

Spiders in a Desert City: What the Behavior and Microclimate of  
Western Black Widows Can Teach Us About the Impacts of Urbanization

by

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## ABSTRACT

As the planet is rapidly urbanizing, understanding the ecological effects of urbanization is a grand challenge for modern biology. For example, increased city temperatures known as the urban heat island effect, disproportionately impact nocturnal taxa and this consideration is widely overlooked. Slight shifts in the thermal microclimate have a cascade of ramifications that directly impact species density and distribution. Animal behavior is a trait that may explain why some species thrive after urbanization when others go locally extinct. In this study I followed 22 adult females of the western black widow, *Latrodectus hesperus*, from both urban and undisturbed Sonoran Desert habitats. First, I began looking for differences between urban and desert spiders under field conditions: boldness, voracity, web size and body condition. Both urban and desert spiders were then brought to the laboratory to see how their behavior changed. I found no behavioral differences between urban and desert spiders in the field or the laboratory. I did find that spider behavior differed between the field and the laboratory. Specifically, boldness in the laboratory was significantly lower compared to the field. Voracity was more repeatable in the laboratory versus the field, and boldness was strongly positively correlated with voracity in the laboratory, but not in the field. These behavioral shifts from the field to the laboratory favor the conclusion that black widow behavior is highly plastic and context dependent. Lastly, I monitored web temperature of black widow microhabitat continuously for an entire year using iButton data loggers. I found microhabitat temperatures differences between urban and desert sites were greatest at night and absent during the daytime. I uncovered a seasonal effect with the highest

magnitude temperature difference occurring during the springtime. Additionally, behavior was significantly correlated with field temperatures; the boldest spiders come from the warmest webs. However, I found little evidence that temperature predicts spider body condition or voracity, and body condition does not predict its behavioral expression. My results highlight the importance of studying animal behavior to increase understanding of the factors that shape distribution and density in a lethal pest species.

## DEDICATION

To my mother Susie: for a lifetime worth of sacrifice that you have accumulated to afford me a better life and always believing in my endeavors.

To my wife Valerie: for your inspiration to pursue a meaningful existence and your willingness to endure my constant quest for knowledge. I am forever grateful to you for lending unwavering support.

To my girls Alexis and Lumen: for allowing me to view the world through innocent eyes once again and giving me the motivation to help shape a bright future for all the critters that call this place home.

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## CHAPTER 1

# RELATIVE BEHAVIORAL PLASTICITY IN BLACK WIDOW SPIDERS: BEHAVIORAL DIFFERENCES BETWEEN URBAN AND RURAL SPIDERS IN BOTH THE FIELD AND LABORATORY

### **Introduction**

Understanding the threats that organisms encounter when faced with human induced rapid environmental change (HIREC) is a grand challenge for ecologists in the Anthropocene (Sih et al., 2010; 2011). Urban habitats are considered prominent features of the Earth's surface and are one of the most prevalent examples of HIREC (Vitousek et al., 1997). It is estimated that by the year 2050, 68.4% of the human population will live in urban areas, in contrast to 55.3% in 2018 (United Nations, 2018). Urbanization in the United States is most rapid in the southern and western regions of the country, particularly in the desert Southwest where population growth from 1950 to 2010 outpaced the United States as a whole by twice as much per decade (Mackun, 2019). Thus, the study of urbanization helps us understand how to promote wildlife coexistence in the human-dominated world.

Alterations to the natural landscape due to urbanization include converting vegetation into novel structures, fragmenting habitat with roads and buildings, adding pollution from light, sound, and chemicals, increasing disturbance regimens created by humans, and the widespread dispersal of exotic species (McKinney, 2002, 2006; Shochat et al., 2006; Sih et al., 2011). Some of these changes can lead to the phenomena known as the “urban heat island effect” (UHI). This occurs when urban temperatures are



significantly elevated compared to surrounding rural areas (Benita et al., 2015; Oke, 1978). In 101 cities sampled across Asia and Australia, the UHI rated an average temperature difference of 4.1 °C (Santamouris, 2020). Urban heat island intensity has been found to be greatest during the nighttime (Benita et al., 2015) and during dry seasons (Jauregui et al., 1992; Kim & Baik, 2002), which makes arid regions particularly vulnerable to a greater magnitude temperature difference. Based on statewide annual precipitation for the previous century, six of the ten driest states in the U.S. are among the Southwest region including the top four; Nevada, Arizona, Utah, and New Mexico (NOAA, 2021). This makes the U.S. desert Southwest an ideal location to study UHI impacts on microclimates.

As natural habitat becomes altered via urbanization, species richness and evenness are impacted. Humans directly modify biodiversity by habitat fragmentation, the introduction of non-native species, habitat loss and by changing water availability, soil composition and the immediate urban microclimate (Kowarik, 2011). Generally speaking, for all taxa groups under intense urbanization (in city cores), species richness is reduced in comparison to more natural rural areas (Lagucki et al., 2017; McKinney, 2008; Piano et al., 2020; Shochat et al., 2010). Some studies, however, have reported neutral (Christie and Hochuli, 2009; Saari et al., 2016) and even positive UHI-biodiversity relationships (Hill et al., 2017; Paul and Myer, 2001). This ambiguity in biodiversity with relation to urbanization is a compelling finding to fuel the further study of urbanization.

In addition to richness, abundance is also transformed with similar varying results. In a desert city, due to supplemental year-round irrigation, higher than normal arthropod abundances can be supported during the naturally dry seasons when these desert species would normally be dormant or absent in the undisturbed wildland (Bang and Faeth, 2011). In some instances, an increased arthropod (prey) abundance, allows spider densities to brim due to a relaxation of competition for prey (Gardiner et al., 2021). On the other hand, niche theory states that abundance can also be limited by either abiotic or biotic factors (Pocheville, 2015). For instance, adverse microclimate conditions that fall outside an ectotherms thermal niche can restrict activity, reproduction, and foraging which can all lead to population declines (Sinervo et al., 2010). As more urban areas are being created to facilitate the ever-growing human population, preserving biodiversity becomes increasingly meaningful.

Native species challenged by urbanization typically go locally extinct if they are poorly adapted to the urban conditions, or they persevere and ultimately benefit from urbanization if they are preadapted to the urban conditions. (Lee & Thornton, 2021; McDonnell & Hahs, 2015; Shochat et al., 2006, 2010). Understanding how these few urban winners can capitalize on these novel environments and in some cases arrive at population densities found nowhere else in nature has profound significance. For one, the species can be viewed as a pest, which is defined as a plant or animal that causes annoyance or harm to humans or their property. There are many pests that present a human health concern due to the transmission of diseases, impact on human agriculture and some even hold safety concerns over biotoxicity (Robinson, 1996). These concerns

are often followed by a strategy that requires abrupt intervention and ultimately eradication. The ramifications of this can be detrimental to the biological community as a whole. Secondly, knowledge of the mechanisms that allow species to become abundant is the first step in reconciliation ecology and conservation management (Rosenzweig, 2003). Completely controlling the population size of many species is impossible yet being able to manage some of the population may give enough room from other taxa to exist (Shochat et al., 2010). Yet it remains unclear the mechanism contributing to this split in the taxa post-urbanization and what provides the ability for some to endure the HIREC (Shochat et al., 2006).

Animal behavior may help explain why some animal populations decline and go locally extinct and others thrive in urban areas. One way that sheds light on the ability to cope with ecological change is the capacity to modify behavior and life histories through adaptive behavioral plasticity (Ditchkoff et al., 2006). Certain behaviors are suggested to be beneficial to city life and can help with understanding how these individuals persist and thrive. For example, boldness demonstrates an individual's inclination to take risks, and some taxa living within urbanized environments are bolder than rural conspecifics (Miranda et al., 2013; Scales et al., 2011; Uchida et al., 2019). However, bold individuals are often also more active in urbanized situations. This increased activity could positively impact foraging success, help maintain territory or assist in finding a mate (Réale et al., 2007; Sol et al., 2013; Sprau and Dingemanse, 2017). Although, being bold also has its disadvantages and is likely not advantageous to all species experiencing urbanization. Thus, predictions of boldness will vary across taxa and the urban-rural gradient.

Just one singular behavior may not be representative of a species' success following urbanization, but rather a suite of behaviors working together. Such suites of correlated behaviors are termed “animal personality” or “behavioral syndromes” (Bell, 2007; Gosling, 1998; Kaiser and Müller, 2021; Sih et al., 2004). Behavioral syndromes are defined as consistent individual variation that is correlated across functional contexts (Bell, 2007; Réale et al. 2007; Sih et al., 2004; Steinhoff, 2020). Certain selection pressures might favor a specific set of correlated behaviors in urban ecosystems, potentially explaining explosive population growth. For instance, *Anolis sagrei* lizards found in urban environments were less aggressive, had shorter fleeing distances, and increased their time spent visually exploring novel environments when compared to their rural populations (Lapiedra et al., 2017). Behavioral syndromes like this can promote fitness advantages under different ecological contexts. Alternatively, some behavioral syndromes may be poorly suited to urbanization and result in population declines/extirpation.

Repeatability of a behavioral trait suggests selection for a precise behavior type within an environment. Whereas the absence of repeatability in behavior traits might indicate plasticity, which may be advantageous to endure urbanization as suggested above (Wolf and Weissing, 2012). It remains to be seen if urban success is most often explained by behavioral plasticity or behavioral syndromes suited to urban habitat (Briffa et al., 2008; Sih et al., 2004).

As noted above, studies have documented animals living in disturbed urban ecosystems differing in their behaviors from those inhabiting the complimentary rural

environments. While the majority of urban organism studies have focused on vertebrates (e.g. herpetofauna: Batabyal and Thaker, 2019; Halfwerk et al., 2019; mammals: Mazza et al., 2020; Newsome et al., 2015; Oliveira et al., 2021; avifauna: Luna et al., 2021; Phillips et al., 2020; review: Miranda et al., 2013), significant work has been done showing behavioral variation on invertebrate taxa populations as well (Gallego-Abenza et al., 2020; Kaiser et al., 2018, 2020; Lowe et al., 2014; Tüzün et al., 2015). Arthropods fill essential functional roles in ecosystems (i.e., biological control, decomposition, food web interactions, nutrient cycling, and pollination) which can directly reflect environmental quality. Also, because arthropods have shorter generation times, they have a rapid response to environmental change which make them alluring subjects of urbanization (Kotze et al., 2011).

As one of the most abundant groups of animals on Earth today with over 49,000 described species (World Spider Catalog, 2021), spiders (Araneae) are a group that deserves much attention. They display an array of behavior types that can be readily evaluated (Hernández Duran et al., 2021), which have established their taxonomic group in animal personality studies (Bosco et al., 2017; Daniel & Chaves-Campos, 2021; Golobinek et al., 2021; Sweeney et al., 2013). Many of which have shown correlations between behaviors like aggression, boldness, and voracity. For example, the North American fishing spider, *Dolomedes triton*, demonstrates a wide-ranging behavioral syndrome wherein the boldest individuals are also the most voracious predators, and the most sexually cannibalistic mates (Johnson & Sih, 2005). In contrast, bronze jumping spiders (*Eris militaris*) demonstrate a negative correlation between boldness and voracity

(Royauté et al., 2014). These distinctly different relationships among behavioral traits highlight the diversity found in spider behavior that in and of itself, requires further study.

The western black widow spider, *Latrodectus hesperus* is native to the Sonoran Desert and flourishes in both urban and rural habitats throughout the Southwest United States. Female widow spiders build 3-dimensional cobwebs, anchored to rigid structures of various substrates (e.g., woody shrub, block wall, etc.). They are considered a pest species because they tend to form dense aggregations, which have been estimated to be thirty times more densely populated than rural populations in Phoenix, AZ (Johnson et al., 2012). Furthermore, western black widows have a toxic venom which can be lethal to humans (Brown et al., 2008; Lewitus, 1935). Because they are nocturnal and ectothermic by nature, webs most typically include a refuge for retreat during the daytime hours and extreme heat of the desert summer. Web-building spiders overcome their feeble eyesight through a sit-and-wait foraging strategy, anticipating vibratory cues created by prey physically interacting with their web (Nakata, 2010; Scott & Gries, 2016; Sergi et al., 2021). The recent work on *L. hesperus* has emphasized their behavioral plasticity (e.g., Halpin & Johnson, 2014), including behavioral shifts following exposure to extreme heat (Johnson et al., 2020).

Prior work has documented a 6°C UHI experienced in western black widow refuges at peak breeding season (Johnson et al., 2019). *Latrodectus hesperus* reared in the laboratory at these urban heat conditions, significantly slowed their development, but increased web building activity, voracity, and sibling cannibalism behavior (de Tranaltes

et al., 2021; Johnson et al., 2019, 2020). These variable behaviors and urbanophile tendencies indicate that western black widow spiders are superb candidates to investigate the role of behavioral traits across an urban-rural context.

Past work completed in our laboratory under common garden conditions has shown a striking lack of behavioral differences between laboratory reared urban and desert spiders. Albeit many studies have suggested spider behavioral differences may be accentuated under genuine field conditions (Halpin and Johnson, 2014; Pritchard et al., 2016; Wiggins et al., 2018). This is made even more intriguing by recent data that indicate significant genetic differences between urban and nearby desert widow populations across a handful of Southwest US cities (Miles et al., 2019). Thus, I compared the behavior of voracity (foraging activity) and boldness (risk-proneness) of urban and desert spiders, both in the field and after they had been maintained in the laboratory under a common garden environment.

I first tested the broad hypothesis that western black widows, given their varied genetics and habitats (desert and urban), would differ behaviorally. Because, relative to urban habitats, desert habitats are characterized by 1) more black widow enemies (e.g., wasp parasites), and 2) lower prey availability, I predict that desert spiders will be both bolder and more voracious than individuals from urban habitats. Secondly, I tested the hypothesis that laboratory conditions could remove interesting behavioral differences that are only apparent in a genuine field caught individual. Thus, I predict that western black widow behavioral differences would wane once moved to the laboratory environment.

## **Materials and Methods**

Four urban western black widow populations were followed within the greater metropolitan Phoenix, AZ area and four desert populations were followed in the relatively undisturbed Sonoran Desert surrounding the city (see Figure 1.1). All populations were a minimum of 3.5 km apart from one another. Desert sites were at least 25 km outside of metropolitan Phoenix, in remote locations relatively undisturbed by human development. Populations were chosen only if they contained a minimum of three western black widow females within one hectare. Three to four adult female widows per site were chosen and monitored weekly (desert: n=12; urban: n=10). Focal individuals had to be greater than 5m apart and were marked distinctly on the fourth femur (left and/or right side) with non-toxic paint to aid in the confirmation of their identity over the course of the study.

Field assays were performed between June 17<sup>th</sup> and July 11<sup>th</sup>, 2019, occurring between 2100 and 0000 hours. Behaviors were measured in a set sequence: voracity always occurred first then >15 minutes later, boldness was measured. Spiders were only assayed if 1) they were out in their web not in the refuge and 2) were relatively motionless in foraging posture. Three repeated measures of each assay were conducted throughout the field season with seven days always separating repeated measures. Spiders were weighed immediately following the third and final field assay only. The decision to only weigh one time in the field was made to minimize human disturbance that potentially could lead to web abandonment. Animal body condition was estimated using



the residual index method and calculated as standardized residuals from the line plotting mass over leg length (Jakob et al., 1996; Schulte-Hostedde et al., 2005). At the close of the study, I photographed and then measured the 3rd leg of each spider using ImageJ (v1.53a, National Institutes of Health, Bethesda, MD, U.S.A.). The third leg was used as it has been suggested that front legs are under sexual selection and thus an inadequate standard for body size indices (Huber, 2005).

Voracity was calculated as latency to attack prey and is reported in seconds. A small wooden dowel about 10 cm in length was attached with tape to the end of a rechargeable electric toothbrush. Each trial commenced when a simulated prey item (tip of toothbrush apparatus vibration) was applied to the web 20 cm from the spider (Chuang & Riechert, 2021; Frohlich & Buskirk, 1982). Each trial concluded at the point when the individual first began throwing silk at the artificial prey or after 120 seconds had lapsed.

Boldness is defined as the latency to emerge from inside one's refuge following a standardized disturbance. To simulate a disturbance, spiders were sprayed three times with short bursts of condensed air from approximately 30-40 cm away to initiate a retreat to the web's refuge (Riechert & Hedrick, 1993). Latency to remerge back into the web past the refuge entrance was recorded in seconds to a maximum of 30 minutes, with shorter latencies indicating bolder animals.

At the close of the field assays, all remaining spiders were collected, weighed, and transported to the laboratory. Spiders were given eight weeks to acclimate to their new environment before any behavior assays took place. All spiders were housed individually in transparent 72-liter plastic tubs (57 × 38 × 33 cm). A refuge was attached to the wall

and centered 22cm from the bottom of the container (see Figure 1.2). The refuge was fashioned from a plastic condiment cup, 7cm in diameter, 4.5cm deep, and blacked out by gray utility tape. A 2.5cm hole was cut into the side of the cup for an entrance. A single wooden dowel 50cm in length positioned from the refuge entrance and attached to the opposite end of the arena was used as scaffolding to aid in establishing a web (see Figure 1.2). Spiders were kept on a 12:12 reverse photoperiod at room temperature (24°-26°C) for the duration of the study. Each spider was fed one adult house cricket, *Acheta domesticus*, visually estimated to be roughly 50% of the spider's size each week. Feeding always occurred three days prior to each behavior assay during the study. Laboratory assays took place between August 29<sup>th</sup> and September 12<sup>th</sup>, 2019. The two behavioral assays were conducted exactly as they were in the field. Assays took place approximately one hour after the start of the dark cycle under dim red light. Each spider was weighed no more than 24-hours following each laboratory assay.

### **Statistical analysis**

All statistical tests were performed in SPSS (Ver. 26.0.0.1 for Mac® SPSS, Chicago, IL, USA). Repeatability tests were performed to measure test-retest reliability within each behavioral context using the Intraclass Correlation Coefficients (Boake, 1989; Koo & Li, 2016). A *t*-test was conducted on body mass and body condition between weeks. Nonparametric tests were performed when data were not normally distributed. Repeated measures ANOVA tests were used to examine the pairwise comparison between weeks. Independent samples Mann-Whitney U tests were utilized to

test for the difference in behavior and body condition between spiders from different habitats. Subsequent analyses pooled all 22 spiders across habitat types if no habitat differences were found. Spearman rank-order correlations were run to determine if there were relationships between any of the behaviors and with body condition.

## Results

*Repeatability:* Because I found very few behavioral differences between urban and desert spiders (see below), I pooled spiders from urban and desert habitats and found voracity to be a highly repeatable trait across three measures that were repeated at weekly intervals (field voracity: ICC 0.494,  $F_{21, 42} = 1.942$ ,  $p = .033$ ; laboratory voracity: ICC 0.746,  $F_{21, 42} = 4.779$ ,  $p < .001$ ). Boldness behavior was significantly repeatable only in the laboratory setting not in the field (field boldness: ICC 0.366,  $F_{21, 42} = 1.571$ ,  $p = .105$ ; laboratory boldness: ICC 0.690,  $F_{21, 42} = 3.434$ ,  $p < .001$ ).

Multiple pairwise comparisons of behavior between weeks found significant differences between weeks in the laboratory for voracity (week one:  $22.58 \pm 8.70$  seconds; week two:  $34.27 \pm 10.38$  seconds; week three:  $59.42 \pm 12.16$  seconds). Specifically, post hoc analysis with a Bonferroni adjustment revealed that voracity in the laboratory significantly decreased from week one to three (36.84 (95% CI, 65.49 to 8.18) seconds,  $p < .01$ ), and from week two to three (25.15 (95% CI, 49.18 to 1.11) seconds,  $p < .05$ ), but not from week one to week two (11.69 (95% CI, 35.94 to 12.56) seconds,  $p = .671$ ). For boldness, there were no significant differences between any of the repeated measures between weeks in the field ( $p > .05$ ) or in the laboratory ( $p > .05$ ). Because

repeatability was found to be high and repeated measures ANOVA showed only sporadic differences, I chose to pool repeated measures and ask whether a spider's average behavior differed across habitats and from the field to the laboratory.

*Desert versus urban behavior:* Across urban and desert habitat there were no significant differences in voracity (field:  $U = 45$ ,  $p = .346$ ; laboratory:  $U = 42$ ,  $p = .248$ ; see Figure 1.4) or boldness (field:  $U = 37$ ,  $p = .14$ ; laboratory:  $U = 42$ ,  $p = .254$ ; see Figure 1.5). Additionally, spiders did not significantly differ in body condition between habitats (week three of field assays:  $t_{17} = -.699$ ,  $p = .494$ ; week one of laboratory assays:  $t_{17} = -.693$ ,  $p = .498$ ; week two of laboratory assays:  $t_{17} = -.655$ ,  $p = .521$ ; and week three of laboratory assays:  $t_{17} = -.635$ ,  $p = .534$ ).

*Field behavior vs laboratory behavior:* Spiders were significantly bolder in the field, returning from their refuge almost 20x faster than they did once moved to the laboratory (field:  $394.02 \pm 74.53$  seconds; laboratory:  $7732.55 \pm 1315.25$  seconds,  $z = -4.107$ ,  $p < .001$ ; see Figure 1.6). Voracity did not significantly differ between field and laboratory assays ( $z = -.146$ ,  $p = .884$ ; see Figure 1.4). Field boldness was positively correlated with laboratory boldness ( $r_s(22) = 0.448$ ,  $p = .037$ ), but field voracity was not found to be correlated with laboratory voracity ( $r_s(22) = -.095$ ,  $p = .674$ ). I found significant behavioral correlations in the laboratory between boldness and voracity. In general, spiders that were bolder were also more voracious ( $r_s(22) = 0.535$ ,  $p = .01$ ; see Figure 1.7 & Table 1.1). However, those correlations did not exist in the field (all  $p > .120$ ). Statistically, body condition was not found to be a consistent predictor of any sampled behaviors (see Table 1.1).

I did find a significant difference in the average body mass between each week for spiders. In general, spider mass increased over the course of the study (week three of field assays:  $240 \pm 18$  mg; week one of laboratory assays:  $341 \pm 20$  mg; week two of laboratory assays:  $304 \pm 19$  mg; and week three of laboratory assays:  $407 \pm 20$  mg). Spider mass differed significantly between the final week in the field and the first week of laboratory assays (increase of  $101 \pm 26$  mg,  $t_{21} = -3.818$ ,  $p = .001$ ), and between the second week of laboratory assays and the third and final week of laboratory assays (increase of  $102 \pm 18$  mg,  $t_{21} = -5.701$ ,  $p < .001$ ). However, average mass between the first assay in the laboratory compared to the second laboratory assay dropped slightly (decrease of  $37 \pm 13$  mg,  $t_{21} = 2.769$ ,  $p = .012$ ). Overall, the average spider mass increased significantly between the end of the field assays and the end of the laboratory assays (increase of  $167 \pm 25$  mg,  $t_{21} = -6.663$ ,  $p < .001$ ).

## **Discussion**

The goal of this study was to evaluate two behaviors (voracity and boldness) in two distinct populations of black widow spiders (urban and desert) under two very different scenarios (field and laboratory). Most of the behaviors I assayed were found to be highly repeatable across multiple repeated measures, yet statistically unrelated to animal body condition. I found no evidence that desert and urban spiders differ in body condition or behave differently from each other in the field or the laboratory. However, I uncovered evidence that suggests individual spiders behave quite differently in the field versus the laboratory. Specifically, I show that spiders are bolder in the field compared to

the laboratory but find no differences between field and laboratory voracity. In addition, I found significant behavioral correlations (in the laboratory but not the field) between boldness and voracity, illustrating a laboratory generated behavioral syndrome.

*Desert and urban differences:* As suggested above, desert and urban western black widows are highly diverged genetically (Miles et al., 2019). Phenotypically, past work has shown urban black widows to be larger than their desert counterparts (Johnson et al., 2017). Yet I found no significant body condition or behavioral differences between desert and urban lineages in the field or the laboratory. This is surprising considering the extreme life history that the desert spider endures to reach adulthood and persist, in contrast to spiders living in an urban area where food is abundant. It's possible that despite the profound genetic and habitat differences between urban and desert spiders, finer scale temporal and spatial conditions drive extreme plasticity in behavior. This suggestion is supported by the observation that some urban and desert habitats do not conform to simple expectations. For example, prey diversity is high in some unique urban locales, with levels matching that seen in desert habitat (Trubl & Johnson, 2019). Under conditions of such fine-scale population differences, one would struggle to show profound habitat differences, especially in a trait as labile as behavior is often suggested to be. While habitat differences in black widow behavior remain an interesting possibility (e.g., desert spiderlings exhibit a non-significant trend to be more siblicidal than urban spiderlings, deTranaltés et al., 2020), I found no evidence for these habitat differences in spider behaviors tested in the field and later in a common laboratory environment. A

result that is more consistent with this species being highly plastic in its behavior regardless of habitat.

*Field behavior vs laboratory behavior:* Black widow boldness differed between field and laboratory assays. Spiders were significantly bolder in the field, returning to their web nearly 20x faster after a startle disturbance. This contrasts with the same assays performed in the laboratory after seven weeks of acclimation. Within a laboratory setting, ecological and environmental contexts can be controlled beyond anything resembling natural conditions. Doing so in a neutral environment removes the animal from all natural signals and cues. This gives the researcher great command over variables and an amplified detection of responses to stimulation.

Environmental variation often impacts the behavior of spiders. For example, *Parawixia bistriata*, a social foraging spider, shows greater plasticity in group foraging behavior when coming from a low-prey environment, evidence that resource availability exerts a strong selective pressure on this species behavior (Fernández, 2005). Also, the whip spider *Phrynus longipes*, has been observed less active and aggressive in cavernous environments compared to open environments, presumably due to selection pressures from predation (Chapin, 2015). These studies both demonstrate that natural environments can drive strong selection for distinct behavioral types in different environments.

In this study, spiders exhibited significant variation in behavior between natural and artificial environments, but their behavior was not explained by their body condition (i.e., past foraging success/prey abundance). Spiders were significantly shyer in the novel laboratory setting, evidence of behavioral plasticity. This plasticity can be construed as

adaptive if boldness is necessary in the field where enemies (e.g., parasitic wasps) are common, but extraneous in the laboratory where such enemies are absent. In the wild it pays to be bold because it can lead to foraging success. Shy spiders will likely miss out on a meal if they are not out in their web actively foraging. The hungrier an individual is the bolder they need to be. This was demonstrated by the six-lined trumpeter, *Pelates sexlineatus*, fish become substantially bolder the longer they go without food (Biro & Booth, 2009). In our laboratory food is abundant and frequent, so there is no need to be bold as spiders are very much satiated. This is supported by the average mass increase of spiders throughout the experiment. From the last field day to the start of the laboratory assays, I documented a 42% average mass increase and an additional gain of about half of that by the end of the study. Thus, it is possible that spiders who are fed regularly and satiated resulted in shyer individuals.

The other variable that I measured, voracity, did not statistically differ between field and laboratory assays. In general, spiders in the field maintained similar levels of voraciousness in the laboratory. However, voracity in the laboratory decreased over the course of this investigation. Spiders at the end of the study were found taking an average of 2.5x longer to attack the artificial prey cue compared to the first week of laboratory assays. Earlier work on *L. hesperus*, established that when food abundance increased, spiders took longer to attack prey, killed less and were more wasteful with their prey (Trubl et al., 2011). Here in my study, spiders were never awarded food in conjunction with the assay for voracity. Actual feeding with live prey always occurred three days prior to the voracity trials and never involved the artificial prey vibratory cue. These



measures were taken to preserve the reliability of the voracity test and minimize habituation and laboratory conditioning. Thus, this is additional strong evidence for behavioral plasticity. As the pressures from food limitation are relaxed, voracity behavior starts to shift to a satiated state.

The plastic ability to change behavior based on fine scale environmental differences is suggested to be a key advantage that allows organisms to respond to rapidly changing environmental conditions (Lowry et al., 2013). Evidence for this has been demonstrated using two different orb-weaving spiders, *Zygiella x-notata* and *Nuctenea umbratica*, which inhabit both urban and rural habitats. Kralj-Fišer et al. (2017) found a consistent change in their activity levels when spiders were presented with a novel environment. Spiders can change their activity levels between a familiar setting and a novel one. They interpret this ability to modulate behavior in this scenario as adaptive to urban exploitation. My data support this idea by demonstrating how quickly the western black widow can alter both boldness and voracity behaviors between field and laboratory assays in a relatively short period of time.

*Behavioral syndromes:* Boldness and voracity in the laboratory both proved to be highly repeatable and significantly correlated with each other suggesting a laboratory-generated behavioral syndrome exists in this species (consistent individual differences correlated across contexts). Examples of laboratory generated behavioral syndromes have been illustrated by other spider studies (Johnson & Sih, 2005; Steinhoff et al., 2020) including western black widows (DiRienzo et al., 2020). Bold spiders in my study tended to be the most voracious. The Australian freshwater crayfish (*Cherax destructor*)

exhibited similar correlations where more voracious individuals were also bolder and this correlation corresponded positively with growth rate (Biro et al., 2014), demonstrating that having an active personality leads to higher growth rates. My data, however, show no statistical relationship between body condition and behavior. I found that the laboratory imposes a behavioral correlation in black widows that is divorced from body condition, evidence against the hypothesis that black widow behavior is typified by condition-dependent plasticity.

In a review of behavioral syndromes, Sih et al. (2012) suggests species establishment into a novel environment may require a positive correlation of boldness and foraging activity, noting behaviors of high boldness and high foraging activity are required to be the most successful invaders. Overly cautious (shy) individuals are negatively impacted by human disturbance and less voracious individuals may not have great foraging success, especially with novel prey. Yet my data does not support this claim as variations of this syndrome was found in both habitats (urban and desert) with no clear selective preference in urban systems for highly bold and highly voracious individuals. Thus, I show no evidence that suggests black widows thrive in urban field environments because they possess an adaptive syndrome of high boldness and high voracity.

My finding of a behavioral correlation present in laboratory assays but absent in the field is intriguing. In a recent study by Fisher et al. (2015), *Gryllus campestris* crickets were observed both in the field and the laboratory. They found that while all assayed traits were significantly repeatable in the laboratory, only some were repeatable

in the field setting (exploration and activity). In addition, both exploration and activity in the laboratory correlated with the same behaviors in the field, but boldness was not correlated between the field and laboratory (Fisher et al., 2015). Findings like this, similar to my own, imply there is much diversity between personality traits in nature and within the laboratory environment. Thus, illustrating the ecological significance of animal personality studies carried out only in the laboratory should be viewed with caution until they can be replicated under field conditions.

The question remains, why was a personality present under laboratory conditions, but absent in the field? Voracity was highly repeatable in both field and laboratory. Boldness behavior was significantly repeatable only in the laboratory setting, not in the field. Anti-predator boldness may be highly sensitive to influence from outside factors in comparison to voracity. This influence could be a result of trade-offs that black widows make echoing their microhabitat state, present condition, objective, and current demands. These effects may have impaired the ability to document clear correlations in the field, when in contrast I was able to detect significant correlations in the laboratory. Thus, it is possible that behavioral correlations in black widows from such varied habitats only manifest in novel, low stress environments. Strong selective pressures acting on individuals in the field could dissolve any correlations that have been seen in the predictable environment of a laboratory.

*Conclusion:* Studies comparing field and laboratory behavior are plentiful in the literature (Campbell et al., 2009; Fisher et al., 2015; Herborn et al., 2010; Jandt et al., 2015; Kobler et al., 2009; Pellegrini et al., 2010; Wright et al., 2015; Yuen et al., 2016;

reviewed, Calisi & Bentley, 2009). I show the utility of such a design by highlighting the confounding results. This provides compelling support for the idea that some commonly studied behaviors can be accurately assayed in captivity, but other behaviors are highly context specific. Leading to the notion that if more accurate predictions of natural behavior are to be generated, a more rigorous approach is warranted utilizing both field and laboratory experiments in unison.

I show that wild urban and rural *L. hesperus* populations do not function differently in two fundamental animal behaviors. Instead, my evidence reveals that black widows may actually be succeeding within urbanization due to their ability to plastically modulate behavior or rapidly adapt to novel contexts. Managing biodiversity is an indispensable task in the modern world and especially true for urban communities. The notion that an urban pest is able to thrive not because it is highly locally adapted but instead because it holds extensive phenotypic plasticity poses unique challenges for management. With respect to certain urban pests, modifying the environment can have significant impacts on species with maladapted behaviors but will have little effect when an organism can adjust to the circumstantial changes like the black widow. Thus, as the fields of urban ecology and evolution focuses on categorizing the adaptive traits that explain urban colonization, one must reconsider the oversimplification of such a task. The complexities that determine the need for either behavioral stability or flexibility in any given situation may better our understanding of population stability in human dominated ecosystems.

**Figure 1.1**

***Black Widow Field Sites in the Greater Phoenix, AZ Area***

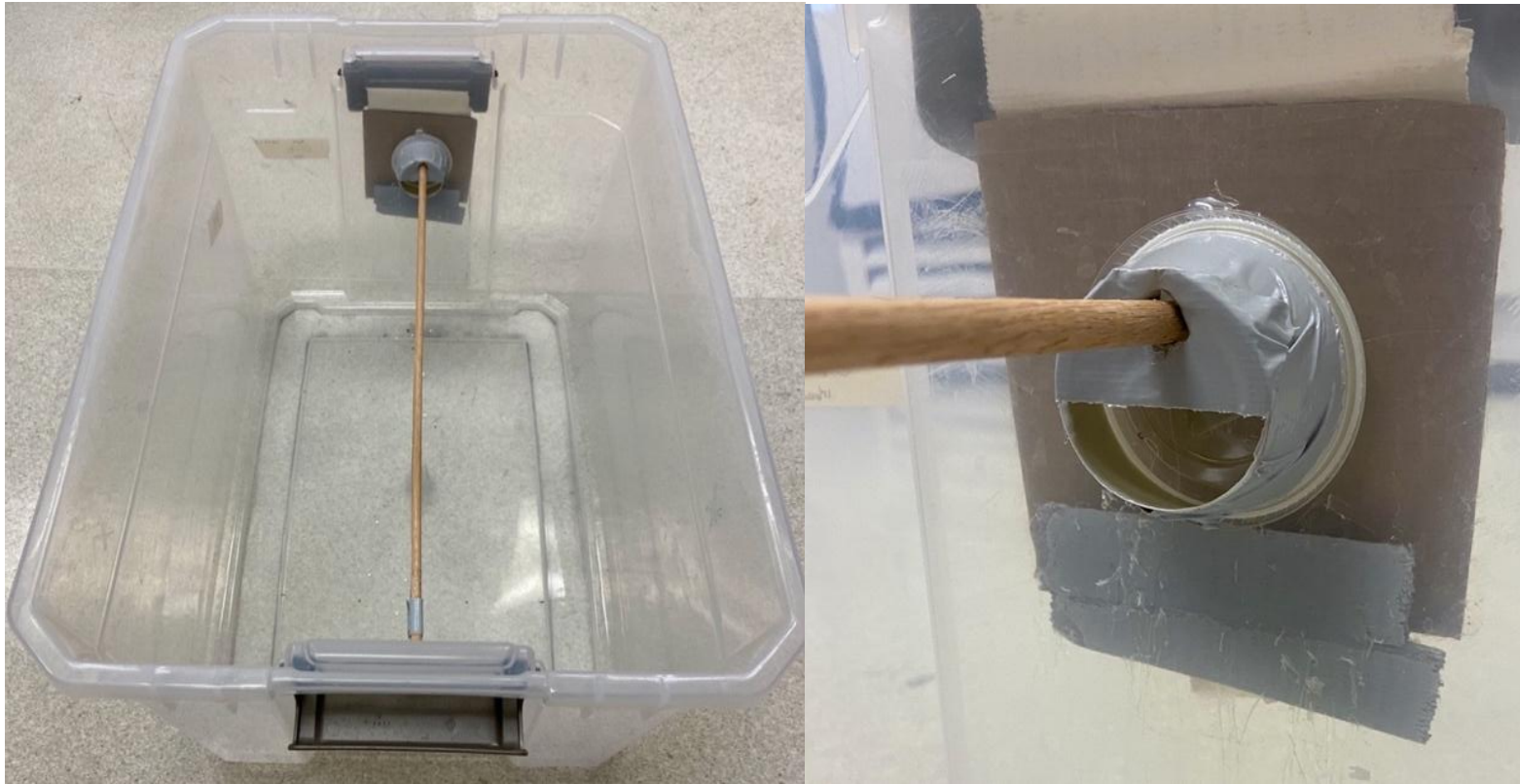


*Note.* Approximate locations of western black widow subpopulations. Desert sites are denoted in yellow. TMW = Table Mesa West, MGU = Moore's Gulch, NRR = New River Road, TME = Table Mesa East. Urban sites are denoted in orange. SSD = Sunrise Drive, SBF = Sunburst Farms, OLI = Olive, CAL = Calvary.



**Figure 1.2**

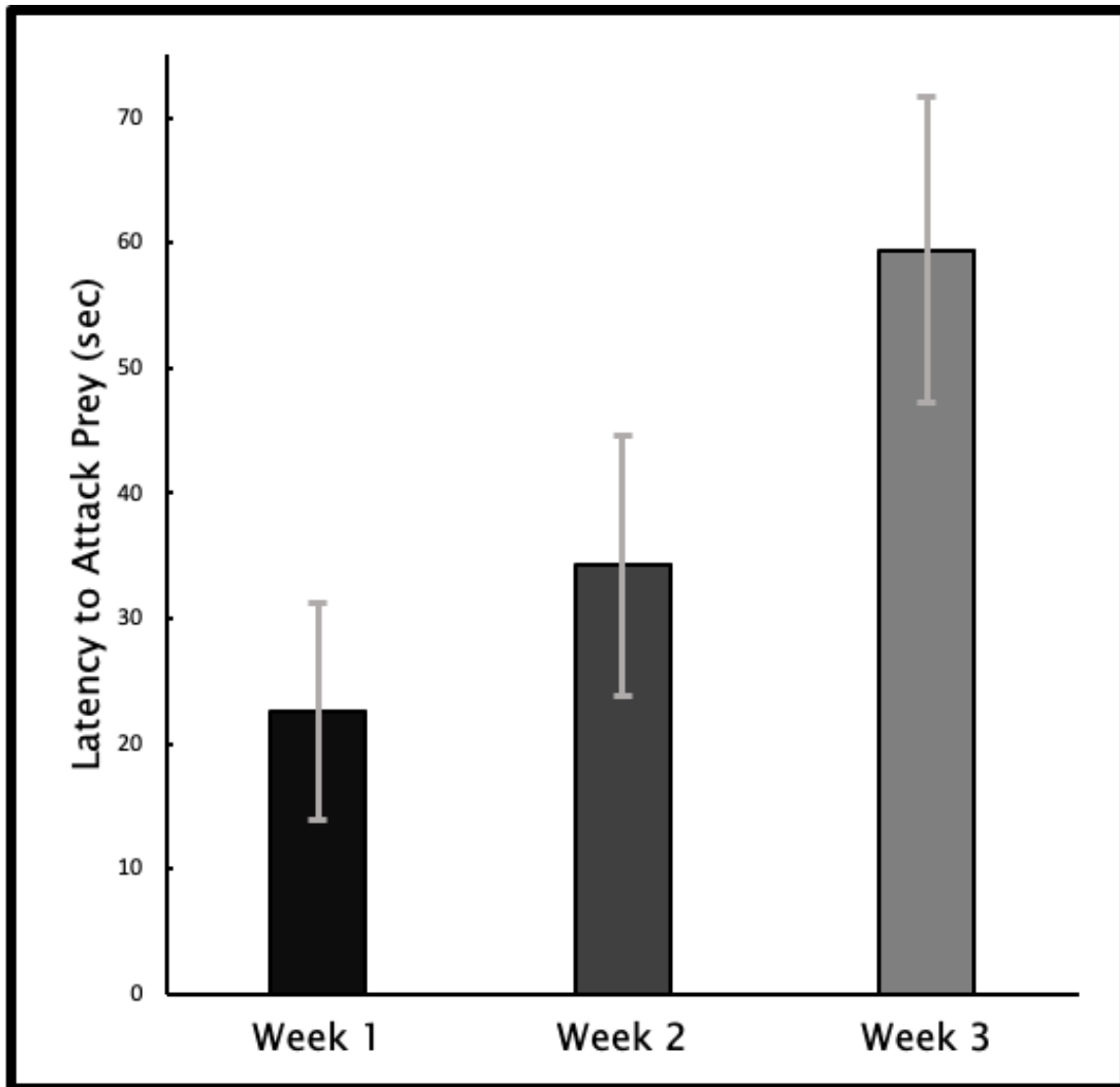
***Laboratory Housing for Western Black Widow Spiders***



*Note.* 72-liter plastic tub outfitted with wooden dowel for scaffolding and a dark refuge secured to the wall (Left). Plastic condiment cup with entrance cut out of the bottom and blacked out with tape to create a secure dark refuge for the spiders to retreat to in the daytime and when startled (Right).

**Figure 1.3**

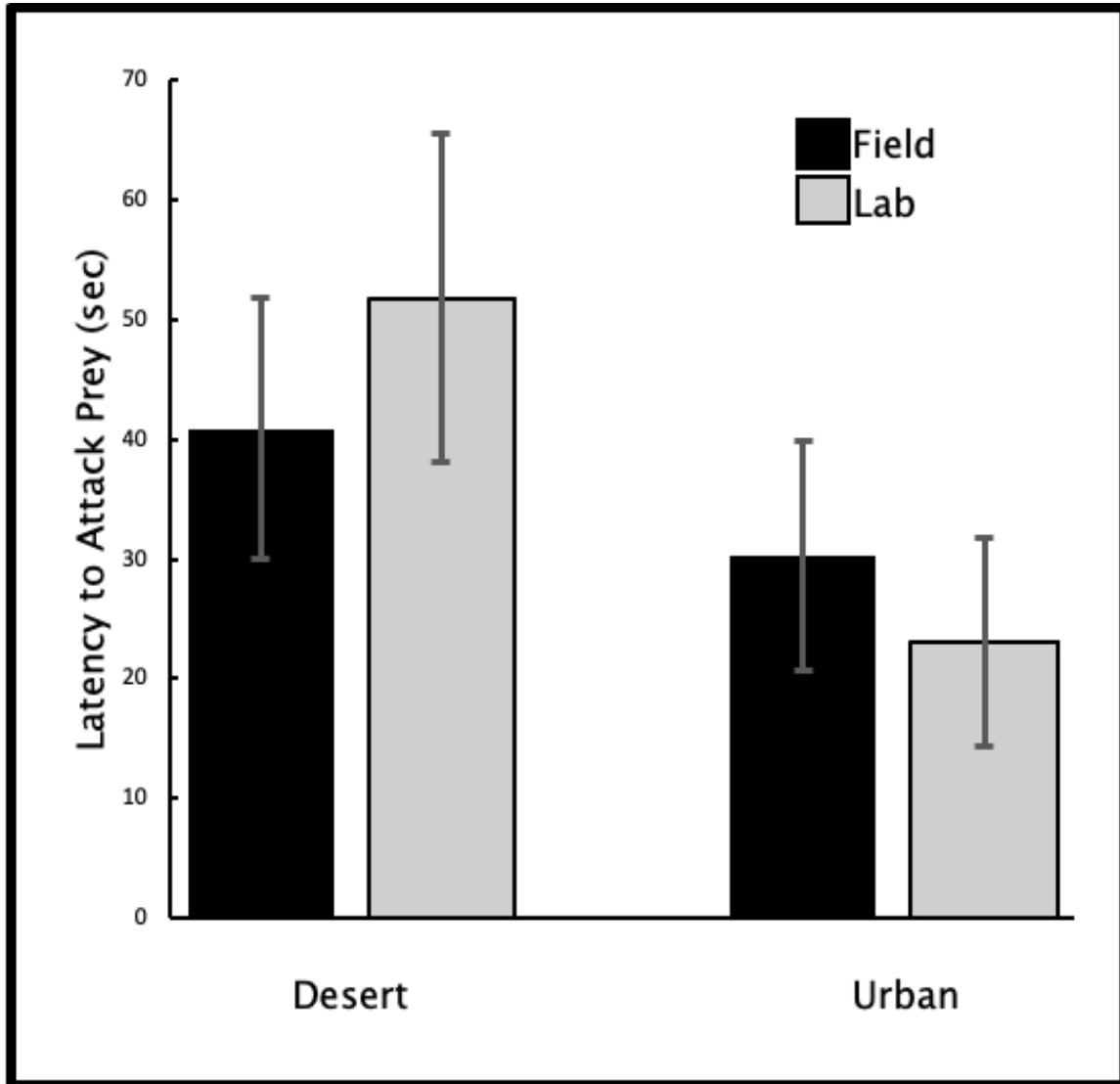
*Mean Spider Voracity by Week in the Laboratory*



*Note.* Average difference between pooled spiders in the laboratory for time to attack artificial prey stimulus. Mean voracity week 1:  $22.58 \pm 8.70$  seconds; week 2:  $34.27 \pm 10.38$  seconds; week 3:  $59.42 \pm 12.16$  seconds (significant decrease from week one to three (36.84 (95% CI, 65.49 to 8.18) seconds,  $p < .01$ ), and from week two to three (25.15 (95% CI, 49.18 to 1.11) seconds,  $p < .05$ ), but not from week one to week two (11.69 (95% CI, 35.94 to 12.56) seconds,  $p = .671$ ) Bars indicate mean estimates and whiskers show the standard error.

**Figure 1.4**

*Desert and Urban Spider Voracity: Field versus Laboratory*

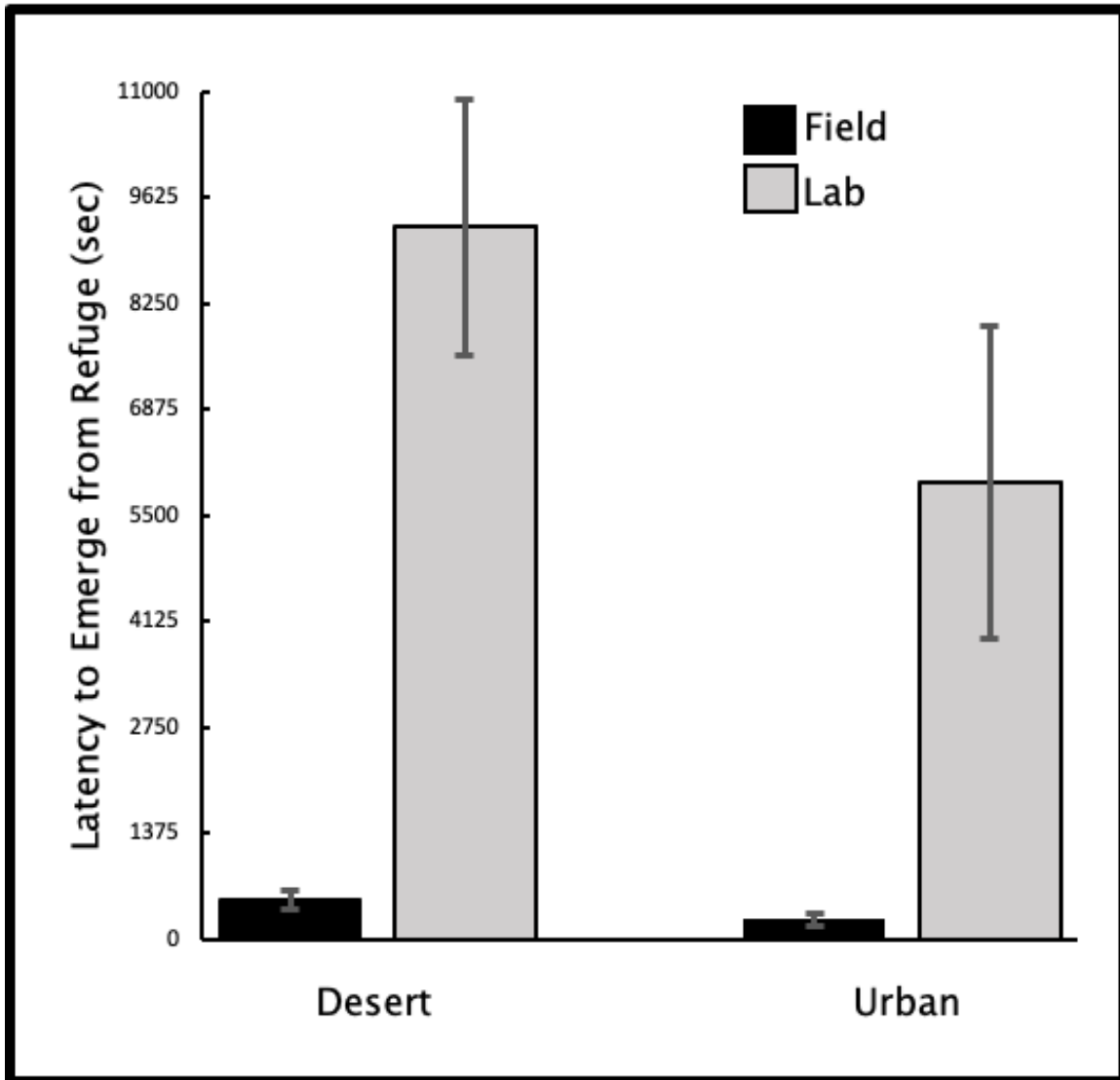


*Note.* Average difference between desert and urban spiders in the field versus the laboratory for time to attack artificial prey stimulus. Voracity in the field between habitats did not differ (desert:  $40.86 \pm 10.88$  seconds, urban:  $30.3 \pm 9.52$  seconds,  $U = 45$ ,  $p = .346$ ) and voracity in the laboratory between habitats did not differ (desert:  $51.81 \pm 13.68$  seconds, urban:  $23.1 \pm 8.69$  seconds,  $U = 42$ ,  $p = .248$ ). Bars indicate mean estimates and whiskers show the standard error.



**Figure 1.5**

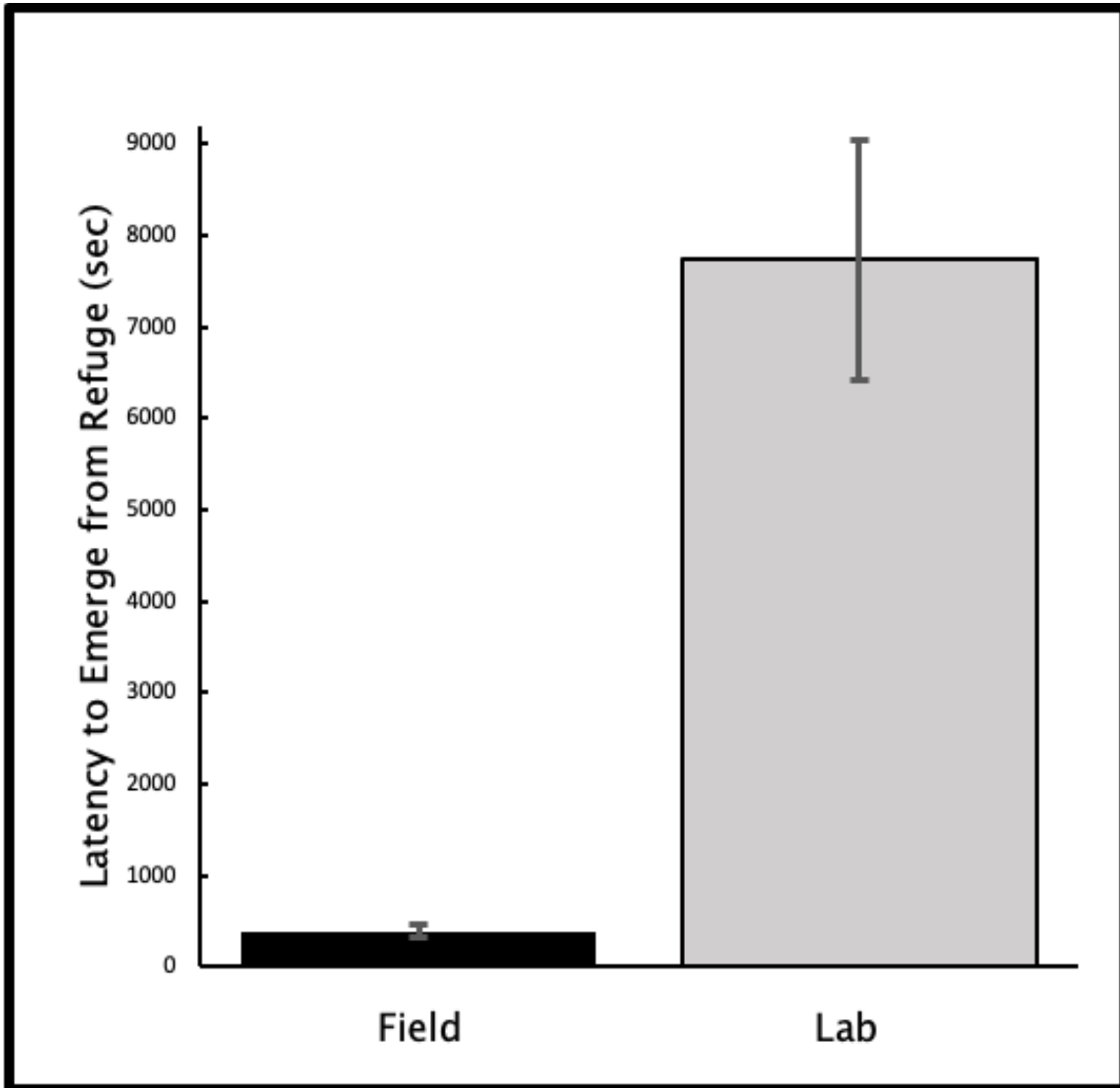
*Desert and Urban Spider Boldness: Field versus Laboratory*



*Note.* Average difference between desert and urban spiders in the field versus the laboratory for latency to emerge from refuge post disturbance. Boldness in the field between habitats (desert:  $510.22 \pm 111.72$  seconds, urban:  $254.56 \pm 79.01$  seconds,  $U = 37$ ,  $p = .14$ ). Boldness in the laboratory between habitats (desert:  $9237.66 \pm 1669.27$  seconds, urban:  $5926.4 \pm 2031.91$  seconds,  $U = 42$ ,  $p = .254$ ). Bars indicate mean estimates and whiskers show the standard error.

**Figure 1.6**

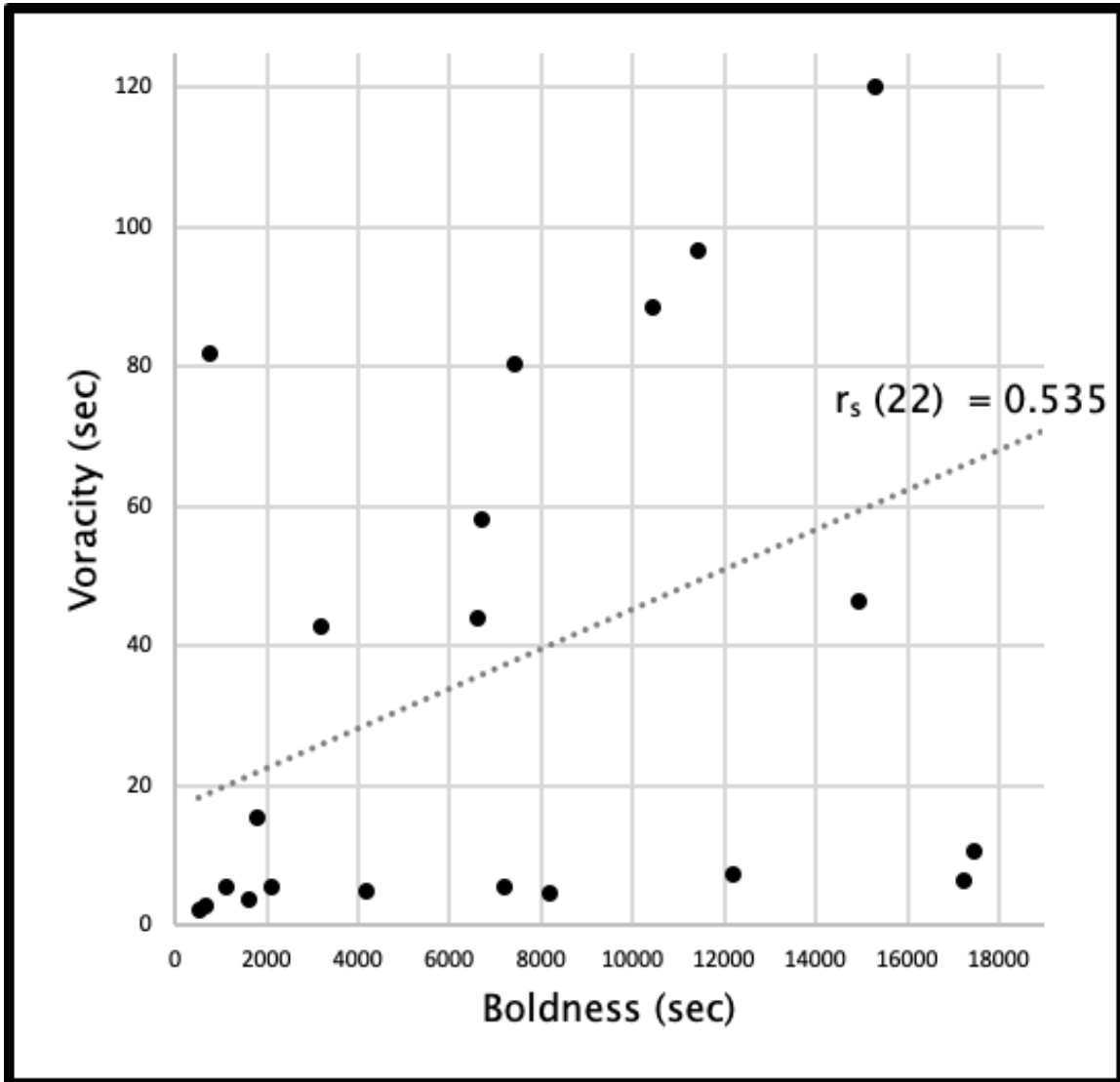
*Average Spider Boldness: Field versus Laboratory*



*Note.* Average difference between all spiders in the field versus the laboratory for latency to emerge from refuge post disturbance. Boldness in the field was significantly higher than boldness in the laboratory (field:  $394.02 \pm 74.53$  seconds, lab:  $7732.55 \pm 1315.25$  seconds,  $z = -4.107$ ,  $p < .001$ ). Bars indicate mean estimates and whiskers show the standard error.

**Figure 1.7**

*Laboratory Correlations Between Voracity and Boldness*



*Note.* Correlation estimates between voracity and boldness averaged across three weeks. Black circles indicate individual spider means and line represents best fit regression ( $r_s (22) = 0.535$ ,  $p = .01$ ).

**Table 1.1***Correlations Between Body Condition, Voracity and Boldness*

Behavior	Week	Body condition		Voracity		Boldness	
		<i>r<sub>s</sub></i> (19)	<b>p</b>	<i>r<sub>s</sub></i> (22)	<b>p</b>	<i>r<sub>s</sub></i> (22)	<b>p</b>
Field							
Voracity	1	-	-	-	-	0.341	.120
Boldness	1	-	-	0.341	.120	-	-
Voracity	2	-	-	-	-	-0.272	.221
Boldness	2	-	-	-0.272	.221	-	-
Voracity	3	0.273	.258	-	-	0.001	.995
Boldness	3	0.203	.405	0.001	.995	-	-
Laboratory							
Voracity	1	0.129	.599	-	-	<b>0.496</b>	<b>.019</b>
Boldness	1	-0.096	.694	<b>0.496</b>	<b>.019</b>	-	-
Voracity	2	0.032	.898	-	-	<b>0.510</b>	<b>.015</b>
Boldness	2	-0.211	.387	<b>0.510</b>	<b>.015</b>	-	-
Voracity	3	-0.212	.383	-	-	0.378	.083
Boldness	3	-0.095	.700	0.378	.083	-	-
Field Mean							
Voracity	-	-	-	-	-	-0.053	.816
Boldness	-	-	-	-0.053	.816	-	-
Laboratory Mean							
Voracity	-	-	-	-	-	<b>0.535</b>	<b>.010</b>
Boldness	-	-	-	<b>0.535</b>	<b>.010</b>	-	-

*Note.* Correlations between behaviors by week for field and laboratory assays. Specifically, between body condition, voracity, and boldness. Values represent Spearman's rank-order correlation coefficients and p-values. Bold values are statistically significant.

## CHAPTER 2

### WESTERN BLACK WIDOW SPIDER HABITAT:

#### HOW DOES THE URBAN HEAT ISLAND IMPACT MICROCLIMATE?

##### **Introduction**

Urban habitats are considered significant features on Earth's surface and are one of the most widespread examples of human induced rapid environmental change (HIREC) (Vitousek et al., 1997). Modifying undamaged ecosystems to further urbanization routinely converts the natural habitat into novel structures which include roads and buildings (McKinney, 2002, 2006; Shochat et al., 2006; Sih et al., 2011). These transformations often lead to the “urban heat island” (UHI) effect; when urban centers experience nighttime temperatures significantly warmer than the adjacent rural areas (Benita et al., 2015; Oke, 1978). During the daytime, large amounts of solar radiation accumulate as stored sensible heat in these impervious urban structures (Yow, 2007). In the nighttime, these surfaces then release the gathered heat overcoming much of the natural cooling experienced in the nocturnal cycle (Lai et al., 2018; Taha, 1997). The impervious surface based UHI has long been a standing contributor to the urban-rural difference in temperatures (Lazzarini et al., 2015; Oke, 1982).

Variations in the UHI intensity have been closely linked to the atmospheric conditions of the region in which the city is situated, mainly temperature and precipitation (Zhao et al., 2014). Water in the form of humidity and precipitation generally has a suppressive quality on the UHI by lowering the radiative charge on

various land surfaces (He, 2018; Oke et al., 1991). For instance, UHI magnitude is often greatest during the dry seasons of the year (Jauregui et al., 1992; Kim & Baik, 2002). This makes arid regions particularly vulnerable to the UHI phenomenon. Although the effects of regional climate on UHI day-to-day fluctuations stem from a mixture of convective, evaporative, and radiative mechanisms (Buyantuyev & Wu, 2010; Kim & Baik, 2002; Zhou et al., 2016a, 2016b). Weather dominates by comparison as the largest UHI control across space and time (Lai et al., 2021).

Much of the UHI research typically concentrates on broad scale urban climatology. These works rely heavily on generic weather station data of the well mixed troposphere or thermal satellite imagery taken of surface temperatures (Jauregui et al., 1992; Kim & Baik, 2002; Zhou et al., 2016b). Both models could be missing significant fine scale climatology necessary to understand the thermal ecology of mesofauna. For instance land surface imagery from a satellite can only measure temperatures from the visible top of a surface (e.g., building roof or tree canopy) but are unable to detect the understory temperatures where terrestrial animals experience temperature. In a lizard microhabitat investigation by Ackley et al. (2015), an interaction was found between distance to shade and sky view. Lizards in shade were more than 30 °C cooler under 10% sky view when compared to lizards that were 2 m from shade. This finding highlights the fine scale microhabitat thermal variation experienced in the city by organisms including humans.

Temperature influences various life history traits and behaviors in most taxa, but this is especially true for ectotherms (Angilletta et al., 2002; Huey and Kingsolver, 1989).

For example, animals may react to daily temperature shifts by being active only when temperatures are within a certain threshold occurring during certain times of the day (Cerdá et al., 1998; Jayatilaka et al., 2011; Kronfeld-Schor & Dayan, 2003). These short- and long-term temperature variations can present challenges for certain species (Gunderson & Stillman 2015; Oms et al., 2017). Maximum upper and lower temperatures regularly influence the density and distribution of flora and fauna, including spider species (Barnes et al., 2019; Davis et al., 2006; Rypstra, 1986; Sentinella et al., 2020). Identifying an organism's environmental limits can aid in understanding their capacity to endure the rapidly expanding, urbanized world and help predict how they may respond. Before we test thermal limits in the laboratory, we need to document the temperatures experienced in the microhabitats of individual species.

The greater Sonoran Desert includes southeastern California, the Baja California peninsula, much of Sonora, Mexico and the southern half of Arizona. Phoenix is the most populous city in the Sonoran Desert and the state of Arizona, which houses roughly 1,680,000 people (U.S. Census Bureau, 2019). Life in this desert can be harsh and unforgiving most of the time. The basic characteristics of this region include very warm temperatures (often  $>38^{\circ}\text{C}$ ), low humidity, and little to no precipitation throughout most of the year with an abrupt but brief rainy period from July to mid-September. Phoenix and its immediate surroundings fall into the Arizona upland subdivision of the Sonoran Desert, characterized uniquely for its relatively higher altitudes and frequent hard winter frosts (Dimmitt, 2015). Much like the rest of the planet, arthropods make up the overwhelming majority of all described animal taxa in the Sonoran Desert. The species

found here exhibit some of the most fascinating behaviors and adaptations that allow them to endure this sweltering desert climate.

The western black widow spider, *Latrodectus hesperus*, is endemic to North America and is considered a pest species as it thrives in conjunction with urbanization, often forming dense aggregations. Specifically, Johnson et al. (2012) estimated urban populations to be thirty times more densely populated than desert populations. Widows spiders are also considered a pest species of medical importance as they possess a toxic venom that can be lethal to humans (Brown et al., 2008; Lewitus, 1935). As nocturnal ectotherms, black widows create 3-D webs that contain strong silk prey-capture fibers that extend to the ground from a protective retreat that provides a refuge for retreat during daytime hours. During the summer in Phoenix, AZ, western black widow refuges experience a 6°C UHI effect (Johnson et al., 2019). There has been significant work with laboratory-reared *L. hesperus*, examining this UHI elevated temperature and its impact on behavior and development. Specifically, it was found that these urban heat conditions significantly slowed their development, but increased web building activity, voracity, and sibling cannibalism behavior (de Tranaltes et al., 2021; Johnson et al., 2019, 2020). However, it should be noted that refuge temperatures do not reflect the microhabitat temperatures experienced by nocturnal western black widows while waiting for prey out in the web structure. Indeed, recent work has examined the relationship between this spider's web building and its foraging behavior. Specifically, *L. hesperus* individuals who used stickier, prey-capture silk lines in their web were also more aggressive (DiRienzo et al., 2020). These studies indicate that western black widow spiders, and the web



microhabitats they create as an extended phenotype, are excellent candidates to further investigate the impact of urbanization generally, and the UHI specifically, on the behavior, ecology, evolution of urban biodiversity.

In this study, I tested the hypothesis that western black widow microhabitats experience significant temperature differences throughout the year because of the UHI. I focused on replicate *L. hesperus* webs from several urban and desert sites to assess what temperatures these spiders experience in the web across the daily cycle for an entire year. I first wanted to quantify what UHI is seen in the webs of these spiders, and then to ask if the pattern of UHI differences held between habitats for both day and night throughout the year. My prediction was that webs would show a nighttime UHI effect throughout the year but not during the daytime. I then asked what magnitude of variation these webs experience from month to month across an entire year. I predicted that web temperatures in the summer months will exhibit a greater degree of variance between habitats and light cycles but will decrease during the cooler months of the year. Finally, I hypothesized that the thermal microclimate had phenotypic consequences. I predicted that spiders would be bolder, more voracious, and have larger webs in warmer areas.

## **Materials and Methods**

The study area was in the greater metropolitan city of Phoenix, Arizona and the accompanying rural desert. Both habitat types occurred within the Sonoran Desert of the Southwest United States. Four urban field sites and four desert field sites were used (see Figure 2.1). All field sites were located a minimum of 3.5 km apart from one another.

Desert sites were located more than 25 km outside of metropolitan Phoenix, in remote locations relatively undisturbed by human development. Field sites were used if they contained a minimum of three adult female western black widows within one hectare of each other. Four to five adult female widows were monitored per site (n= 18 urban, 17 desert).

A Thermochron® iButton® device model DS1921G-F5 was deployed with each focal spider. Devices were programmed to record the ambient air temperature of the spider web at synchronized recurring intervals. The digital thermometer measures temperature in 0.5°C increments and has a temperature range of -40°C to +85°C, with an accuracy of ±1°C in the range of -30° to +70°C (Maxim Integrated Products, Inc., 2015). My procedures followed those of Brooks, Bloniarz & Lerman (2012), with minor modifications described hereafter. Each iButton was first housed inside a small square envelope constructed with a single layer of mylar blanket (aluminized plastic sheeting) 4cm x 2.5cm and held together with a piece of transparent tape (see Figure 2.2). The mylar material was chosen because of its low cost, superior ability to reflect radiant heat, and protect against sudden heat loss due to wind or rain. Once constructed, these mylar envelopes were packaged inside common construction flagging stakes with standard office staples. The flags provided a discreet installation that would not draw attention and ward off theft or vandalism, especially in the urban habitat.

Initial deployment of the flag sensors occurred in occupied adult webs only and had to be greater than 5m apart from one another. Throughout the course of the study, flags remained in place even if the spider vacated their web for any reason including

collection, disturbance, or mortality. I placed flags no less than 20cm from the ground, 5cm away from an object (tree, wall, etc.) and within 0.5m of the foraging area. I define the foraging area as the spider's primary location in the web when not constructing new web lines. This zone of the web was identified prior to flag positioning.

Most flags were anchored in the ground, where a few others were affixed to a nearby structure to make it as close to the foraging area of the web. Each flag was required to be in contact with the silk of the spider's web for the initial placement (see Figure 2.3). Sites were visited biweekly for data download and maintenance. After each visit, flags were returned to the original position but not required to remain in contact with the web to reduce the amount of disturbance. Over the course of the year, fifteen iButtons ( $\approx 42\%$ ) were lost due to theft, vandalism, flood, or battery malfunction. In total, nine urban and eleven desert digital thermometers remained at the end of the study producing 361,364 individual temperature measurements.

Temperature recording began June 17th, 2019 and ended on June 16<sup>th</sup>, 2020. I estimated the nighttime average temperature of the western black widow's microhabitat as the mean temperature from 2100-0000 hr. in 10-minute intervals. These first few hours after nightfall are by far the spider's most active period (RC, personal observation). In contrast I used the 3-hour interval 12 hours later (0900-1200 hr.) as the microhabitat average daytime temperature. I used the mean nighttime web temperatures during a two-week window (June 17th, 2019 to June 30th, 2019) approximately coinciding with most behavioral assays to test for correlations between web temperature and spider phenotypes

(including web size). Interruptions in individual data loggers that lasted more than one day were not used in that respective month's analysis.

Beginning on the night of initial stationing of data loggers, I began conducting assays to measure boldness, voracity, and web dimensions. Behavior assays were performed between June 17<sup>th</sup> and July 11<sup>th</sup>, 2019, occurring between 2100 and 0000 hours. Behaviors were measured in a set sequence: voracity always occurred first then >15 minutes later, boldness was measured. Spiders were only assayed if 1) they were out in their web not in the refuge, and 2) were relatively motionless in foraging posture. Three repeated measures of each assay were conducted throughout the field season with 7 days always separating repeated measures. Measurements were taken for web dimensions one time on the first night of assays only. Dimensions were recorded from the widest portion of the web's length, width, and height. Web volume was calculated as  $L \times W \times H$ .

Voracity was calculated as latency to attack prey and is reported in seconds. A small wooden dowel about 10 cm in length was attached with tape to the end of a rechargeable electric toothbrush. Each trial commenced when a simulated prey item (tip of toothbrush apparatus vibration) was applied to the web 20 cm from the spider (Chuang & Riechert, 2021; Frohlich & Buskirk, 1982). Each voracity assay concluded at the point when the individual first began throwing silk at the artificial prey or after 120 seconds had elapsed with no contact. Boldness was defined as the latency to emerge from inside one's refuge following a standardized disturbance. To simulate a disturbance, spiders were sprayed three times with short bursts of condensed air from approximately 30-40 cm away to initiate a retreat to the web's refuge (Riechert & Hedrick, 1993). Latency to

re-emerge back into the web past the refuge entrance was recorded in seconds to a maximum of 30 minutes, with shorter latencies indicating bolder animals.

At the close of these field assays, all spiders were collected, weighed (mg) and transported to the laboratory where their 3rd leg was photographed and then measured (after Huber, 2005) using ImageJ (v1.53a, National Institutes of Health, Bethesda, MD, U.S.A.). Animal body condition was estimated using the residual index method and calculated as standardized residuals from the line plotting mass over leg length (Jakob et al., 1996; Schulte-Hostedde et al., 2005).

### **Statistical Analysis**

All statistical tests were performed in SPSS (Ver. 26.0.0.1 for Mac® SPSS, Chicago, IL, USA). Spearman rank-order correlations were run to determine if there were relationships between any of the indices. Independent sample *t*-tests were carried out on daily means of web temperatures between urban and desert sites. Independent samples *t*-tests were also conducted on monthly averages of AM and PM temperatures between urban and desert sites. A one-way ANOVA was performed to compare the effect of site on temperature.

### **Results**

Urban and desert web temperature means were compared throughout the year. On average, urban web means were  $2.50 \pm 0.69$  °C warmer than desert web means each day ( $t_{730} = -3.627, p < .001$ ). Daytime temperature means (0900-1200hr) between urban and

desert webs did not differ significantly for any month sampled across the year (*t*-tests, all  $p > .05$ ). However, nighttime temperatures between urban and desert webs significantly differed for each month sampled across the year such that an UHI was present at night across the entire year (*t*-tests, all  $p < .001$ , see Figure 2.5, 2.6 and table 2.1).

There was a significant difference in daytime temperatures between the four urban sites during the year ( $F_{3, 1459} = 34.204, p < .001$ ). However, these urban sites did not experience this variation during the nighttime ( $F_{3, 1459} = 1.469, p = .221$ ). In contrast, temperatures between desert sites significantly differed during the nighttime ( $F_{3, 1460} = 6.060, p < .001$ ) and marginally non-significant during the day ( $F_{3, 1460} = 2.497, p = .058$ ).

The UHI effect was found to be of greatest magnitude during the springtime, where urban web mean temperatures were  $3.45 \pm 0.97$  °C warmer than desert web means daily ( $t_{182} = 3.540, p < .01$ ; see Figure 2.4). In comparison, the winter months displayed the lowest UHI daily temperature mean difference of  $2.07 \pm 0.49$  °C ( $t_{180} = 4.239, p < .001$ ). Summer months produced a mean difference of  $2.28 \pm 0.31$  °C ( $t_{180} = 7.307, p < .001$ ), and the fall season showed a mean difference of  $2.22 \pm 0.83$  °C daily temperature elevation at urban webs ( $t_{182} = 2.665, p < .01$ ).

Temperature was significantly correlated with boldness ( $r_s(17) = -.505, p = .039$ , see Figure 2.7), spiders in warmer webs were found to be bolder. There was no significant correlation of temperature with any other indices (web size,  $r_s(16) = .015, p = .957$ ; voracity, ( $r_s(17) = -.387, p = .125$ ; and body condition,  $r_s(14) = -.152, p = .605$ ).

## Discussion

The goal of this study was to evaluate two broad ideas surrounding the western black widow. I wanted to know precisely what temperatures black widow microhabitats experience in the city and in the desert for an entire year. Secondly, I wanted to know how temperature in the field was affecting phenotypic expression of behavior. I found urban webs to be warmer than desert webs at night for the whole year but not different during the day. Then I found significant temperature variations between urban sites during the daytime but not at night. The opposite finding was true for desert webs, variation in the night but not during the day. The UHI effect documented here is found to be greatest during the springtime and smallest in the winter. Lastly, I found strong evidence that nighttime temperatures black widows experience is correlated with shy/bold behavior, indicating spiders from warmer webs take more risks. Additionally, web temperature was not statistically correlated to voracity, web size, or body condition.

*Black widow UHI daily:* Web temperatures during the daytime show little variation between the rural desert and urban sites. These findings hold true throughout the entire year. The daytime UHI effect is relatively absent in black widow microhabitats likely due to the arid nature of the region. Zhou et al. (2016a) found the temperature during the daytime for five arid/semi-arid cities in China to have insignificant differences between the rural to city core gradient, suggesting little daytime UHI. They have attributed this result in these dry areas compared to the other regions to the low vegetation activity. In contrast, I found nighttime web temperatures significantly warmer in urban areas when compared to desert sites. I generally have found black widow webs

out in the desert closely associated with vegetation (e.g., native trees, shrubs, grasses, and cacti) and near the cooler valley xeroriparian habitats of the dry riverbeds and washes. At urban sites I still find black widow webs associated with vegetation but also very closely associated with the built environment (e.g., buildings and concrete block walls). Urban heat is captured by the surfaces in urban landscapes (e.g., asphalt roads and concrete buildings), which exhibit thermal and radiative properties that contribute variously to warming the ambient air temperature (Oke, 1982). A black widow web that is attached exclusively to a cinder block wall with a concrete foundation will likely experience the brunt of that thermal release in the nighttime when spiders of the desert have minimal thermal radiative surfaces to deal with. My finding that western black widows are confronted with the UHI effect only during the nighttime hours and not during the daytime, confirms what is already known from similar broad scale urban climatology studies (Lazzarini et al., 2013; Sun et al., 2009).

I found pronounced site differences (i.e., spatial complexity) in urban ecosystems in the daytime, but no such spatial patchiness at night. The temperature of urban webs during the daytime is highly variable. This site variation in the city during the day can most likely be explained by variation in landscape design. Similar research on land surface temperatures has described this very phenomenon. Buyantuyev & Wu (2010) found the magnitude of intra-urban land surface temperatures in the Phoenix area to be equal and sometimes greater than the urban to desert comparison. Their evidence suggests a strong relationship among exotic vegetation and pavements with air temperature. The areas with non-native plants are cooler than areas dominated by



concrete and asphalt. Similarly, a study in the Phoenix area using two commonly found urban lizard species, found microhabitats in mesic residential landscapes during the daytime in summer, 5-10 °C cooler than landscapes contrived of native desert plants (Ackley et al., 2015). They suggest mesic landscaping offers the highest potential for lizard activity and duration due to the preferred temperature range found in comparison to similar bare, native, xeric and oasis microhabitats. These studies demonstrate that Phoenix experiences a temperature mosaic of hot and cold spots that cover the city. The proximity of black widow webs to irrigated grasses, non-native trees and human structures likely influence the wide range of temperatures detected during the daytime. In the nighttime, many urban plants do not contribute to much of the variation as they halt most of the evapotranspiration cooling effects, which 70 -90% of the total release takes place during the daytime photoperiod (Snyder et al., 2003). The nocturnal cycle then transitions into a concrete and asphalt dominated landscape that overwhelmingly releases stored heat from the daytime sunlight (Taha, 1997), effectively muting the contributors of cool air variation. From a nocturnal species viewpoint, these daytime variations have little impact on microhabitat as they are not active when this is occurring. The nighttime temperatures found in this study indicate that western black widows are all experiencing similar temperatures in the city.

Conversely, temperature variation among desert sites is most pronounced at night, with a marginal difference at night. This can similarly be explained by natural landscape characteristics. In the desert, the landscape is almost completely occupied by desert adapted vegetation and void of the staggering amount of human architecture found in the

city. Many areas across the spatial geography of the Sonoran Desert ecosystem are dominated by only one or two plant species, and this is especially true for the sandy flats (Parker, 1991). What vegetation that does occur is a combination of native trees, shrubs, and cacti. This combination of plants has varying evapotranspiration timing; trees peak during the day and succulents at night (Consoli et al., 2013; Wagle & Kakani, 2014). For instance, the prickly pear cactus *Opuntia ficus-indica*, found throughout Arizona, contributes only 10% of the total daily evapotranspiration release during the daytime photoperiod (Consoli et al., 2013). At night, this too creates a temperature mosaic of hot and cold spots that cover the landscape. The proximity of black widow webs to succulent plants, native trees and bare soil likely influences the wide range of temperatures detected in the desert during the nighttime highlighting the varied conditions of the microclimate. Moreover, in the daytime, desert-adapted plants do not contribute much air cooling as they conserve most of the evapotranspiration for the evening hours. Thus, it can be said that much of the natural Sonoran landscape is in a water conservation state during the daytime, essentially removing many sources of air cooling we are seeing at night but not seeing during the day. Hence, the daytime web temperatures found in the desert indicate that western black widows are all experiencing similar temperatures when they are least active.

*Black widow UHI seasonality:* Across all seasons, I observed urban microclimates to be significantly warmer than desert microclimates, which is reflective of the UHI effect (Benita et al., 2015; Oke, 1978). In the springtime this variation was most distinct, displaying the widest average temperature differences between the two habitats. In

contrast, wintertime showed the narrowest average temperature difference between the two habitats, with summer and fall seasons presenting temperature differences only slightly larger than the winter. This goes against the presumption that the UHI is generally greatest in the summer and smallest in the winter (Brazel et al., 2007; Du et al., 2021; Imhoff et al., 2010). My data are consistent with other studies showing that urban centers across the globe have a varied seasonality to the UHI effect. For example, in Seoul, Korea, the UHI intensity was found to be smallest in the summer and largest in the fall/winter. This is explained by correlations with the intensity of sea breeze circulations that occur seasonally (Kim & Baik, 2002). Another study by Zhou et al. (2016b) found multiple UHI variations across three neighboring regions in China. In northwestern regions the UHI magnitude was greatest in the winter and spring, the northeastern region was strongest in the winter, and the southeastern region was largest in the summer. Additionally, they found significant correlations with air temperature and precipitation across all regions; areas that received high annual precipitation displayed the smallest UHI effect. In my study, precipitation was not measured, but average monthly precipitation for the last 20 years highlights May/June as the driest months and July/August receiving the most rainfall (National Weather Service, 2021). This finding aligns perfectly with the seasonal magnitude of UHI effect that we are seeing in the microhabitat of black widows. Black widow webs experience the greatest UHI effect during the springtime when Phoenix rainfall is close to non-existent. Once summer temperatures start to peak, the rainy “monsoon” season moves in and reduces the UHI effect. A similar study conducted just south of Arizona in Jalisco, Mexico found the UHI

of the city Guadalajara was greatest during the months of November to April, with a peak UHI magnitude during March (Jauregui et al., 1992). They found that as soon as the rainy season began temperature contrasts declined considerably. This further helps explain the seasonal UHI found in black widow microhabitats which is likely associated with annual precipitation.

*Temperature correlations:* Ectotherms make up the large majority of species on this planet. Because of this it is crucial to understand how the typical daily temperature experienced by an organism affects an individual's phenotypic expression of behavior. In the field, I observed the boldest spiders linked with warm webs and shyer individuals from slightly cooler webs. Temperature is known to affect metabolic rate which has physiological effects that can impact behavioral expression (Pang et al., 2011). Like my results, Forsatkar et al. (2016) found a positive correlation with temperature on boldness behaviors of Siamese fighting fish *Betta splendens*. They tested various behavioral assays and found slightly warmer waters positively increased activity and boldness levels (Forsatkar et al., 2016). In another study, the spider *Erigone atra*, generated different dispersal phenotypes reared under different temperatures in the laboratory during development; cooler temperatures favored ballooning (distant dispersal) and warmer temperatures favored repelling (near dispersal) (Bonte et al., 2008). These examples show clear effects of temperature on animal phenotypes, including spiders. However black widows in this study show no statistical correlation of temperature with body condition, web size or voracity.

Although I did not find a statistically significant difference in boldness between spiders from desert and urban lineages (see chapter 1), here I have demonstrated that the boldest spiders come from the warmest webs which consequently occur in the urban habitat. Being bold means an individual is likely to take risks, which helps foraging success, locating mates, and defending territory (Réale et al., 2007; Sol et al., 2013; Sprau and Dingemans, 2017). My findings show urban webs are warmer than the desert, and the boldest spiders are often found in the warmest webs.

Over the past few decades there has been a great deal of investigation into the effects of heat islands generated from urban centers (He et al., 2021; Oke, 1973; Taha, 1997). Most highlight the impact the UHI has on human well-being and heed warnings of increasing concern with the looming consequences of contemporary climate change. The economics necessary to abate this human discomfort and health concern often overshadow the other implications of heat related complications. Here I offer insight from the western black widows' perspective when challenged by this ordeal for an entire year. This is one of the few microclimatic investigations of this scale. The iButton temperature data loggers proved to be powerful devices used to assess thermal variation in both undisturbed and cityified ecosystems. I demonstrated their usefulness for documenting fine scale effects of the UHI which provides a more refined awareness of the ecological consequences.

A primary goal was to use the temperature estimates to better understand the complex thermal experience of this pest species. Secondly, this dataset was intended to help calibrate future UHI models which can be used in experimental design. With this

investigation plus previous work on *L. hesperus* refuge temperatures (Johnson et al., 2019), we now have the best available version of what this species' thermal lives look like in nature. Ectothermic taxa are of special concern in these ecosystems because thermal environments are an important regulator of species interactions (Wittman et al., 2010). Temperature determines when certain species are active and for how long in the season. This sets the stage for determining which population sustains/grows and which one declines. Nocturnal taxa are disproportionately living under increasingly warmer temperatures in urban areas and this consideration is widely overlooked. If further warming persists globally in urban habitats, temperatures could possibly exceed the tolerance limits of Theridiidae species (Barnes et al., 2019). Broadly speaking the understanding of how urban diversity tolerates UHI and climate change will be required to help conserve biodiversity.

**Figure 2.1**

*Western Black Widow Field Sites in the Greater Phoenix, AZ Area*



*Note.* Approximate locations of western black widow subpopulations. Desert sites are denoted in yellow. TMW = Table Mesa West, MGU = Moores Gulch, NRR = New River Road, TME = Table Mesa East. Urban sites are denoted in orange. SSD = Sunnyside Drive, SBF = Sunburst Farms, OLI = Olive, CAL = Calvary.



**Figure 2.2**

***Digital Thermometer Housing for Western Black Widow Spider Webs***



*Note.* Assembly of flag sensors. Individual parts pictured: iButton digital thermometer (Left), construction flag in white (Top), and Mylar envelope (Bottom). Photograph taken by R. Clark.



**Figure 2.3**

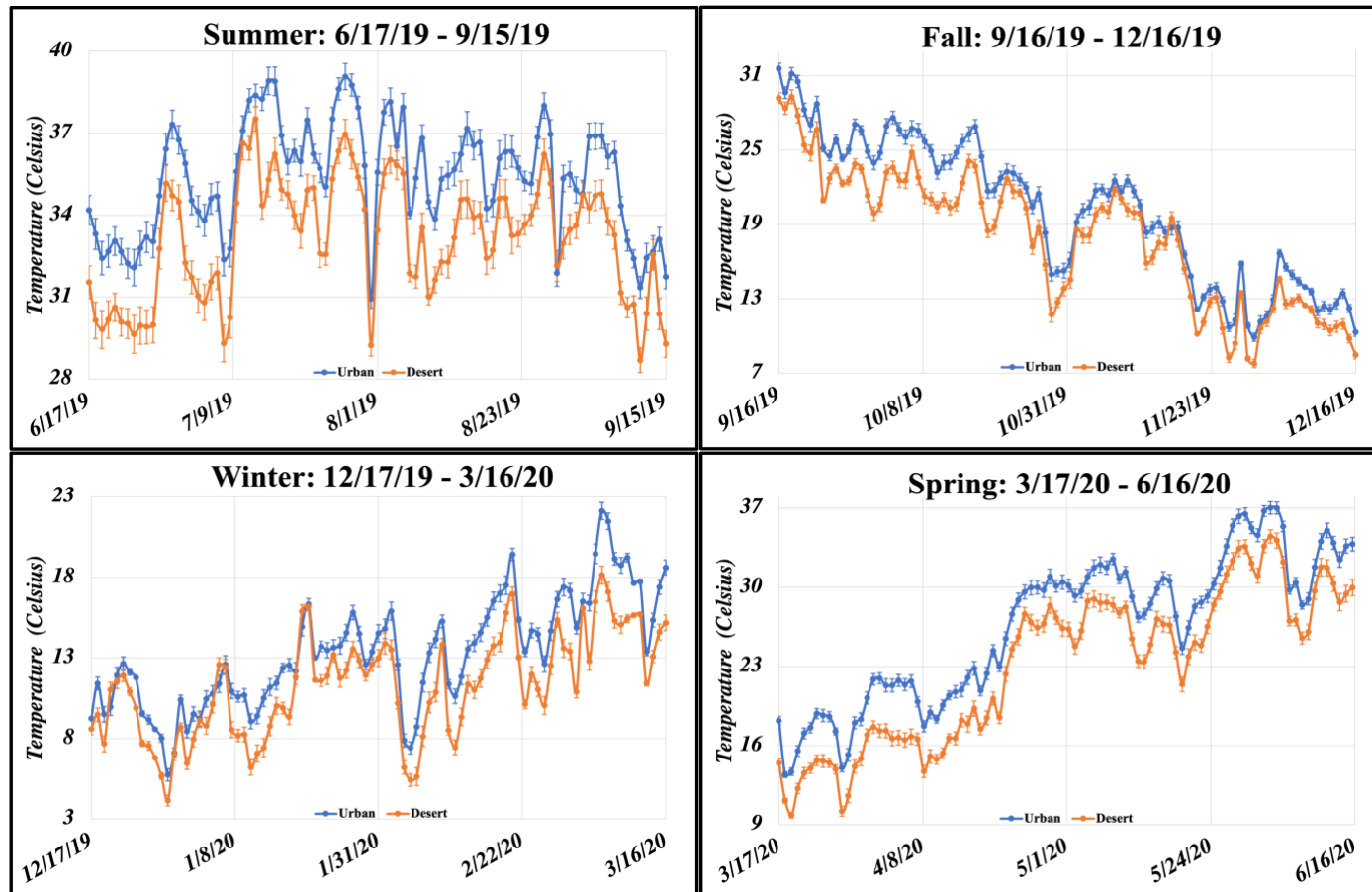
***Digital Thermometer Flag Deployed in a Western Black Widow Spider Web***



*Note.* Close-up photo of activated thermometer flag deployed. Picture details the flag in the web structure contacting spider web silk. Photograph taken by R. Clark.

Figure 2.4

*Daily Black Widow Web Temperature Means by Habitat*

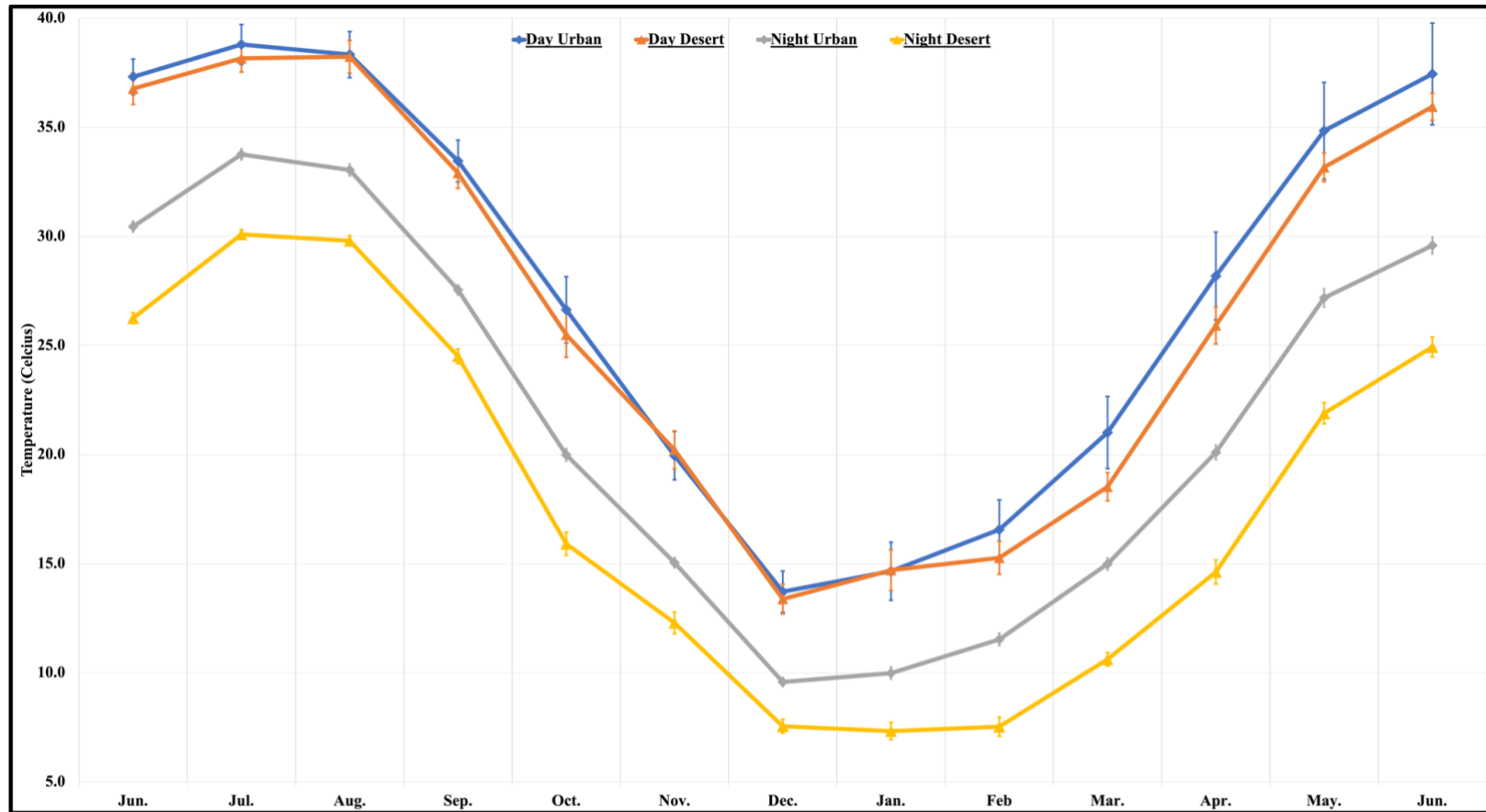


51

*Note.* Urban and desert black widow daily variation of web temperature by season. Assays commence June 17th, 2019 and conclude June 16th, 2020. Points indicate daily mean temperature estimates and whiskers show the standard error.

Figure 2.5

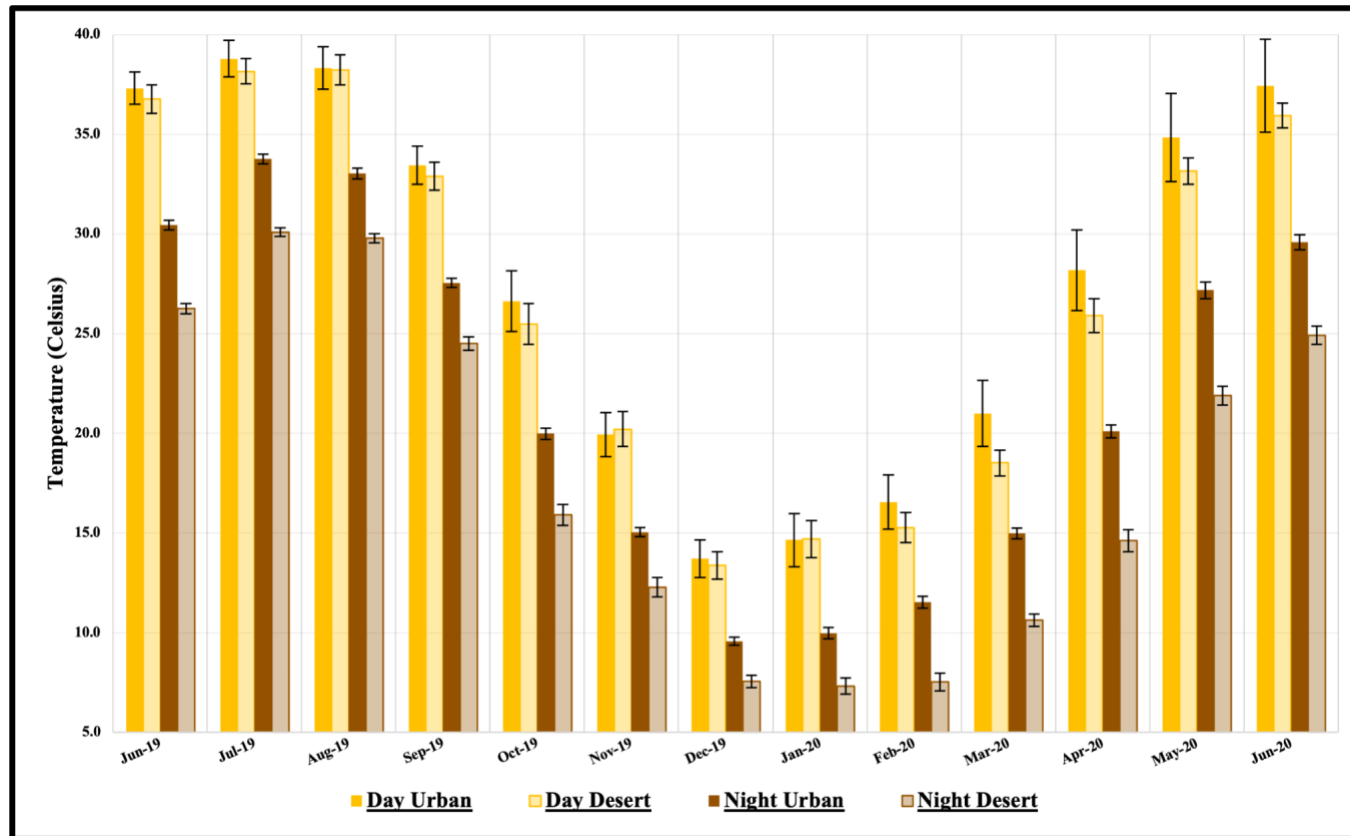
Line Graph of Average Monthly Web Temperature



Note. Urban and desert spider webs during the daytime (0900-1200hr) versus the nighttime (2100-0000hr). Assays commence June 17th, 2019 and conclude June 16th, 2020. Points indicate monthly mean estimates and whiskers show the standard error.

Figure 2.6

Bar Graph of Average Monthly Web Temperature



Note. Urban and desert spider webs during the daytime (0900-1200hr) versus the nighttime (2100-0000hr). Assays commence June 17th, 2019 and conclude June 16th, 2020. Bars indicate monthly mean estimates and whiskers show the standard error. Temperature between habitats did not statistically differ for any month shown in the daytime but did differ in the nighttime for all months reported (see table 2.1 for statistics). Bars indicate mean estimates and whiskers show the standard error.

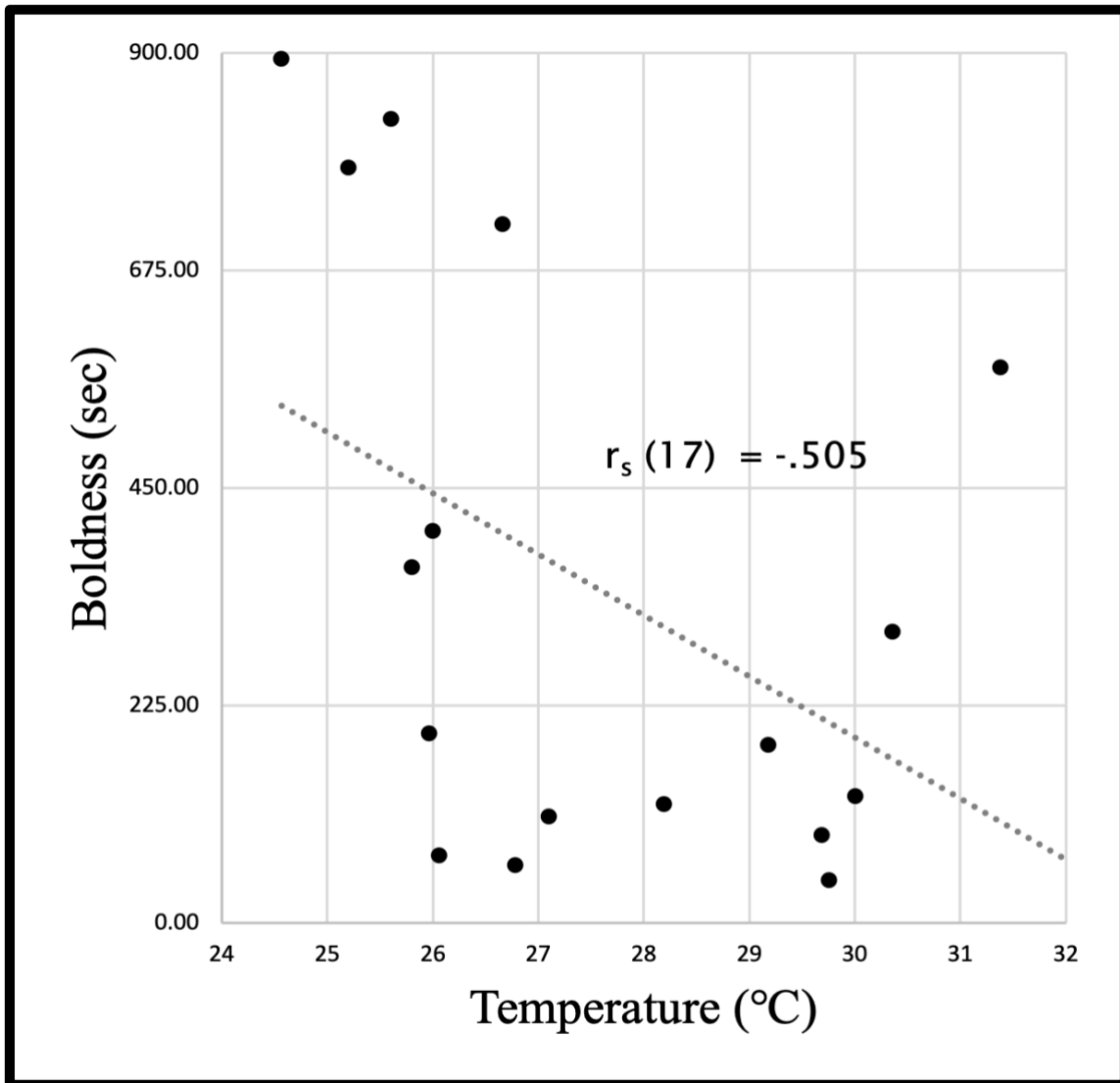
**Table 2.1*****Day versus Night Web Temperature Averages per Month by Habitat***

Date	Site	N	Day (0900-1200hr)				Night (2100-0000hr)			
			Mean	SE	<i>t</i> (df)	p	Mean	SE	<i>t</i> (df)	p
06/2019*	Desert	17	36.8	0.700	-0.499 (33)	.621	26.3	0.248	<b>-12.012 (33)</b>	<b>&lt;.001</b>
	Urban	18	37.3	0.811			30.4	0.245		
07/2019	Desert	17	38.2	0.630	-0.584 (29)	.564	30.1	0.221	<b>-11.048 (29)</b>	<b>&lt;.001</b>
	Urban	14	38.8	0.915			33.8	0.249		
08/2019	Desert	16	38.2	0.747	-0.076 (29)	.940	29.8	0.235	<b>-9.139 (29)</b>	<b>&lt;.001</b>
	Urban	15	38.3	1.057			33.0	0.268		
09/2019	Desert	13	32.9	0.704	-0.446 (27)	.659	24.5	0.333	<b>-7.759 (27)</b>	<b>&lt;.001</b>
	Urban	16	33.5	0.957			27.5	0.228		
10/2019	Desert	13	25.5	1.027	-0.626 (24)	.537	15.9	0.528	<b>-6.802 (18.3)</b>	<b>&lt;.001</b>
	Urban	13	26.6	1.515			20.0	0.282		
11/2019	Desert	13	20.2	0.875	0.185 (23)	.855	12.3	0.494	<b>-5.053 (16.9)</b>	<b>&lt;.001</b>
	Urban	12	20.0	1.104			15.0	0.231		
12/2019	Desert	13	13.4	0.687	-0.292 (22)	.773	7.6	0.315	<b>-5.46 (19.6)</b>	<b>&lt;.001</b>
	Urban	11	13.7	0.943			9.6	0.196		
01/2020	Desert	13	14.7	0.931	0.031 (22)	.976	7.3	0.395	<b>-5.303 (22)</b>	<b>&lt;.001</b>
	Urban	11	14.7	1.333			10.0	0.279		
02/2020	Desert	12	15.3	0.759	-0.848 (21)	.406	7.5	0.433	<b>-7.54 (21)</b>	<b>&lt;.001</b>
	Urban	11	16.6	1.361			11.5	0.289		
03/2020	Desert	12	18.5	0.644	-1.496 (20)	.150	10.6	0.309	<b>-10.407 (20)</b>	<b>&lt;.001</b>
	Urban	10	21.0	1.656			15.0	0.270		
04/2020	Desert	11	25.9	0.849	-1.036 (21.1)	.320	14.6	0.553	<b>-8.286 (19)</b>	<b>&lt;.001</b>
	Urban	10	28.2	2.014			20.1	0.332		
05/2020	Desert	11	33.1	0.661	-0.709 (9.4)	.496	21.9	0.482	<b>-8.119 (18)</b>	<b>&lt;.001</b>
	Urban	9	34.8	2.220			27.2	0.413		
06/2020*	Desert	11	35.9	0.622	-0.629 (9.1)	.544	24.9	0.451	<b>-7.641 (18)</b>	<b>&lt;.001</b>
	Urban	9	37.4	2.330			29.6	0.385		

*Note.* Values represent the results of independent samples *t*-tests conducted on the daytime and nighttime average temperatures at both desert and urban black widow webs. Bold values are statistically significant. \*June 2019 only includes the second half of the month and June 2020 only includes the first half of the month.

**Figure 2.7**

*Correlations Between Web Temperature and Boldness*



*Note.* Correlation estimates between mean nighttime web temperature and spider boldness averaged across three weeks. Individuals at warmer locations were found to be boldest ( $r_s(17) = -.505$ ,  $p = .039$ ). Black circles indicate individual spider means and the line represents best fit regression.

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