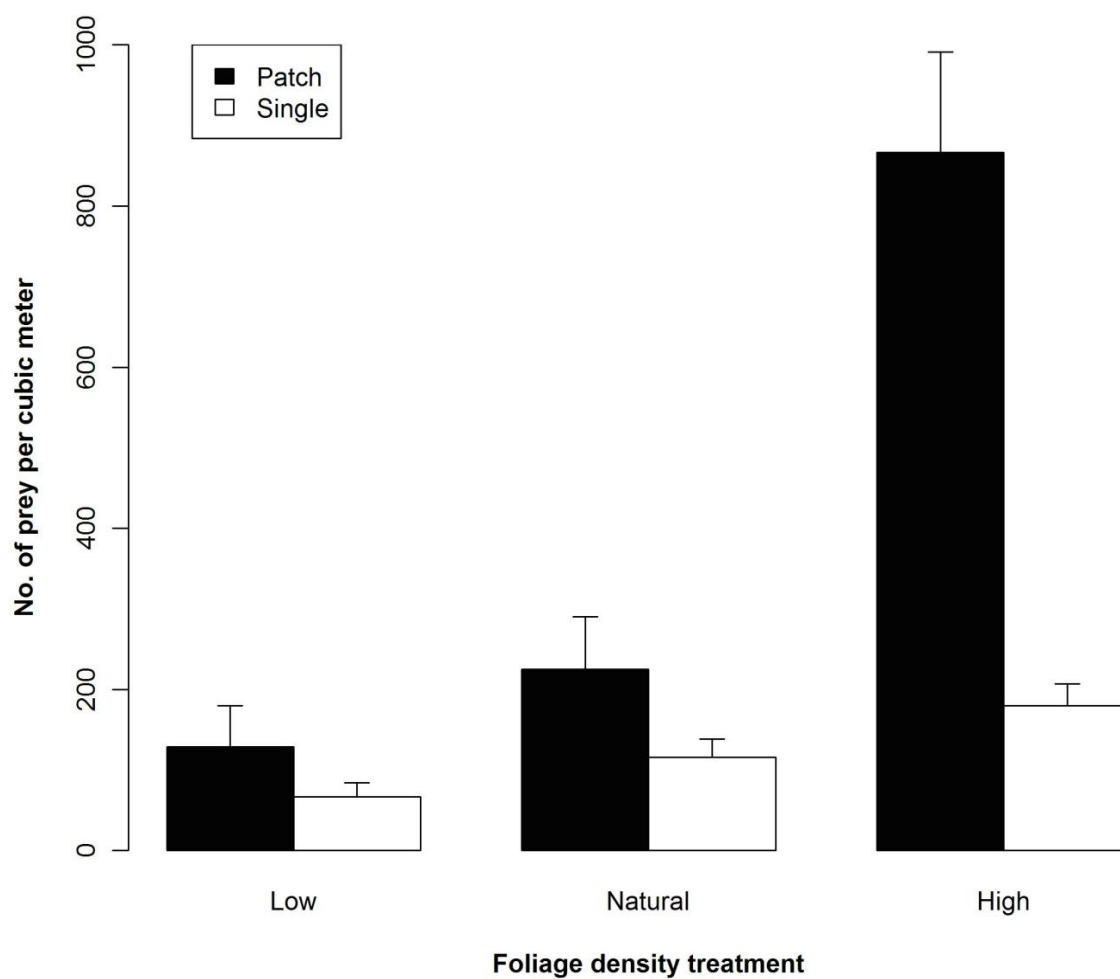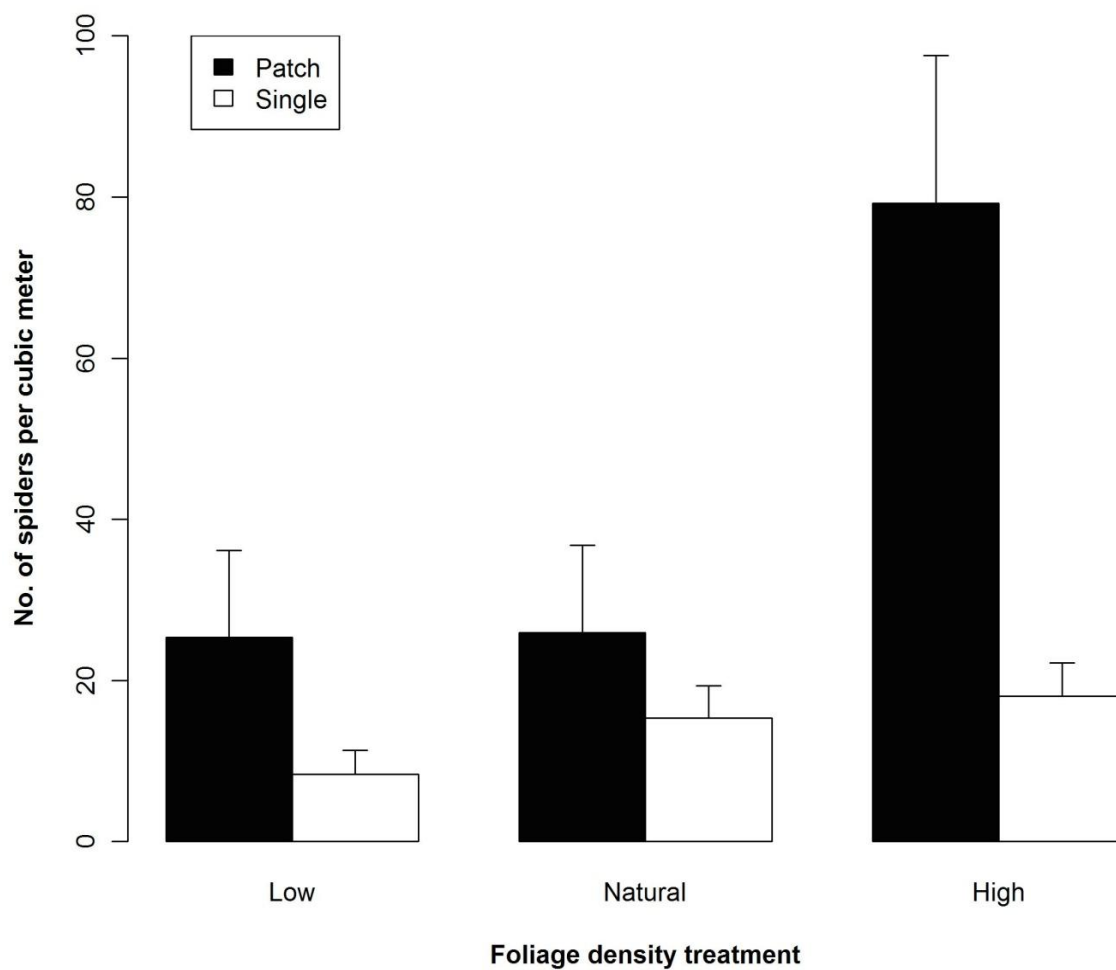
Figure 4.2.—Spider densities from shrubs sampled in 2008 and sorted by two different spatial contexts and three different foliage density treatments. Graphs show means with standard errors. Means and standard errors were back-transformed from square-root transformed estimates.

CHAPTER 5

SUMMARY AND GENERAL CONCLUSIONS

The studies outlined in this dissertation were conducted to determine the relative importance of prey availability and shrub architecture on the distribution, abundance, and biodiversity of spiders in a shrub-steppe ecosystem of northern Utah. In general, we found that prey availability varied with changes in shrub architecture and that both prey availability and shrub architecture influenced spider abundance and species richness (Chapter 2). Spider species diversity, however, was influenced mostly by changes in shrub architecture. Spider species and family compositions were also associated with changes in shrub architecture, but neither guild composition nor prey composition responded to such changes. Although it is generally thought that structurally complex habitats are beneficial to organisms, some spiders were deterred by such habitats. Dense vegetation can be less suitable if, for example, it impedes their mobility (Stratton et al. 1979; Hatley & MacMahon 1980; Stevenson & Dindal 1982) or provides less suitable substrates for web attachment (Hatley & MacMahon 1980; Uetz & Hartsock 1987; Marc & Canard 1997; Balfour & Rypstra 1998; Tsai et al. 2006).

When we analyzed the data using structural equation modeling (Chapter 3), we found that shrub architecture influenced spider abundances directly and indirectly via prey availability. The direct effect of shrub architecture had less explanatory power than the direct effect of prey availability, though the total effects (i.e., the sum of direct and indirect pathways) of each factor were more similar in strength. In addition, spider species richness was not directly related to shrub architecture and was only marginally

related to prey availability. Both factors, however, influenced species richness indirectly

through accompanied changes in spider density. An analysis of the total effects of prey

availability and shrub architecture on species richness revealed that they were similar in

predictive strength. Finally, shrub architecture affected spider species diversity directly,

as well as indirectly. Prey availability was not directly associated with spider species

diversity but was indirectly related through spider density. The total effect of prey

availability on species diversity, however, was negligible. Although the relevance of our

study is dependent on whether our measure of prey reflects true resource availability for

spiders, our results are supported by the observation that more than half of the prey items

collected in this study belong to families Cicadellidae and Miridae, both of which are

regularly fed upon by spiders (Nyffeler et al. 1992; Lang et al. 1999).

Surrounding vegetation structure was also found to impact the abundance of

spiders and their prey (Chapter 4). Overall abundances were greater on high foliage

density shrubs, especially when those shrubs were surrounded by shrubs of similar

architectures. We also found that spider and prey compositions were influenced by

surrounding vegetation structures. Interestingly, prey compositions did not differ among

treatments in the study from Chapter 2 where shrub architecture varied only at the scale

of a single shrub. Prey may have responded more to variation in shrub architecture at

broad than at fine spatial scales since they are able to readily move across the landscape

to assess resources (Krawchuk & Taylor 2003; Stoner & Joern 2004; Hewitt et al. 2005).

In conclusion, our results suggest that structural complexity increases the total

abundance and diversity of spiders and other arthropods and that variation in prey

availability is partly responsible for patterns of spider community organization. Future studies should continue to evaluate how habitat structure interacts with other environmental variables to affect community dynamics. For example, microclimate could be an important intermediary variable since structurally complex habitats offer a variety of microhabitat types that differ in physical conditions (Riechert & Tracy 1975; Bell et al. 2001; Byrne 2007). Finally, although results from this study warrant further investigation, we show that structural equation models provide additional insight into ecological patterns and processes and recommend that they be used to strengthen understanding of ecological effects through intervening variables.

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APPENDICES

Appendix A.1.—List and numbers of non-Araneae arthropods collected from sagebrush at Hardware Ranch WMA, northern Utah, 2007-2008. Values represent pooled numbers collected from shrubs across all treatment combinations and sampling dates. An asterisk (*) indicates superfamily rank.

Order	Family	Total number collected
Acari		144
Archaeognatha	Machilidae	11
Coleoptera	Buprestidae	4
	Carabidae	26
	Cerambycidae	1
	Chrysomelidae	1649
	Coccinellidae	128
	Curculionidae	19
	Dermestidae	11
	Elateridae	1
	Histeridae	18
	Melyridae	66
	Mordellidae	5
	Scarabeidae	1
	Staphylinidae	1
	Tenebrionidae	1
Collembola	Entomobryidae	5
	Sminthuridae	53
Dermaptera	Forficulidae	2
Diptera	Bombyliidae	1
	Cecidomyiidae	14
	Chironomidae	12
	Chloropidae	68
	Culicidae	2
	Phoridae	18
	Pipunculidae	3
	Sarcophagidae	1
	Sciaridae	27
	Simuliidae	10
	Tachinidae	9
	Tephritidae	35
	Ulidiidae	8
Hemiptera	Anthocoridae	4
	Cercopidae	109
	Cicadellidae	3049
	Dictyopharidae	24
	Lygaeidae	42
	Membracidae	59
	Miridae	2967
	Nabidae	253

Appendix A.1.— (continued from previous page)

Order	Family	Total number collected
	Ortheziidae	7
	Pentatomidae	23
	Psyllidae	47
	Reduviidae	11
	Rhopalidae	3
	Scutelleridae	5
	Tingidae	39
Hymenoptera	Braconidae	28
	Chalcidoidea *	201
	Chrysididae	2
	Cynipoidea *	18
	Halictidae	1
	Ichneumonidae	2
	Vespidae	1
Lepidoptera	Lycaenidae	7
	Noctuidae	299
	Nymphalidae	2
	Pterophoridae	1
Mantodea	Mantidae	1
Neuroptera	Chrysopidae	3
	Hemerobiidae	3
	Myrmeleontidae	1
	Raphidiidae	8
Odonata	Coenagrionidae	2
Orthoptera	Acrididae	57
	Rhaphidiphoridae	2
	Tettigoniidae	32
Psocoptera	Liposcelidae	100
	Psocidae	75
Thysanoptera		87
Total		9929

Appendix A.2.—List and numbers of spider taxa collected from sagebrush at Hardware Ranch WMA, northern Utah, 2007-2008. Values represent pooled numbers of adult specimens collected from shrubs across all treatment combinations and sampling dates.

Family	Species	Total number collected
Araneidae	*Aculepeira packardi* (Thorell 1875)	1
	Hypsosinga funebris (Keyserling 1892)	1
	Metepeira foxi Gertsch & Ivie 1936	60
Dictynidae	*Dictyna idahoana* Chamberlin & Ivie 1933	6
	Emblyna piratica (Ivie 1947)	57
	Emblyna reticulata (Gertsch & Ivie 1936)	85
Gnaphosidae	*Micaria gertschi* Barrows & Ivie 1942	31
	Unidentified	1
Linyphiidae	*Erigone dentosa* O. P.-Cambridge 1894	9
Lycosidae	*Pardosa utahensis* Chamberlin 1919	7
Mimetidae	*Mimetus aktius* Chamberlin & Ivie 1935	2
Oxyopidae	*Oxyopes scalaris* Hentz 1845	133
Philodromidae	*Ebo pepinensis* Gertsch 1933	157
	Philodromus histrio (Latreille 1819)	161
	Philodromus sp.	3
	Thanatus formicinus (Clerck 1757)	27
	Tibellus oblongus (Walckenaer 1802)	12
Salticidae	*Evarcha hoyi* (Peckham & Peckham 1883)	2
	Habronattus americanus (Keyserling 1885)	42
	Pelegrina clemata (Levi & Levi 1951)	690
	Phidippus johnsonii (Peckham & Peckham 1883)	24
	Sassacus papenhoei Peckham & Peckham 1895	18
	Synageles idahoanus (Gertsch 1934)	55
Theridiidae	*Chrysso pelyx* (Levi 1957)	1
	Dipoena nigra (Emerton 1882)	81
	Theridion petraeum L. Koch 1872	22
	Theridion sp.	7
Thomisidae	*Mecaphesa lepida* (Thorell 1877)	3
	Xysticus cunctator Thorell 1877	1
	Xysticus gulosus Keyserling 1880	2
	Xysticus montanensis Keyserling 1887	43
Total		1744

Appendix A.3.—List and numbers of non-Araneae arthropods collected from sagebrush at Hardware Ranch WMA, northern Utah, in July of 2008, and sorted by two different spatial context treatments. Values represent pooled numbers collected from shrubs across all foliage density and prey attractant treatment combinations.

Order	Single shrubs	Patch shrubs
Acari	69	21
Archaeognatha	2	5
Coleoptera	104	18
Collembola	24	1
Dermaptera	2	0
Diptera	42	5
Hemiptera	1503	638
Hymenoptera	49	7
Lepidoptera	26	18
Neuroptera	0	5
Orthoptera	22	14
Psocoptera	18	17
Thysanoptera	33	1
Total	1894	750

Appendix A.4.—List and numbers of adult spider taxa collected from sagebrush at Hardware Ranch WMA, northern Utah, in July of 2008, and sorted by two different spatial context treatments. Values represent pooled numbers of adult specimens collected from shrubs across all foliage density and prey attractant treatment combinations.

Family	Species	Single shrubs	Patch shrubs
Araneidae	*Hypsosinga funebris* (Keyserling 1892)	1	0
	Metepeira foxi Gertsch & Ivie 1936	2	0
Dictynidae	*Dictyna idahoana* Chamberlin & Ivie 1933	1	0
	Emblyna piratica (Ivie 1947)	10	6
	Emblyna reticulata (Gertsch & Ivie 1936)	22	8
Gnaphosidae	*Micaria gertschi* Barrows & Ivie 1942	6	0
	Unidentified	1	0
Linyphiidae	*Erigone dentosa* O. P.-Cambridge 1894	0	1
Oxyopidae	*Oxyopes scalaris* Hentz 1845	13	8
Philodromidae	*Ebo pepinensis* Gertsch 1933	26	4
	Philodromus histrio (Latreille 1819)	6	4
	Thanatus formicinus (Clerck 1757)	3	0
	Tibellus oblongus (Walckenaer 1802)	0	2
Salticidae	*Habronattus americanus* (Keyserling 1885)	7	1
	Pelegrina clemata (Levi & Levi 1951)	161	61
	Phidippus johnsonii (Peckham & Peckham 1883)	0	1
	Sassacus papenhoei Peckham & Peckham 1895	2	2
	Synageles idahoanus (Gertsch 1934)	9	3
Theridiidae	*Dipoena nigra* (Emerton 1882)	5	0
	Theridion petraeum L. Koch 1872	3	1
	Theridion sp.	2	2
Thomisidae	*Xysticus montanensis* Keyserling 1887	6	1
Total		286	105

Appendix B.1.—Photographs illustrating an experimental A) low foliage density shrub, B) natural (or control) foliage density shrub, and C) high foliage density shrub.

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Spears, L.R. 2012. Prey availability mediates spider response to shrub architecture: a structural equation modeling approach. Intermountain Graduate Research Symposium, Utah State University, Logan, UT.

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Spears, L.R. and J.A. MacMahon. 2009. Effects of insect availability and shrub architecture on spider abundance and diversity: an experimental study of spiders in a shrub-steppe ecosystem. Ecological Society of America Annual Meeting, Albuquerque NM. (Poster)

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Spears, L. and J.F. Cavitt. 2001. The effects of avian pox on plumage coloration in male house finches (*Carpodacus mexicanus*). Senior Thesis in Zoology. Utah Academy of Sciences, Arts and Letters, Salt Lake City, UT.

Spears, L. 2001. Patterns of ranging and resource utilization in mantled howler monkeys (*Alouatta palliata*). Senior Project in Anthropology. Student Research Conference, Department of Anthropology and Sociology, Weber State University, Ogden, UT.

ADDITIONAL RESEARCH EXPERIENCE

Assisted Amy Croft (Ph.D. candidate in Ecology, Utah State University) with rare plant surveys in the upper Las Vegas wash. Summer 2009.

Assisted Dr. James MacMahon (Utah State University) and Charlie Crisafulli (USDA Forest Service Pacific Northwest Research Station) with monitoring of small mammals on lands disturbed by the 1980 eruption of Mount St. Helens. Summer 2005.

Assisted Dr. Dwayne Meadows (Weber State University) with studying the distribution and relative abundance of molluscs in the national forests of Utah. Summer 2001.

Advanced Field Course in Primate Behavior and Ecology, Ometepe Biological Field Station, Nicaragua. Summer 2000.

Field Course in Tropical Botany, Ethnobotany, and Mayan Culture, Belize. Summer 1998.

VOLUNTEER WORK

Adoption Counselor, Email and Social Media Coordinator, Silent Auction Committee Member (Annual Moondog Ball Charity Event), Four Paws Rescue, Logan, UT. 2009-present.

President, Anthropology Club, Weber State University, Ogden, UT. 2000-2001.

Wildlife Care Assistant, Ogden Nature Center, Ogden, UT. 2000.

Historian, Anthropology Club, Weber State University, Ogden, UT. 1999-2000.