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

Patricia Trubl · Theresa Gburek · Lindsay Miles ·
J. Chadwick Johnson

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

P. Trubl (✉) · T. Gburek · L. Miles
School of Life Sciences, Arizona State University, PO Box 874501, Tempe, AZ 85287-4501, USA
e-mail: Patricia.Trubl@asu.edu

J. C. Johnson
Division of Mathematical and Natural Sciences (2352), Arizona State University at the West Campus,
4701 W. Thunderbird Rd, Glendale, AZ 85306, USA

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
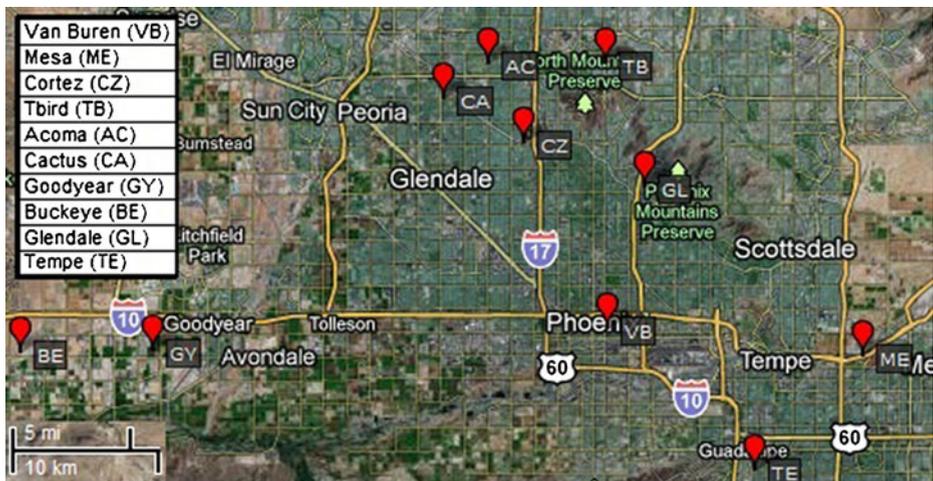

Fig. 1 A map of the urban black widow aggregations studied in Phoenix, Arizona

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 (m³)	Spider density (per m²)	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 mm². 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
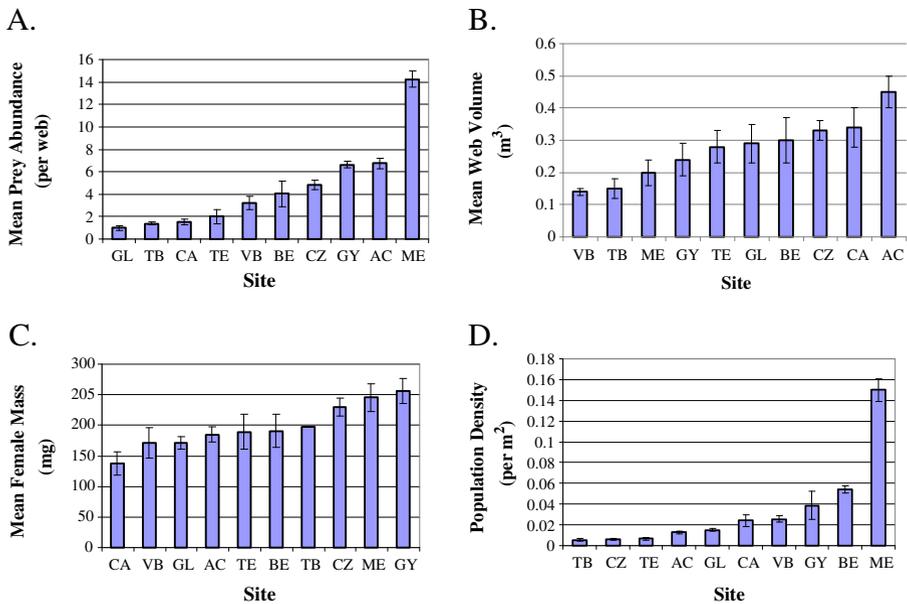
Fig. 2 Spatial variation in biotic variables among black widow spider aggregations. **a** Mean number of prey items per focal female web ($F_{1,9}=12.957$, $p=0.006$). **b** Mean web volume ($N=6$–17 webs/site) ($F_{9, 201}=2.24$, $p=0.086$). **c** Mean female spider mass ($N=6$–17 females/site) ($F_{9, 200}=4.54$, $p=0.006$). **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 (m³)	Female mass (mg)	Prey abundance (per web)	Population density (per m²)
% 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 (m³)					–	$R^2=0.209$ $F_{1,8}=$ 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 $p=0.001$
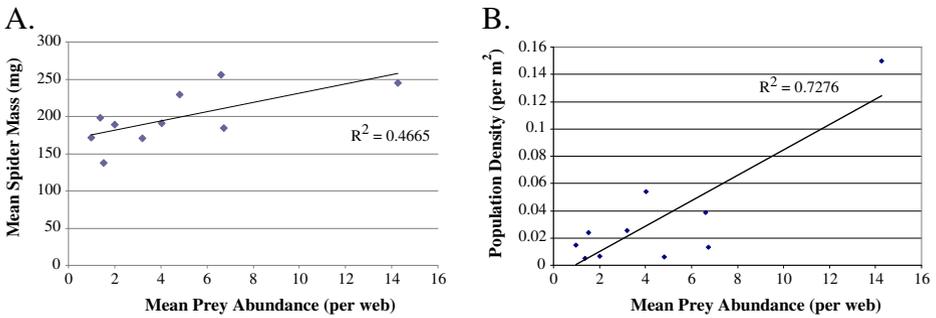
Fig. 3 Prey abundance has a positive relationship with **a** body mass ($F_{1,8}=6.995$ $p=0.029$) and with **b** population density ($F_{1,8}=21.368$ $p=0.002$)

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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