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COMMUNITY-LEVEL EFFECTS OF VEGETATION ARCHITECTURE AND PREY
AVAILABILITY: A STUDY OF GROUND-DWELLING ARTHROPODS IN A
SHRUB-STEPPE ECOSYSTEM

by

Mary E. Pendergast

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

of

DOCTOR OF PHILOSOPHY

in

Ecology

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2011

ABSTRACT

Community Level Effects of Vegetation Architecture and Prey Availability: A Study of
Ground-dwelling Arthropods in a Shrub-steppe Ecosystem

by

Mary E. Pendergast, Doctor of Philosophy

Utah State University, 2011

Major Professor: Dr. James A. MacMahon
Department: Biology

Changes to vegetation architecture within a natural habitat can have profound impacts upon ecological community function, but the relative influence of vegetation architecture itself and potential indirect influences of associated food resources are often difficult to disentangle. I present the results of a three-year study designed to address the community level impacts of changes in big sagebrush (*Artemisia tridentata*) architecture and associated prey availability upon the ground-dwelling arthropod community. Three experimental sagebrush architecture treatments (low, intermediate, and high foliage density) and two levels of prey insect availability treatment (natural and baited/increased prey availability) were imposed in a sage-steppe ecosystem. The ground-dwelling spider (top predators) and insect (prey) response to all combinations of the six treatments were assessed through abundances in pitfall traps. Chapter 2 demonstrates that changes in a single shrub's architecture did not markedly impact prey arthropod availability on the

ground, though an overall increase in arthropod abundance was detected within baited shrubs. This indicates changes to vegetation architecture do not impact prey insect availability for ground-dwelling spiders. Thus, changes in shrub architecture and not the associated prey base directly alter the ground-dwelling spider community. Chapter 3 shows that architectural manipulation of a single sagebrush directly influences the ability of certain ground-dwelling spider guilds to persist beneath the shrub. Data within Chapters 2 and 3 support the conclusion that vegetation architecture directly affects ground-dwelling spider community structure and composition. Finally, Chapter 4 explores how the relative impacts of vegetation architecture and prey availability upon ecological communities can shift depending upon the spatial context in which the manipulations take place, given the differences in mobility of species within the ground-dwelling spider and insect prey communities. Within this study, Diurnal and Nocturnal Wanderers responded to manipulations in prey availability at a larger spatial context (patches of 15 shrubs) while more stationary Trappers and Ambushers did not. Through simultaneous manipulation of vegetation architecture (*Artemisia tridentata*, big sagebrush) and associated insect prey base in different spatial contexts, this dissertation demonstrates that vegetation architecture directly affects ground-dwelling spider community organization at the species and guild levels of diversity. Shifts in spider (predator) functional diversity can ultimately impact arthropod decomposer and herbivore populations, influencing fundamental ecosystem processes such as decomposition and productivity.

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CHAPTER 1

INTRODUCTION

Patterns in species abundance and distribution have informed understanding of ecological system processes (Andrewartha and Birch 1954), with theoretical and practical applications. A variety of biotic and abiotic variables explain patterns in the composition and organization of species within an ecosystem. Because species operate at a variety of spatial scales, incorporation of spatial contexts reveals the complexity of factors responsible for observed patterns in ecological communities (Whittaker 1956, Wiens 1989, Putman 1994, Belovsky et al. 2004).

Ecological patterns are observed at several levels of biological organization ranging from individuals to the biosphere. Interactions that occur among different groups of species form community level patterns of organization. Often, redundancy of species within functional groups maintains ecosystem stability (Smith 1972, Lawrence and Wise 2004, Shultz et al. 2006, Schmitz 2009). Thus, diversity and abundance at the functional group level is frequently more reflective of primary factors influencing a community organization than species level diversity alone. Recognizing species and functional group distribution patterns and the factors behind them will help explain underlying processes of community organization and stability.

Habitat structure is one factor known to influence community-level diversity and organization (MacArthur and MacArthur 1961, Pianka 1961, Uetz 1977, Scheidler 1990, Weeks and Holtzer 2000, Cardoso et al. 2008). Community composition (presence and absence of species or groups) and structure (abundances within species or groups) are closely tied to habitat structure, diversity and complexity. Abundance and distribution of

resources, including food, is also linked to habitat structure as are various microhabitat variables, including light, moisture, and temperature, that determine the ability of species to persist and reproduce in a given area. As a result, habitat structure plays a central role in understanding species composition (presence/absence) and structure (species abundances) in communities.

Vegetation architecture, a primary form of habitat structure, influences microhabitat and structural attributes that differentially affect species composition within a community. Community-level responses to architectural change are measured by diversity, abundance and richness of species and functional guilds. Guilds, groups of organisms exploiting the same resources in a similar manner, are commonly used to describe community organization (Whittaker 1956, MacArthur and Wilson 1967, Root 1973, Hatley and MacMahon 1980, Holt 1984, Wing 1984, Hawkins and MacMahon 1989, Benke and Wallace 1997, Heino et al. 2003).

Altering the foliage density, volume and heterogeneity of architecture considerably impact guild, functional group and species diversity as well as overall ecological community composition (Pianka 1973, Allen 1975, Cardoza et al. 2008). Measuring arthropod community response is a practical means of assessing the ecological impacts of vegetation architectural manipulation, as arthropods are easily collected, represent a variety of trophic levels and functional groups and are incredibly speciose. To date, most of these studies analyzed the influence of vegetation architecture on foliage-dwelling arthropod communities or the influence of ground surface-litter on ground-dwelling communities (Hatley and MacMahon 1980, Brandt 1998, Halaj et al. 2000,

Halaj et al. 2008, Sanders et al. 2008). This study investigates the influence of the vegetation canopy architecture on the ground-dwelling spider community. Ground-dwelling spiders, in particular, are the dominant arthropod predators in many terrestrial ecosystems (Uetz 1977, Weeks and Holtzer 2000, Cardoso 2008). These top predators affect the diversity and abundance of other arthropods in a range of experimental systems, including sage-steppe, agricultural, old-field, and forest litter communities (Wing 1984, Hurd 1990, Riechert and Lawrence 1997, Wise 2004). The relevance of spiders has been established in managing insect communities and as useful indicators of habitat change (Sanders et al. 2008, Maleque et al. 2009, Woodcock et al. 2009, Petillon et al. 2010). Shifts in spider guild composition often change predator functional diversity impacting arthropod decomposer and herbivore populations, subsequently influencing fundamental ecosystem processes such as decomposition and productivity (Schmitz 2009). The insect prey base and ground-dwelling spiders represent a broad range of trophic levels and functional groups, or guilds, within a community and are readily sampled across terrestrial habitats.

Guilds have been described in various ways for the spider communities based on prey-capture methods (Turnbull 1973, Uetz 1977, Wing 1984, Ehmann and MacMahon 1996). A spider guild classification similar to that used by Abraham (1980) was adopted for this study. The classification includes 'Diurnal Wanderers,' 'Nocturnal Wanderers,' 'Ambushers,' and web-spinners, referred to as 'Trappers' herein. Ground-dwelling insect communities utilizing habitat similar to their spider predators are organized by trophic levels in community studies rather than guilds as they represent a broad range of feeding

types (Parmenter and MacMahon 1984, Didham et al. 1996, Brussard et al. 1998).

Some of these trophic groups or functional feeding groups include ‘Predators,’ ‘Herbivores,’ ‘Omnivores,’ and ‘Detritivores.’

The direct mechanism(s) that links vegetation architecture to ground-dwelling spider community organization is seldom explored. It has been suggested that influences of vegetation architecture on spider communities result from spiders, as predators, responding to the suitability of the physical structure of the plant in or under which they live. By sheltering from wind, improving microclimate variables or protecting them from other predators, vegetation architecture has a profound impact on spider communities (Enders 1975, Bultman and Dewitt 2008). This concept implies the nature of the vegetation architecture directly influences the spider community rather than any biotic characteristics of the plant itself. In addition, the insect prey base may also respond to the difference in vegetation architecture. Thus, spiders may respond indirectly to shifts in prey base rather than directly to changes in vegetation architecture. Many positive relationships between vegetation heterogeneity, complexity and density and insect abundance and diversity have been documented (Root and Chaplin 1976, Brown 1984, Wright et al. 1998). Often vegetation architecture also provides associated insects with a food resource (Strong 1979) and refugia from predators (Price et al. 1980, Evans 1997, de Souza and Martins 2005). Insect prey abundance is influenced by a variety of microhabitat variables. Despite the cause, change in abundance and distribution of insect prey influences the presence of spider species and guilds within a community in conjunction with habitat structure (Smith 1972, Crowley 1978, Crowder and Cooper

1982, Wing 1984, de Souza and Martins 2005). When investigating the possible effects of vegetation architecture on the ground-dwelling spider community, the associated prey base must also be considered. Thus, simultaneous manipulation of both vegetation architecture and prey availability is required. The potential indirect effect of vegetation architecture on the spider prey base must be evaluated before the existence of a direct effect of vegetation architecture on the ground-dwelling spider community can be determined.

Given the differences in mobility within the ground-dwelling spider and insect prey communities the spatial context in which experimental manipulation occurs must be considered when determining the influence of vegetation architecture. Thus, a spatial context approach is required to adequately understand the impacts of habitat alteration on an ecological community, because the surrounding matrix may impact the relative importance of an architectural change to community organization (Levins and Culver 1971, Crowley 1978, Perry 1995, Law 2000, Hewitt et al. 2002, Belovsky et al. 2004, Murphy and Lovett-Doust 2004, Galle 2008, Kapoor 2008, Horvath et al. 2009, Oberg 2009, Siira-Pietikainen and Haimi 2009, Magura et al. 2010, Opatovsky et al. 2010). Habitat structure and other environmental variables also differentially influence community functional diversity and organization depending upon spatial context (Pearman 2002, Chust et al. 2003, De Mas et al. 2009). Given that members of a community utilize variable spatial scales of habitat, a multiple spatial context approach to studies of habitat change broadens the generality and applicability of this experimental

fieldwork (Levins and Culver 1971, Crowley 1978, Perry 1995, Law 2000, Hewitt et al. 2002, Belovsky et al. 2004).

Both ground-dwelling spider and insect responses to vegetation architectural change will aid in disentangling the influences of habitat structure and prey availability on community structure. This study examines the relative impacts of vegetation architecture, prey availability and spatial context alterations on community-level organization in a natural system. A community of ground-dwelling arthropods in a shrub-steppe system was used to address four ecological questions:

Questions

- 1.) Does manipulation of vegetation architecture affect ground-dwelling spider diversity and guild structure?
- 2.) Does manipulation of vegetation architecture affect ground-dwelling arthropod diversity and trophic structure?
- 3.) Do changes in prey availability influence spider guilds and species diversity?
- 4.) Do impacts of vegetation architecture and prey availability manipulations on ground-dwelling spider community organization differ among spatial contexts?

To address these questions, a 3 x 2 x 2 factorial design was employed. The three experimental factors included: three levels of vegetation architecture manipulations, two levels of prey availability amendments and two levels of spatial context. The field site was a continuous landscape of shrub-steppe habitat managed by the Utah Division of Wildlife Resources, Hardware Ranch, Cache County, UT. *Artemisia tridentata*,

hereafter, big sagebrush, is dominant in the shrub-steppe area and was used for experimental manipulations.

In the second chapter of this dissertation, a detailed explanation of the experimental design, implementation of shrub manipulations and pitfall-trapping methods is given. The second chapter primarily investigates the influences of vegetation architecture and prey availability manipulations on the ground-dwelling spiders' potential prey base. The central hypothesis within Chapter 2 states that increased prey availability due to baiting treatments within the shrub canopy architecture would increase the abundance of potential spider prey on the ground. Further, I investigate whether manipulating shrub canopy architecture impacts the overall ground prey abundance or diversity through correlated change in foliage density or biomass. The impacts of vegetation architecture, or lack thereof, will suggest the presence or absence of an indirect effect of change in foliage density or biomass and a subsequent shift in insect prey base. Without evidence of a shift in ground prey abundance, vegetation architecture impacts on the ground-dwelling spider community are likely a result of a direct effect, as documented in the third chapter.

In the third chapter, the ground-dwelling spider community response to vegetation architecture, prey availability and spatial context treatments is described. I hypothesized that some ground-dwelling spider guilds would respond to the vegetation architecture manipulations as well as the prey availability alterations and that the community-level response would vary between the different levels of spatial context.

The fourth chapter explores the importance of spatial context with regard to the previous manipulations to vegetation architecture and prey availability. The main hypothesis in this chapter states that spider guilds will have different responses to architectural and prey manipulations depending upon spatial context given their varying levels of mobility. I also expected any general impacts of vegetation architecture on community organization to be magnified as the spatial context of manipulation was increased.

To conclude, the fifth chapter synthesizes the results of the three data chapters and provides perspective upon the implications of the findings, reviewing my original ecological questions.

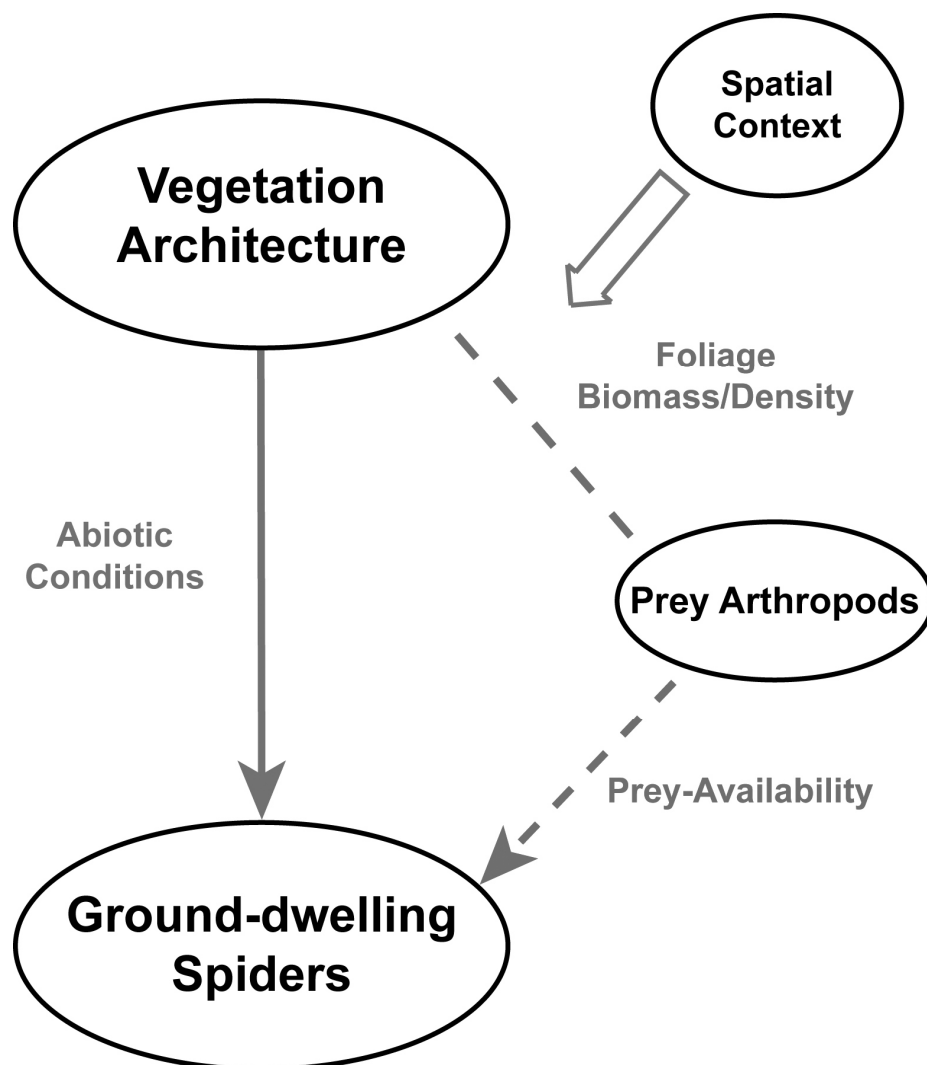


Figure 1.1. A flow diagram representing the potential direct and indirect effects of vegetation architecture, prey arthropods and spatial context on the ground-dwelling spider community.

CHAPTER 2

ARTHROPOD COMMUNITY INFLUENCES OF VEGETATION ARCHITECTURE:
AN EXPERIMENTAL STUDY IN A SHRUB-STEPPE ECOSYSTEM**Abstract**

Many studies demonstrate the influence of vegetation architecture on ecological community organization. Chapter 3 illustrates an example of a ground-dwelling spider community responding to the canopy architecture change to single shrubs. Whether spider communities are directly altered by architecture change or indirectly influenced through a shift in prey base due to a change in foliage density or biomass is unknown. To determine if shrub architecture affects the spider community directly or indirectly, varied levels of vegetation architecture (low, intermediate and high foliage density) and prey availability (baited and un-baited) on big sagebrush (*Artemisia tridentata*) were created within a shrub-steppe ecosystem. This study investigates the influences of these manipulations on the insect prey base of the shrub-steppe ground-dwelling spider community. The majority of insect Orders and arthropod subclasses as well as feeding guilds responded to prey availability treatments but not to changes in vegetation architecture, with few exceptions. These data support findings that the ground-dwelling spider community responds directly to changes in vegetation architecture and not indirectly through a shift in prey base with a change in foliage biomass.

Introduction

Habitat structure and prey availability are among the important factors determining ecological community structure and composition (Turnbull 1973, Lawton 1983, Gardner et al. 1995, Tews et al. 2004). This study sought to distinguish the relative influences of habitat structure and prey availability on ground-dwelling arthropod community composition both at the functional group and species level and whether these factors directly affect the community.

The potential response of the ground-dwelling arthropod community to changes in vegetation architecture and prey availability also informs other work evaluating the influence of these factors upon the ground-dwelling spider community. As described in Chapter 3, changes in vegetation architecture influenced ground-dwelling spider community composition and structure. To determine whether vegetation architecture directly affects the spider community, as these observations suggest, evaluating what influence vegetation architecture has upon the insect community is warranted. If the ground-dwelling spiders' potential prey base was not influenced by the vegetation architecture manipulations, then an indirect effect of changes to plant biomass or foliage density upon prey abundance or diversity was unlikely to exist. Therefore, the ground-dwelling spider community was directly affected by changes in vegetation architecture.

Literature describing the relationships between vegetation architecture and arthropod abundance and diversity often focuses on foliage-dwelling species (Leather 1986, Andow and Prokrym 1990, Bell et al. 2000, Goncalves-Alvim and Fernandes 2001, Garcia et al. 2010). Most foliage-dwelling arthropods are not considered the ground-

dwelling spider 'prey base' (Fagan and Denno 2004). This would suggest that a ground-dwelling spider community responses are a direct effect of vegetation architectural attributes and are not indirectly affected through changes in prey availability due to change in foliage density or biomass.

Ground-dwelling prey insects are exposed to the same abiotic microhabitat conditions as ground-dwelling spiders. Consequently, the response of some arthropod functional groups to vegetation architecture manipulations may mimic responses observed within some ground-dwelling spider guilds (Geiger 1965). Given the wandering nature of many ground-dwelling arthropods, whether single shrub vegetation architectural changes impact the arthropod prey base may be varied across the functional groups. Considering the diversity of potential prey arthropods for the ground-dwelling arthropod community this study assumes an increase in arthropod abundance across different functional groups and insect Orders increases prey available to ground-dwelling spiders and other predatory arthropods.

To further separate the relative influences of habitat structure and prey availability upon the ground-dwelling arthropod community, the abundance of potential prey was altered within each architectural treatment (Hatley and MacMahon 1980, Lawton 1983, Wing 1984, Schowalter et al. 2005, Pearson 2009). The ground-dwelling arthropod community was monitored by pitfall-trapping to assess possible responses to architectural changes that address two ecological hypotheses:

H₁: Ground-dwelling arthropod Order and functional group (classification by food source) abundance, diversity and richness will not be influenced by the vegetation architecture changes to the sagebrush canopy.

H₂: Ground-dwelling arthropod abundance, diversity and richness within Order and functional group will increase in the baiting treatments.

Methods

Field experiment

Hardware Ranch, a Wildlife Management area in Cache County, Utah (41.61 N, 111.57 W) contains a continuous landscape of shrub-steppe habitat managed by the Utah Division of Wildlife Resources. At an elevation of 1,694.7 meters and mean annual precipitation of 3.6 cm, sagebrush dominates this shrub-steppe and was used for experimental manipulations of habitat structure.

Simultaneous manipulations of vegetation architecture, and prey availability in the spider community were represented using a 3 x 2 factorial design. The influence of shrub architecture on ground dwelling arthropods was addressed by manipulating 150 individual sagebrush shrubs. Experimental shrubs were chosen at random in an approximately 2 ha area of sagebrush habitat. The distance between experimental shrubs was always at least 10 m and the physical measurements of shrub height, long width axis and the perpendicular axis to it were between 0.4 and 1.0 m. Shrub architecture was varied at three levels: 1) removing 50% of the shrub canopy by cutting branches produced the 'low' foliage density treatment group, 2) tying the shrub branches and binding the entire canopy together with jute, without removing any canopy, represented

the 'high' foliage density treatment group, and 3) reference or unaltered shrubs served as controls or the 'intermediate' foliage density treatment group (Hatley and MacMahon 1980, Lawton 1983, Schowalter et al. 2005).

The second experimental factor, altering potential prey abundance, consisted of two levels: insect-attractant baited and un-baited shrubs. The bait consisted of pig offal and honey to attract a variety of arthropod groups (Wing 1984). Four bait cups were suspended in each shrub, two pig offal and two honey-filled cups, with hole punched lids. Bait was in place two weeks before arthropod sampling to allow time for detection of bait and for colonization by predators (spiders) (Ehmann and MacMahon 1996). Containers were replenished with fresh bait before each sample period to ensure similar freshness or levels of attractant. During the prey attracting experiment, the same number of empty bait containers was suspended from the un-baited shrubs to control for adding containers to the system (Robinson 1981, Wing 1984). Baited and un-baited levels of prey treatments were evenly distributed across all three levels of vegetation architecture, creating six treatment combinations.

Pitfall Trapping Methods

To sample the ground-dwelling arthropod community, two 7.4 cm diameter × 11.2 cm deep pitfall traps were installed, flush with the ground, beneath each experimental shrub. One pitfall was placed on the north side of the shrub and the other on the south to be sure that the orientation of each trap was consistent. Due to the lack of significant differences, North and South pitfall catches were later combined into one sample for each shrub. Each pitfall trap was covered with a slightly elevated wooden tile

to prevent surface litter from entering the trap and flooding while traps were active (Clayton 2001). Traps were filled to a 2 cm depth with a propylene glycol and water solution (1:1 diluted antifreeze) for a five day sampling period once a month in June, July, and August of 2007 and 2008. Arthropods caught in pitfall traps were sorted to Order and counted. Insect Orders represented in pitfall traps included Archaeognatha, Dermaptera, Orthoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera and Hymenoptera, in addition to non-insect arthropod members of the subclasses Acarina and Collembola.

All arthropods were identified to the taxonomic level necessary to sort them into functional feeding groups (classified by food type) (Bland 1978). Herbivores consisted of Orthoptera, Hemiptera, and the Coleoptera families: Chrysomelidae, Curculonidae, Cerambycidae and Elateridae. Acarina, mites, were the predominant members of the Predator feeding group along with Coleoptera families: Cantharidae, Carabidae and Coccinellidae. The vast majority of the Omnivores were comprised of Hymenoptera, more specifically Formicidae (ants), with far fewer Dermaptera and Diptera. The Detritivore feeding group included beetle families: Scarabaeidae and Tenebrionidae, but was mostly represented by subclass Collembola and Order Archaeognatha (Appendix 3).

Quantifying prey availability

The prey availability treatment was quantified based on the non-spider arthropods captured in pitfall traps beneath experimental shrubs. The arthropod community diversity and abundance was calculated to confirm an increase in prey availability for ground-dwelling spiders under baited shrubs compared to un-baited shrubs.

Quantifying shrub foliage density

Foliage density and shrub volume were quantified based on physical measurements of height, width and length for each shrub and digital photographs taken before and after architecture treatments were implemented in June of 2007. Each photograph was taken 1.5m distant from each shrub with a portable white backdrop behind the shrub. A black and white image of each photograph was created using Photoshop 7.0 (Adobe Systems Incorporated, San Jose, California, USA). Shadows that interfered with the contrast of the shrub canopy against the white background were removed using the 'select color range' option and 'eyedropper' tool. Using the magnetic lasso tool with the 'threshold' option, the shrub canopy was selected. Next, the 'histogram' option was used to find the percentage of black (vs. white) pixels within the selected area to quantify foliage density. To obtain the area of foliage cover, the same photo manipulations were conducted but instead of using the magnetic lasso around the shrub canopy, the lasso was used to select the entire photo area. This area of foliage metric provides a measure of cover or shade cast on the ground by the three different shrub architecture forms. The measured area of cover as well as the amount of cover within the canopy area should suggest potential differences in quality of shade experienced by ground-dwelling arthropods under each architecture type.

Statistical analyses

To test for effects of vegetation architecture, prey availability, vegetation architecture \times prey availability and sample date on the ground-dwelling arthropod community, permutational multivariate analyses of variance (MANOVA) were

performed using the Adonis function in the Vegan package in Program R (Anderson 2001, McArdle and Anderson 2001, Oksanen et al. 2008). The MANOVA analyses included two forms of community level data: a presence/absence matrix describing community composition and a matrix incorporating abundance of arthropod Orders and functional groups describing community structure. Using the Bray-Curtis index, distance matrices were created and 1,000 permutations of the raw data creating F -tests used to give P -values. The MANOVA was conducted for each sample month separately as well as across samples to ensure there were no false significances due to permutation constraints when combining sample periods in the Adonis function. The MANOVA only denoted community differences among experimental treatments, not the direction of any differences in community measures of diversity and abundance.

To determine the direction of differences in common community measures due to experimental treatments, arthropod Order and functional group data were used to produce three diversity metrics: the Shannon-Weiner diversity index based on richness and evenness of functional groups and Order diversity. Sample date explained the greatest amount of the data. As a result each sample date was analyzed separately for all diversity metrics. To analyze each month separately, a two-factor ANOVA was conducted using Program R to test for any fixed effects of vegetation architecture treatments, prey availability treatments and the architecture \times prey treatment interaction. Functional group analyses were conducted for each of the four feeding groups, using the two-factor ANOVA model. The relationship between vegetation architecture and ground-dwelling arthropods was further examined by conducting repeated ANOVAs across all treatment

groups to detect differences in Order and functional group diversity and overall arthropod abundance. Response variables were square root transformed to meet the assumption of normality when required. *P* values less than 0.05 were considered statistically significant.

Results

Shrub foliage density

Cut shrubs had the lowest canopy density with a mean of 50.95% black pixels within the shrub canopy. Reference shrubs had 66.59% mean of black pixels and tied had 82.04% mean. Tied shrubs had the highest canopy density but covered the least amount of area in the total photo space with 17.31% black pixels followed by cut with 26.37% and reference with 27.64% (average t-statistic = -14.347, *P* <0.001).

Effects of vegetation architecture on ground-dwelling arthropod Orders and functional groups

A single shrub manipulation of vegetation architecture had a significant effect upon arthropod community composition and structure at the functional group level (Table 2.2). At the Order level, vegetation architecture significantly affected arthropod community structure but not composition.

Univariate analysis of community measures across all sample dates only showed significant effects of vegetation architecture in August of 2007 for functional group diversity, functional richness and for Order diversity (Table 2.3). Of the four arthropod functional groups, only the Predators significantly responded to vegetation architecture treatments (Table 2.4 a). Significantly fewer arthropods within the Predator functional

group were found in low density shrubs compared to both reference and high density shrubs in July and August of 2007. Of the eight arthropod Orders only Hymenoptera, mostly ants, were significantly influenced by vegetation architecture in June of 2007. More ants were captured beneath low density shrubs compared to reference and high density shrubs (Table 2.4 b).

Effects of prey availability on ground-dwelling insect Orders and functional groups

Single shrub prey availability treatments significantly altered arthropod community composition at the insect Order level but not at the functional group level. Insect community structure was significantly affected by prey treatment at both the arthropod Order and functional level (Table 2.2).

Univariate analysis of arthropod abundance, functional diversity, functional richness, Order diversity and Order richness results across all sample dates revealed that prey availability significantly affected all of these measures except functional richness and diversity (Table 2.3). Baited shrubs had significantly higher arthropod Order and functional group diversity, richness and abundance values (Table 2.3).

Prey availability treatments most significantly affected the Predator functional group (Table 2.4 a). Within reference shrubs, significantly more Predators were captured beneath baited shrubs than un-baited shrubs. Of the eight arthropod Orders Coleoptera, Archaeognatha and Acarina were all significantly increased in the baited treatment group (Table 2.4 b). Overall arthropod abundance was increased by 26 % beneath baited shrubs compared to un-baited shrubs ($F = 3.917$, $P = 0.008$).

Interactive effects of prey availability on ground-dwelling arthropod Orders and functional groups

Community structure results showed a significant interaction of baiting treatments and vegetation architecture both at the arthropod functional group and Order level (Table 2.2). Univariate analysis of community measures of arthropod abundance, functional diversity, functional richness, Order diversity and Order richness results, across all sample dates, showed no significant interactive effects of prey availability and vegetation architecture treatments with the exception of August 2008 for arthropod abundance alone (Table 2.3). In both sample months arthropod abundance was significantly greater beneath baited shrubs within the low foliage density architecture treatments.

Of the four arthropod functional feeding groups Predators and Detritivores were significantly influenced by the prey availability x vegetation architecture interaction (Table 2.4 a). Within baited shrubs, Predator abundance was significantly less beneath low density shrubs compared to high density and reference shrubs. Detritivore abundance was significantly greater beneath reference than low and high density shrubs within the baited treatment group. Of the eight arthropod Orders, Archaeognatha, Collembola (subclass Entognatha) and Acarina (subclass Arachnidae) responded to a prey availability x vegetation architecture interactive effect (Table 2.4 b). Only Acarina and Archaeognatha responded to shrub architecture, with reference and baited shrubs having higher abundances over un-baited, low or high density shrubs.

Discussion

This study evaluated how changes in vegetation architecture and prey availability alter the ground-dwelling arthropod community organization. I first predicted that beneath a single experimental shrub, ground-dwelling arthropod abundance, diversity and richness at the Order and functional level would not be influenced by changes to vegetation architecture within the sagebrush shrub canopy given the presumed lack of change to the ground-surface litter. However, changes to vegetation architecture did influence two specific groups within ground-dwelling arthropod community – Predators (consisting primarily of mites) and some Detritivores (specifically Archaeognatha). Both affected groups are found almost exclusively in leaf-litter, which suggests that the decrease in their numbers is a result of decrease in leaf-litter under low foliage density treatments where 50% of the canopy had been removed. Vegetation architecture change significantly altered both community composition and structure at the arthropod functional group level. Community structure was altered by vegetation architecture manipulations at the arthropod Order level (Table 2.2). The significant results for the influence of vegetation architecture on the non-spider ground-dwelling arthropods may also be explained by an anomaly in the single sample month out of the six sample months where the single shrub spatial context was addressed. Community measures of functional diversity, richness and Order diversity were only significantly impacted in August 2007 (Table 2.3) and it is unclear as to why this sample month was the exception. However, none of the eight arthropod Orders responded to changes in vegetation architecture with the exclusion of Acarina (mites) and Archaeognatha (bristletails) (Table 2.4 b). Predators,

primarily consisting of mites, were the only arthropod functional group to respond to changes in vegetation architecture (Table 2.4 a). Mites, although potential arthropod prey for the ground-dwelling spiders, are likely to be responding to changes in abiotic ground surface variables much like their spider predators and not shifts in foliage density or biomass from architecture manipulation. The same explanation holds for the bristletails in this study as they are found in the leaf-litter and are responding only to the high-foliage density treatments and likely its decrease in canopy cover on the ground not a reduction in biomass in the low-foliage density treatments. Thus, both the mite and bristletail responses to vegetation architecture change do not support the concept of an indirect effect of change in arthropod prey base resulting from change in shrub foliage density or biomass.

My second hypothesis stating that ground-dwelling arthropod abundances within Order and functional groups as well as diversity and richness will be increased by the arthropod baiting treatments was largely supported. Although an interactive vegetation architecture x prey availability effect was present, prey treatments had a significant impact on community structure both at the arthropod functional group and Order level as well as community composition at the Order level (Table 2.2). Prey availability treatments were also responsible for the vast majority of the significant effects on community measures of functional diversity, richness and Order diversity and richness (Table 2.3). This suggests that the ground-dwelling arthropod community's response in this experiment is principally governed by the prey treatments in the study rather than changes in the shrub canopy architecture.

Three of the eight arthropod groups: (Coleoptera, Archaeognatha and subclass: Acarina) that are considered potential ground-dwelling spider prey had significantly higher abundances beneath baited experimental shrubs. Again, the ground-dwelling arthropod community general responses to changes in prey availability and not vegetation architecture support the concept that changes in foliage density or biomass are not governing arthropod prey abundances on the ground. Therefore, any ground-dwelling spider community response to vegetation architecture change described in the next chapter is likely a direct effect of the architecture itself and not a change in prey base (Chapter 3).

After analyzing the ground-dwelling arthropod community responses to simultaneous manipulation of vegetation architecture and prey availability, the overall impact of change in biomass or foliage density does not directly impact arthropod abundance, diversity or richness. This is not usually the case for shrub or foliage-dwelling arthropod communities whose food is associated with the plant biomass of the vegetation architecture they live in. Generally, an increase or decrease in plant biomass results in a corresponding increase or decrease in the associated arthropod community's abundance (Lawton 1983, Gardner et al. 1995, Johnston and Holberton 2009, Siira-Pietikainen and Haimi 2009). Instead, the ground-dwelling arthropod response to changes in the above canopy architecture is probably due to abiotic variables on the ground and possible interactions with the arthropod baiting treatments.

Although some interactive effects of vegetation architecture and prey availability impacted the captured arthropod community, most members of the ground-dwelling

community considered to be part of the spider prey base, were weakly influenced by changes in the above shrub canopy architecture. This supports the claim that vegetation architecture directly influences the ground-dwelling spider community (Chapter 3). Both the ground-dwelling spider and arthropod community responses to vegetation architecture manipulations in this sage-steppe ecosystem support the concept that shrub canopy changes influence the ground-dwelling community organization as well as the importance of considering spatial context. This concept may also demonstrate its importance in studies that aim to use spiders and other arthropods as indicators for ecological change when assessing impacts of habitat management strategies.

Table 2.1. Standard deviation, standard error of mean and mean percent of black pixels in the shrub canopy portion of each experimental shrub photo for the effects of shrub architectural treatments.

Shrub Treatment	Std Dev (px)	S.E.M. (px)	Mean %	
			black pixels in canopy	black pixels in photo area
CUT = low density	6.341	0.978	50.954	17.310
REFERENCE	5.348	0.806	66.589	27.645
TIED = high density	3.749	0.696	82.042	26.371

Comparison	df	t statistic	<i>P</i>
CUT vs REFERENCE	84	-12.382	<0.001***
CUT vs TIED	84	-16.531	<0.001***
TIED vs REFERENCE	84	-13.511	<0.001***

Table 2.2. *F* and *P*-values from MANOVA analysis of vegetation architectural and baiting treatments upon arthropod community composition (based on presence/absence) and community structure (incorporating abundance) at the arthropod functional group and Order levels.

Community Level	Treatment	Community Composition		Community Structure	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Functional	Architecture	2.519	0.040	3.667	0.005
	Prey	1.270	0.267	4.859	0.011
	ArchitecturexPrey	0.278	0.851	2.899	0.023
Order	Architecture	1.557	0.149	4.285	0.019
	Prey	5.756	0.009	4.595	0.019
	ArchitecturexPrey	0.943	0.416	2.905	0.009

Table 2.3. Degrees of freedom, *F*-statistics and *P*-values from ANOVAs for statistically significant effects of vegetation architectural and baiting treatments on arthropod abundance, Order diversity and richness; as well as functional diversity and richness. Values were reported only when $P < 0.05$.

Dependent Variable	Treatment	df	<i>F</i>	<i>P</i>	Date
Abundance	Prey Baiting	1	4.817	0.029	July-08
	ArchitecturexPrey	2	7.081	<0.001	August-08
Functional Diversity	Architecture	2	0.263	0.006	August-07
Functional Richness	Architecture	2	3.213	0.042	August-07
Order Diversity	Prey Baiting	1		0.001	August-08
	Architecture	2	3.141	0.045	August-07
Order Richness	Prey Baiting	1	8.778	0.003	August-08

Table 2.4. Degrees of freedom, *F*-statistics and *P*-values from ANOVAs for effects of vegetation architectural and baiting treatments and interactions on arthropod abundance within **a**: functional groups and **b**: arthropod Orders.

a	Shrub Architecture			Prey Baiting			Architecture x Prey		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Herbivores	2	1.658	0.191	1	1.350	0.246	2	0.752	0.472
Predators	2	11.071	<0.001	1	6.939	0.009	2	9.122	<0.001
Omnivores	2	1.805	0.165	1	0.915	0.339	2	1.045	0.352
Detritivores	2	1.090	0.337	1	3.351	0.068	2	8.788	<0.001

b	Shrub Architecture			Prey Baiting			Architecture x Prey		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Coleoptera	2	1.028	0.358	1	56.328	<0.001	2	0.591	0.554
Orthoptera	2	3.190	0.061	1	0.962	0.322	2	2.098	0.123
Hymenoptera	2	0.541	0.582	1	0.001	0.972	2	0.127	0.881
Hemiptera	2	0.256	0.774	1	1.626	0.201	2	1.167	0.311
Diptera	2	0.051	0.950	1	0.148	0.701	2	3.239	0.059
Acarina	2	9.219	<0.001	1	5.107	0.024	2	8.217	<0.001
Collembola	2	1.939	0.144	1	2.111	0.146	2	8.666	<0.001
Archaeognatha	2	14.18	<0.001	1	25.52	<0.001	2	9.685	<0.001

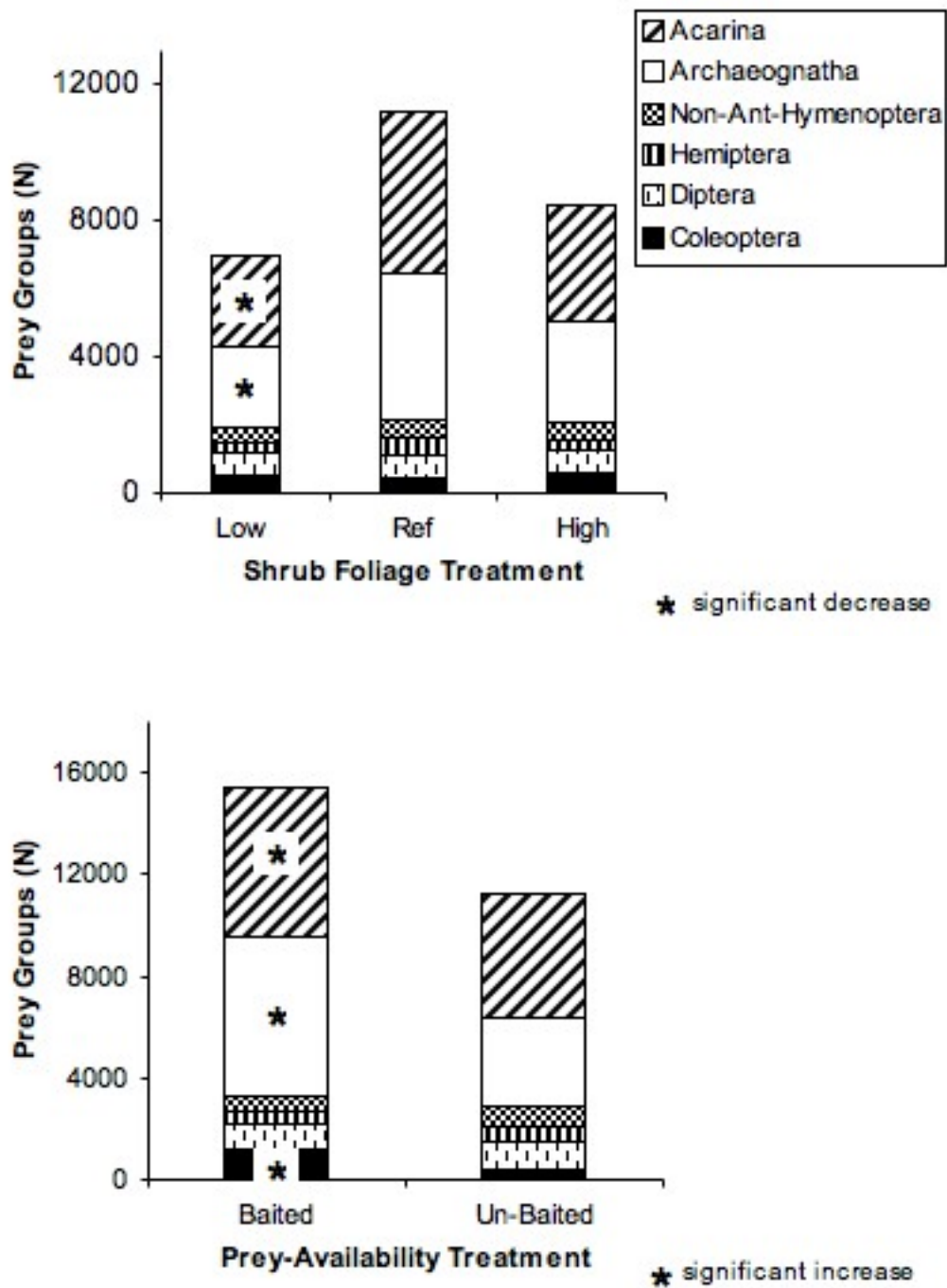
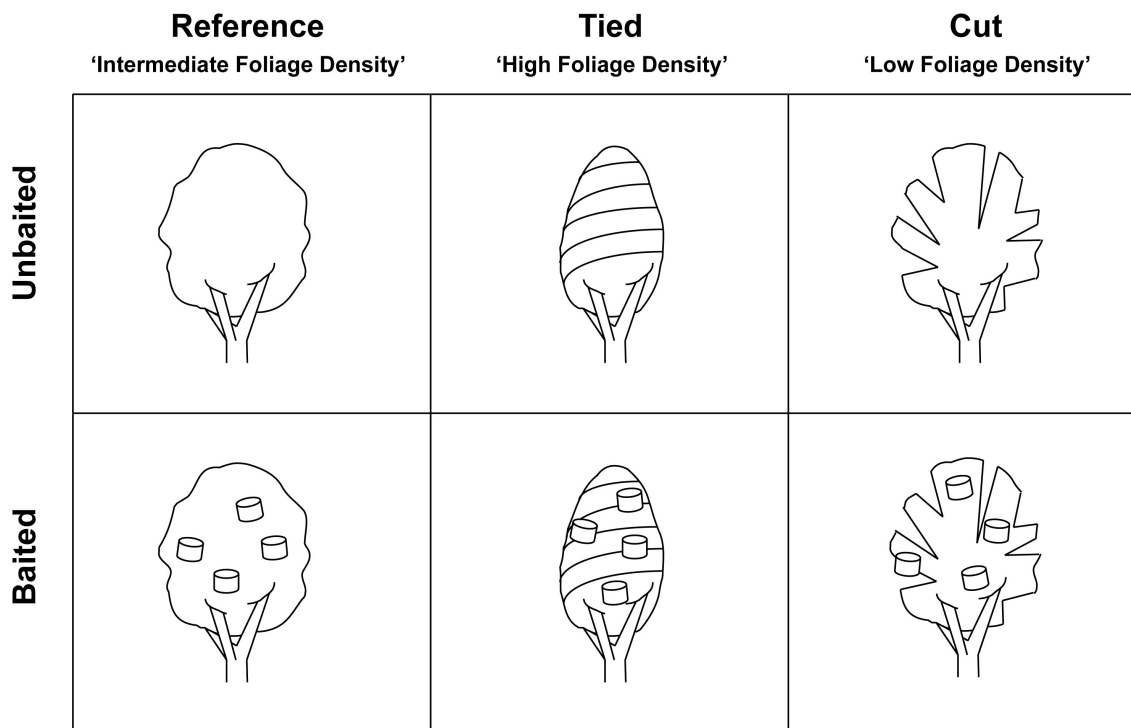


Figure 2.1. Arthropod relative abundances compared across vegetation architecture and prey baiting treatments.

Single Shrub Context (June/July/August 2007, 2008)



Appendix 1. Experimental design for single shrub vegetation architecture and prey availability manipulations of sagebrush.

Reference**Cut****Tied****Baited**

Appendix 2. Experimental shrub photos of three levels of vegetation architecture and a baited shrub.

Appendix 3. Insect Order and family composition of 5 functional feeding groups (defined by food source) collected from pitfall traps in the sage-steppe ecosystem of Hardware Ranch of Cache County, Utah.

Functional Group (food source)	Order	Family (when needed for functional classification)
HERBIVORE	Coleoptera	Cerambycidae
		Chrysomelidae
		Curculionidae
		Elateridae
	Hemiptera	Aphidae
		Cicadellidae
		Coreidae
		Fulgoridae
		Lygaeidae
		Membracidae
		Pentatomidae
		Rhopalidae
		Thyrecoridae
Tingidae		
Lepidoptera		
Orthoptera		
PREDATOR	*Acarina (subclass of Arachnidae)	
	Coleoptera	Cantharidae
		Cleridae
		Coccinellidae
	Hymenoptera	Chalcidoidea
		Pompiliidae
Sceliphronidae		
OMNIVORE	Dermaptera	
	Diptera	Bibionidae
		Chironomidae
	Hymenoptera	Formicidae
DETRITIVORE	Archaeognatha	
	Coleoptera	Scarabaeidae
		Tenebrionidae
	*Collembola	(subclass of Entognatha)
PARASITOID	Hymenoptera	Vespidae

* subclass

CHAPTER 3

SPIDER COMMUNITY INFLUENCES OF HABITAT STRUCTURE AND PREY
AVAILABILITY: AN EXPERIMENTAL STUDY IN A SHRUB-STEPPE
ECOSYSTEM

Abstract

Vegetation architecture plays a central role in determining shrub-dwelling spider community organization. This concept, however, is less thoroughly investigated for ground-dwelling spider communities nor in different spatial contexts. Whether spider communities are directly altered by architecture change or indirectly influenced through a shift in prey base is also undefined for shrub-steppe communities. To determine shrub architecture effects on the spider community, levels of vegetation architecture (low, intermediate and high foliage density) and prey availability (baited and un-baited) were simultaneously varied on big sagebrush (*Artemisia tridentata*) within a shrub-steppe ecosystem. The ground-dwelling spider community response to treatments was determined from abundance and diversity values calculated from spiders collected in pitfall traps. Experimental shrub results showed vegetation architecture strongly influenced the spider community richness and evenness at the guild and species levels while prey availability had no effect on the spider community. These results suggest that the ground-dwelling spider community is directly influenced by vegetation architecture changes to a single shrub.

Introduction

Habitat structure plays a central role in determining species presence within ecological communities through microhabitat variables, such as light, moisture and temperature. These microhabitat variables directly influence the presence and abundance of some species within a community (Smith 1972, Crowley 1978, Crowder and Cooper 1982). Thus, direct mechanisms underlying species community organization and structure may be determined through alteration of vegetation architecture (Holt 1984, Wing 1984, Ehmann and MacMahon 1996, de Souza and Martins 2005, Loeser et al. 2006, Sackett et al. 2008, Bridle et al. 2009, De Mas et al. 2009, Petillon et al. 2010).

Spiders are potential indicators of shifts in ecosystem processes resulting from vegetation architecture change (Churchill 1997, Cardoso et al. 2008, Cristofoli et al. 2010) as they are common, taxonomically diverse and play major ecological roles (Wise 1993). These top predators are classified into specialized feeding guilds that directly and indirectly impact other arthropods (Fagan and Hurd 1991, Wise 1993, Lawrence and Wise 2004, Shultz et al. 2006, Sanders et al. 2008, Schmitz 2009), making them an integral part of the ground-dwelling community (Chen and Wise 1999, Wise et al. 1999, Wise 2004, Schmitz 2009). Species-rich spider communities influence prey arthropod abundance and indirectly impact ecosystem processes by stimulating or depressing abundances within insect functional groups, such as detritivores and subsequently altering decomposition rates (Kajak 1995, Lawrence and Wise 2004, Wise 2004, Lensing and Wise 2006, Chatterjee et al. 2009, Gontijo et al. 2010). Likewise, spider communities

are constrained by the population densities of their prey (Chen and Wise 1999, Wise et al. 1999, Marko et al. 2009).

Due to the differences in mobility across feeding guilds, ground-dwelling spiders occupy a wide variety of microhabitats at several spatial scales (Denno et al. 2004, Langellotto and Denno 2004, Mallis and Hurd 2005). Changes in habitat structure, such as above ground vegetation architecture or ground surface litter, alter the microhabitats in which the ground-dwelling spiders reside (Bultman and Dewitt 2008). Consequently, spiders are effective responders to abiotic variables that are tied to overall habitat quality at many spatial scales and contexts (Cardoso et al. 2008, Kapoor 2008, Smith et al. 2008, Maleque et al. 2009, Uetz et al. 2009).

Natural variation, experimental manipulation and artificial models of vegetation architecture significantly impact shrub-dwelling spider community composition (presence and absence of species or guilds) and structure (abundances within species or guilds) (Wing 1984, Ehmann and MacMahon 1996, Halaj et al. 2000, Heikkinen and MacMahon 2004, Corcuera et al. 2008). However, the potential direct and indirect mechanisms that link vegetation architecture to ground-dwelling spider community organization have not been determined. Recent studies have looked at how the vegetation architecture influences forest leaf-litter habitats (Halaj et al. 1998, Wise 2004, Uetz et al. 2009). Whether changes in above ground vegetation architecture and prey availability affect the shrub-steppe ground-dwelling spider community is unknown (Enders 1975, Halaj et al. 2000, Galle 2008, Halaj et al. 2008, Pinto-Leite et al. 2008, Schuldt et al. 2008). Specifically, the ground-dwelling spider community may be directly

affected by architectural change, or architectural change may alter the associated insect prey, thus indirectly affecting the spider community.

To determine the direct and indirect influences of vegetation architecture upon the spider community, simultaneous manipulation of both architecture and prey availability is necessary. An ecological community that rapidly responds to experimental changes in prey base and habitat structure is required to observe the relative impacts of each factor. In shrub-steppe ecosystems dominated by *Artemisia tridentata*, hereafter, big sagebrush, vegetation architecture can be altered to create varying levels of architecture and prey availability. The ground-dwelling arthropod response can be monitored to assess the community-level impacts of architectural and prey availability.

To separate the influences of habitat structure and prey availability upon ground-dwelling spider community composition, shrub-steppe habitat structure was altered by manipulating sagebrush architecture while simultaneously amending prey availability (Hatley and MacMahon 1980, Lawton 1983, Wing 1984, Schowalter et al. 2005, Pearson 2009). When evaluated in a natural shrub-steppe habitat, these experimental manipulations allow us to address two ecological hypotheses. First, changes in sagebrush architecture directly affect ground-dwelling spider community organization. Second, changes in prey availability within sagebrush canopies will not impact ground-dwelling spider community organization given their ground-based hunting strategies.

Methods

Field experiment

Hardware Ranch, a Wildlife Management area in Cache County, Utah (41.61 N, 111.57 W) contains a continuous landscape of shrub-steppe habitat managed by the Utah Division of Wildlife Resources. At an elevation of 1,694.7 meters and mean annual precipitation of 3.6 cm, sagebrush dominates this shrub-steppe and was used for experimental manipulations of habitat structure.

Simultaneous manipulations of vegetation architecture and prey availability in the spider community were represented in a 3 x 2 factorial design. The influence of shrub architecture on ground dwelling spiders was addressed by manipulating 150 individual sagebrush shrubs. Experimental shrubs were chosen at random in an approximately 2 ha area of homogeneous sagebrush habitat. The distance between experimental shrubs was always at least 10 m and the physical measurements of shrub height, the long width axis and the perpendicular axis to it were between 0.4 and 1.0 m. Shrub architecture was varied at three levels: 1) removing 50% of the shrub canopy by cutting branches produced the 'low' foliage density treatment, 2) tying the shrub branches and binding the entire canopy together with jute, without removing any canopy, represented the 'high' foliage density treatment, and 3) reference or unaltered shrubs served as controls or the 'intermediate' foliage density treatment (Hatley and MacMahon 1980, Lawton 1983, Schowalter et al. 2005).

The second experimental factor, altering potential prey abundance, consisted of two levels: insect-attractant baited and un-baited shrubs. The bait consisted of pig offal

and honey in Order to attract a variety of insect groups (Wing 1984). Two plastic cups with holes in the lids containing pig offal and two with honey were suspended uniformly in each experimental shrub canopy. Bait was in place two weeks before arthropod sampling to allow time for insects to detect the bait and for colonization by the predators (spiders) (Ehmann and MacMahon 1996). Containers were replenished with fresh bait before each sample period to ensure similar freshness or levels of attractant. The same number of empty bait containers was suspended in un-baited shrubs to control for adding containers to the system (Robinson 1981, Wing 1984). Baited and un-baited levels of prey treatments were evenly distributed across all three levels of vegetation architecture, creating six treatment combinations (Appendix 1) to augment a possible loss in prey available when tying shrubs or removing foliage from the shrub canopy. All baiting and architecture shrub treatment combinations were randomly distributed across the shrub-steppe landscape.

Pitfall trapping methods

To sample the ground-dwelling arthropod community, two 7.4 cm diameter × 11.2 cm deep pitfall traps were installed, flush with the ground, beneath each single shrub. One pitfall trap was placed on the north side of the shrub and the other on the south to be sure that the trap orientation was consistent. Due to the lack of significant differences, north and south pitfall catches were later combined into one sample for each shrub. Each pitfall trap was covered with a slightly elevated wooden tile to prevent surface litter from entering the trap or flooding while traps were active (Clayton 2001). Traps were filled to a 2 cm depth with a propylene glycol and water solution (1:1 diluted

antifreeze) for a five-day sampling period once a month in June, July, and August of 2007 and 2008. Arthropods caught in pitfall traps were sorted to Order and counted. Spiders were identified to species and classified into one of four feeding guilds based on similarities in hunting strategies: Ambushers, Diurnal Wanderers, Nocturnal Wanderers and Trappers (sensu Abraham 1980). Ambushers included members of the families Thomisidae, Philodromidae and Mimetidae as they are sit-and-wait predators. Lycosidae, Salticidae, and Oxyopidae, which have good vision and are active runners during the day, were included in the Diurnal Wanderer guild. Nocturnal Wanderers consisted of the families Clubionidae, Gnaphosidae and Anyphaenidae. These spiders are active runners who hunt at night and retreat under foliage and litter during the day. The families Theridiidae, Dictynidae, Agelenidae, Amaurobiidae, Linyphiidae, Tetragnathidae and Araneidae were all considered Trappers, as they are all web-building spiders. Immature spiders were only included in the study if species and gender were identifiable.

Quantifying prey availability

Prey availability was quantified based on the non-spider arthropods captured in pitfall traps beneath experimental shrubs. Insect community diversity and abundance was calculated to confirm an increase in potential prey availability for ground-dwelling spiders under baited shrubs compared to un-baited shrubs. Given that insect abundance and diversity are not the only measures of prey availability, further investigation into the insect community response to both prey availability and vegetation architecture treatments was warranted (see Chapter 2). Given the diversity of potential prey

arthropods for the ground-dwelling spider community this study assumes an increase in arthropod abundance across different functional groups and insect Orders increases prey available to ground-dwelling spiders and other predatory arthropods.

Quantifying shrub foliage density

Foliage density and shrub volume were quantified based on physical measurements of height, width and length for each shrub and digital photographs taken before and after architecture treatments were implemented in June of 2007. Each photograph was taken 1.5m distant from each shrub with a portable white backdrop behind the shrub. A black and white image of each photograph was created using Photoshop 7.0 (Adobe Systems Incorporated, San Jose, California, USA). Shadows that interfered with the contrast of the shrub canopy against the white background were removed using the 'select color range' option and 'eyedropper' tool. Using the magnetic lasso tool with the 'threshold' option, the shrub canopy was selected. Next, the 'histogram' option was used to find the percentage of black (vs. white) pixels within the selected area to quantify foliage density. To obtain the area of foliage cover, the same photo manipulations were conducted but instead of using the magnetic lasso around the shrub canopy, the lasso was used to select the entire photo area. This area of foliage metric provides a measure of cover or shade experienced by ground-dwelling spiders.

Statistical analyses

To test for effects of vegetation architecture, prey availability, vegetation architecture \times prey availability and sample date on the ground-dwelling spider

community, permutational multivariate analyses of variance (MANOVA) were performed using the Adonis function in the vegan package in Program R (Anderson 2001, McArdle and Anderson 2001, Oksanen et al. 2008). MANOVA analyses included two forms of community level data: a presence/absence matrix describing community composition and a matrix incorporating abundance of spider species and guilds describing community structure. Using the Bray-Curtis index, distance matrices were created and 1,000 permutations of the raw data creating *F*-tests used to give *P*-values. The MANOVA was conducted for each sample month separately, as well as across samples using mean relative abundances, to ensure there were no false significances due to permutation constraints when combining sample periods in the Adonis function. The MANOVA only denoted community differences among experimental treatments, not the direction (i.e. increase or decrease) of any differences in community measures of diversity and abundance.

To determine the direction of differences in community measures due to experimental treatments, spider species and guild data were used to produce diversity metrics: the Shannon-Wiener diversity index based on richness and evenness of spider guilds (referred to as “guild diversity”) and species diversity. Sample date explained the most variance in the data in a series of ANOVAs. As a result each sample date was analyzed separately for all diversity metrics. To analyze each month in each year separately, a two-factor ANOVA was conducted using Program R to test for any fixed effects of vegetation architecture treatments, prey availability treatments and the architecture \times prey treatment interaction. Spider guild analyses were conducted for each

of the four feeding guilds, using the two-factor ANOVA model (Table 2.3). I further examined the relationship between vegetation architecture and ground-dwelling spiders by conducting repeated ANOVAs across all treatment groups to detect differences in species and guild diversity, richness, evenness and overall spider abundance. Response variables were square root transformed to meet the assumption of normality when required. *P* values less than 0.05 were considered statistically significant.

Results

7, 618 individual spiders were identified, representing 38 species, 14 families and four guilds (Appendix 4). Insect Orders represented in pitfall traps included Collembola, Archaeognatha, Dermaptera, Orthoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera and Hymenoptera, in addition to non-insect arthropod members of the subclass Acarina (see Chapter 2). These arthropod groups are all potential prey items for ground-dwelling spiders (Nyffeler 1999).

Shrub foliage density

Each of the vegetation architecture treatment groups had significantly different percentages of black pixels in the photographed canopy based on simple paired T-tests (see Chapter 2).

Effects of vegetation architecture and prey availability treatments

Multivariate analyses of shrub architecture demonstrated that changes to a single shrub altered the associated ground-dwelling spider community composition (determined

using a presence/absence matrix) and structure (determined using an abundance matrix) at species level (Table 3.1). Community structure and evenness were also altered at the species level. These results were consistent across individual and pooled sample months.

Univariate results for 2007 revealed that ground-dwelling spiders had lower abundance in June and lower species diversity in August within high foliage density treatments. In 2008, high foliage density treatments also yielded consistently lower spider abundance and richness in both June and August (Figure 3.2). At the guild level, high foliage density shrubs had consistently lower spider diversity and richness in August of both 2007 and 2008. High foliage density shrubs also had significantly lower abundances within guilds in June 2007. Diurnal Wandering and Trapper guilds had significantly lower abundances in the high foliage density shrub treatment group (Table 3.3). There were no significant interactions for shrub architecture and prey availability across all analyses. Low and reference foliage density architecture treatments were not statistically significantly different from each other for ground-dwelling spider diversity or richness at the guild or species levels. No significant influences of the prey availability treatment were detected in the single shrub manipulations. This was consistent at the spider species and guild level (Table 3.1).

Table 3.1. *F* and *P*-values from MANOVA analysis of the effects of vegetation architecture manipulations on ground-dwelling spider community composition (based on presence/absence) and community structure (incorporating abundance) of guilds and species.

Community Level	Treatment	Community Composition		Community Structure	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Guild	Architecture	2.507	0.039	2.038	0.121
	Prey	0.837	0.453	0.169	0.691
	Arch x Prey	1.46	0.218	0.933	0.341
Species	Architecture	34.419	<0.001	22.02	<0.001
	Prey	2.437	0.098	1.021	0.303
	Arch x Prey	1.953	0.13	0.212	0.643

Table 3.2. Degrees of freedom, *F*-statistics and *P*-values for statistically significant ANOVA results of vegetation architectural and prey availability treatments on spider abundance, species diversity and guild diversity. Values were reported only when $P < 0.05$.

Dependent Variable	Treatment	df	<i>F</i>	<i>P</i>	Date
Guild Diversity	Architecture	2	3.968	0.021	August-07
	Architecture	2	3.555	0.031	August-08
Spider Abundance	Architecture	2	3.881	0.023	June-07
	Architecture	2	4.929	0.009	June-08
Species Diversity	Architecture	2	4.117	0.018	August-07
	Architecture	2	4.294	0.016	June-08

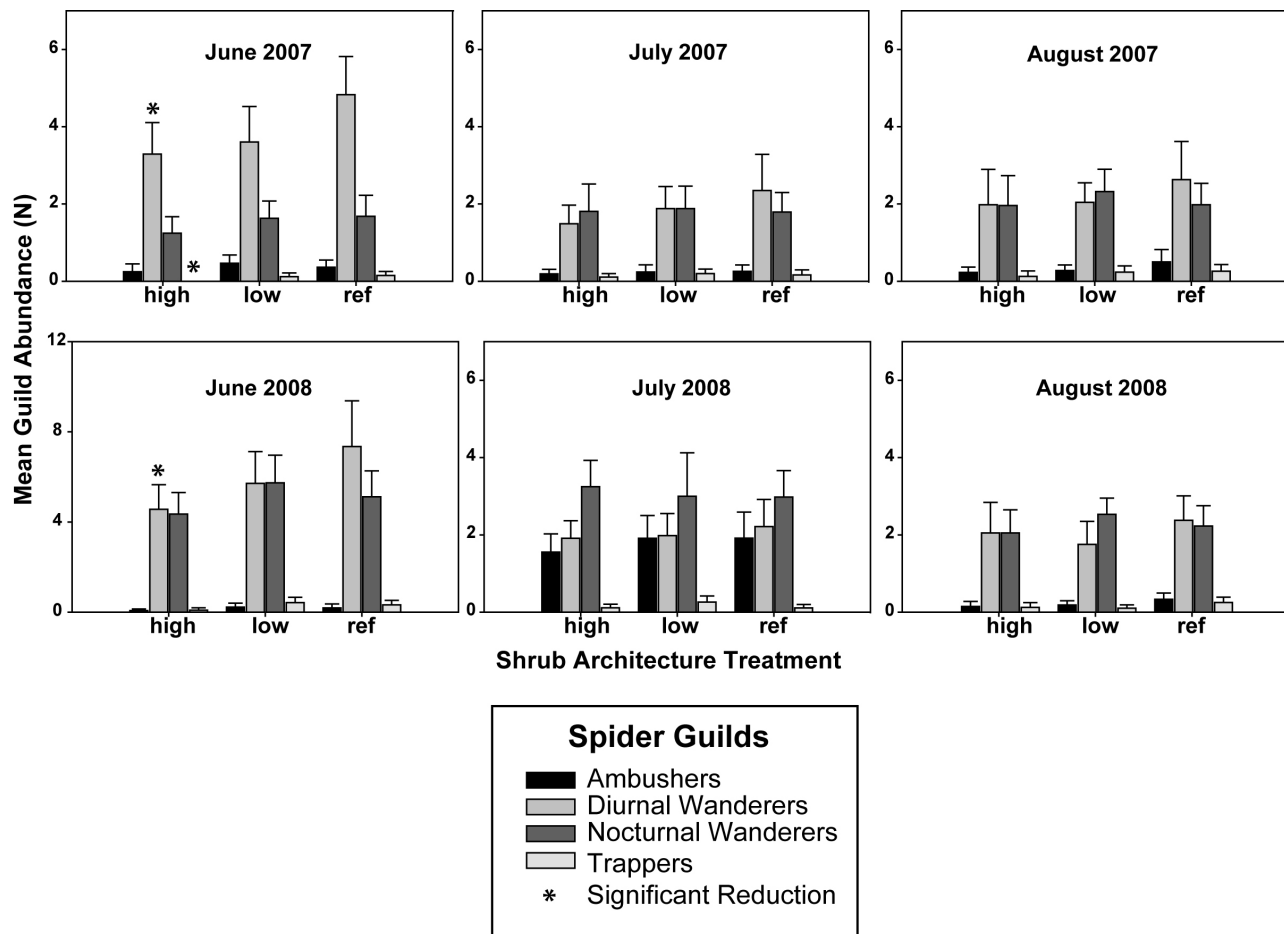


Figure 3.1. Mean Guild abundance compared across vegetation architectural treatments for each sample date. Error bars represent 1 SE.

Table 3.3. Results from ANOVA (degrees of freedom, *F*-statistics and *P*-values) for statistically significant effects of vegetation architectural and prey availability treatments on abundance in each spider guild. Values were only reported when $P < 0.05$.

Guild Abundance	Architecture Treatment	df	<i>F</i>	<i>P</i>	Date
Diurnal Wanderers	High density	2	3.448	0.039	June-07
	High density	2	3.562	0.032	June-08
Trappers	High density	2	3.599	0.029	June-07
	High density	2	3.708	0.024	June-08

Discussion

Altering vegetation architecture and prey availability produced two consistent patterns in ground-dwelling spider community organization. First, shrub architecture primarily influenced ground-dwelling spider community composition and structure with single shrub manipulations. Second, prey availability had no detectable impact on ground-dwelling spider community composition and structure within single shrub manipulations. The ground-dwelling spider response to single shrub architectural manipulation and not to prey base manipulation indicates a direct effect of vegetation architecture on the community, supporting the second hypothesis that, prey availability changes in the shrub canopy will not impact the ground-dwelling spider community.

Tied experimental shrubs with increased foliage density resulted in a compression of the shrub canopy and a decrease in canopy cover area on the ground. These shrubs had significantly reduced spider abundance and diversity at the species and guild levels. The Diurnal Wanderer guild population was also significantly reduced in the high foliage

density architectural treatments (Table 3.3). Since Diurnal Wanderers are active during the day they are subject to higher temperatures and increased vapor pressure deficit on the ground compared to members of other guilds who are nocturnal or less mobile during the day (Huey 1991, Schmitz et al. 1997, Joern et al. 2006). It follows that fewer Diurnal Wanders would be captured under tied or high foliage density shrubs, given the high foliage density architecture treatments have a decreased area of foliage cover, resulting in a decrease in area of shade and potentially higher surrounding ground temperature. Thus, shrub architecture with greater area of canopy cover, creating cooler and more humid microhabitat conditions, may support more Diurnal Wanderers.

Trapper guild abundance was also significantly lower in the high foliage density treatments compared to the reference and low foliage density treatments. Trappers collected within this study, primarily scattered-line weavers, depend upon the construction of various webs within leaf-litter to ensnare prey items (Turnbull 1973). Thus, Trappers are likely subject to the similar ground surface microhabitat requirements as the Diurnal Wanderers and share the same need for increased canopy cover, which is not afforded by the high foliage density architecture treatment. Both the Diurnal Wanderer and Trapper guild responses support the first hypothesis stating: changes in sagebrush architecture directly impact ground-dwelling spider community organization.

Warmer temperatures may also explain the lack of significant influences of vegetation architecture and prey availability in July and August of both years. Increased radiant energy and resulting ground surface temperatures likely governed ground-dwelling spider behavior within this period (Joern et al. 2006). Strategies to avoid

desiccation may take precedence over food acquisition, decreasing movement and feeding time during the warmer months.

Two years of study across six sample periods support the observation that vegetation architecture is a primary factor, and likely a direct effect, determining ecological community structure (MacArthur and MacArthur 1961, Scheidler 1990, Uetz and Hodge 1990, Weeks and Holtzer 2000). If the ground-dwelling spider community was impacted indirectly through a change in foliage density or biomass from single shrub architecture manipulations, resulting in a shift in insect prey, then single shrub prey availability treatments should have impacted the community similarly to architectural manipulations. The lack of spider community response to altered prey availability in a single shrub suggests a direct effect of vegetation architecture is present. However, to rule out the indirect influence of architectural changes upon insect prey and the subsequent spider community, detailed analysis of the ground-dwelling insect community was warranted (Chapter 2).

The relative importance of vegetation architecture was found to be much greater than that of prey availability from a ground-dwelling perspective and single shrub spatial context. A multiple spatial context approach may be helpful in understanding the influences of habitat alteration on ground-dwelling arthropod communities, because functional diversity and community organization are differentially influenced by the spatial context in which habitat structure changes occur (Pearman 2002, Chust et al. 2003, De Mas et al. 2009). Whether this same observation occurs at a larger spatial scale in a shrub-steppe ecosystem is investigated in the next chapter.

Appendix 4. Family and species composition of four spider guilds (defined by hunting strategy) collected from pitfall traps in the sage-steppe ecosystem of Hardware Ranch of Cache County, Utah.

Guild (hunting strategy)	Family	Species	
DIURNAL WANDERER (diurnal, active)	Gnaphosidae	<u>Micaria</u> sp.	
	Lycosidae	<u>Pardosa</u> <u>utahensis</u>	
		<u>Alopecosa</u> <u>kochii</u>	
	Oxyopidae	<u>Oxyopes</u> <u>scalaris</u>	
		<u>Habronattus</u>	
	Salticidae	<u>americanus</u>	
		<u>Phidippus</u> <u>johnsoni</u>	
		<u>Salticus</u> <u>peckhamae</u>	
	NOCTURNAL WANDERER (nocturnal, active)	Clubionidae	<u>Chiracanthium</u>
			<u>inclusum</u>
<u>Castianeira</u> <u>descripta</u>			
Gnaphosidae		<u>Castianeira</u> sp.	
		<u>Callilepis</u> <u>eremella</u>	
		<u>Drassodes</u> <u>neglectus</u>	
		<u>Drassodes</u> sp.	
		<u>Drassyllus</u> <u>lamprus</u>	
		<u>D. nannellus</u>	
		<u>D. notous</u>	
		<u>Gnaphosa</u> <u>sericata</u>	
		<u>Haplodrassus</u> <u>bicornis</u>	
		<u>Zelotes</u> <u>puritanus</u>	
		<u>Z. subterraneus</u>	
AMBUSHER (sit-and-wait)	Mimetidae	<u>Mimetus</u> sp.	
	Philodromidae	<u>Ebo</u> sp.	
		<u>Philodromus</u> <u>histrion</u>	
		<u>Thanatus</u> <u>coloradensis</u>	
	Thomisidae	<u>T. formicinus</u>	
		<u>Misumenops</u> sp.	
		<u>Xysticus</u> <u>gulosus</u>	
		<u>X. montanensis</u>	
			<u>X. locuples</u>

TRAPPER (web building)	Amaurobiidae	<u>Titanoeca nigrella</u>
	Agelenidae	<u>Teganaria</u> sp.
	Araneidae	<u>Metepeira foxi</u>
	Dictynidae	<u>Dictyna</u> sp.
	Linyphiidae	<u>Spirembolus mundus</u>
		<u>Spirembolus</u> sp.
		<u>Erigone</u> sp.
	Theridiidae	<u>Theridion petraeum</u>
<u>Theridion</u> sp.		

CHAPTER 4

SPATIAL CONTEXT ALTERS COMMUNITY INFLUENCES OF VEGETATION
ARCHITECTURE VS. PREY AVAILABILITY: AN EXPERIMENTAL STUDY IN A
SHRUB-STEPPE ECOSYSTEM

Introduction

A spatial context approach is required to adequately understand the impacts of vegetation architecture manipulation on an ecological community, because the surrounding matrix may impact the relative importance of an architectural change upon different functional groups (Pearman 2002, Chust et al. 2003, De Mas et al. 2009).

Vegetation architecture and other habitat variables differentially influence community functional diversity and organization depending upon spatial context (Cady 1983).

Here, the influences of spatial context, vegetation architecture and prey availability are investigated using the same ground-dwelling spider community in the same shrub-steppe ecosystem with the same set of experimental field manipulations as in the previous chapter (see Chapter 3). The additional experimental factor, spatial context, has two levels: 1) a single manipulated shrub within a patch of untreated shrubs, hereafter ‘single shrub context’ and 2) a manipulated shrub surrounded by a patch of similarly treated shrubs, hereafter ‘shrub patch context.’

By simultaneously manipulating vegetation architecture, prey availability and spatial context, three hypotheses were examined:

H₁: Ground-dwelling spider abundance and diversity will be altered by changes to vegetation architecture within the sagebrush shrub canopy in single shrub and shrub patch context and the ground-dwelling prey will be unaffected.

H₂: Arthropod-baiting treatments within sagebrush canopies will increase the ground-dwelling spider abundance and diversity by increasing potential prey availability in both spatial contexts.

H₃: The relative influences of vegetation architecture and prey availability on ground-dwelling spider community organization will differ between spatial contexts.

Methods

Field experiment

In the Hardware Ranch, Wildlife Management area in Cache County, Utah (41.61 N, 111.57 W), a sage-steppe ecosystem dominated by *Artemisia tridentata* (hereafter big sagebrush), vegetation architecture was altered to create two spatial contexts: 1) 'single shrub context' and 2) 'shrub patch context'. Single shrub context consisted of a center or focal shrub that was experimentally manipulated and was surrounded by reference shrubs. Shrub patch context patches contained a focal experimental shrub surrounded by a patch of similarly manipulated shrubs. Each patch consisted of approximately 15 shrubs in a 2.5 m radius from a focal shrub. Patch size was chosen to account for the average daily distance traveled by spiders, approximately 2 meters, although many ground-dwelling spiders can cover much more area throughout the day (Clayton 2001). Patches were also selected to be at least ten meters apart. Fifteen replicate patches of each of the combinations of vegetation architecture and prey availability levels were established

(Appendix 5). Within these spatial contexts, the ground-dwelling spider community was monitored to assess the community response to architectural changes.

Pitfall Trapping Methods

To sample the ground-dwelling arthropod community, two 7.4 cm diameter × 11.2 cm deep pitfall traps were installed, flush with the ground, beneath each experimental shrub and the focal shrub of the experimental patches. One pitfall was placed on the north side of the shrub and the other on the south to be sure that the orientation of each trap was consistent and any influence of direction was accounted for. North and South pitfalls were later combined into one sample for each shrub. Each pitfall trap was covered with a slightly elevated wooden tile to prevent surface litter from entering the trap and flooding while traps were active (Anderson 2001, McArdle and Anderson 2001, Oksanen et al. 2008). Traps were filled to a 2 cm depth with a propylene glycol and water solution (1:1 diluted antifreeze) for a five-day sampling period once a month in July of 2009 and in a shrub patch context in July of 2009.

Statistical analyses

To test for effects of vegetation architecture, prey availability, vegetation architecture × prey availability and sample date on the ground-dwelling arthropod community, permutational multivariate analyses of variance (MANOVA) were performed using the Adonis function in the Vegan package in Program R (Joern et al. 2006). The MANOVA analyses included two forms of community level data: a presence/absence matrix describing community composition and a matrix incorporating

abundance of insect functional groups and Orders; spider species and guilds, describing community structure. Using Bray-Curtis index, distance matrices were created and 1,000 permutations of the raw data creating F -tests used to give P -values. The MANOVA only denoted community differences among experimental treatments, not the direction of any differences in community measures of diversity and abundance.

To determine the direction of differences in common community measures due to experimental treatments, arthropod functional group and Order as well as spider guild and species data were used to produce three diversity metrics: the Shannon-Weiner diversity index based on richness and evenness of functional groups/guild, Order/species diversity and total arthropod abundance. Sample date explained the greatest amount of the data. As a result each sample date was analyzed separately for all diversity metrics. A two-factor ANOVA was conducted using Program R to test for any fixed effects of vegetation architecture treatments, prey availability treatments and the architecture \times prey treatment interaction. Functional group and guild analyses were conducted for each of the arthropod groups, using the two-factor ANOVA model. The relationship between vegetation architecture and ground-dwelling arthropods was further examined by conducting ANOVAs across all treatment groups to detect differences in species/Order and guild/functional group diversity and overall spider/insect abundance. Response variables were square root transformed to meet the assumption of normality when required.

Results

Insect community response

Vegetation architecture treatments (reference, low and high foliage density) showed no significant differences in insect community composition based on a presence/absence data of insect functional groups and Orders in a shrub patch context. In addition, vegetation architecture in the shrub patch context had no significant effect upon insect community structure, based on abundance data for insect functional groups and Orders. Prey availability treatments in the shrub patch contexts significantly altered insect community composition at the insect Order level but not at the functional group level. Insect community structure, however, was significantly affected by prey treatment at both the insect Order and functional level within the shrub patch contexts (Table 4.1 a).

Of the four insect functional groups, Predators were the only group influenced by vegetation architecture (Table 4.2 a). Both Predators and Detritivores were impacted by the prey availability treatments. Predators and Detritivores were both significantly impacted by the vegetation architecture x prey availability interaction. Detritivore abundance was increased by 19% under baited reference shrubs compared to baited tied shrubs ($F = 5.002$, $P = 0.032$) Predator abundance was 27% greater under baited reference shrubs compared to baited tied shrubs ($F = 24.40$, $P < 0.001$).

Spider community response

Multivariate analyses of prey availability treatments revealed species level differences in ground-dwelling spider community structure (abundance matrix) and composition (presence/absence matrix) in the shrub patch context. No significant

vegetation architecture x prey availability interaction or vegetation architecture main effect was present at the spider species or guild level for community composition or structure (Table 4.1 b).

Prey availability treatments significantly impacted both Nocturnal and Diurnal Wanderer abundances at the patch spatial context (Table 4.2 b). Diurnal Wanderer abundance increased by 65% under baited patches ($F = 5.388, P = 0.023$) and Nocturnal Wanderer abundance increased by 100% ($F = 6.802, P = 0.011$). Ambushers and Trappers had no detectable impact of prey availability treatments in patch context. Baited shrub patches had significantly greater spider abundance within both cursorial spider guilds: Nocturnal and Diurnal Wanderers (Figure 4.1). None of the four spider guilds had a statistically significant response to the vegetation architecture treatments in the patch sample month of July. Warmer temperatures may explain the lack of significant influences of vegetation architecture as in the single shrub context studies in July of 2007 and 2008 (Chapter 3). Increased radiant energy and resulting ground surface temperatures likely governed ground-dwelling spider behavior within this period. Strategies to avoid desiccation may take precedence, resulting in a lack of observed habitat preference within the month of July.

Table 4.1 a, b. *F* and *P*-values from MANOVA analysis of arthropod community composition (based on presence/absence) and community structure (incorporating abundance) for **a**: arthropods and **b**: spiders at the patch spatial context.

a		Community Composition		Community Structure	
Community Level	Treatment	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Functional	Architecture	0.563	0.633	1.007	0.425
	Prey	2.889	0.082	5.055	0.005
	ArchitecturexPrey	0.838	0.433	1.344	0.239
Order	Architecture	1.124	0.346	2.092	0.431
	Prey	3.890	0.011	9.984	<0.001
	ArchitecturexPrey	1.252	0.255	1.166	0.302

b		Community Composition		Community Structure	
Community Level	Treatment	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Guild	Architecture	1.047	0.378	0.544	0.586
	Prey	14.896	<0.001	2.865	0.041
	ArchitecturexPrey	3.487	0.066	0.517	0.823
Species	Architecture	0.936	0.384	1.735	0.191
	Prey	9.922	0.002	7.735	0.007
	ArchitecturexPrey	2.876	0.075	1.349	0.693

Table 4.2 a, b. Degrees of freedom, *F*-statistics and *P*-values of ANOVAs for effects of experimental patch treatments and interactions on the abundance within **a**: arthropod functional groups and **b**: spider guilds.

a	Shrub Architecture			Prey Availability			Architecture x Prey		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Herbivores	2	0.782	0.459	1	0.070	0.792	2	1.194	0.306
Omnivores	2	0.361	0.697	1	1.586	0.210	2	2.014	0.137
Predators	2	4.942	0.008	1	24.40	<0.001	2	6.520	0.002
Detritivores	2	0.054	0.947	1	5.002	0.032	2	4.268	0.016

b	Shrub Architecture			Prey Availability			Architecture x Prey		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Diurnal W.	2	0.382	0.684	1	5.388	0.023	2	1.238	0.297
Nocturnal W.	2	1.362	0.263	1	6.802	0.011	2	1.556	0.218
Ambushers	2	1.146	0.324	1	0.006	0.939	2	0.097	0.908
Trappers	2	0.647	0.527	1	0.224	0.638	2	0.591	0.556

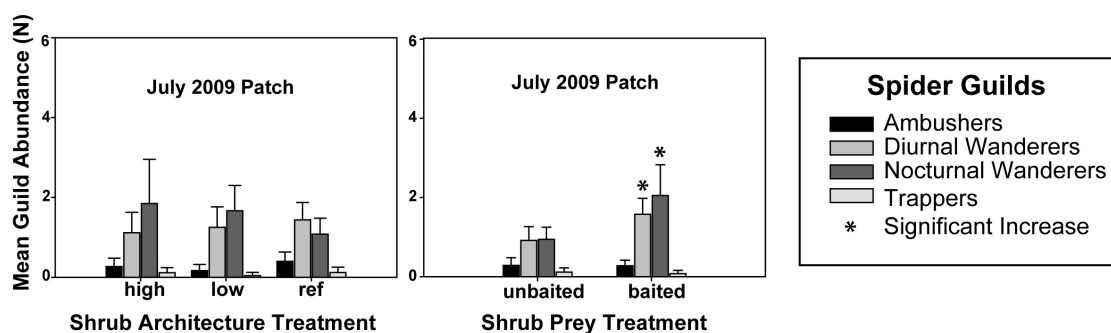


Figure 4.1. Mean guild abundance compared across vegetation architectural treatments and prey availability treatments of shrub patches. Error bars represent 1 SE.

Discussion

How changes in vegetation architecture and prey availability alter the ground-dwelling arthropod community organization in two different spatial contexts was evaluated in this chapter. The first hypothesis stated that within both the single shrub and patch context, ground-potential spider prey abundance, diversity would be influenced by vegetation architecture treatments but prey arthropod richness at the Order and functional level would not be influenced by changes to vegetation architecture within the sagebrush shrub canopy. In support of the second portion of this hypothesis, changes to vegetation architecture did influence the overall ground-dwelling arthropod community in the shrub patch context. At the single shrub spatial context, however, vegetation architecture change significantly altered both community composition and structure at the arthropod functional group level and community structure alone at the insect Order level (Chapter 2). Predators, primarily consisting of mites, were the only functional group of the four to respond to changes in vegetation architecture changes. Consistently, mites responded only to the tied or increased foliage density vegetation architecture treatment rather than the foliage removal treatments. Therefore, mites are likely to be responding to changes in abiotic ground surface variables much like their spider predators and not shifts in foliage density or biomass from architecture manipulation. The same explanation holds for the Detritivores in this study as they are found in the leaf-litter and are responding only to the high-foliage density treatments and likely its decrease in canopy cover on the ground not a reduction in biomass in the low-foliage density treatments. Thus, both the Predator and Detritivore response to vegetation architecture change does not support the concept an

indirect effect of change in insect prey base resulting from change in shrub foliage density or biomass. Also, in support of this hypothesis, insect community composition and structure at the insect Order and functional group level were not influenced by changes to vegetation architecture at the shrub patch spatial context.

In the shrub patch context, the prey treatments had the only significant effects on community structure both at the arthropod functional group and Order level as well as community composition at the insect Order level. Thus, any influences of vegetation architecture on the ground-dwelling spider community are unlikely to be a result of an indirect effect insect prey base change.

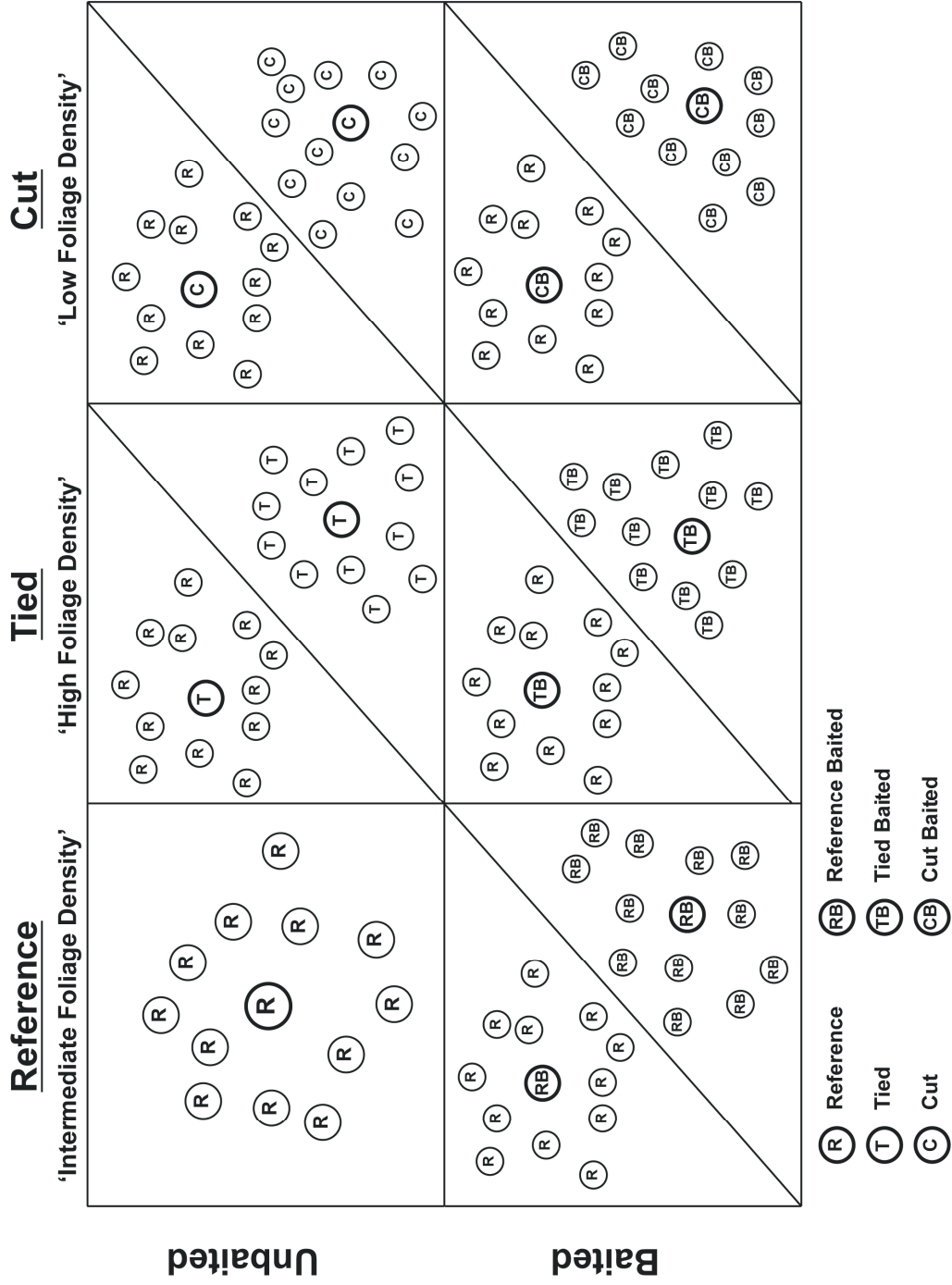
An entirely different spider community response to architectural and prey availability manipulations was found at the shrub patch spatial context compared to the single shrub spatial context results in Chapter 3. The Diurnal and Nocturnal Wanderer guilds had higher abundance and diversity in the baited patches compared to un-baited patches. These results support the second hypothesis that changes in prey availability within sagebrush canopies will increase abundance and diversity in the ground-dwelling spider community. This increase was only detected when the prey treatment occurred in a multiple shrub context. Due to the greater mobility of the two Wanderer guilds, as compared to Ambushers and Trappers, it follows that Wanderers would be markedly impacted by an increase in prey availability occurring within a larger spatial context. These results support the third hypothesis stating that impacts of vegetation architecture and prey availability on ground-dwelling spider community organization differ between spatial contexts. Bait treatments within the patch context may have increased prey

availability to a large degree, negating any detectable influence of architecture treatment upon spider community organization. However, vegetation architecture did not detectably alter the spider community within un-baited patches.

A single manipulated shrub in the context of reference shrubs yielded a community-level response to architectural and not prey availability manipulation (Chapter 3). In contrast, an experimental shrub in the context of similarly manipulated shrubs yielded a community-level response to prey availability and not architecture. Thus, considering different spatial contexts is critical when evaluating ecological communities containing members with varied levels of mobility. One spatial context is not sufficient when assessing community level impacts of habitat change.

Spatial context may be particularly important when considering the lesser-studied ground-dwelling spider community as well as other ecological communities with wandering members. This concept may also prove its relevance in studies that aim to use spiders and other arthropods as indicators for ecological change when assessing effects of management strategies.

Patch Context (July 2009)



Appendix 5. Experimental design for shrub patch vegetation architecture and prey availability manipulations of sagebrush.

CHAPTER 5

CONCLUSIONS

The importance of habitat structure has been studied extensively across a variety of ecological communities. Whether in rainforests or desert scrub habitats structure plays a significant role in community organization and functioning (MacArthur and MacArthur 1961, Pianka 1966, Uetz 1977, Hatley and MacMahon 1980, Scheidler 1990, Weeks and Holtzer 2000, Halaj and Wise 2002, Cardoso et al. 2008). Much of the historic literature has investigated the influence of habitat structure in the context of vegetation architecture and the species living within the architecture of interest. These studies often leave questions as to whether the observed influences of vegetation architecture on ecological communities are a result of the architecture itself or traits of the vegetation tied to food or prey resources. Difficulties in disentangling the relative influences of habitat structure and associated food or prey base impede the ability to make practical inferences about the factors behind community organization. Given the increased call for rapid bioassessment methods and standards for measuring habitat change (Mallis and Hurd 2005, Halaj et al. 2008, Schmitz 2009), it is necessary to determine the direct and indirect mechanisms linking vegetation architecture to ecological community organization and function.

As the literature addressing the connections between community organization and vegetation architecture expands, many studies with examples at the species, trophic and guild levels are discovering direct impacts of vegetation architecture changes. More complicated patterns suggest multiple indirect effects are linked to food and prey associated with vegetation and the spatial context in which the vegetation changes occur

have also been documented (Whitehouse et al. 2002, Wiser and Buxton 2008).

Through simultaneous manipulation of vegetation architecture (*Artemisia tridentata*, big sagebrush) and associated insect prey base in different spatial contexts, this dissertation demonstrates that vegetation architecture directly affects ground-dwelling spider community organization at the species and guild levels of diversity.

A common theme within the data chapters is the importance of spatial context when evaluating the ground-dwelling arthropod community responses to changes in vegetation architecture. Depending upon the natural history traits of a given spider guild or insect functional group, responses to experimental manipulations differed between spatial contexts. For instance, in Chapter 3, Diurnal Wanderers were impacted by vegetation architecture manipulations in a single shrub context but not in single shrub prey availability treatments until they occurred in the shrub patch context (Chapter 4). This response pattern was also observed in overall community measures of abundance, diversity and richness both for spider species and guilds. In contrast, in Chapter 2, the ground-dwelling insect community responded to prey availability manipulations in both the single shrub and shrub patch contexts. Architecture treatments yielded a response in the single shrub context for only one insect functional group, Predators. The ground-dwelling arthropod community consists of a variety of different guilds and functional feeding groups, which utilize resources and space differently. Therefore, it is beneficial to include spatial context as a factor when assessing an arthropod community's response to habitat changes.

Chapters 3 and 4 Conclusions

Although previous studies have determined that foliage-dwelling spider communities respond to changes in vegetation architecture (Hatley and MacMahon 1980, Brandt 1998, Halaj et al. 2008, Sanders et al. 2008), whether manipulations of shrub canopy architecture would influence the ground-dwelling spider community in the context of a single shrub or shrub patch manipulation was unknown. I hypothesized that there would be changes in the ground-dwelling spider community composition (presence/absence) and structure (abundances) across the different architectural treatment groups and spatial contexts. The hypothesis that single shrub architectural manipulations influence ground-dwelling spider community composition and structure was supported both at the species and guild levels (Chapter 3). Any effects of vegetation architecture manipulations would be expected to increase in the shrub patch context as compared to the single shrub context. There were no main effects or interactive effects of vegetation architecture detected in the shrub patch context. Instead, prey availability alterations seemed to govern ground-dwelling spider community composition and structure at the shrub patch context. These results support the main hypothesis of Chapter 4, that impacts of vegetation architecture and prey availability on ground-dwelling spider community organization differ among spatial contexts. Baiting treatments within the patch context may have increased prey availability to a large degree, negating any detectable influence of architecture treatment upon spider community organization. This was only observed in one sample month, July 2009. Warmer temperatures in that sample month may also explain the lack of significant influences of vegetation architecture.

Strategies to avoid desiccation may take precedence over food acquisition, decreasing spider movement and resulting in a lack of observed patterns in habitat preference during the month of July.

Still, across two field seasons and six sample periods, single shrub architectural manipulations influenced relative abundance, diversity and richness both at spider species and guild levels with no significant effects of prey availability. The lack of spider community response to altered prey availability in a single shrub context also suggests a direct effect of vegetation architecture is present. If the ground-dwelling spider community were impacted indirectly through a shift in prey base, resulting from a change in foliage density or biomass due to single shrub architecture manipulations, then single shrub prey availability and architectural treatments should have impacted the community similarly.

The significant reduction in Diurnal Wanderer and Trapper guild abundance within the ‘high foliage density’ or tied single shrub treatment group also supports the concept of a direct effect of vegetation architecture on the ground-dwelling spider community. Due to a similar ground-surface temperature and vapor pressure deficit thresholds, both guilds may share the same requirements for canopy cover amount, which is not afforded by the tied architecture treatment. Thus, a single shrub’s canopy architecture directly influences the ability of certain ground-dwelling spider guilds to persist beneath it. The Chapter 3 data support the observation that vegetation architecture has a direct effect on ground-dwelling spider community structure and composition. However, to rule out the possible indirect influences of architectural changes upon insect

prey and the subsequent spider community, it was important to assess the ground-dwelling insect community available as spider prey in the different experimental treatments.

Chapter 2 Conclusions

In Chapter 2, I quantified the ground-dwelling arthropod response to changes in vegetation architecture and arthropod baiting treatments. Given that ground-dwelling spiders and their prey base are likely exposed to the same abiotic microhabitat conditions, the response of some of the potential prey functional groups might mimic responses observed within certain spider guilds in Chapter 2. However, the hypothesis was that overall ground-dwelling arthropod community measures would be relatively unaffected by vegetation architecture manipulations. I did not predict insects to be overwhelmingly reduced in abundance or diversity resulting from changes in plant biomass or foliage density with respect to the different architectural treatments. I did hypothesize that arthropod abundance and diversity would increase with the baiting prey availability treatment. Although significant responses to vegetation architecture were present in two specific arthropod groups, both expectations that 1) no marked reduction in prey arthropods would result from architectural manipulations and yet 2) the spider community would respond to changes in vegetation architecture; were largely met. Insect community measures of abundance, diversity and richness were significantly increased by the baiting prey availability treatment. Overall community structure both at the insect functional group and Order level as well as community composition at the Order level were significantly impacted by the prey availability treatment. Across all six

sample periods single shrub architecture manipulations only influenced arthropod community measures in August of 2007. Of the four arthropod functional groups, predators, mainly consisting of mites, were the only group to respond to changes in vegetation architecture. This is consistent with the earlier suggestion that specific groups might be responding to changes in abiotic microhabitat conditions much like their ground-dwelling spider predators and not shifts in foliage density or biomass from shrub architecture manipulations.

Synthesis

After simultaneous consideration of the ground-dwelling spider and arthropod communities' responses, the direct community organization-vegetation architecture mechanism has been refined. Although some interactive effects of vegetation architecture and prey availability impacted the ground-dwelling arthropods, members of the community considered to be part of the spider prey base were not largely influenced by changes in the shrub canopy architecture (Chapter 2). Therefore, it is a reasonable conclusion that the ground-dwelling spider community is responding directly to vegetation architecture manipulations (Chapter 3) and not indirectly through a shift in prey base. This research also suggests the importance of the spatial context in which a habitat change occurs. The relative influences of vegetation architecture and prey availability manipulations shifted depending on the spatial context for both the ground-dwelling spider and insect communities. As in other spatial context studies, this study supports the concept that the role of the surrounding matrix needs to be better understood. By establishing the importance of colonization and dispersal processes as well as the

environmental differences in each spatial context determining the persistence of different species in a given ecological community, the role of the matrix can be clarified (Whitehouse et al. 2002, Wisser and Buxton 2008). This study may have implications for management of arthropod communities in shrub-steppe habitats as well as other natural or agricultural ecosystems by demonstrating the relevance of spatial context and the relative impacts of vegetation architecture and prey availability on this ground-dwelling spider community.

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CURRICULUM VITAE

MARY E. PENDERGAST

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Utah State University
Department of Biology
5305 Old Main Hill
Logan, UT 84322-5305

OBJECTIVE

Pursuing a conservation scientist position working at the nexus of research, education and outreach toward practical ecological management.

DEGREES

Utah State University Logan, UT (2005-2011)

Department of Biology / Ecology Center
PhD, Ecology. 2011

Principle Researcher, Community level effects of vegetation architecture and prey availability, an experimental field study of ground-dwelling arthropods in a shrub-steppe ecosystem

- Set up experimental field study and collected data in the summers of 2006-2009
- Conducted species level identifications arthropod community
- Completed my comprehensive exams in December of 2006, obtaining candidacy status
- Performed statistical analyses on a subset of the data and presented to research committee as well as an annual ecology conference in 2007.
- Continued field sampling and completed statistical analyses for dissertation.

Graduate Advisor, Dr. James A. MacMahon

Saint Mary's College Notre Dame, IN (2000-2004)

Bachelor of Science, Biology with a Chemistry Minor

Advisor, Dr. David M. Sever

RESEARCH / PROFESSIONAL EXPERIENCE

Nature Conservancy Consultant Salt Lake City, UT (March 2010-present)

Principle Researcher, Effects of current mosquito abatement strategies on the aquatic insect community, a pilot study at the Great Salt Lake Shorelands Preserve

- Drafted a proposal and budget accepted by TNC, Salt Lake City office
- Conducted order level identifications of aquatic insect community

- Performed statistical analyses on of the data and presented to Great Salt Lake Shorelands Manager, Director of Conservation and Outreach and Education Coordinator
 - Currently drafting new inclusive budget for a longer term follow up study to begin
- Director of Conservation, Dr. Chris Montague/ Shorelands Manager, Chris Brown/ Outreach Coordinator, Heidi Nedreberg*

National Bison Range Wildlife Refuge Moiese, MT (Fall 2004)

Field Researcher and Technician,

- Set up experimental field enclosures for arthropod community
- Conducted species level identifications arthropod community
- Performed laboratory tests on water and soil samples collected in the field

Principle Investigator, Dr. Gary Belovsky

University of Notre Dame Environmental Research Center Land O'Lakes, WI (Summer 2004)

Teaching Assistant of Environmental Field Course, Field Technician,

- Advised students on personal research projects
- Prepared field and lab portions of class
- Assisted in small mammal trapping studies around vernal ponds

Principle Investigators, Dr. Karen Francl and Dr. Gary Belovsky

University of Montana Flathead Lake Biological Station Polson, MT (Summer 2003)

REU, Field Researcher, Data Analysis, and Author, Bufo boreas in Parafluvial Ponds of the Nyack Floodplain

- Recorded water quality measurements
- Analyzed population sizes, regional migration of toads, survival and growth of tadpoles
- Obtained GPS readings of parafluvial ponds
- Designed methods for pit tagging and tracking of individual toads
- Analyzed data and presented results to committee

Principle Investigators, NSF Dr. Jack Stanford, Dr. Art Mckee

“Biocomplexity study of the Nyack Floodplain” funded by the National Science Foundation

University of Notre Dame Environmental Research Center Land O'Lakes, WI (Summer 2002)

Field Researcher, Data Analysis, and Author,

An Experimental Study on the Effects of Climate Change on Primary Consumer Behavior of *Camnula pellucida* in the Field

- Designed methods for observing grasshopper behavior in the field
- Constructed enclosures and observed grasshoppers in the field
- Analyzed data within SYSTAT and presented results to committee

Villanova University Villanova, PA (Summer 2001)*Researcher, Laboratory Work*

The Absorptive Capabilities of Carbon Nanofibers on Metal Cations in Water

- Performed synthesis of Carbon Nanofibers
- Tested for removal of metal cations
- Overall study of water remediation presented to a committee

Principle Investigators, Dr. Carol Bessel

RELEVANT COURSEWORK

Saint Mary's College and the University of Notre Dame, IN

Biology Concepts	Environmental Field Biology
Comparative Vertebrate Anatomy	Calculus for Life Sciences
Physics	Animal Behavior
Genetics	Organic Chemistry
Microbiology	Structures of Biomolecules
Molecular Biology	Economic Botany
Vertebrate Natural History	Ecology

As Student enrolled in Practicum in Environmental Field Biology

Aquatic Ecology, Stream Ecology, Wetland Ecology, Aquatic Entomology, Callback Surveying, Tracking and Trapping, Spotlighting, Herpetology, and Ornithology

Utah State University, Logan, UT

Landscape Ecology	Insect Systematics and Evolution
Graduate Ecology	Soil Genesis and Morphology
Biometry	Linear Regression and Time Series
Biogeography	Design of Experiments
Environmental Biophysics	

TEACHING

Salt Lake Community College, Salt Lake City, UT

Introductory Biology, Spring 2011

Utah State University, Logan UT

Human Anatomy, Spring 2005, Summer 2006, Summer 2007, Summer 2008, Summer 2009, Spring 2010

Field Botany, Summer 2005, Spring 2006

Biodiversity of Utah, Fall 2006

Introductory Biology, Fall 2005, Spring 2007, Fall 2007, Spring and Fall 2008, Spring 2009

University of Notre Dame, South Bend, IN

Environmental Field Research, Summer 2004

PUBLICATIONS / PRESENTATIONS

Pendergast, M. E. and J. A. MacMahon. Spatial context affects importance of habitat structure vs. prey availability on a ground-dwelling spider community, an experimental field study in a shrub-steppe ecosystem. *In progress*

Pendergast, M. E. Direct and indirect effects of shrub architecture and prey availability on ground-dwelling arthropods. *In progress*

Pendergast, M. E. and J. A. MacMahon. Community level effects of vegetation architecture and prey availability, an experimental field study of ground-dwelling spiders in a shrub-steppe ecosystem. Ecology Society of America Annual Meeting, San Jose CA, August 5 – 10, 2007

AWARDS AND SCHOLARSHIPS

2010	Ecology Center Assistantship in March from Utah State University, Ecology Center
2009	School of Graduate Studies Dissertation Fellowship from Utah State University
2007-2009	Ecology Center Research Award at Utah State University, Ecology Center
2008	Datus M. Hammond Memorial Scholarship, Utah State University, Department of Biology
2004	George Juanda Bick Nature Award for outstanding achievement in environmental biology of the graduating class at Saint Mary's College
2004	Notre Dame Chapter of Sigma Xi Scientific Research Society Award for outstanding research of the graduating class at Saint Mary's College
2000-2004	Ladies of Notre Dame and Saint Mary's Scholarship
2000-2004	Saint Joseph County Scholarship

PERSONAL INTERESTS/ACTIVITIES

Marathon Running	Insect Collection and Identification
Trail Running	Bird Watching
Cross-fit Training	Wildlife Painting/Sketching
Triathlons	Wilderness/Backcountry Preparedness
Martial Arts	Nature Conservancy Volunteer at Great Salt Lake Preserve