Population Ecology and Stoichiometry of the Western Black Widow Spider:

From Solitary Desert Predator to Urban Pest.

by

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ABSTRACT

Human-induced rapid environmental change (HIREC) influences nearly all of Earth's ecosystems through processes such as urbanization. Previous studies have found that urbanization influences biodiversity patterns, often yielding an increase in the abundance of a few urban-adapted taxa at the expense of native species diversity. The western black widow spider, *Latrodectus hesperus*, is a medically-important pest species that often forms dense urban subpopulations (i.e., infestations) relative to the low-density subpopulations found throughout undisturbed, desert habitat. Here, I employ field and laboratory studies to examine the population ecology and stoichiometry of this urban pest to increase our understanding of the mechanisms underlying its success.

The population ecology of ten black widow subpopulations spread across metropolitan Phoenix, AZ was examined during the peak breeding season (June-August). This study revealed that arthropod prey abundance, female mass and population density of females showed significant spatial variation across the ten subpopulations. Additionally, prey abundance and foraging success, measured as the number of carcasses found in webs, were a strong determinant of female mass and population density within each subpopulation.

To test the mechanisms that drive black widow infestations, I used ecological stoichiometry to examine the nutrient (nitrogen and phosphorus) composition of spiders and arthropod prey from urban habitat, desert habitat and a laboratory diet regime. These studies revealed that (1) spiders are more nutrient rich than cricket prey in the field, (2) spider subpopulations exhibit significant spatial variation in their nitrogen composition, (3) nutrient composition of urban spider subpopulations does not differ significantly from Sonoran desert subpopulations, (4) laboratory-reared spiders fed a diet of only laboratory-reared crickets are more nitrogen and phosphorus limited than field-captured spiders, and (5) cannibalism by laboratory-reared spiders alleviated phosphorus limitation, but not nitrogen limitation, when compared to field-captured spiders. This work highlights the need to examine the population ecology of species relationships, such as predator-prey dynamics, to fully understand the fecundity and population growth of urban pest species. Moreover, the integration of population ecology and stoichiometry illustrates the need to address mechanisms like nutrient limitation that may explain why urban pest populations thrive and native species diversity suffers following HIREC.

DEDICATION

To my son, Adam: for his love, patience, support and understanding when I could not spend the time with him that he deserved.

To my parents, Joseph and Barbara Tafoya: for their love and support as they encouraged me to further my education and helped me take care of Adam, so that I could complete this study and this thesis. Thank you.

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Chapter 1

INTRODUCTION

Human-Induced Rapid Environmental Change and Urbanization

Anthropogenic disturbances (recently termed ‘human-induced rapid environmental change’ (HIREC; Sih et al., 2010; 2011) impact nearly all of Earth’s ecosystems, and present ecologists with a ‘grand challenge’ (Vitousek et al., 1997; Sih et al., 2010). HIREC has been divided into five categories, (1) habitat loss/fragmentation, (2) the spread of exotic species, (3) harvesting by humans, (4) pollutants, and (5) climate change (Sih et al., 2011). All categories of HIREC are found within urban ecosystems (Munn et al., 2002; Grimm et al., 2008). Indeed, urbanization is a pervasive form of HIREC because more than 50 % of the human population now lives in urban centers and this figure is expected to increase to 72 % by the year 2025 (United Nations, 2012). These fast growing urban populations drastically alter the landscape and the abiotic (e.g., water availability) and biotic (e.g., decomposition) processes within them (Grimm et al., 2008). In particular, urban habitats exhibit decreased temporal variation and heightened spatial variation in many abiotic and biotic variables compared to surrounding wild lands (reviewed in Shochat et al., 2006). Moreover, these changes in abiotic and biotic processes cause stress on biological communities and ecosystem functions within cities and beyond city boundaries (Collins et al., 2000; Grimm et al., 2008). Thus, urbanization provides a study system for ecologists to understand the implications of HIREC on natural ecosystems.

Biodiversity and Urban Exploiters

Biodiversity influences several ecosystem processes (e.g., nutrient cycling), and habitats with higher species richness enhance ecosystem services (e.g., pollination; see

Duffy, 2008). Moreover, habitats with higher species richness are more resilient to disturbance (Tilman & Downing, 1994; Tilman, 1996). Therefore, understanding the patterns of biodiversity within an ecosystem is critical because biodiversity influences overall ecosystem functioning. Furthermore, ecosystems collectively regulate biogeochemical processes (Loreau et al., 2001) and changes in biodiversity patterns can disrupt such processes.

Although many factors influence biodiversity, urbanization often reduces native diversity at the expense of a few urban-adapted taxa (Blair, 1996; Mckinney, 2002; Shochat et al., 2010; but see Bolger et al., 2008 for contradictory findings). Within urban habitat, species can be grouped into three categories, 'urban avoiders', 'urban adapters' and 'urban exploiters' (Mckinney, 2006). These categories are often associated with a gradient of urbanization. For example, in the most highly urbanized areas (e.g., urban core) there are abundant populations of urban exploiters, small populations of urban adapters and the absence of urban avoiders (reviewed in McKinney, 2006).

The patterns of biodiversity within urban habitats are relatively well studied, but the underlying mechanisms that allow urban exploiters to thrive in urban habitats are poorly understood (Shochat et al., 2006). Urban exploiters are predicted to dominate highly productive habitats where food resources are high and seasonality is dampened (e.g., continuous inputs of nutrients and water) (Shochat et al., 2006; 2010; Faeth et al., 2012). Additionally, urban exploiters may generally rely on human provided resources over natural resources (reviewed in McKinney, 2002; 2006). For example, in urban habitats the predominant food types for avian species consist of seeds and other plant material (Davies et al., 2009). Thus, avian species that are able to exploit the dominant food resource (e.g., bird seed feeders) are going to be more persistent in urban habitats than insectivorous species, which are relatively rare in urban habitats (Chance & Walsh, 2006; Kark et al., 2007; Fuller et al., 2009). However, we need a better understanding of the mechanisms that drive biodiversity patterns within cities.

Specifically, we need a better understanding of the abiotic mechanisms behind the success of urban exploiters. For example, are urban exploiters able to thrive in urban habitats because of their ability to cope with the changes in diet breadth and nutrient composition that typically follow urbanization (Smith & Carlile, 1993; Kurosawa et al., 2003; Ciminari et al., 2005; Bateman & Fleming, 2012)? Most often, urban exploiters are omnivores, typified by a wide diet breadth (Kark et al., 2007; Bateman & Fleming, 2012). However, we know very little about the physiological mechanisms that would allow urban exploiters to cope with changes in nutrient availability. For example, compared to wild lands, urban soils often contain high amounts of nitrogen (N), but not phosphorus (P) (Baker et al., 2001; Metson et al., 2012). Thus, as N levels rise, plants are more likely to be limited by other nutrients such as P (Bobbink et al., 2010). However, studies showing how the variation of N and P in urban habitats influence higher trophic levels are rare (Singer & Battin, 2007; Tsoi et al., 2011; Tao & Hunter, 2012).

Ecological Stoichiometry

One approach used to quantify the nutrient dynamics of an ecosystem is ecological stoichiometry (Sterner & Elser, 2002). Ecological stoichiometry allows for the quantification of multiple chemical elements (most often carbon (C), nitrogen (N), and phosphorus (P)) in ecological interactions (Sterner & Elser, 2002). In particular, stoichiometry allows us to view the role of elemental imbalances (e.g., C: N ratios) in shaping key ecological processes (e.g., food web dynamics) (Sterner & Elser, 2002). Among trophic levels there is an imbalance in the amount of nutrients (e.g., N & P) available between a consumer and their food source (Fagan et al., 2002; Sterner & Elser, 2002; Denno & Fagan, 2003). For example, herbivores contain 10-20 times the amount of nutrients in their tissues than what is available in autotrophs (Elser et al., 2000). Thus, this imbalance suggests that herbivores are subject to strong nutrient limitation. As a result, herbivores employ a variety of different tactics to combat nutrient limitation via generalist feeding strategies to feeding across multiple trophic levels (Hägele & Rowell-Rahier, 1999; Denno & Fagan, 2003). Recently, the imbalance between consumers and their food sources has been identified in higher trophic levels (Fagan et al., 2002; Denno & Fagan, 2003). For example, spiders contain significantly more N in their tissues than herbivorous prey which makes spiders especially vulnerable to N limitation (Fagan et al., 2002). Thus ecological stoichiometry can be used to identify changes in nutrient flow in habitats that house reduced species richness.

Historically, stoichiometric theory predicts that consumers strictly regulate N and P homeostasis regardless of diet nutrient availability (Sterner & Elser, 2002). However, recent evidence supports the idea that consumers vary in their degree of nutrient homeostasis (Bertram et al., 2008; Small & Pringle, 2010; González et al., 2011; Tsoi et al., 2011; El-Sabaawi et al., 2012a; 2012b). Deviation from a strict nutrient homeostasis may contribute to the success of invasive species (Naddafi et al., 2009; Persson et al., 2010). For example, plasticity in nutrient homeostasis allows for organisms to adapt to nutrient poor diets by allocating fewer nutrients to new tissues (Elser et al., 2003). In contrast, in environments where there is a surplus of nutrients, plasticity in nutrient homeostasis allows for nutrients to be stored and used later for growth (Sterner & Schwalbach, 2001; Raubenheimer & Jones, 2006). Persson et al. (2010) reviewed the regulation of nutrient homeostasis among consumer taxa and found that the degree of variation from strict homeostasis cannot be identified as a group or even species-level trait. Instead, the degree of variation from nutrient homeostasis may be largely determined by local environmental conditions.

Recently, intraspecific organismal stoichiometric variation has been linked with environmental heterogeneity, where nutrient (N & P) tissue composition is determined by the environmental variables defining a particular locale (Small & Pringle, 2010; Tsoi et al., 2011; El-Sabaawi et al., 2012a; 2012b). In these studies, environmental conditions such as the overall biogeochemical setting (El-Sabaawi et al., 2012a) and variability in food quality (El-Sabaawi et al., 2012b) are determinants of organismal stoichiometry more so than biological factors such as lineage, body size, or life-history phenotype. Thus, ecological stoichiometry can be used to look at the effects of spatial heterogeneity, typical of urban habitat, on the nutrient interactions of urban exploiters.

A Native Urban Exploiter, the Western Black Widow Spider

Among arthropods, spiders are good biological indicators used for conservation and management planning because they are key predators that regulate insect populations in natural and urban ecosystems (Riechert & Bishop, 1990; Shochat et al., 2004). Within urban habitat, increased productivity often leads to decreased spider diversity, but an increase in the abundance of a few spider taxa (Shochat et al., 2004). The western black widow spider, *Latrodectus hesperus* (Araneae, Theridiidae) is native to the Sonoran Desert and has become a predatory urban exploiter within the disturbed habitats of Phoenix, AZ. Female black widows spend the majority of their time in webs, which are large, three dimensional cobwebs with an area of dense silk that serves as a refuge (Zevenbergen et al., 2008; Johnson et al., 2011). Adult male black widows do not build webs, feed very little, and instead spend the majority of their adult lives searching for females (Kasumovic & Andrade, 2004). Within urban habitats, widow spiders are considered pest species because they readily form dense infestations and their venom is particularly dangerous to humans (Lewitus, 1935; Orlova et al., 2000; Brown et al., 2008). Black widows are generalist predators and have a broad diet in nature (Hódar & Sánchez, 2002; Salomon, 2011). However, black widows in urban Phoenix may experience increased prey abundance, but reduced prey diversity relative to spiders inhabiting undisturbed Sonoran desert habitat (Bang & Faeth, 2011). Thus, spatial variation in prey diversity and/or nutrient availability across habitat types (urban-desert) and within urban habitat (e.g., across different municipalities) may help explain the success of black widows as urban exploiters.

Thesis Outline

To better understand the mechanisms that drive urban exploiter populations, I integrated the population and ecosystem ecology of a native urban exploiter, the western black widow spider, *L. hesperus*. My research objectives were to determine (1) how variation in abiotic and biotic variables influences black widow subpopulations across urban Phoenix and (2) determine the mechanisms that allow urban exploiters to cope with changes in diet breadth and nutrient availability associated with urban environments. This work was organized around six main questions, outlined below.

1) How does low Temporal Variation and Spatial Heterogeneity Influence Urban Black Widow Subpopulations? In order to identify the underlying mechanisms that allow black widows to thrive in urban habitats, I first needed to quantify the variation in population dynamics among black widow subpopulations. I followed 10 black widow subpopulations across the greater metropolitan Phoenix area over the peak of their breeding season (June-August). Locales were followed if they met the following criteria: (1) were a minimum of 8km apart from one another, (2) commercial sub-habitats with xeric landscaping, and (3) contained a minimum of 10 adult female black widows (within 5,000 m^2) in the initial census. The abiotic variables I measured from each locale included (1) the percent of impervious surface area (e.g., cement) as a measure of disturbance and indirect measure of temperature, (2) the time lapsed from urban site development (years), and (3) wall length (m) as a measure of available web building substrate. Biotic variables collected from each locale were percent vegetation, prey abundance, web volume, female mass, and population density of females. I predicted that black widow subpopulation dynamics would exhibit little variation across the peak of the breeding season (June-August), but would exhibit significant variation across subpopulations more so than within a subpopulation.

2) How do Bottom-up Resources (i.e., Prey Abundance) Influence Urban Black Widow Subpopulation Dynamics? Spiders are prey-limited in nature and prey abundance directly influences spider population dynamics (Rypstra 1985, Wise, 1975; 1979; 1993). Within urban ecosystems, there is an increased abundance of arthropods relative to surrounding wild lands (Cook & Faeth, 2006; Bang & Faeth, 2011). I collected prey abundance as the number of prey carcasses per focal female web, which also measured female foraging success. I predicted that prey abundance will positively correlate with female mass, web volume and population density of females. Thus, locales that house higher prey densities should contain more high-conditioned female black widows that build and maintain larger webs.

3) How does the Stoichiometry of Urban Black Widow Predators Differ from a Common Urban Prey Item? Once I quantified the variation in abiotic and biotic factors that influenced black widow subpopulations across urban Phoenix, I examined the nutrient composition of the black widow spider to determine its potential role in ecosystem processes. According to Fagan et al. (2002) predatory arthropods contain more nutrients in their tissues than their herbivorous prey. Thus, organisms that are limited to a diet low in nutrients may not be able to acquire enough nutrients needed for growth, tissue maintenance and reproduction (Fagan & Denno, 2004). In order to determine if black widows faced potential nutrient limitation, I looked at the stoichiometry of one prey item, the decorated cricket, (*Gryllodes sigillatus*) because it was the only prey item that was found consistently across the 10 black widow subpopulations. I predicted that urban black widow spiders (predators) will contain more nutrients (N & P) in their tissues than crickets (prey).

4) How does Spatial Heterogeneity Influence Black Widow and Cricket C: N: P? Plasticity in nutrient homeostasis is often influenced by both biological and environmental factors (Persson et al., 2010). In an aquatic system, overall biogeochemical setting (El-Sabaawi et al., 2012a) and variability in food quality (El-Sabaawi et al., 2012b) are stronger determinants of organismal stoichiometry more so than biological factors such as lineage, body size, or life-history phenotype. Thus, I was interested in how environmental factors may influence the stoichiometry of black widows and crickets across the 10 locales. I predicted that black widows and crickets would exhibit more variation in their stoichiometry across subpopulations than within a subpopulation.

5) How does C: N Ratios Differ Between Urban and Desert Black Widows and Available Prey? Compared to surrounding wild lands, urban habitats house reduced species richness, but increased abundances of a few arthropod-taxa (Cook & Faeth, 2006; Bang & Faeth, 2011). Black widows are generalist predators and have a broad diet in nature (Hódar & Sánchez, 2002; Salomon, 2011). Thus, black widow subpopulations may experience changes in nutrient availability due to differences in prey composition. I predicted that black widows in urban habitats will have higher C: N ratios (i.e., lower N content) relative to desert black widows because of reduced species richness (e.g., reduced nutrient availability). Additionally, I predict that available arthropod prey species will have higher C: N ratios in urban habitats relative to desert habitats.

6) How does Black Widow Stoichiometry Differ when fed a Single- and Mixed-Species Diet in the Laboratory? In order to determine the degree to which diet influences black widow stoichiometry, I fed laboratory-reared black widows either a single- or mixed-species diet. Single-species diets consisted of a laboratory- reared *G. sigillatus* (fed a single food source) weekly for eight weeks. Mixed-species diets consisted of a laboratory-reared cricket (fed a single food source) weekly for four weeks and then a conspecifics (fed a laboratory-reared cricket) weekly for four weeks. These diets represent possible diets of black widows across urban subpopulations. I predicted that black widows fed a diet of only crickets would be more nutrient-limited (N & P) than black widows fed a mixed- species diet and field captured spiders (allowed to fed on available prey). Additionally, I predicted that black widows fed a mixed- species diet would have similar nutrient body content to black widows captured from the field.

Chapter 2

VARIATION IN THE STOICHIOMETRY OF AN URBAN PREDATOR-PREY SYSTEM: THE WESTERN BLACK WIDOW SPIDER AND DECORATED CRICKET ACROSS METROPOLITAN PHOENIX, AZ.

Abstract

Human-induced rapid environmental change (HIREC) influences nearly all of Earth’s ecosystems through processes such as urbanization. For example, transformation of the Sonoran desert by the recent and rapid development of metropolitan Phoenix, Arizona has decreased native species diversity while increasing the abundance of a few urban-adapted taxa termed ‘urban exploiters’. Unfortunately, the mechanisms driving biodiversity patterns in cities are poorly understood. For instance, it is unclear if urban exploiters have a superior ability to adapt to changes in nutrient availability typical of urban habitat. Ecological stoichiometry is a tool used to identify nutrient imbalances in food web interactions. Here, we used ecological stoichiometry to quantify the nutrient composition (carbon: nitrogen: phosphorus) of a predator-prey interaction between two urban pests found throughout Phoenix, Arizona--the western black widow spider (*Latrodectus hesperus*) and the decorated cricket (*Gryllodes sigillatus*). Spiders (predators) contained significantly more nitrogen than crickets (prey) in the field. In addition, both spider and cricket subpopulations from different sites across urban Phoenix differed in terms of their C: N ratios; though cricket nutrient composition at a site did not predict spider nutrient composition. Surprisingly, the stoichiometry of urban widow subpopulations did not differ significantly from that of undisturbed, Sonoran desert subpopulations; but both urban and desert spiders were significantly more nutrient rich than our F1 laboratory stocks. For example, *L. hesperus* captured from the field were significantly more nitrogen- and phosphorus- rich than spiders reared in the laboratory on

a controlled diet of only laboratory-reared *G. sigillatus.* Interestingly, cannibalism by laboratory-reared spiders alleviated phosphorus limitation, but not nitrogen limitation, when compared to field-captured spiders. These results show that black widows shift their nutrient composition in relation to changes in the elemental composition of their prey, which may factor in the success of urban exploiters and controlling infestations of *L. hesperus.*

Introduction

Anthropogenic disturbances (recently termed 'human-induced rapid environmental change' (HIREC; Sih et al., 2010; 2011) impact nearly all of Earth's ecosystems, and present ecologists with a 'grand challenge' (Vitousek et al., 1997; Sih et al., 2010). Urbanization is a pervasive form of HIREC because more than 50 % of the human population now lives in urban centers and this figure is expected to increase to 72 % by the year 2025 (United Nations, 2012). These fast growing urban populations drastically alter the landscape and cause stress on biological communities and ecosystem functions within cities and beyond city boundaries (Collins et al., 2000; Grimm et al., 2008). Thus, urbanization provides a study system for ecologists to understand the implications of HIREC on natural ecosystems.

Urbanization often influences biodiversity patterns such as a reduction in native diversity at the expense of a few urban-adapted taxa termed 'urban exploiters' (Blair, 1996; Mckinney, 2002; Shochat et al., 2010; but see Bolger et al., 2008 for contradictory findings). However, the mechanisms that allow for urban exploiters to thrive in urban habitats are poorly understood (Shochat et al., 2006). For example, one model suggests that an increase in water supplementation and primary productivity allows for urban exploiters to thrive within urban environments (Shochat et al., 2006; 2010). This relationship between primary productivity, increased abundance of urban exploiters, and decreased species richness appears in urban habitats for avian (Shochat et al., 2010) and predatory arthropod taxa (e.g., spiders; Shochat et al., 2004; Cook & Faeth, 2006). In contrast, another model suggests that abundance of urban exploiters does not depend on vegetation at a site, but instead generally relies on human provided resources (e.g., bird feeders; reviewed in McKinney 2002; 2006). Thus, it remains unclear the degree to which abiotic and biotic factors influence the population dynamics of urban exploiters.

Specifically, we need a better understanding of the mechanisms that contribute to the increased abundances of urban exploiters and reductions in urban biodiversity. We suggest that ecological interactions following urban disturbance must be better understood to predict how biological communities will respond to urbanization. For example, urban habitats contain fewer top-level arthropod predator taxa than surrounding natural habitats, which may alter ecosystem functioning across urban habitat (Cook & Faeth, 2006). Thus, comparing ecological interactions between natural and urban habitats is essential for understanding the physiological mechanisms by which urban exploiters thrive in urban environments.

Urban exploiters may thrive in urban habitats because of their ability to cope with changes in diet breadth and nutrient composition that typically follow urbanization (Smith & Carlile, 1993; Kurosawa et al., 2003; Ciminari et al., 2005; Bateman & Fleming, 2012). For example, in urban habitats the predominant food types for avian species consist of seeds and other plant material (Davies et al., 2009). Thus, avian species that are able to exploit the dominant food resource are going to be more persistent in urban habitats than insectivorous species, which are relatively rare in urban habitats (Chance & Walsh, 2006; Kark et al., 2007; Fuller et al., 2009). However, the physiological mechanisms that allow for urban exploiters to cope with changes in nutrient availability are not well studied. For example, in urban areas, soils often contain high amounts of nitrogen (N), but not phosphorus (P) compared to wild lands (Baker et al., 2001, Metson et al., 2012). Thus, as N levels rise, plants are more likely to be limited by other nutrients such as P (Bobbink et al., 2010). However, studies showing how variation in N and P in urban habitats influence higher trophic levels are rare (Singer & Battin, 2007; Tsoi et al., 2011; Tao & Hunter, 2012).

Ecological stoichiometry allows for the quantification of multiple chemical elements (most often carbon (C), nitrogen (N), and phosphorus (P)) in ecological interactions (Sterner & Elser, 2002). In particular, stoichiometry allows us to view the role of elemental imbalances (e.g., C: N ratios) in shaping key ecological processes (e.g. food web dynamics) (Sterner & Elser, 2002). In terrestrial systems, there is an imbalance in the amount of nutrients (N & P) available between trophic levels (e.g., autotrophs-herbivores) (Fagan et al., 2002; Sterner & Elser, 2002; Denno & Fagan 2003; González et al., 2011). For instance, spiders contain significantly more N in their tissues than most predatory insects and herbivorous prey which makes spiders especially vulnerable to N limitation (Fagan et al., 2002). Thus, ecological stoichiometry can be used to identify nutrient constraints of urban exploiters and their role in ecosystem processes.

A central premise of stoichiometric theory is that consumers are expected to regulate N and P homeostasis regardless of diet nutrient availability (Sterner & Elser, 2002). However, recent evidence supports the idea that consumers vary in their degree of nutrient homeostasis (Bertram et al., 2008; Small & Pringle, 2010; González et al., 2011; Tsoi et al., 2011; El-Sabaawi et al., 2012a; 2012b). Organisms showing plasticity in nutrient homeostasis may be more likely to adapt to variable environments such as urban environments (Persson et al., 2010). Plasticity in nutrient homeostasis allows for organisms to adapt to nutrient poor diets by allocating fewer nutrients to new tissues (Elser et al., 2003). In contrast, in environments where there is a surplus of nutrients, plasticity in nutrient homeostasis allows for nutrients to be stored and used later for growth (Sterner & Schwalbach, 2001; Raubenheimer & Jones, 2006).

Persson et al. (2010) reviewed the regulation of nutrient homeostasis among consumer taxa and found that the degree of variation from strict homeostasis cannot be identified as a group or even species-level trait. Instead, the degree of variation from nutrient homeostasis is determined by both biology and environmental factors. For example, intraspecific stoichiometric variation has been linked with environmental heterogeneity, where nutrient (N & P) tissue composition is determined by the environmental variables defining a particular locale (Small & Pringle, 2010; Tsoi et al., 2011; El-Sabaawi et al., 2012a; 2012b). Thus, in urban food webs, ecological stoichiometry provides a framework for understanding the implications of HIREC because it allows ecologists to examine the relationship between environmental and biological constraints on the stoichiometry of urban exploiters. Determining the abiotic and biotic factors that influence intraspecific stoichiometric variation of urban exploiters may aid in predicting biodiversity patterns between urban sub-habitats.

Recently, arthropods have been the focus of studies on both ecological stoichiometry (Denno & Fagan, 2003; Fagan & Denno, 2004; González et al., 2011) and the effects of urbanization on biodiversity (McIntyre, 2000; McIntyre et al., 2001; Raupp et al., 2010). Arthropods play an important role in ecosystem functioning and are indicators of environmental disturbance because they are speciose, have short generation times, and occupy multiple trophic levels (McIntyre, 2000; McIntyre et al., 2001). Among arthropods, spiders are biological indicators used for conservation and management planning because spiders are key predators that control insect populations in natural and urban ecosystems (Riechert & Bishop, 1990; Shochat et al., 2004).

The western black widow spider, *L. hesperus* (Araneae, Theridiidae) is native to the Sonoran Desert and has become an urban predatory exploiter of Phoenix, AZ. Female black widows spend the majority of their time in webs, which are large, three dimensional cobwebs with an area of dense silk that serves as a refuge (Zevenbergen et al., 2008; Johnson et al., 2011). Adult male black widows do not build webs, feed very little, and instead spend the majority of their adult lives searching for females (Kasumovic & Andrade, 2004). Within urban Phoenix, female black widow spiders often form dense subpopulations (i.e., infestations) that vary in mean spider mass and population density across commercial urban sub-habitats (see Appendix A). In our prior work, we found that variability in prey abundance across urban Phoenix predicted mean spider mass and population density of subpopulations, rather than abiotic factors (e.g., impervious surface area) (see Appendix A).

In a study of black widows from a costal sand-dune habitat, black widows were found to be polyphagous predators known to prey across at least eight different orders of arthropods (Salomon, 2011). However, black widows in urban Phoenix may experience increased prey abundance, but reduced prey diversity (sub-habitats with xeric landscape, studied herein) relative to spiders inhabiting undisturbed Sonoran desert habitat (Bang & Faeth, 2011). The data from Bang and Faeth (2011) indicate that desert black widows have access to prey across 31 different families whereas urban black widows have access to prey from 18 families in xeric landscaped sub-habitats. For example, within urban habitat, one of the most abundant prey items consistently found across metropolitan Phoenix, AZ was the decorated cricket, (*Gryllodes sigillatus*). Thus, black widow subpopulations may experience changes in nutrient availability due to differences in prey composition.

To better understand how black widow stoichiometry may be influenced by changes in diet composition, we quantified the stoichiometry of black widows and their prey in urban habitats, desert habitats and a laboratory diet regime. This study was conducted over a two year period with year one focusing on the inter- and intra-specific stoichiometric differences in two urban arthropod pest species, the western black widow spider and one of its most common urban prey items--the decorated cricket (see Appendix A). Year two focused on differences in the stoichiometry of black widows and multiple prey types from urban and desert habitats. Here we test the general prediction that (1) N and P body contents will be higher in predators than in herbivores. We also test, within species, if (2) black widows and crickets deviate from strict nutrient (N & P) homeostasis across urban sub-habitats.

We contrast these urban stoichiometric data with the nutrient levels of black widows and a variety of arthropod prey collected from undisturbed Sonoran desert habitat —predicting (3) that desert widows and their prey will be more nutrient-rich than their urban counterparts because of the reduced arthropod prey availability to black widows in urban habitats (Bang & Faeth, 2011). Lastly, we compare the stoichiometry of these urban and desert field samples with laboratory reared *L. hesperus.* Specifically, we predicted (5) that laboratory spiders fed a single- species diet will be nutrient poor (N & P) compared to field populations allowed to fed freely on available prey. Additionally, we test the general prediction that (6) predators allowed to fed across multiple trophic levels will reduce nutrient limitation.

Methods

2010 Collection Protocol. Penultimate instar and adult female *L. hesperus* were collected from ten sites located across metropolitan Phoenix, AZ from 15 August to 15 September. We selected these sites based on the following criteria: (1) land-use type was commercial with xeric landscaping, (2) sites had to be a minimum of 8 km apart from one another, and (3) sites had a minimum of 10 penultimate to adult female black widow spiders (within 5,000 m^2) from initial census. The ecology of these ten sites has been described by Trubl et al. (2012) (see Appendix A) (Fig 1). Black widow webs were located visually during daylight hours, and spiders were captured at night when they are active in their webs (n = 11 - 14 spiders per site). Confirming our earlier observations (see Appendix A), *G. sigillatus* was an abundant prey type, found consistently at all 10 urban widow sites, and we observed cricket carcasses frequently in urban black widow webs (Trubl, per. obs.). *G. sigillatus* is found in urban habitats, including the metropolitan Phoenix area, and is not found in Sonoran desert habitat (Smith & Thomas, 1988; Bang & Faeth, 2011). Adult *G. sigillatus* were hand-collected at each site within a 10 m^2 area of webs. Crickets and spiders were hand-collected the same evening at each site. Crickets and spiders were stored at -20^{o}C for later chemical analysis (see below).

2011 Collection Protocol. From 15 August – 15 September, penultimate and adult female black widow spiders and arthropod prey (n = 2-8 species) were collected from (1) five disturbed, urban sites across Phoenix, AZ, not previously sampled in the 2010 collection and (2) five undisturbed, Sonoran desert sites (Fig 2). Urban sites were sampled for arthropods based on the requirements as described in Trubl et al. (2012) (see Appendix A). Desert sites were sampled if they met the following criteria: (1) during an initial census, sites had to contain a minimum of 2 black widow females within 5,000 m^2

and (2) sites had to be a minimum of 20 km. apart from one another. Black widow webs were located visually during daylight hours and spiders were captured at night when they were active in their webs (2-3 female spiders per site). Arthropod prey were hand-collected from our desert and urban sites. Because we were primarily interested in the diversity of Sonoran desert arthropod prey and their nutrient value to black widows, we captured any ground-dwelling arthropod prey species that came within 20 m^2 of a widow's web and when possible collected up to three individuals of each prey species. We visited each site twice, randomly over the month, spending three hours each time searching for prey. Arthropods were stored at -20^{o}C for later chemical analysis (see below).

Laboratory Reared Samples. In order to establish a baseline for black widow stoichiometry, we put F1 spiders (offspring of urban-caught females) on a controlled laboratory diet wherein they fed solely on laboratory-reared *G. sigillatus*. Following egg sac emergence, we housed offspring communally for two weeks. During this period, each family was fed 20 flightless fruit flies (*Drosophila melanogaster*) twice weekly, and no attempt was made to limit cannibalism among widows. After two weeks, surviving juvenile spiders were separated to avoid cannibalism and raised individually in transparent plastic boxes (4 x 4 x 5 cm.) on three fruit flies twice weekly for a month. At that time, we shifted to weekly feedings of an individual cricket (50-75% of the focal female's mass) until spiders reached sexual maturity.

One hundred and thirty, F2 generation, *G. sigillatus* were reared to adulthood on an *ad libitum* diet of Purina Cat Chow® and water. Ten of these crickets were used for chemical analysis at adulthood (see below). The remaining 120 crickets were used to feed the F1 generation, adult female *L. hesperus* (n = 20) described above. These spiders were fed a cricket (75- 100% of focal female spider's mass) weekly for four weeks before being assigned to one of two feeding treatments (n = 10 spiders per treatment). The first group of black widows continued to feed on a cricket (75- 100% of focal female's mass) weekly for four weeks, while their counterparts were fed an adult female black widow (75-100% of the focal female's mass) weekly for four weeks. Black widows used as conspecific prey for the first three feedings (weeks 1-3) were F1 generation spiders reared under the same conditions as focal females (see above). For the final conspecifics feeding (week 4), black widows used as prey were captured from the field. These field-caught spiders were captured from urban habitat 1-2 molts from maturity and fed a diet of only laboratory-reared *G. sigillatus* before being used as prey. One week following the fourth (final) feeding, all twenty focal spiders were stored at -20^{o}C for later chemical analysis (see below).

Sample Preparation and C and N Determination. All arthropod samples were dried at 60^{o}C for 120 hours. Dried arthropods from 2011 and the laboratory diet regime were weighed to the nearest hundredth of a milligram using a Sartorious M5P microbalance. Arthropod prey were then ground individually into a homogenous powder using a Spex Certiprep 800 D ball mill. Widows were not ground into a homogenous powder because they more readily ground into a paste. To access carbon (C), nitrogen (N), and phosphorus (P) body content we used a sub-sample of each body segment (cephalothorax, abdomen, and legs). Approximately 5 mg of powder (2.5 mg for C & N analysis and 2.5 mg for P analysis) from each individual prey were used to access C and N and P body content. Some prey individuals from our 2011 field collection failed to produce 5 mg. of powder. These individuals were combined with other individuals of the same species to allow us to assess the stoichiometry of this taxa rather than the stoichiometry of individuals. If we had more than one individual from a species that was large enough to be sampled individually, we used average values for a stoichiometric measure per species. We used a PerkinElmer 2400 CHN elemental analyzer to quantify C and N contents (percentage of dry mass). Percent recovery in C and N assays were determined by comparison to apple leaves and Acetanilide standards (obtained from the U.S. National Institute of Standards and Technology, U.S. Department of Commerce).

Phosphorus Analysis. We measured total P content in widows and crickets from the 2010 field collection and laboratory diet manipulation by microwave acid digestion (CEM MARS 5, Arizona State University, AZ, U.S.A.). Analysis was performed spectrophotometrically on an inductively coupled plasma optical emission spectrometer (ICP-OES; Themo iCAP6300, Arizona State University, AZ, U.S.A.). Total P was converted to percentage of dry mass for comparative purposes. This method was chosen because it yields a higher percent recovery of P compared to other common methods (see Tanner et al., 1999). Two milliliters of concentrated HNO_3 (70 % by weight) was added to each individual sub-sample. After cooling, the solution was transferred to a 20-mL volumetric flask and diluted to volume with Nano water. Percent recovery in P assays was determined by comparison to bovine muscle standards (obtained from the U.S. National Institute of Standards and Technology, U.S. Department of Commerce).

Statistical Analysis. All statistical tests were performed in SPSS (Ver. 17.0 for Windows® SPSS, Chicago, IL, USA). The Shapiro-Wilk goodness-of-fit test was used to ensure that data met normality assumptions. Elemental percents were log10(x+1) transformed to meet assumptions of normality. Unless otherwise noted, all tests were done on the following list of dependent measures: % C, % N, % P, C: N, C: P and N: P.

We used a univariate ANOVA to test for spatial variation (collection site as a random factor) in both widow and prey populations. Additionally, we used a univariate ANOVA to test for an effect of diet type (field caught versus laboratory diets) on nutrient values. Paired t-tests were used to examine stoichiometric differences between predators and prey. Linear regressions were run to look for (1) relationships between predator and prey stoichiometry, (2) relationships between stoichiometry and biotic parameters measured in Trubl et al. (2012) (see Appendix A), (3) if C: N ratios were influenced by body size (measured as dry mass (mg.)) in widows from desert and urban habitats and (4) if C: N: P was influenced by body size in widows from the laboratory diet regime. As we performed multiple tests (n = 6 stoichiometric measures) in many of these analyses, we employed a Bonferroni correction (0.05/6 = 0.008) to account for the inflated probability of finding a significant difference.

Results

Stoichiometry of Black Widow Spiders and Crickets Collected from Urban Habitat (2010).

Body size is a strong predictor of C: N ratios in black widow spiders ($F_{1, 44} = 31.497$, $R^2 = 0.423$, $P < 0.0001$), but not crickets ($F_{1, 23} = 0.306$, $P = 0.586$). In our 2010 field collection across urban Phoenix habitat, black widow spiders exhibited significantly lower C: P ratios (t =17.1; *d.f.* = 9; $P < 0.001$) and N: P ratios (t = 17.0; *d.f.* = 9; $P < 0.001$) when compared to herbivorous cricket prey (Fig. 3a, b). Additionally, spiders were more N (t =3.14; *d.f.* = 9; P = 0.006) and P (t = 24.6; *d.f.* = 9; $P < 0.001$) rich than cricket prey (Fig. 4a, b). Both C: N ratios (t = 2.67; *d.f.* = 9; P = 0.013) and % C (t =2.03; *d.f.* = 9; P = 0.024) were higher in crickets than spiders, but these differences were not statistically different after a Bonferroni adjustment for multiple tests (Fig. 3c, 4c).

We found significant spatial variation across urban Phoenix spider subpopulations in C: N ratios ($F_{9,\,115} = 8.253$, $P < 0.001$, Fig 5a). Crickets showed similar evidence of site variation, but spatial variation in crickets was not statistically significant after a Bonferroni adjustment for multiple tests (Fig. 5b). Additionally, % N of black widows was highly variable across the ten sites ($F_{9,\,119} = 5.561$, $P < 0.001$). In contrast, % C and % P stoichiometry of black widows and crickets did not vary across the greater metropolitan Phoenix area (Table 2). Urban black widow biotic population parameters measured previously (see Appendix A; e.g. prey abundance, spider mass and population density) were poor predictors of urban black widow and cricket stoichiometry (Table 3). In addition, cricket (prey) stoichiometry at each urban site proved to be a poor predictor of the black widow stoichiometry at those sites (Table 4 far left column).

Stoichiometry of Black Widows and Arthropod Prey from Urban and Desert Habitats (2011). Body size was not a significant predictor in C: N ($F_{1,\,41} = 0.053$, $P = 0.820$) ratios of urban prey, but was in desert prey with larger individuals containing higher C: N ratios ($F_{1,\,34} = 20.215$, $P < 0.0001$). The C and N stoichiometry of black widow subpopulations and arthropod prey were not significantly different across our 5 urban sites and our 5 desert sites (Table 5). Perhaps surprisingly, urban black widows did not differ in C, N stoichiometry from desert black widows, and urban arthropod prey did not differ in C, N stoichiometry from desert arthropod prey (Table 6). Because we found no differences between urban and desert black widow stoichiometry, we lumped our 5 urban sites with our 5 desert sites and found that % C ($F_{9,\,26} = 1.332$, $P = 0.292$), % N ($F_{9,\,26} = 1.013$, $P = 0.292$) and C: N ratios ($F_{9,\,26} = 1.004$, $P = 0.473$) did not exhibit site variation among these 10 sites. The C, N stoichiometry of potential arthropod prey collected from these 10 urban and desert sites did not predict black widow stoichiometry (Table 4). Furthermore, potential prey species richness did not differ between desert and urban habitats (t = 1.835; *d.f.* = 4; P = 0.07).

Black Widow Spider and Cricket Stoichiometry Across 2010-2011. Because we found no differences between urban and desert black widow stoichiometry in 2011 (see above) and we found no significant differences between the 2010 and 2011 urban sampling periods (% C: $F_{1, 131}$ = 3.467, P = 0.065, % N: $F_{1, 134}$ = 0.281, P = 0.597, and C: N ratio: $F_{1, 131}$ = 2.057, P = 0.154), we pooled our ten 2010 and ten 2011 sites and found a strong effect of spatial variation in % N ($F_{19, 146}$ = 2.97, P < 0.001; Fig 6a) and C:N ratios ($F_{19, 142}$ = 4.511, P < 0.001; Fig. 6b), but not for % C ($F_{19, 143}$ = 1.838, P = 0.025).

Because crickets from urban sites in 2011 showed no significant spatial variation in % C ($F_{4, 13}$ = 2.445, P = 0.122), % N ($F_{4, 13}$ = 1.790, P = 0.215) and C: N ratio ($F_{4, 13}$ = 1.817, P = 0.210), and cricket stoichiometry from urban sites in 2010 and 2011 did not differ (% C: $F_{1, 109}$ = 1.979, P = 0.162, % N: $F_{1, 109}$ = 0.179, P = 0.673, and C: N ratio: $F_{1, 109}$ = 0.883, P = 0.349), we pooled our 10 sites from 2010 and 5 urban sites from 2011 and found cricket stoichiometry was not significantly influenced by site (% C: $F_{14, 109}$ = 1.697, P = 0.069, %N: $F_{14, 111}$ = 1.557, P = 0.106, & C: N ratio: $F_{14, 109}$ = 2.138, P = 0.016).

Stoichiometric Differences Between Field-caught and laboratory-reared spiders and crickets. Crickets fed a controlled laboratory diet (see Methods) did not differ from crickets collected from urban Phoenix habitat in C: N ($F_{1, 105}$ = 0.565, P = 0.454), C: P ($F_{1, 103}$ = 0.338, P = 0.562), or N: P ($F_{1, 106}$ < 0.001, P = 0.989) ratios. In contrast, laboratory-reared black widow spiders fed solely on laboratory-reared *G. sigillatus* were more C rich and nutrient (N and P) limited than field-captured black widows (urban & desert) that fed on available field prey (Fig. 7). Cannibalism supplementation for this laboratory-reared spider group did not relax N limitation (Fig. 7). In contrast, cannibalism supplementation for this laboratory-reared spider group significantly increased % P ($F_{1,129} = 27.584$, $P < 0.001$) and decreased C: P ($F_{2, 134} = 28.044$, $P < 0.001$) and N: P ($F_{2, 138} = 29.451$, $P < 0.001$) ratios to levels seen in field-caught, urban spiders (Fig. 8).

In the laboratory, black widows fed a diet of only crickets were not more nutrient rich or nutrient poor than the crickets they fed on (N: t =0.937; *d.f.* = 9; P = 0.187, P : t =0.645; *d.f.* = 9; P = 0.2675; C:N : t =1.502; *d.f.* = 8; P = 0.086, C:P : t =0.393; *d.f.* = 8; P = 0.353, N: P : t =0.762; *d.f.* = 9; P = 0.2325). However, black widows fed conspecifics contained more P (t = 4.061, *d.f.* = 8; P = 0.002) and had lower C: P (t = 4.22, *d.f.* = 8; P = 0.002) and N: P (t = 6.17, *d.f.* = 8; $P < 0.001$) ratios than crickets. In these laboratory-reared animals, cricket stoichiometry was a poor predictor of black widow stoichiometry (Table 4, far right column).

Discussion

As expected, urban black widows were significantly more nutrient rich than cricket prey in the field. However, in our laboratory diet regime, spiders fed solely on laboratory-reared crickets were no more nutrient rich or poor than their prey (i.e., laboratory-reared crickets). Subpopulations of spiders and crickets varied in their C and N stoichiometry (but not P) across metropolitan Phoenix. Interestingly, black widow C: N ratios did not significantly differ between desert and urban habitats. Laboratory-reared black widows fed a diet of only laboratory-reared *G. sigillatus* were more N- and

P- poor than black widows that fed freely on available prey in the field. Cannibalism supplementation for these laboratory-reared black widows increased P- richness, but not N- richness, to levels comparable to that seen in field-caught spiders. We discuss the implications of these results below.

Interspecific Stoichiometric Variation. In the laboratory, black widows on a diet of only crickets were not more nutrient rich or nutrient poor than their laboratory-reared cricket prey. However, in the field black widows were more nutrient rich than cricket prey, supporting the notion that carnivorous predators are more N-rich than their herbivorous prey (Fagan et al., 2002; Fagan & Denno, 2004; Fig 3, 4). Possible explanations for differences in N tissue content among trophic levels are detailed elsewhere (Fagan et al., 2002; Denno & Fagan, 2003). Nitrogen differences in body content between herbivores and predators may stem from diet, where predators consume more N than herbivores. Alternatively, herbivores and predators may differentially allocate N to body structures (e.g., muscle versus other lower-N structures) because of foraging strategy (e.g., grazer vs. hunter) or exoskeleton investment (e.g., amount of protein relative to chitin). However, we did not measure the diet nutrient composition of crickets or measure the nutrient composition of different body structures to determine the cause of interspecific stoichiometric variation of black widows and their prey.

Interestingly, we found trophic level differences in P with predators (spiders) containing a higher P body content than herbivores (crickets) in urban habitats (Fig 3, 4). This result is consistent with González et al. (2011) who showed that, on average, invertebrate predators contain higher amounts of P in their tissues than herbivores and detrivores. However, Woods et al. (2004) did not find P tissue content to differ based on trophic level in terrestrial invertebrates. According to Fagan and Denno (2004), consumers that contain more nutrients in their tissues than their food source may face severe nutrient limitation because consumers may not be able to acquire the amount of nutrients essential for growth, tissue maintenance, and reproduction. Since black widows are more nutrient rich than crickets in the field, this would suggest that black widows constrained to a diet of only crickets may be subject to strong nutrient limitation (see below).

Intraspecific Stoichiometric Variation. In addition to the stoichiometric differences between field caught and laboratory-reared spiders discussed above, we also found significant C and N variation across urban-locales. Cricket prey showed a similar site effect for C and N stoichiometry (Fig 5). Body size and phylogeny are often strong predictors of variation in invertebrate stoichiometry, but these results are mixed across invertebrate taxa (Fagan et al., 2002; Woods et al., 2004; Bertram et al., 2008; Martinson et al., 2008; Hambäck et al., 2009; Visanuvimol & Bertram, 2010; González et al. 2011). In particular, body size in invertebrates often has a negative relationship with body stoichiometry, where larger individuals contain fewer nutrients (e.g., N & P) in their tissues than smaller individuals. The relationship between N body content and body size in insects is thought to arise from differential dilution by low-N gut content (Fagan et al., 2002). It does not appear that the intraspecific nutrient variation we document here is explained by body size in crickets. However, in black widows body size can account for 42% of the variation in C: N ratios. Surprisingly, the wet mass of black widows showed significant spatial variation across the 10 urban subpopulations (see Appendix A), but was a poor predictor of black widow stoichiometry (Table 3). Additionally, we did not find any environmental variation that could explain nutrient variation across locales. Future work should incorporate environmental differences (e.g., water supplementation &

productivity) among sites in relation to intraspecific stoichiometric variation of urban pest species across sub-habitats.

Similarly, in aquatic systems, spatial variation significantly influences the intraspecific stoichiometric variation of predatory arthropods (e.g., damselflies & back swimmers; Tsoi et al., 2011) and fish (e.g., guppies & Neotropical stream fish; El-Sabaawi et al., 2012a; 2012b). In these studies, environmental conditions such as the overall biogeochemical setting (El-Sabaawi et al., 2012a) and variability in food quality (El-Sabaawi et al., 2012b) are determinants of organismal stoichiometry more so than lineage, body size, or life-history phenotype. However, the biotic variables (female mass, population density & prey abundance) that varied across the 10 black widow subpopulations (see Appendix A) did not significantly predict black widow stoichiometry (Table 3).

The shift in body stoichiometry of black widows from the field (allowed to feed on available prey) versus black widows in the laboratory (constrained to a single-species diet) may be an adaptation to cope with potential nutrient limitation. Shifts in body stoichiometry such as these may contribute to the success of invasive species. For example, an invasive species, the zebra mussel (*Dreissena polymorpha*) may be able to reduce nutrient limitation by shifting their tissue stoichiometry in response to changes in the elemental composition of their food source allowing them to exploit novel environments (Naddafi et al., 2009). The potential for black widows to shift their body stoichiometry may contribute to the underlying success of black widows (e.g., infestations; see Appendix A) in novel environments such as urban ecosystems.

Differences in interspecific and intraspecific organismal stoichiometry of consumers can have important implications for differential nutrient cycling in ecosystems (Elser & Urabe, 1999). Notably, predators are starting to receive attention for their role in regulating nutrient cycling (Schmitz et al., 2010). Specifically, spiders indirectly regulate nutrient cycling via predation of herbivores (i.e., reduces rates of herbivory) and nutrients derived from their debris (e.g., feces, silk, prey carcasses) (Hodkinson et al., 2001; Romero et al., 2006; 2008a; Gonçalves et al., 2011). Furthermore, the role that spiders play in nutrient cycling can be spatially dependent. For example, Bromeliad plants in open grassland systems depend on spiders for N and the amount of N in plants is positively correlated with spider density (Romero et al., 2008b). Indeed, we have previously shown that population density of black widows varies across locales (Appendix A). Thus, the relationship between locale and stoichiometric variation in organisms may contribute to differences in nutrient cycling across urban sub-habitats.

Arthropod C and N Stoichiometry from Urban and Desert Habitats. C and N stoichiometry in black widow spiders from urban and desert habitats revealed that urban black widows are no more nutrient poor or rich than their desert counterparts. Arthropod diversity available as prey for black widows is reported to be higher in desert habitats relative to urban Phoenix habitats (Bang & Faeth, 2011). In contrast, urban widows are subject to decreased prey diversity but increased abundance of a limited number of arthropod prey species. Nevertheless, urban black widows are able to maintain N levels in their tissues despite the presumed reduced prey diversity.

It is conceivable that the diversity of arthropod prey available to urban black widows may be greater than previously thought. Indeed, our censuses revealed only a slight, non-significant increase in prey diversity for desert sites relative to urban sites (Table 1). More striking within this limited sample was the presence of outlier sites within each habitat type that harbored twice the prey diversity seen at other sites. This latter finding suggests that spatial variation within urban habitat (caused, for example, by differential water or N supplementation across city municipalities) may be greater than variation across urban and desert habitats. For instance, in the laboratory diet regime, black widows fed only crickets had significantly higher C: N ratios (i.e., lower N body content) than the 10 urban sub-populations combined (Fig 7). However, in comparing the C: N ratios of laboratory spiders fed only crickets to the C: N ratios of the 10 urban spider subpopulations individually, there were a few sites (e.g., GY & BE, see Fig 6) that did not differ in C: N ratios from the C: N ratios of the laboratory diet regime. These results suggest that prey species composition may vary widely across urban sub-habitats causing variation in C: N ratios across the urban landscape. Future work needs to begin from the premise that urbanization leads to spatial heterogeneity within the urban landscape, and continue to search for the variables (abiotic & biotic) that drives this patchiness.

Additionally, C: N ratios of arthropod prey available to black widows did not vary between urban and desert habitats. As expected, body size in arthropod prey was a strong predictor of prey C: N ratios in desert habitats with larger individual prey containing lower C: N ratios (i.e., lower N body content) than smaller individual prey. However, body size in arthropod prey was a poor predictor of prey C: N ratios in urban sub-habitats. One explanation for the release of body size as a determining factor in urban arthropod C: N ratios may stem from a surplus of N typical of urban environments. Within urban Phoenix, human-mediated N inputs are an order of magnitude higher than N inputs in surrounding Sonoran desert habitat (Baker et al., 2001). In an aquatic system, human- mediated nutrient inputs increased consumer nutrient composition (Singer & Battin, 2007). However, we did not find urban arthropod prey to be more nutrient rich than desert arthropod prey.

Alternatively, measuring the entire N content of prey from urban and desert habitats may be a poor predictor of what is available for spider consumption. Black widow spiders partake in extra oral digestion and as a result, cannot digest N that may be stored in the exoskeleton (e.g., chitin) of arthropod prey (Cohen, 1995; Foelix, 1996; Denno & Fagan, 2003; Wilder & Eubanks, 2010). Indeed, black widows are known to "waste" much of the prey biomass they take (Trubl et al., 2011), though it is unknown if this discarded prey contains valuable nutrients. Discarded prey remains from the spider *Pisaura mirabilis* contained similar amounts of C and N compared to the C and N contents of whole prey (Lang & Klarenberg, 1997). Similarly, spiders did not ingest all the protein content available across a range of prey types and the percent of protein that spiders were able to ingest varied by prey species (Wilder et al., 2009; Wilder & Rypstra, 2010). Determining the amount of nutrients black widows select from different prey species in urban and natural environments may explain the lack of differences in C: N ratios of black widows despite differences in prey species diversity.

Laboratory Diet Influences on Black Widow Stoichiometry. Laboratory-fed black widows were significantly more nutrient limited than black widows captured from urban and desert field sites (see Fig 7). Notably, despite the presumed lack of prey diversity in urban habitat (Bang & Faeth, 2011), urban black widows were significantly more nutrient rich than laboratory-raised spiders fed on a single prey type. Indeed, our laboratory spiders were not only more nutrient poor than field spiders, but they were also no more nutrient rich than their food source, laboratory-raised crickets. Multiple prey species diets increase growth, development and survival in many generalist predators (Bilde & Toft, 2000; Oelbermann & Scheu, 2002). In contrast, generalist predators on a single species diet experience reduced survival and reproduction compared to mixed diets (Evans et al., 1999; Toft & Wise, 1999). Here, we show that nutrient limitation is one mechanism underlying the poor performance of organisms on restricted diets. Thus, a single prey species diet like the one we provided for spiders in the laboratory, and which many arthropod ecologists rely upon for their laboratory populations, may not provide adequate nutrients required for optimal growth and reproduction for generalist predators.

Cannibalism Influences on Black Widow Stoichiometry. Several studies suggest that intraguild predation (including cannibalism) may serve as a mechanism for consumers to deal with N limitation (Wolcott & Wolcott 1984; Denno & Fagan, 2003; Okuyama, 2008). However, our results suggest that cannibalism does not alleviate N- limitation in black widows. In contrast, to our knowledge this is the first study to show cannibalism as a mechanism relaxing P limitation. Our data suggest that laboratory-reared spiders allowed to cannibalize show increased P levels comparable to the P levels found in field-caught spiders (Fig. 8). Phosphorus is an element tightly linked to the growth rate of invertebrates (Elser et al., 2001; Perkins, 2004, Jeyasingh & Weider, 2007; Huberty & Denno, 2006). Recently, dietary P availability has been linked with reproduction in *Daphnia* with low P diets causing reduced egg size and egg survival (Urabe & Sterner, 2008). However, when comparing P demand over ontogeny in *Daphnia,* juveniles required more P than adults for reproduction (Nakazawa, 2011).

Understanding P demand over ontogeny for higher trophic levels may help predict community dynamics. For example, if juvenile spiders require more P, then they may be more likely to engage in intraguild (e.g., cannibalism) predation than adult spiders, suppressing predatory arthropod populations. Additionally, adult spiders that are P-limited, perhaps from a low diversity diet, may partake in cannibalism to acquire P for reproduction. Therefore, environments dominated by a single prey species (including laboratory environments and perhaps all heavily disturbed environments) are likely to present arthropod predators with P limitation. Cannibalism may offer a means to cope with P limitation. Thus, population growth of nutrient-limited spiders may suffer both in terms of the direct effects of nutrient limitation on growth, survival and reproduction, and the indirect effects of nutrient-limited spiders cannibalizing each other.

Conclusion

In conclusion, black widows are successful urban exploiters. Here we have shown that black widows may thrive in urban habitats, in part, by their ability to deviate from a strict elemental composition when restricted to a single- species diet. Additionally, cannibalism may be a behavioral mechanism for black widows to cope with P-limitation in urban sub-habitats that house fewer prey species. Black widows are important to ecosystem processes in urban habitats because of their potential to regulate insect populations and differentially regulate nutrient cycling across urban sub-habitats. Future work should study how shifts from elemental homeostasis influence black widow performance and reproduction across urban sub-habitats. The integration of population dynamics and ecological stoichiometry is an area which can identify the mechanisms that drive urban exploiter populations and ultimately shape biodiversity patterns in urban ecosystems. Thus, work in this area can lead to better management strategies in controlling urban exploiter populations to maintain or even increase biodiversity. Additionally, understanding how HIREC impacts ecosystem processes such as food web dynamics and nutrient cycling can lead to maintaining ecosystem health in highly disturbed environments.

Table 1. Description of black widow spider collection sites in 2011 from urban and desert sub-habitats in Arizona.

Site	Habitat Type	Habitat Description	Prey Species Richness
CB	Urban	Commercial sub-habitat with xeric landscaping	3
ME2	Urban	Commercial sub-habitat with xeric landscaping	7
TE2	Urban	Commercial sub-habitat with xeric landscaping	3
DT	Urban	Commercial sub-habitat with xeric landscaping	3
GC	Urban	Commercial sub-habitat with xeric landscaping	4
AF	Desert	Desert wash	4
PE	Desert	Desert wash	8
EC	Desert	Mountain with rocky outcroppings	7
CF	Desert	Desert wash	2
TU	Desert	Desert wash	7

*Table 2. Carbon, nitrogen, and phosphorus stoichiometry of black widow spiders and crickets collected in 2010 across the greater metropolitan Phoenix, AZ area. P-value marked with * indicates statistically significant value after Bonferroni correction (P = 0.008).*

Organism	Stoichiometry	Mean ± SE	ANOVA
Black Widow Spider	% C	48.018 ± 0.558	$F_{9, 117} = 2.758$, $P < 0.01$
	% N	11.88 ± 0.123	$F_{9, 119} = 5.561$, $P < 0.001$*
	% P	1.386 ± 0.04	$F_{9, 119} = 0.43$, $P = 0.062$
	C : N	4.099 ± 0.072	$F_{9, 115} = 8.253$, $P < 0.001$*
	C : P	37.38 ± 1.169	$F_{9, 117} = 1.775$, $P = 0.081$
	N : P	9.14 ± 0.193	$F_{9, 119} = 0.937$, $P = 0.496$
Decorated Cricket	% C	50.06 ± 0.198	$F_{9, 95} = 1.176$, $P = 0.321$
	% N	10.95 ± 0.084	$F_{9, 97} = 2.039$, $P = 0.044$
	% P	0.765 ± 0.008	$F_{9, 96} = 1.9$, $P = 0.062$
	C : N	4.594 ± 0.042	$F_{9, 95} = 2.488$, $P = 0.014$
	C : P	66.67 ± 0.791	$F_{9, 93} = 1.574$, $P = 0.136$
	N : P	14.56 ± 0.189	$F_{9, 96} = 2.061$, $P = 0.042$

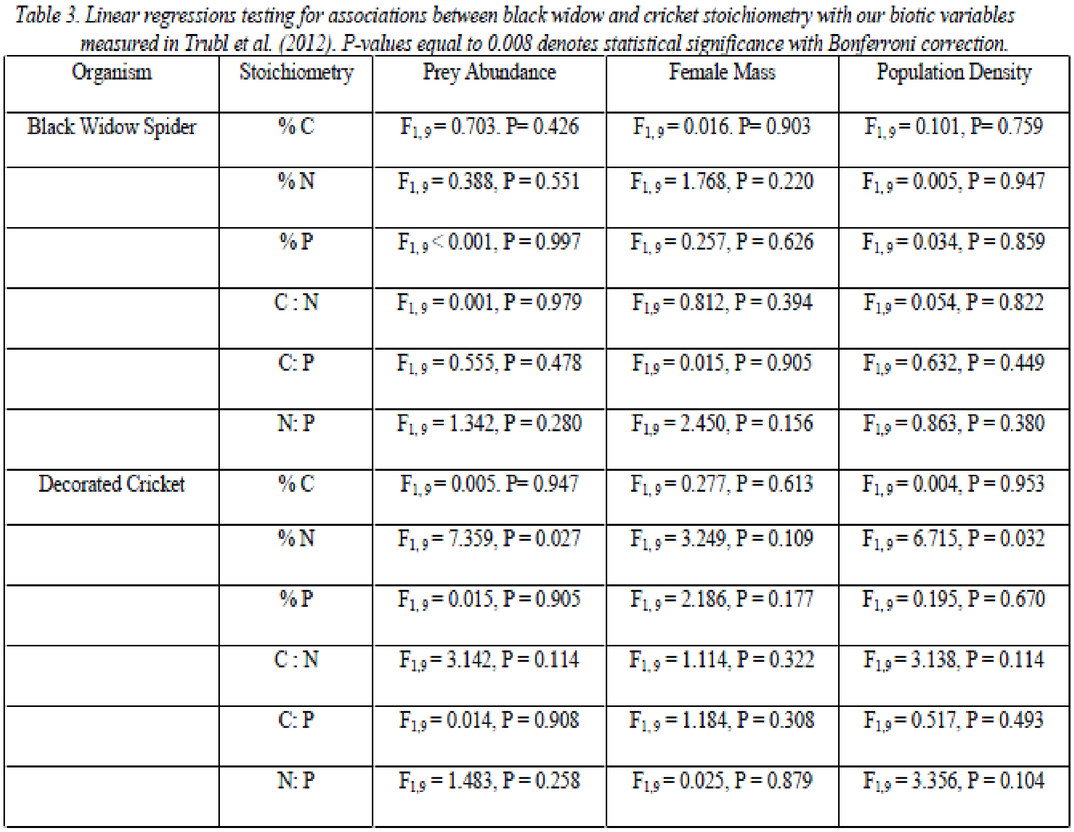

Table 3. Linear regressions testing for associations between black widow and cricket stoichiometry with our biotic variables measured in Trubl et al. (2012). P-values equal to 0.008 denotes statistical significance with Bonferroni correction.

Organism	Stoichiometry	Prey Abundance	Female Mass	Population Density
Black Widow Spider	% C	$F_{1,9} = 0.703$. P= 0.426	$F_{1,9} = 0.016$. P= 0.903	$F_{1,9} = 0.101$, P= 0.759
	% N	$F_{1,9} = 0.388$, P = 0.551	$F_{1,9} = 1.768$, P = 0.220	$F_{1,9} = 0.005$, P = 0.947
	% P	$F_{1,9} < 0.001$, P = 0.997	$F_{1,9} = 0.257$, P = 0.626	$F_{1,9} = 0.034$, P = 0.859
	C : N	$F_{1,9} = 0.001$, P = 0.979	$F_{1,9} = 0.812$, P = 0.394	$F_{1,9} = 0.054$, P = 0.822
	C: P	$F_{1,9} = 0.555$, P = 0.478	$F_{1,9} = 0.015$, P = 0.905	$F_{1,9} = 0.632$, P = 0.449
	N: P	$F_{1,9} = 1.342$, P = 0.280	$F_{1,9} = 2.450$, P = 0.156	$F_{1,9} = 0.863$, P = 0.380
Decorated Cricket	% C	$F_{1,9} = 0.005$. P= 0.947	$F_{1,9} = 0.277$, P = 0.613	$F_{1,9} = 0.004$, P = 0.953
	% N	$F_{1,9} = 7.359$, P = 0.027	$F_{1,9} = 3.249$, P = 0.109	$F_{1,9} = 6.715$, P = 0.032
	% P	$F_{1,9} = 0.015$, P = 0.905	$F_{1,9} = 2.186$, P = 0.177	$F_{1,9} = 0.195$, P = 0.670
	C : N	$F_{1,9} = 3.142$, P = 0.114	$F_{1,9} = 1.114$, P = 0.322	$F_{1,9} = 3.138$, P = 0.114
	C: P	$F_{1,9} = 0.014$, P = 0.908	$F_{1,9} = 1.184$, P = 0.308	$F_{1,9} = 0.517$, P = 0.493
	N: P	$F_{1,9} = 1.483$, P = 0.258	$F_{1,9} = 0.025$, P = 0.879	$F_{1,9} = 3.356$, P = 0.104

Table 4. Linear regressions testing for associations between arthropod prey stoichiometry and black widow stoichiometry in field and laboratory populations.

Stoichiometry	Urban 2010 (crickets)	Urban-Desert 2011 (mixed)	Laboratory (crickets)
% C	$F_{1,9} = 1.449$, $P = 0.263$	$F_{1,11} = 0.157$, $P = 0.700$	$F_{1,8} = 0.368$, $P = 0.563$
% N	$F_{1,9} = 3.301$, $P = 0.107$	$F_{1,11} = 2.263$. $P = 0.163$	$F_{1,9} = 0.102$, $P = 0.757$
% P	$F_{1,9} = 1.243$, $P = 0.297$	-	$F_{1,9} = 0.002$, $P = 0.969$
C :N	$F_{1,9} = 1.881$, $P = 0.207$	$F_{1,11} = 2.857$, $P = 0.122$	$F_{1,8} = 0.017$, $P = 0.899$
C: P	$F_{1,9} = 0.044$, $P = 0.838$	-	$F_{1,8} = 1.067$, $P = 0.336$
N: P	$F_{1,9} < 0.001$, $P = 0.988$	-	$F_{1,9} = 0.504$, $P = 0.498$

Table 5. Carbon and nitrogen stoichiometry of black widow spiders and arthropod prey collected in 2011 across an urban and desert gradient.

Organism	Habitat Type	Stoichiometry	ANOVA
Black Widow Spider	Urban	% C	$F_{4,14} = 1.111$, $P = 0.404$
		% N	$F_{4,14} = 2.796$, $P = 0.085$
		C:N	$F_{4,14} = 1.507$, $P = 0.272$
	Desert	% C	$F_{4,11} = 1.133$, $P = 0.414$
		% N	$F_{4,11} = 0.388$, $P = 0.811$
		C:N	$F_{4,11} = 0.581$, $P = 0.686$
Arthropod Prey	Urban	% C	$F_{4,19} = 1.709$, $P = 0.2$
		% N	$F_{4,19} = 0.914$, $P = 0.481$
		C:N	$F_{4,19} = 1.483$, $P = 0.257$
	Desert	% C	$F_{4,29} = 1.709$, $P = 0.179$
		% N	$F_{4,29} = 0.716$, $P = 0.589$
		C:N	$F_{4,29} = 1.332$, $P = 0.286$

Table 6. Black widow spiders and arthropod prey do not differ in their carbon and nitrogen stoichiometry between urban and desert habitats.

Organism	Stoichiometry	ANOVA	Urban Mean ± SE	Desert Mean ± SE
Black Widow Spider	% C	$F_{1, 26} = 2.714$, $P = 0.112$	44.9 ± 0.872	47.2 ± 1.09
	% N	$F_{1, 26} = 0.153$, $P = 0.699$	12.1 ± 0.347	11.9 ± 0.462
	C:N	$F_{1, 26} = 0.153$, $P = 0.699$	3.8 ± 0.214	4.06 ± 0.211
Arthropod Prey	% C	$F_{1, 49} = 0.099$, $P = 0.755$	48.3 ± 0.63	48.6 ± 15.5
	% N	$F_{1, 49} = 0.224$, $P = 0.638$	11.9 ± 4.14	11.7 ± 6.68
	C:N	$F_{1, 49} = 0.070$, $P = 0.793$	4.14 ± 0.149	4.19 ± 3.11

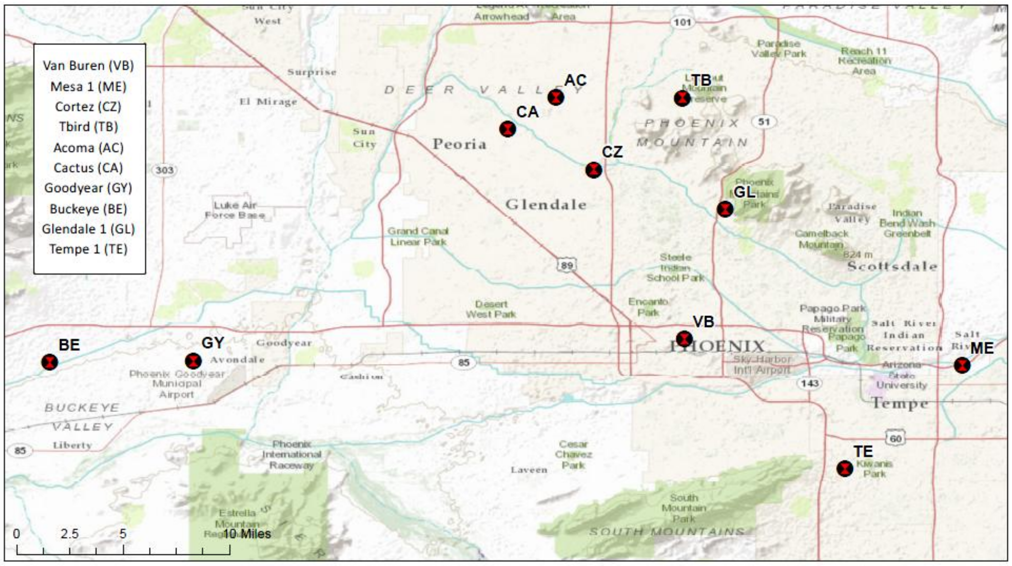

Figure 1. A map of the urban black widow subpopulations from 2010 studied in Phoenix, AZ.

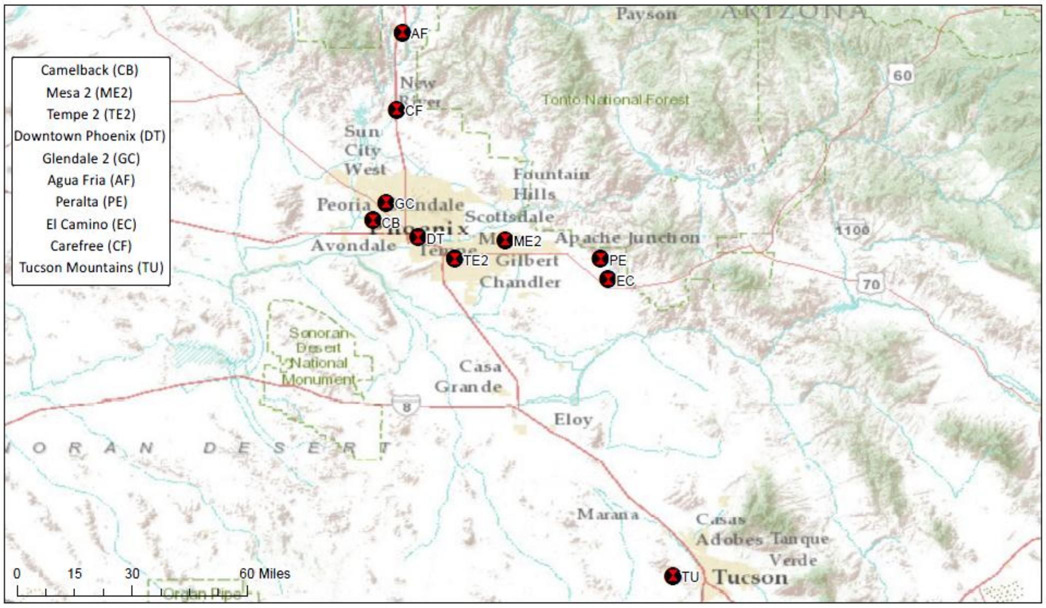

Figure 2. A map of the urban and desert black widow subpopulations from 2011 studied in Arizona.

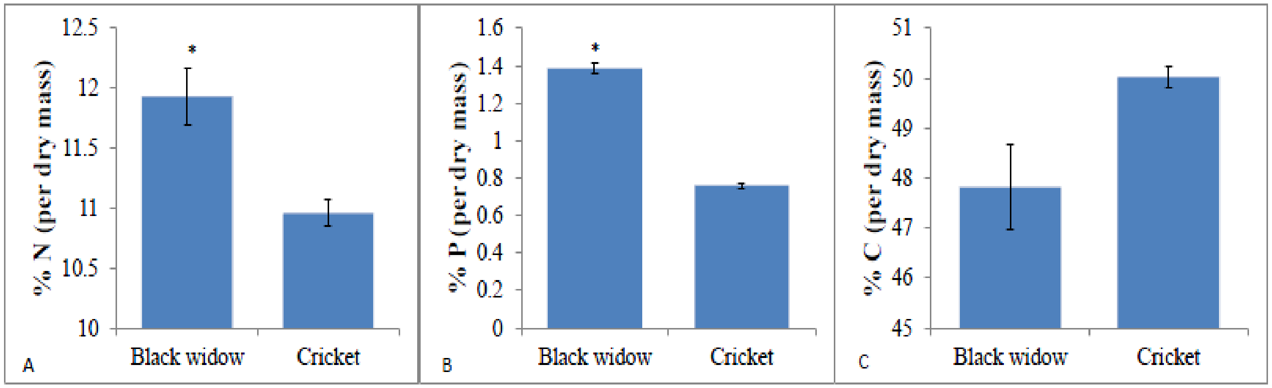

Figure 3. Black widows are more a N (t =3.14; *d.f.* = 9; P = 0.006) and b P (t =24.609; *d.f.* = 9; P < 0.001) rich and contain less c C (t =2.03; *d.f.* = 9; P =0.024) than herbivorous cricket prey. Values represent mean ± se. Asterisk above columns denote significant (P = 0.001) differences between treatment groups.

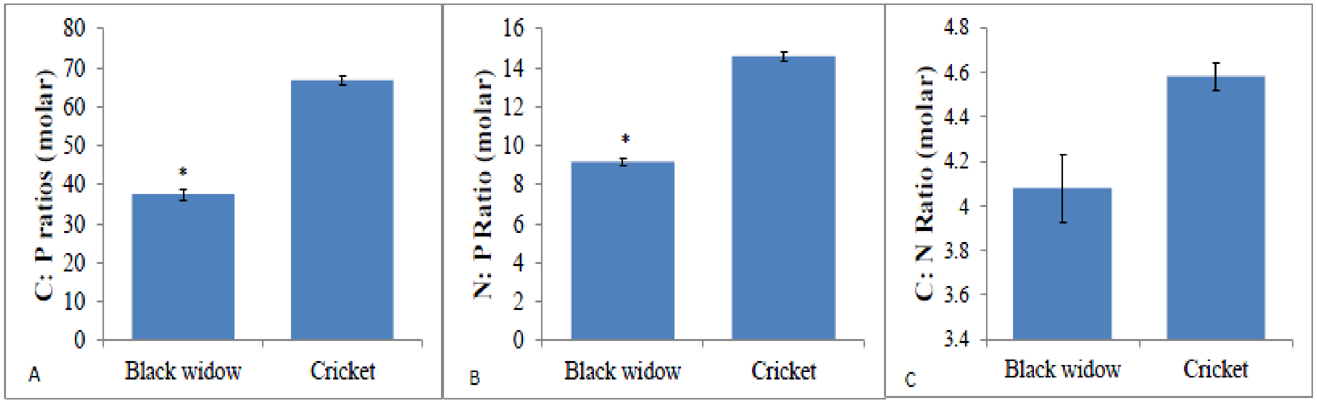

Figure 4. Black widows contain lower a C: P (t =-17.156; *d.f.* = 9; $P < 0.001$), b N:P (t = -17.047; *d.f.* = 9; $P < 0.001$) and c C:N (t =2.67; *d.f.* = 9; P = 0.013) ratios than herbivorous cricket prey. Values represent mean ± se. Asterisk above columns denote significant (P = 0.001) differences between treatment groups.

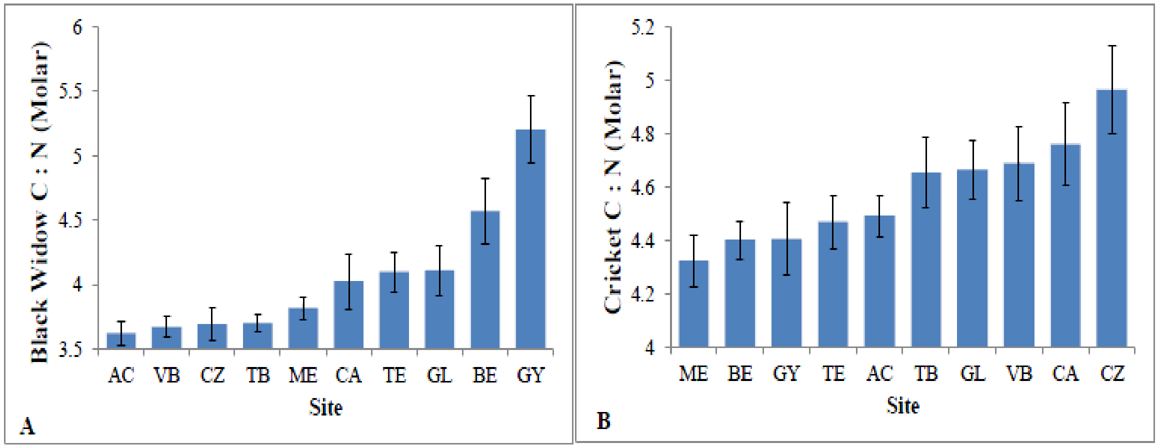

Figure 5. Spatial variation in the C: N ratios among a. urban black widow spider subpopulations ($F_{9,115} = 8.253$, $P < 0.001$) (N = 8-14 females/site) b. urban adult cricket subpopulations ($F_{9,95} = 2.488$, $P = 0.014$) (N= 8-11 adults located within metropolitan crickets/site) Phoenix, AZ, U.S.A. Values represent mean ± se. For location of sites on the x axis, see Trubl et al. (2012).

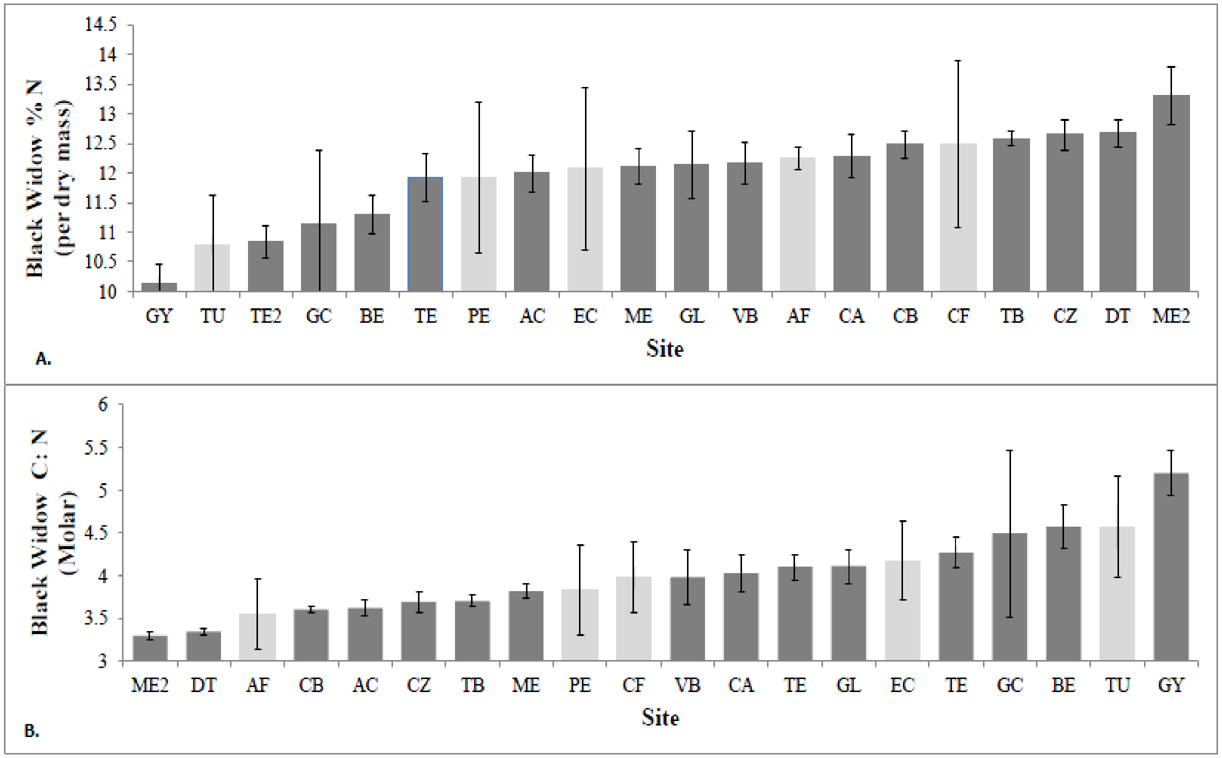

Figure 6. Spatial variation in C:N ratios among black widow spiders from 2010 and 2011 across an urban-desert gradient (N = 2-14 females/site). a. Percent nitrogen content ($F_{19, 146}$ = 2.97, $P < 0.001$) and b. C:N ratios ($F_{19, 142}$ = 4.511, $P < 0.001$). Values represent mean ± se. For location of sites on the x axis, see table 1, 2. Light gray bars denote desert sites and dark grey bars denote urban sites.

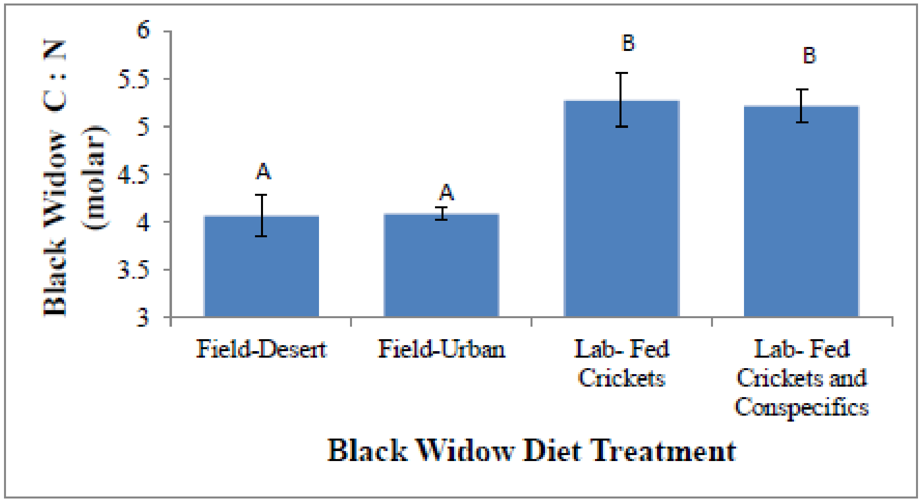

Figure 7. Cricket and conspecific laboratory diets create nitrogen limitation in black widows when compared to black widows feeding freely on avaliable prey in urban and desert habitats. Stoichiometry of urban and desert widows (N = 12-120) on a field diet were compared to lab-reared spiders fed a diet of only lab-reared crickets (N = 9) and spiders fed a diet of crickets and lab-reared black widow spiders (N = 10). Values represent mean ± se. Letter differences above columns denote significant (P = 0.001) differences between treatment groups ($F_{2,133} = 17.218$, $P < 0.001$).

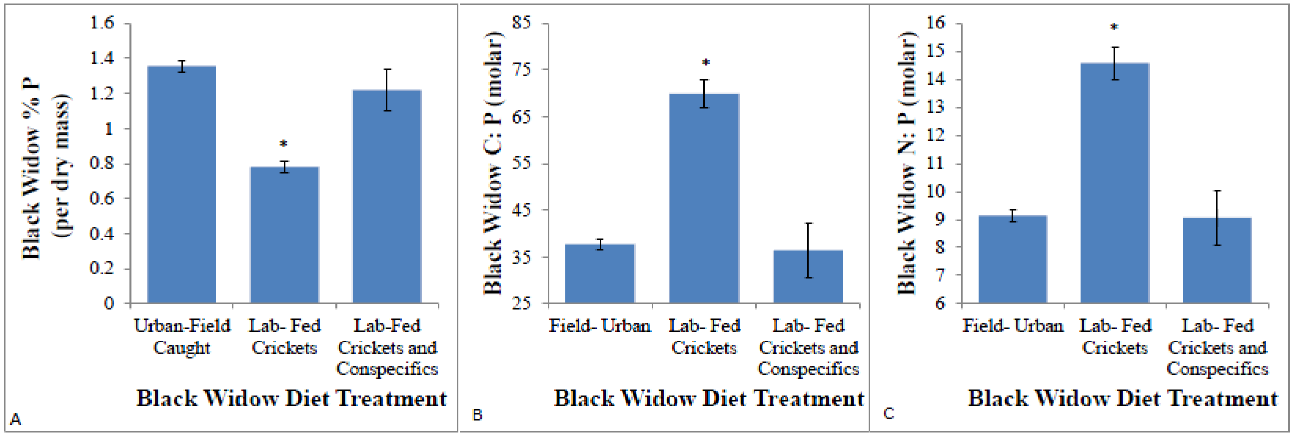

Figure 8. Cannibalism diet supplementation decreases phosphorus, but not nitrogen limitation in lab-reared black widow spiders when compared to urban-field caught black widows. Stoichiometry of urban widows (N = 113-120) on an urban field diet were compared to lab-reared spiders fed a diet of only lab-reared crickets (N = 9-10) and spiders fed a diet of crickets and lab-reared black widow spiders (N = 10). Values represent mean ± se. Asterisk above columns denote significant (P = 0.001) differences between treatment groups a % P ($F_{1,129}$ = 27.584, P < 0.001) b C:P ratios ($F_{2,134}$ = 28.044, P < 0.001) and c N:P ratios ($F_{2,138}$ = 29.451, P < 0.001).

Chapter 3

GENERAL DISCUSSION

In my thesis work, I focused on two research topics that integrated the population and ecosystem ecology of an urban exploiter, the western black widow spider. Here, I have shown that female back widows form infestations across the greater Phoenix metropolitan area. Within urban habitat, black widow subpopulations are significantly influenced by site in terms of female mass and population density. Additionally, the prey abundance within a site was a strong determinant of female mass and population density. Furthermore, I used ecological stoichiometry to view the potential role that black widow infestations may play in ecosystem functioning across urban sub-habitats. Black widows exhibit significant levels of intraspecific stoichiometric variation (1) across urban sub-habitats and (2) among spiders reared in the laboratory on single- and mixed- species diets. These results suggest that black widow infestations are driven by bottom up resources across urban sub-habitats. Additionally, the ability for black widows to deviate from an elemental homeostasis may, in part, contribute to the success of this urban exploiter.

Organisms showing plasticity in nutrient homeostasis may be more likely to adapt to variable environments such as urban environments (Persson et al., 2010). For example, the zebra mussel is an invasive species that is able to shift its body nutrient ratios in response to changes in the nutrient composition of their food (Naddafi et al., 2009). The shift in nutrient requirements may allow for zebra mussels to invade novel environments with low nutrient availability. Similarly, black widows were able to shift their elemental body composition when fed a single- and mixed- species diet. In the field, black widows were more nutrient rich than their cricket prey. Then in the laboratory, black widows were similar in their nutrient composition as their cricket prey. This deviation from elemental homeostasis may allow for black widows to thrive in urban sub-habitats that house high abundances of a few arthropod prey species (e.g., crickets, reduced nutrient availability).

Persson et al., (2010) reviewed the regulation of nutrient homeostasis among consumer taxa and found that the degree of variation from strict homeostasis cannot be identified as a group or even species-level trait. Instead, the degree of variation from nutrient homeostasis is determined by both biology and environmental factors. For example, in black widow subpopulations across metropolitan Phoenix, AZ, site is a strong determinant of C: N ratios, whereas this relationship was not as strong in predicting cricket C: N ratios. Indeed 42% of the variation in C:N ratios of black widows can be contributed to body size, where some sites housed heavier widows with less N body content (i.e., higher C:N ratios) than other sites. However, within the 10 urban subpopulations collected in 2010, female wet mass and prey abundance were a poor predictor of black widow C: N ratios. This result suggests that prey quantity is more important in housing dense infestations of heavy, fecund females. However, our laboratory diet regime suggests that black widows may alleviate nutrient limitation from poor prey quality through behavioral mechanisms such as cannibalism. Future work should integrate the behavioral and physiological mechanisms involved in the inter- and intra-specific elemental composition of urban pest species across urban sub-habitats.

Much work remains to be done in determining the mechanisms that allow for urban exploiters to thrive in urban habitats, ultimately changing biodiversity patterns across sub-habitats. The nutrient composition of urban exploiters is one approach in understanding how some species are able to thrive over others in urban habitats. However, as we have seen here and in other works, there are many aspects of biology and environment that may influence the nutrient composition of an organism. Additionally, understanding the role that urban exploiters partake in ecosystem functioning across sub-habitats can lead to better management planning to maintain or limit pest populations. Ultimately, understanding how urban exploiters thrive as a result of HIREC can better inform conservation strategies in increasing biodiversity and ecosystem functioning in highly disturbed environments.

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APPENDIX A

BLACK WIDOW SPIDERS IN AN URBAN DESERT: POPULATION VARIATION IN AN ARTHROPOD PEST ACROSS METROPOLITAN PHOENIX, AZ

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Black widow spiders in an urban desert: Population variation in an arthropod pest across metropolitan Phoenix, AZ

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Abstract The effects of urban disturbance are critical to understand, as the majority of the world's population now resides in urban centers. For example, urbanization often leads to reduced species diversity at the expense of a few urban-adapted taxa. However, it remains unclear why some taxa thrive following human disturbance whereas others do poorly. The western black widow spider, *Latrodectus hesperus,* thrives in disturbed, urban habitat—often forming dense aggregations (i.e., infestations) relative to typical low-density, desert populations. We examined the population dynamics of ten black widow aggregations spread across metropolitan Phoenix, AZ, during the peak of the breeding season (June–August). Here we show that prey abundance, female mass, web volume and population density exhibit minimal temporal variation across the breeding season, but that prey abundance, female mass and population density show significant spatial variation across the ten urban aggregations. Our measure of prey abundance and foraging success, the number of prey carcasses found in black widow webs, shared a strong positive relationship with female mass and population density, but not with web volume. Surprisingly, female mass, web volume and population density were not correlated with each other. The abiotic variables we measured at each site did a poor job of explaining black widow population parameters, although we did find a marginal trend for more recent developments to harbor denser black widow aggregations. Our findings support the generalization that urbanization heightens spatial variation, and we suggest that local urban prey abundance is influential in promoting urban infestations full of heavy, fecund female black widows. Studies of the population ecology of urban pests are necessary to identify the mechanisms allowing some species to thrive following human disturbance while much native biodiversity is lost following urbanization.

Keywords *Latrodectus hesperus* · Urbanization · Spatial variation · Population dynamics

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Introduction

Understanding the impacts of 'human-induced rapid ecological change' (HIREC) has recently been described as a 'grand challenge' for ecologists (Sih et al. 2010). Given that half the world's population now lives in urban centers, and this figure is projected to increase 19% over the next 40 years (United Nations Population Division 2007), we need to understand the effects of urbanization on ecosystems. Generally, urbanization is thought to result in the loss of native species diversity at the expense of a handful of urban-adapted taxa termed 'urban exploiters' by Blair (1996). Thus, urbanization is thought by many to result in the biological homogenization of urban environments (Blair 1996; McKinney 2006). However, urban habitat should not be thought of as monotypic environments. Indeed, urbanization can result in a variety of sub-habitats, and the result is not always decreased diversity (Mckinney 2008; Van Keer et al. 2010). Thus, the mechanisms by which urban exploiters can locally dominate urban ecosystems, thus reducing native species diversity in many cases, need to be better understood (Bonier et al. 2007; Shochat et al. 2010).

Recent studies suggest that urban environments can exhibit a dampening of temporal variation (reviewed in Shochat et al. 2006), thought to arise from 1) an urban heat island effect (Hinkel et al. 2003) that results in decreased seasonal variation in temperatures (i.e., warmer winters) and/or 2) year-round water supplementation (Shochat et al. 2004). Both urban aseasonality and year-round water supplementation are factors that increase urban primary productivity, and this heightened resource availability may favor urban exploiters over many other taxa (Shochat et al. 2006). For example, the house gecko (*Hemidactylus frenatus*), an invasive urban exploiter, is thought to have displaced the native gecko species *Lepidodactylus lugubris* by outcompeting it for preferred (large) prey that are associated with urban habitat (Petren et al. 1993; Petren and Case 1996). Thus, the artificially inflated levels of productivity associated with urbanization may favor the competitive efforts of urban exploiters.

In contrast, spatial variation may have the opposite effect, as variation in disturbance patterns within the urban landscape can lead to fragments of distinct urban habitat at various spatial scales. For example, at a broad scale, fish assemblages differ among urban habitats across California watersheds (Marchetti et al. 2006). One reason suggested for these diversity differences across watersheds is the presence/absence of highly competitive invasive species (Marchetti et al. 2006). At a finer scale, species diversity of carabid beetles varies over a rural–urban gradient within Hiroshima City, Japan (Ishitani et al. 2003). Specifically, beetle abundance and species richness decreases in urban habitat relative to rural areas. However, Ishitani et al. (2003) notes that this pattern seen within Hiroshima City is not universal because cities differ in their 1) age, 2) spatial structure/configuration and 3) intensity of human disturbance. Consequently, urban populations may vary greatly from each other to the extent that urbanization causes habitat fragmentation.

Most obviously, staggered development in urban areas leads to variation in habitat age and intensity of disturbance, and this can lead to variation in urban biodiversity (Crooks et al. 2004). For example, urbanization has been used as a vehicle to test the intermediate disturbance hypothesis (Connell 1978). Areas of moderate urban disturbance have been suggested to support the highest species diversity (Blair 1996, 1999; Blair and Launer 1997). For example, Blair (1999) found more species of birds and butterflies in intermediately developed sites relative to highly urbanized or undisturbed sites. However, McKinney (2008) suggests that an intermediate disturbance hypothesis predicts urban diversity for plants better than it does for invertebrates and non-avian vertebrates. In line with this taxonomic emphasis, bird abundance is often highest in intermediately developed sites

(Blair 1999, 2004), whereas butterfly abundance declines as a site becomes more developed (Blair 1999). Thus, the degree of local urban disturbance affects species abundance differently for different taxa.

Arthropod communities have received much attention over the past decade as an indicator for environmental disturbance (e.g. urbanization) because they have short generation times, are speciose and occupy multiple trophic levels (McIntyre 2000). Moreover, recent studies suggest that habitat structure and land use within urban environments can shape the composition and trophic dynamics of arthropod communities (McIntyre et al. 2001; Marussich and Faeth 2009). In particular, spiders are key predators that control insect populations in disturbed and undisturbed ecosystems (Riechert and Bishop 1990; Shochat et al. 2004). Within urban habitat, increased productivity is often associated with decreased spider diversity but heightened abundances of a subset of spider taxa (Shochat et al. 2004; but see Van Keer et al. 2010 for an example of heightened urban spider diversity). Shochat et al. (2004) found that water supplementation (e.g. agriculture and mesic residential landscaping) in Phoenix, AZ, supports a lower diversity of spider taxa but a higher abundance of wolf spiders (Lycosidae) relative to desert remnants and xeric landscaping. Thus, the transformation of the Sonoran desert into Phoenix has resulted in reduced spider diversity, and the emergence of a few spider taxa that thrive in the disturbed environment and have become very abundant.

The western black widow spider (*Latrodectus hesperus*) is native to the Sonoran desert and thrives in disturbed, urban habitat throughout the desert southwest including the Phoenix, AZ, metropolitan area. Widow spiders were not found to be a superabundant urban exploiter in Phoenix by Shochat et al. (2004), presumably because the sampling protocols they utilized (e.g. pitfall trapping) failed to adequately represent web-building spiders like black widows that spend most of their time in webs or in hard- to- access refuges (see below). Indeed, the black widow is a pest species in Phoenix because of both its propensity to form dense populations in urban areas (see data below) and the toxicity of its venom to humans (Lewitus 1935; Brown et al. 2008). Female widow spiders build large, 3-dimensional cobwebs that usually include a refuge (e.g. underside of a bench, crevice in a block wall) and strong, prey-ensnarement draglines that are attached to the ground (Johnson et al. 2011; Zevenbergen et al. 2008). We examined the urban population dynamics of the western black widow spider throughout the peak of its breeding season (June–August) across replicate sites within metropolitan Phoenix, AZ. Here, we test the general hypothesis that urban population dynamics are characterized by low temporal variation and high spatial variation. Thus, we predict that prey abundance, female web volume, female body condition and the population density of black widows within an aggregation will exhibit: 1) little variation across the breeding season (June–Aug) and 2) significantly more variation between aggregations than within an aggregation. Moreover, we predict that the four biotic variables listed above are likely to be positively correlated such that sites with abundant prey will support dense aggregations of high-condition females that are able to build and maintain large webs. Lastly, we predict that variation in abiotic factors (e.g. age of development, ground cover type and web-building substrate) may also predict black widow population parameters.

Methods

Study area

Phoenix, AZ, was the second fastest- growing- city in the United States over the past decade (24.6% increase), currently estimated to house 6.4 million people (United States Census

2010). Here, the Sonoran desert has rapidly undergone an extreme land transformation into urban habitat (e.g. agriculture, industry and residences; Knowles-Yanez et al. 1999). As a result, Phoenix is an urban ecosystem typified by increased local temperatures, supplemental water usage, decreased biodiversity and altered food webs compared to surrounding, undisturbed Sonoran desert habitat (reviewed in Shochat et al. 2006). Phoenix is an ideal laboratory of urban ecology and HIREC given the speed at which it has become urbanized (Knowles-Yanez et al. 1999) and this is a focus of the Central Arizona-Phoenix Long-Term Ecological Research (CAP-LTER) project.

Site selection

Ten black widow aggregations across the greater Phoenix metropolitan area were monitored during the peak of their breeding season (June–August) in 2010 (see Fig. 1). Sites were chosen to represent a broad sample across urban Phoenix. Although we did not intentionally follow sites along an urban-desert continuum, our sites nevertheless varied widely in both biotic and abiotic parameters (see Table 1 and Fig. 1). Sites were followed if they met the following criteria: 1) sites had to be a minimum of 8 km apart from one another and 2) sites had to contain a minimum of 10 females (within 5,000 m^2) in the initial census. All sites were commercial subhabitats with xeric landscaping. Sites were censused biweekly for population density. Webs were located visually and, if spiders were in refuge, we confirmed that the web was occupied by dangling live prey in the web until the web's occupant emerged.

Habitat description

All sites ran parallel to a road and had a wall (made of cement, brick, or pipe) as a backdrop. We quantified percent of impervious ground cover and vegetation abundance at each site using five replicate, 5 m × 5 m (25 m^2) plots that were randomly distributed across the site. Sample plots were always initiated at the base of the wall running parallel to the road as this was the structure that most spiders used to build their web. We also measured the length of

Fig. 1 A map of the urban black widow aggregations studied in Phoenix, Arizona

Table 1 Summary data for black widow aggregations throughout Metropolitan Phoenix, AZ

Aggregation	% Impervious surface	% Vegetation	Wall length (m)	Age of development (years)	Female mass (mg)	Female web volume (m^3)	Spider density (per m^2)	Prey abundance (per focal web)
Van Buren (VB)	39.67±14.85	1.66±0.93	739.81	11	170.72±25.03	0.3±0.07	0.0256	3.20
Thunderbird (TB)	41.66±12.13	6.28±5.97	182.5	12	198±0.27	0.29±0.06	0.0053	1.36
Mesa (ME)	80±16.33	0	188.55	2	245.2±23.02	0.33±0.03	0.15	14.26
Goodyear (GY)	8.94±8.92	1.11±0.69	179.28	8	255.98±19.91	0.14±0.01	0.0387	6.61
Tempe (TE)	4.92±4.20	23.13±5.67	174.57	12	189.2±28.41	0.15±0.03	0.0066	2
Glendale (GL)	37.05±2.1	22.04±3.07	15.5	53	171.74±10.41	0.28±0.05	0.015	0.99
Buckeye (BE)	6.18±3.80	2.35±2.29	159.62	5	190.72±27.34	0.45±0.05	0.054	4.03
Cortez (CZ)	30.66±10.79	0	2821.1	38	229.39±14.56	0.2±0.04	0.006	4.82
Cactus (CA)	80.28±3.72	7.42±2.69	275.05	25	137.33±18.72	0.24±0.05	0.0241	1.52
Acoma (AC)	35.84±4.08	8.42±5.14	384.08	41	184.68±12.26	0.34±0.06	0.013	6.73

wall available at each site. The age of development for each site was obtained from county parcel data and expressed as the number of years elapsed from site development to 2010.

Focal females

Ten female widows per site were randomly chosen and monitored weekly. Focal females were uniquely marked on the dorsum with Testor's® non-toxic enamel paint to allow us to confirm their identity across the season. Focal female webs were censused weekly for prey carcass abundance. Females were then captured and weighed (mg). We minimized damage to webs by dangling live prey in the web to lure females to the edge of their web for safe capture. Although females were absent from their webs we measured the dimensions (L × W × H cm) of each web and calculated web volume in mm^2. In the event that a focal female went missing she was replaced with a randomly chosen female. Focal females were determined to be missing if they had not emerged after 10 min of live prey dangling in the web and if there were visual indications of web abandonment (e.g. absence of new threads). Data were only included in analyses if females were present for a minimum of three consecutive weeks.

Statistical analysis

SPSS software (Ver. 17.0 for Windows® SPSS, Chicago, IL, USA) was used for all statistical analyses, and summary statistics presented are mean ± standard error. Repeated-measures ANOVA was employed to test for seasonal variation in prey abundance, population density, female mass and web volume. Univariate ANOVA was used to test for spatial variation (collection site as a random factor) using prey abundance, population density, female mass and web volume as dependent measures. Linear regressions were run to look for relationships among these biotic factors, as well as the abiotic habitat variables listed in Table 1. All data were normally distributed unless otherwise noted. One of our sites proved to be an outlier for many variables (site ME in Table 1 and Fig. 1). We include this dense infestation in all of the analyses below, as its exclusion did not change our finding that sites vary significantly.

Results

Biotic and abiotic variables measured at each site are summarized in Table 1. Figure 1 provides a map of urban Phoenix and the locations of our sites. Repeated-measures ANOVA showed no effect of temporal variation (seasonality within the breeding season) on prey abundance ($F_{2,\ 18}=2.17$, $p=0.18$), population density ($F_{4,\ 8}=2.42$, $p=0.13$), female mass ($F_{2,\ 200}=0.60$, $p=0.62$) or web volume ($F_{2,\ 201}=0.55$, $p=0.59$). In other words, widow population parameters changed very little across the breeding season. Thus, we averaged each measure across the season to look for spatial differences among urban sites. Across Phoenix, our ten sites proved to be highly variable in terms of prey abundance ($F_{1,\ 9}=12.957$, $p=0.006$), female mass ($F_{9,\ 200}=4.54$, $p=0.006$) and population density ($F_{9,\ 41}=165.63$, $p<0.001$; Fig. 2). Web volume showed similar evidence of site variation, but these differences were not significantly different ($F_{9,\ 201}=2.24$, $p=0.086$).

Relationships between the biotic and abiotic variables measured at each site are summarized in Table 2. Very few of these relationships proved statistically significant. However, prey abundance shared a positive relationship with both female mass ($R^2=0.4665$, $F_{1,8}=6.995$ $p=0.029$) and population density ($R^2=0.7276$, $F_{1,8}=21.368$ $p=0.002$; Fig. 3). This

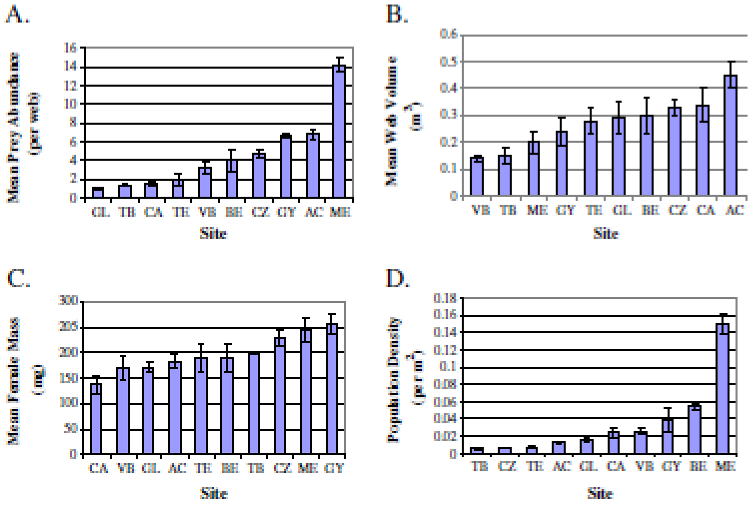

Fig. 2 Spatial variation in biotic variables among black widow spider aggregations. **a** Mean number of prey items per focal female web ($F_{1,9}$=12.957, p=0.006). **b** Mean web volume (N=6–17 webs/site) ($F_{9,\ 201}$=2.24, p=0.086). **c** Mean female spider mass (N=6–17 females/site) ($F_{9,\ 200}$=4.54, p=0.006). **d** Mean population density (N=3–5 measures per site) ($F_{9,\ 41}$=165.63, p<0.001)

latter relationship between prey abundance and population density was the only result in Table 2 that proved marginally significant after employing a conservative Bonferroni adjustment for the multiple tests run. Nevertheless, we also found a trend for a site's age (time since development) to influence black widow population density such that newer developments (more recent disturbance) house denser widow aggregations (R^2=0.2403, $F_{1,8}$=4.924, p=0.062). Age of development was log-transformed to meet normality assumptions (Shapiro-Wilk test: W=0.9488, n=10, p=0.6541).

Discussion

The limited snapshot of temporal variation across the breeding season measured here did not yield significant differences across the season. In contrast, the results from this study support the contention that urban habitats are spatially heterogeneous and that this variation can be significant even at the relatively small spatial scales studied here (see Fig. 1). We found significant effects of spatial variation on prey abundance, female mass and population density. In addition, prey abundance was positively related to both female mass and population density. Lastly, we found a trend for more recently disturbed habitats to support denser black widow populations.

Most notable in our dataset is the extent to which habitats within urban Phoenix varied spatially from each other. Perhaps it should not be surprising that human disturbance creates distinct, and sometimes pronounced, habitat fragmentation. Date of development, socio-economic status, land-use type, mode of irrigation, landscaping type/frequency and pesticide

Table 2 Linear regressions testing for associations between our abiotic and biotic variables

	% Impervious surface	% Plant cover	Wall length (m)	Age of site (years)	Web volume (m^3)	Female mass (mg)	Prey abundance (per web)	Population density (per m^2)
% Impervious surface	–	R^2=0.051 $F_{1,8}$= 0.425 p=0.533	R^2=0.004 $F_{1,8}$= 0.03 p=0.860	R^2=0.001 $F_{1,8}$= 0.084 p=0.779	R^2=0.024 $F_{1,8}$= 0.20 p=0.667	R^2=0.044 $F_{1,8}$= 0.37 p=0.56	R^2=0.123 $F_{1,8}$= 1.124 p=0.320	R^2=0.230 $F_{1,8}$= 2.398 p=0.16
% Vegetation		–	R^2=0.142 $F_{1,8}$= 1.32 p=0.284	R^2=0.187 $F_{1,8}$= 1.94, p=0.201	R^2=0.067 $F_{1,8}$= 0.572 p=0.471	R^2=0.205 $F_{1,8}$= 2.07 p=0.188	R^2=0.277 $F_{1,8}$= 3.07 p=0.117	R^2=0.176 $F_{1,8}$= 1.71 p=0.226
Wall length (m)			–	R^2=0.091 $F_{1,8}$= 1.02 p=0.342	R^2=0.0563 $F_{1,8}$= 0.477 p=0.509	R^2=0.059 $F_{1,8}$= 0.499 p=0.500	R^2=0.008 $F_{1,8}$= 0.002 p=0.964	R^2=0.058 $F_{1,8}$= 0.499 p=0.5
Age of development (years)				–	R^2=0.0078 $F_{1,8}$= 0.546 p=0.481	R^2=0.121 $F_{1,8}$= 2.38 p=0.161	R^2=0.119 $F_{1,8}$= 4.63 p=0.063	R^2=0.262 $F_{1,8}$= 13.29 p=0.007
Web volume (m^3)					–	R^2=0.209 $F_{1,8}$= 1.48 p=0.258	R^2=0.035 $F_{1,8}$= 0.295 p=0.602	R^2=0.124 $F_{1,8}$= 1.273 p=0.292
Female mass (mg)						–	R^2=0.4602 $F_{1,8}$= 6.82 p=0.031	R^2=0.209 $F_{1,8}$= 2.40 p=0.160
Prey abundance (per web)							–	R^2=0.74 $F_{1,8}$= 22.7 p=0.001

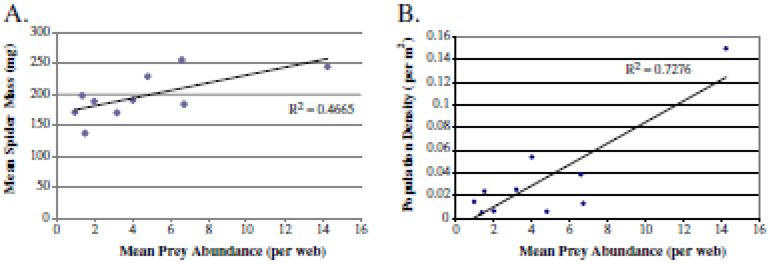

Fig. 3 Prey abundance has a positive relationship with a body mass ($F_{1,8}$=6.995 p=0.029) and with b population density ($F_{1,8}$=21.368 p=0.002)

use are but a few examples of the ways in which Phoenix neighborhoods differ from each other. The composition of arthropod communities is known to vary across urban sub-habitats depending on many of these factors (Bolger et al. 2000; McIntyre et al. 2001; Cook and Faeth 2006). The black widow aggregations we found tended to be concentrated in commercial areas containing xeric landscaping. Thus, black widow habitat preferences appear to eliminate a great deal of the available urban habitat variation. Nevertheless, even within these commercial habitats, we found significant site variation in prey abundance, female mass and population density.

A common theme in the literature on urban ecology is the suggestion that species richness and/or abundance decrease in highly disturbed urban habitat and peak in moderately disturbed urban habitats (e.g. carabid beetle richness, Alaruikka et al. 2002; butterfly richness, Blair and Launer 1997). Perhaps the spatial variation we documented in black widow population parameters can be attributed to the notion that widows thrive best in areas of moderate disturbance. Anecdotally, we noticed that our densest sites were the ones that had a unique disturbance regime, such that irrigation and impervious surfaces were abundant, but human traffic (e.g. landscaping) was minimal. In support of this, our densest aggregation was found adjacent to a car dealership in southeast Phoenix (site ME in Figs. 1 and 2 and Table 1). The ground cover at this site was 80% cement and this site had the highest prey abundance, but we noted anecdotally that this area experienced almost no human disturbance via landscaping. Thus, urban environments that minimize impervious surfaces (concrete) and are not irrigated but that include regular landscaping may be best suited to reduce black widow population growth.

Our indirect measure of widow prey abundance/foraging success was a good predictor of female mass and population density. Thus, we provide support for the bottom-up view that population growth in this urban pest is regulated by prey availability. The arthropod prey being found in black widow webs (primarily crickets, cockroaches, ants and beetles) are likely responding to local water supplementation (Cook and Faeth 2006), but surprisingly we found no relationship between the prevalence of vegetation at a site (an indirect indicator of water supplementation) and black widow populations. We have previously shown that black widows readily track prey availability in urban habitats by using foraging kairomones that shape microhabitat preferences for areas laden with chemical cues from common urban prey (Johnson et al. 2011). Thus, taken together, our results suggest xeric landscaping with native, drought-adapted plants that do not require water supplementation would be an excellent choice for any homeowner, business or municipality eager to limit the population growth of black widows and their prey.

Our prey carcass measure of prey availability is admittedly an indirect estimate and has at least one drawback. Many of the females studied here maintained their refuge in small crevices such as a pipehole on the side of a block wall. Narrow refuges such as this made it impossible for us to census prey carcasses that had been taken by the spider back into the recesses of their retreat. As such, our indirect measure is certainly an underestimate of foraging success, but we have no reason to believe this estimate is biased in favor of certain sites over others. Our more direct, traditional attempts to measure prey availability through pitfall traps were unsuccessful. Most importantly, our traps were routinely disturbed by pedestrians and groundskeepers, and this effect is likely to be biased heavily towards sites that experienced significant human traffic.

Relaxed prey limitation is not the only hypothesis that could explain the spatial patchiness of urban black widow population success. For example, pollution and heavy metal stress limits the reproductive output of a European wolf spider (Hendrickx et al. 2003, 2008). Alternatively, urban black widows may face variation in the risk that their enemies (predators and parasites) pose. We did not quantify enemy risk in this study as it remains unclear what the black widow's primary enemies are. Most obviously, black widows are cannibalistic (e.g. 5 conspecific prey found in webs in this study), and the explosive population growth of urban populations may eventually be limited by intraspecific competition and/or cannibalism. Alternatively, our laboratory studies note that black widows are readily consumed by the Mediterranean house gecko, (*Hemidactylus turcicus*), a superabundant urban, invasive species in Phoenix (Johnson et al. 2011). Our field censuses also provide anecdotal evidence that frit flies (Chloropidae) are a regular parasite on black widow egg sacs from undisturbed Sonoran desert habitats but not on egg sacs from urban Phoenix habitats. Future work should begin to construct an urban food web including black widows and attempt to discern what, if any, urban organisms present a significant constraint to black widow population growth.

In conclusion, urban Phoenix aggregations of black widows are spatially distinct in terms of their prey abundance, average female mass and population density. In contrast, within sites, these variables do not differ significantly across the breeding season. Thus, black widows reinforce the generalization that urban disturbance reduces seasonality and introduces spatial differentiation. Our future efforts will be focused on further identifying the urban variables that promote local population growth/decline. These works will both inform local communities on how to manage their urban ecosystem to discourage black widows without the use of pesticides, as well as add to our conceptual understanding of what factors make some species outstanding urban exploiters at the expense of biodiversity.

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APPENDIX B

PERMISSIONS FROM CO-AUTHORS

Appendix A, Black widow spiders in an urban desert: Population variation in an arthropod pest across metropolitan Phoenix, AZ was coauthored with Theresa Gburek, Lindsay Miles and J. Chadwick Johnson. The coauthors have given permission for the inclusion of this study in this thesis