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Ecological stoichiometry of the black widow spider and its prey from desert, urban and laboratory populations

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ABSTRACT

Ecological stoichiometry (ES) offers a framework to identify the mechanisms that allow pest species to thrive following human-induced rapid environmental change (HIREC). Specifically, ES links the biochemical composition of an organism to their growth and reproduction, which influences population growth and ecosystem dynamics. We used ES to quantify the nutrient composition (C: N, C: P, and N: P) of the western black widow spider (*Latrodectus hesperus*) and its prey (from desert and urban) and laboratory populations. Urban field spider and cricket subpopulations exhibited spatial variation in their C: N ratios. Urban field spider C: N, C: P, and N: P ratios were significantly different from urban crickets, but in the laboratory population, spiders and cricket C: N, C: P, and N: P ratios did not vary. Relative to urban spiders, desert spiders had lower C: P and N: P, but C: N did not differ. In the laboratory population, spiders had higher C: N, C: P, N: P ratios than field-caught spiders. Moreover, cannibalism by laboratory-reared spiders lowered C: P and N: P ratios, but not C: N ratios. We suggest such intraspecific variation may be one mechanism that allows urban pests to thrive following HIREC.

1. Introduction

Human-induced rapid environmental change (HIREC; Sih et al., 2010) impacts nearly all of Earth's ecosystems and presents ecologists with a ‘grand challenge’ (Vitousek et al., 1997; Sih et al., 2010). Urbanization is a pervasive form of HIREC because fast-growing urban populations drastically alter the landscape, altering biological communities and ecosystem function within cities and beyond city boundaries (Collins et al., 2000; Grimm et al., 2008). In terms of biodiversity, urbanization often compromises native diversity at the expense of a few urban-adapted taxa termed ‘urban exploiters’, (McKinney, 2002; Shochat et al., 2010; but see Bolger et al., 2008 for contradictory findings). These urban exploiters, whether they be native or exotic species, have the potential to homogenize ecological communities, both within and among cities (Blair, 1996; McKinney, 2006). Thus, trophic interactions following urban disturbance must be quantified to appreciate the implications of urbanization for biodiversity (Shochat et al., 2006). For example, urbanized deserts contain fewer top-level arthropod predators than surrounding desert habitat, which may alter ecosystem function across the urban-desert continuum (Cook and Faeth, 2006). Thus, comparing ecological interactions across a continuum of urbanization is essential for understanding the mechanisms by which urban exploiters thrive in urban environments.

One mechanism for the success of urban exploiters may be their ability to cope with the reduction in diet breadth and nutrient diversity that typically follows urbanization (Kurosawa et al., 2003; Bateman and Fleming, 2012). Ecological stoichiometry (ES) offers a framework to identify nutrient requirements and limitations of organisms through the quantification of carbon (C), nitrogen (N), and phosphorus (P) in ecological interactions (Sterner and Elser, 2002). Specifically, ES allows us to view the role of elemental imbalances (e.g. C: N ratios) in shaping key ecological processes (e.g. food web dynamics; Sterner and Elser, 2002). Terrestrial systems exhibit imbalances in the amount of nutrients (N and P) available between trophic levels (e.g. herbivores-predators; Denno and Fagan, 2003; González et al., 2011; Ludwig et al., 2018). For instance, spiders are more prone to N limitation because they contain significantly more body N than most arthropod prey (Fagan et al., 2002). Recent studies use ES to show how nutrients are distributed across trophic levels in urban environments (Singer and Battin, 2007; Tsoi et al., 2011; Ludwig et al., 2018). Thus, ES can be used to identify nutrient constraints of urban exploiters and their role in ecosystem processes.

A central premise of stoichiometric theory is that consumers are expected to regulate N and P homeostasis regardless of nutrient availability (Sterner and Elser, 2002). Recent data, however, suggest that consumers exhibit intraspecific variation in nutrient composition even

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after controlling for factors such as ontogeny and body size (Bertram et al., 2008; Tsoi et al., 2011; González et al., 2011; El-Sabaawi et al., 2012a, b; El-Sabaawi et al., 2014). In terrestrial arthropod food webs, body size can account for intraspecific variation in P (Woods et al., 2004; González et al. 2011, 2018; Wiesenborn, 2013), but not N content in arthropods (González et al., 2011). Phosphorus content is tightly correlated in arthropods during ontogeny due to the growth rate hypothesis but is relaxed when P is not limiting for growth (Elser et al., 2003). Organisms showing plasticity in nutrient composition may be better able to adapt to variable environments such as cities (Persson et al., 2010). Plasticity in nutrient composition allows for organisms to adjust to nutrient-poor diets by allocating fewer nutrients to new tissue (Elser et al., 2003) or allows for nutrients to be stored and used later for growth when nutrients are in surplus (Raubenheimer and Jones, 2006). Persson et al. (2010) reviewed the regulation of nutrient homeostasis among consumer taxa and found the degree of variation from strict homeostasis cannot be identified as a group or even species-level trait. Instead, the degree of variation from nutrient homeostasis is determined by both genetic and environmental factors. For example, intraspecific stoichiometric variation can correspond to environmental heterogeneity (Bertram et al., 2008), such that nutrient composition is determined by the availability and quality of food sources at a particular locale (Tsoi et al., 2011; El-Sabaawi et al., 2012a, b). Determining the factors that influence intraspecific stoichiometric variation of urban exploiters may aid in predicting biodiversity patterns between urban subpopulations.

Arthropods play an important role in ecosystem functioning and are indicators of environmental disturbance because they are species-rich, have short generation times, and occupy multiple trophic levels (McIntyre et al., 2001). Among arthropods, spiders are often urban exploiters and are key predators that control insect populations in urban ecosystems (Shochat et al., 2004). The western black widow spider, *Latrodectus hesperus* (Araneae, Theridiidae) is native to the Sonoran Desert and has become an urban exploiter throughout Phoenix, Az and many western cities. Female black widow spiders often form dense subpopulations (i.e. infestations) that vary in mean spider mass and subpopulation density across commercial urban subpopulations within urban Phoenix (Trubl et al., 2012). Previously, we have shown that local prey abundance across urban Phoenix predicts spider mass and population density of subpopulations, rather than abiotic factors (e.g. % impervious surface area) (Trubl et al., 2012).

L. hesperus are polyphagous predators, preying across at least eight different orders of arthropods (Salomon, 2011), including their cannibalistic tendencies (Johnson et al., 2010; Salomon, 2011). Black widows in urban Phoenix likely experience increased prey abundance, but reduced prey diversity relative to spiders inhabiting undisturbed Sonoran desert habitat (Bang and Faeth, 2011). The data from Bang and Faeth (2011) indicate desert black widows have access to 31 different ground-based arthropod families, whereas urban black widows have access to only 18 families in xeric landscaped subpopulations. For example, within urban Phoenix habitat, one of the most abundant prey items consistently found in black widow webs is the Decorated cricket, (*Gryllodes sigillatus*) (Trubl pers. obs.). This cricket is super-abundant within the metropolitan Phoenix area, but absent from the surrounding Sonoran desert habitat (Bang and Faeth, 2011). Thus, black widow subpopulations may experience changes in nutrient availability due to differences in types and diversity of prey available.

We quantified the stoichiometry (molar ratios of C: N, C: P, and N: P) of black widows and their prey from replicate field (urban and desert) habitats, and a laboratory-reared population (single species diet and cannibalism diet) to document stoichiometric variation. Following the literature outlined above, we predicted, first, that black widow predators would be more nutrient rich than their herbivorous prey, and would thus have lower C: N, C: P, and N: P than their cricket prey. Second, we quantified levels of intraspecific variation in C: N, C: P, and N: P among replicate field (urban and desert) habitats—predicting i) that body-size would account for intraspecific variation in C: N, C: P, and N: P ratios due to the negative allometric relationship found in several arthropod taxa (Woods et al., 2004; González et al., 2011) and ii) greater variation among populations than within subpopulations due to spatial variability in elemental availability (El-Sabaawi et al., 2012a, b, 2014). Third, while Trubl et al. (2012) documented spatial variation in prey abundance, spider mass, and population density among urban widow subpopulations, we nevertheless predict that the success of urban black widows may stem, in part, from their ability to forage with plasticity— selectively foraging on multiple species or different nutrients from a single species to balance nutrient composition (Mayntz et al., 2005). As such, we predict biotic parameters such as prey abundance, spider mass, and population density may not drive the stoichiometry of a species with behavioral plasticity.

Additionally, we compared the stoichiometry of spiders from urban and desert field populations and predicted that in some situations intraspecific variation might not be sufficient to allow urban spiders to optimally balance nutrients. As such, we predicted urban spiders might have higher C: N, C: P, and N: P ratios than desert spiders due to decreased prey diversity in urban habitats (Bang and Faeth, 2011). Finally, we compared the stoichiometry of these urban and desert field samples with laboratory-reared organisms—predicting that single-species laboratory diets would compromise nutrient levels relative to field-caught organisms (El-Sabaawi et al., 2012b). While we acknowledge that there are many variables that differentiate urban, desert and laboratory reared spiders besides nutrient availability, we nevertheless think this population-level comparison can shed some insight into the role of prey availability and stoichiometry. Lastly, we supplemented the single-species diet of some laboratory-reared spiders with conspecific prey to test the prediction that cannibalism may relax nutrient imbalances (Denno and Fagan, 2003).

2. Methods

2.1. Field study

2.1.1. Urban population

Penultimate instar and adult female *L. hesperus* were collected from ten subpopulations from 15 August to 15 September 2010 and an additional five subpopulations from 15 August to 15 September 2011 for a total of 15 subpopulations located across metropolitan Phoenix, AZ (Fig. 1). We selected these subpopulations based on the following criteria: (1) land-use type was commercial with xeric landscaping, (2) subpopulations were a minimum of 8 km apart from one another, and (3) subpopulations had a minimum of 10 penultimate or adult female black widow spiders (within 5000 m^2) from initial census. The ecology of the ten subpopulations from 2010 has been described elsewhere (Trubl et al., 2012). Black widow webs were located visually during daylight hours, and spiders were captured at night when they are active in their webs (n = 11–14 spiders per site). Confirming our earlier observations (see Trubl et al., 2012), *G. sigillatus* was an abundant prey type, found consistently at all 15 urban widow subpopulations, and we observed cricket carcasses frequently in urban black widow webs (Trubl, pers. obs.). Adult *G. sigillatus* were collected live at each site within a 10 m^2 area of webs. Crickets and spiders were collected on the same evening at each site. Crickets and spiders were stored at −20 °C for later chemical analysis (see below). Biotic parameters (prey abundance, spider mass, and population density) from Trubl et al. (2012) were compared to spider C: N, C: P, and N: P collected from the ten subpopulations in 2010.

2.1.2. Desert population

Penultimate instar and adult female *L. hesperus* were collected from five Sonoran Desert subpopulations from 15 August to 15 September 2011 (Fig. 1). Desert subpopulations were sampled if they met the following criteria: (1) during an initial census, subpopulations had to

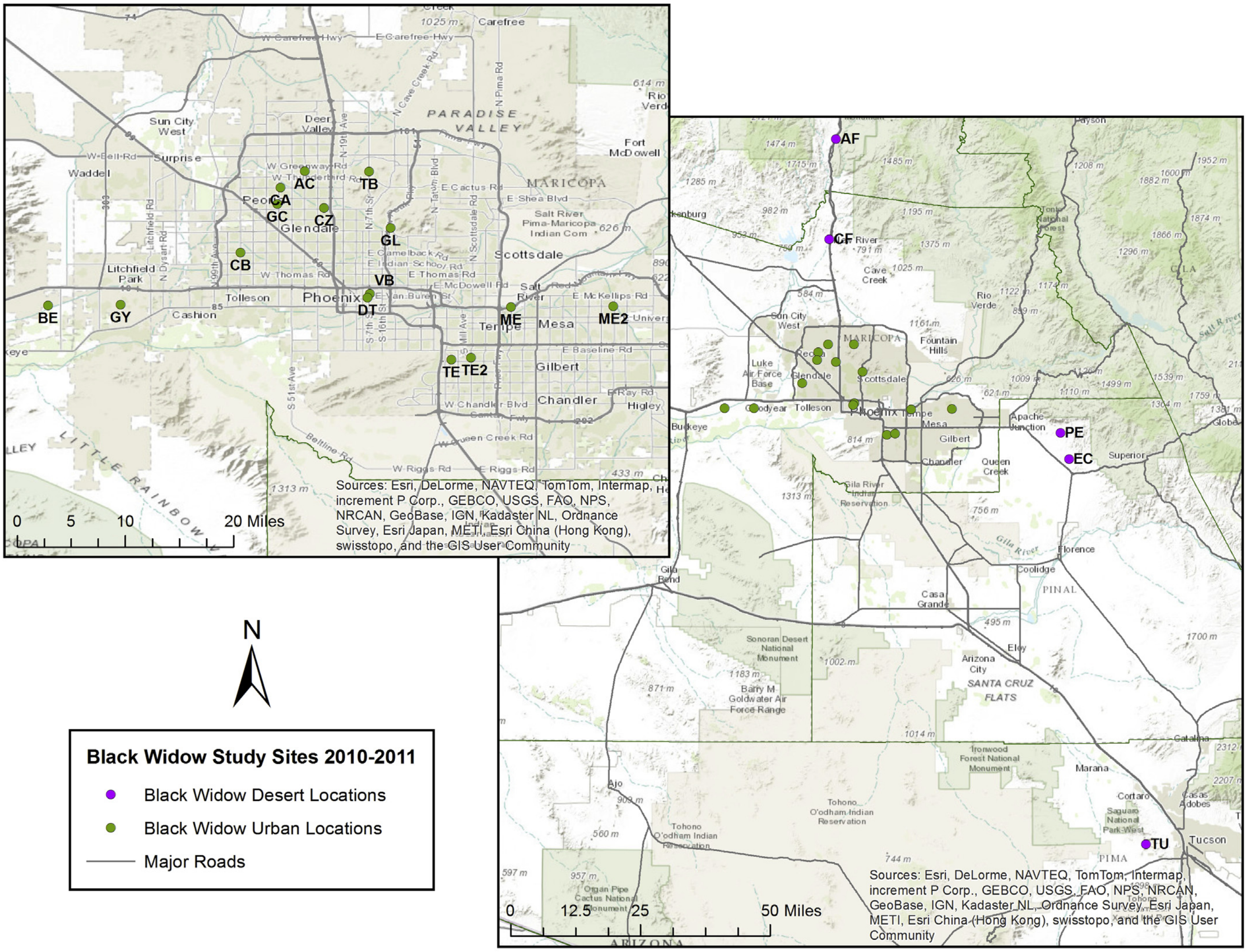

Fig. 1. A map of the urban and desert black widow subpopulations from 2010 to 2011 studied in Arizona. The top left image depicts the 15 urban subpopulations across the greater Phoenix metropolitan area. The bottom right image is an overall map of the 15 urban and 5 desert subpopulations.

contain a minimum of two black widow females within 5000 m^2 (desert black widow subpopulations are significantly less densely populated than urban subpopulations, Johnson et al., 2012) and (2) subpopulations had to be a minimum of 8 km apart from one another. Black widow webs were located visually during daylight hours and spiders were captured at night when they were active in their webs. Arthropod prey were hand-collected from our desert subpopulations. We captured any ground-dwelling arthropod prey species that came within 20 m^2 of a widow's web, and when possible collected up to three individuals of each prey species. We visited each site twice, spending three hours at each visit searching for prey. Arthropods were stored at −20 °C for later chemical analysis (see below).

2.2. *Laboratory study*

One hundred and thirty, F_2 generation, *G. sigillatus* were reared to adulthood on an *ad libitum* diet of Purina Cat Chow® and water. Ten of these crickets were used for chemical analysis at adulthood (see below). The remaining 120 crickets were used to feed the F_1 spider generation described below.

Female spiders used in this experiment were unrelated F_1 laboratory-reared offspring of spiders collected from urban habitats in Phoenix, AZ. Following egg sac emergence, we housed offspring communally for two weeks and during this time each family was fed 20 flightless fruit flies (*Drosophila melanogaster*) twice weekly. No attempt was made to limit cannibalism among spiderlings at this stage. Surviving juvenile spiders were separated to avoid cannibalism and raised individually in transparent plastic boxes (4 × 4 × 5 cm) on three fruit flies twice weekly for a month. At that time, we shifted to weekly feedings of an individual cricket (50–75% of the focal spider's mass) until spiders reached sexual maturity.

2.2.1. *Single species diet*

Female spiders (n = 10) were fed a cricket (75–100% of focal female spider's mass) weekly for eight weeks. One week following the fourth (final) feeding, all ten focal spiders were stored at −20 °C for later chemical analysis (see below). Spiders fed a single species diet were used as a baseline to compare a nutrient limited population to the laboratory population fed conspecifics (see below) and the field (urban and desert) populations.

2.2.2. *Cannibalism diet*

Female spiders (n = 10) were fed a cricket (75–100% of focal female spider's mass) weekly for four weeks. The following four weeks, females were hand-fed an adult female black widow (75–100% of the focal female's mass) weekly. Black widows used as conspecific prey were fed on laboratory crickets for six weeks prior to being used as conspecific prey. One week following the fourth (final) feeding, all ten

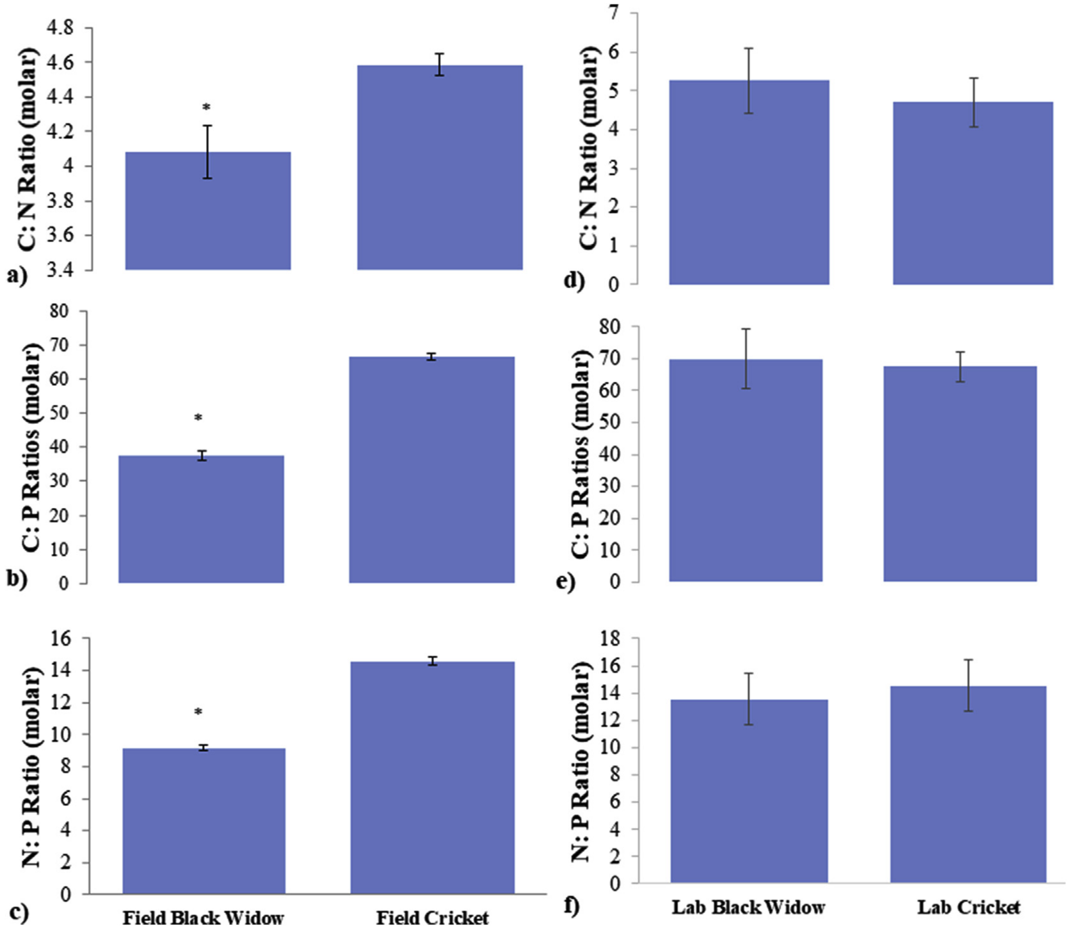

Fig. 2. Spatial variation in the C: N ratios among urban black widow spider subpopulations ($F_{9,\ 115} = 8.3$, $P < 0.001$) (N = 8–14 females/site) and urban adult cricket subpopulations ($F_{9,\ 95} = 2.5$, $P = 0.014$) (N = 8-11 adults located within metropolitan crickets/site) Phoenix, Ariz., U.S.A. Values represent mean ± se.

focal spiders were stored at −20 °C for later chemical analysis (see below).

2.3. Sample preparation and C, N, and P determination

Samples were dried at 60 °C for 120 h. Samples from 2011 and the laboratory-reared population were weighed to the nearest microgram using a Sartorious M5P microbalance. Prey samples were ground individually into a homogenous powder using a Spex Certiprep 800 D ball mill. A portion of each body segment (cephalothorax, abdomen, and legs) from each spider was used to estimate carbon (C), nitrogen (N), and phosphorus (P) body content. Approximately 5 mg of powder (2.5 mg for C and N analysis and 2.5 mg for P analysis) from each individual prey was used to access C, N, and P body content. Some prey individuals from our 2011 field collection failed to produce 5 mg of powder. These individuals were combined with other individuals of the same species to allow us to assess the stoichiometry of such taxa rather than the stoichiometry of individuals. In species that produced more than 5 mg of powder, we sampled individuals separately and used the mean stoichiometric measure per species.

We used a PerkinElmer 2400 CHN elemental analyzer to quantify C and N contents (percentage of dry mass). Total P content was measured by microwave acid digestion (CEM MARS 5, Arizona State University, AZ, U.S.A.). Analysis was performed spectrophotometrically on an inductively coupled plasma optical emission spectrometer (ICP-OES; Themo iCAP6300, Arizona State University, AZ, U.S.A.). Total P was converted to percentage of dry mass for comparative purposes. This method was chosen because it yields a higher percent recovery of P compared to other common methods (see Tanner et al., 1999). Two milliliters of concentrated HNO_3 (70% by weight) was added to each individual sub-sample. After cooling, the solution was transferred to a 20 mL volumetric flask and diluted to volume with Nano water. Percent recovery in P assays was determined by comparison to bovine muscle standards (obtained from the U.S. National Institute of Standards and Technology, U.S. Department of Commerce). The C: N, C: P, and N: P ratios were calculated in molar units.

2.4. Statistical analysis

All statistical tests were performed in SPSS (Ver. 17.0 for Windows® SPSS, Chicago, IL, USA). The Shapiro-Wilk goodness-of-fit test was used to ensure data met normality assumptions. Unless otherwise noted, all tests were done on the following list of dependent measures: C: N, C: P and N: P. Thus, ratios were used as a measure of nutrient abundance, and we interpret low C: N and C: P values as indicative of nutrient richness. We used a univariate ANOVA to test for spatial variation (collection site as a random factor) in both widow and prey populations. Additionally, we used a univariate ANOVA to test for an effect of population type (urban, desert and laboratory-reared) on nutrient values. T-tests were used to examine stoichiometric differences between predators and prey. Linear regressions were run to look for (1) relationships between predator and prey stoichiometry with spider body size as a covariate, (2) relationships between stoichiometry and biotic parameters measured in Trubl et al. (2012) with spider body size as a covariate, (3) if C: N ratios were influenced by body size (dry weight in mg) in widows from desert and urban habitats and (4) if C: N, C: P, and N: P was influenced by body size in widows from the laboratory diet regime. We employed a Bonferroni correction (0.05/3 = 0.017) to account for the inflated probability of finding a significant difference among the different elemental ratios within and across species.

3. Results

3.1. Spatial variation in stoichiometry of arthropod urban field populations

The 2010 urban field collection across urban Phoenix habitat revealed significant intraspecific spatial variation in **C: N** across spider ($F_{9,\ 115} = 8.3$, $p < 0.001$) and cricket ($F_{9,\ 95} = 2.5$, $p = 0.014$) subpopulations (Fig. 2). Spatial variation across urban subpopulations in **C: P** and **N: P** ratios was less notable (black widow **C: P** $F_{9,117} = 1.8$, $p = 0.081$; **N: P** $F_{9,119} = 0.94$, $p = 0.496$; crickets **C: P** $F_{9,93} = 1.6$, $p = 0.136$; **N: P** $F_{9,96} = 2.1$, $p = 0.042$).

Urban black widow biotic subpopulation parameters measured previously (Trubl et al., 2012; e.g. prey abundance, spider mass and population density) were poor predictors of urban black widow and cricket stoichiometry (prey abundance **C: N** $F_{1,\ 9} = 0.002$, $p = 0.969$; **C: P** $F_{1,\ 9} = 0.347$, $p = 0.572$; **N: P** $F_{1,\ 9} = 1.254$, $p = 0.295$; spider mass **C: N** $F_{1,\ 9} = 1.141$, $p = 0.317$; **C: P** $F_{1,\ 9} = 0.106$, $p = 0.753$; **N: P** $F_{1,\ 9} = 2.088$, $p = 0.186$; population density **C: N** $F_{1,\ 9} = 0.051$, $p = 0.827$; **C: P** $F_{1,\ 9} = 0.659$, $p = 0.440$; **N: P** $F_{1,\ 9} = 1.036$, $p = 0.339$). Cricket (prey) stoichiometry at each urban site proved to be a poor predictor of the black widow stoichiometry at those subpopulations (**C: N** $F_{1,\ 9} = 1.88$, $P = 0.207$; **C: P** $F_{1,\ 9} = 0.044$, $p = 0.838$; **N: P** $F_{1,\ 9} < 0.001$, $p = 0.988$). Lastly, in urban habitats, black widow spiders had significantly lower **C: P** ratios ($t = 17.2$; *d.f.* = 9; $p < 0.001$), **N: P** ($t = 17.0$; *d.f.* = 9; $p < 0.001$) and **C: N** ($t = 2.67$; *d.f.* = 9; $p = 0.013$) than their cricket prey (Fig. 3).

3.2. Comparison of C: N, C: P, and N: P ratios in desert and urban field arthropods

C: N, **C: P**, and **N: P** ratios did not differ significantly among our five urban subpopulations or five desert subpopulations for either black widow stoichiometry or prey stoichiometry (all $p > 0.1$). Because we found no differences between urban and desert black widow stoichiometry, we lumped our five urban subpopulations with our five desert subpopulations and found that **C: N** ($F_{9,\ 26} = 1.004$, $p = 0.473$), **C: P** ($F_{9,\ 24} = 1.693$, $p = 0.176$) and **N: P** ratios ($F_{9,\ 24} = 0.629$, $p = 0.756$) did not exhibit significant site variation. Additionally, body size in black widows from urban and desert habitats was a poor predictor of **C: N** ratios ($F_{1,\ 26} = 0.015$, $p = 0.904$), **C: P** ratios ($F_{1,\ 24} = 1.001$, $p = 0.327$), and **N: P** ratios ($F_{1,\ 24} = 0.491$, $p = 0.490$). The **C: N** ratios of the arthropod prey collected from these ten urban and desert subpopulations did not predict black widow stoichiometry ($F_{1,\ 11} = 2.86$, $p = 0.122$). Perhaps our measures of prey species **C: N, C: P**, and **N: P** did not differ between desert and urban habitats ($t = 1.84$; *d.f.* = 4; $p = 0.07$).

C: N, C: P, and **N: P** ratios did not differ significantly among the ten urban subpopulations from 2010 and the five urban subpopulations from 2011 for black widows (all $p > 0.8$). Because there were no significant differences between sampling years (**C: N:** $F_{1,\ 131} = 2.06$; $p = 0.154$, **C: P:** $F_{1,\ 129} = 2.90$; $p = 0.091$, and **N: P:** $F_{1,\ 132} = 2.55$; $p = 0.113$) we pooled the black widow stoichiometry data for our urban subpopulations from 2010 ($n = 10$) and 2011 ($n = 5$) to compare the ES of urban and desert spiders. **C: N** ($F_{1,\ 141} = 8.057$, $p = 0.98$) did not differ significantly between the urban and desert populations, but desert black widows had lower **C: P** ($F_{1,\ 140} = 8.06$, $p = 0.005$) and **N: P** ($F_{1,\ 143} = 14.00$, $p = 0.0003$) than urban black widows (Fig. 4).

3.3. Stoichiometry of arthropods from field and laboratory populations

Urban-field crickets collected from across metropolitan Phoenix were similar in their **C: N** ($F_{1,\ 105} = 0.565$; $p = 0.454$), **C: P** ($F_{1,\ 103} = 0.338$; $p = 0.562$), **N: P** ($F_{1,\ 106} < 0.001$; $p = 0.989$) ratios to laboratory-reared crickets fed a controlled laboratory diet. However, laboratory-reared black widow spiders fed solely on laboratory-reared *G. sigillatus* contained higher **C: N, C: P**, and **N: P** than field-captured black widows (urban and desert) that fed on available field prey (Fig. 4). Cannibalism supplementation for the laboratory-reared spider group significantly decreased **C: P** and **N: P**, but not **C: N,** to levels seen in field-caught, urban spiders (Fig. 4). Furthermore, laboratory-reared black widows fed conspecifics had lower **C: P** ($t = 4.22$, *d.f.* = 8; $p = 0.002$) and **N: P** ($t = 6.17$, *d.f.* = 8; $p < 0.001$) ratios than when fed a single-species diet of laboratory-reared crickets (Fig. 4). Whereas, laboratory-reared black widows fed a diet of only crickets were stoichiometrically similar to the crickets they fed on (Fig. 3).

4. Discussion

Our results document the interspecific and intraspecific variation in C: N, C: P, and N: P ratios of black widow spiders and crickets from field (urban and desert) and laboratory populations. As expected, urban, field-caught black widows had significantly lower C: N, C: P, and N: P ratios than their herbivorous, field-caught cricket prey. Urban spider and cricket subpopulations both showed significant spatial variation across urban Phoenix habitat in C: N, but C: P and N: P ratios showed less spatial patchiness. Black widows displayed significant intraspecific variability in C: N, C: P, and N: P ratios (Fig. 4). Black widow C: N did not differ between desert and urban habitats, but C: P and N: P were lower in desert widows than their urban counterparts. Laboratory-reared black widows fed a diet of only crickets were more nutrient limited than black widows that fed freely on available prey in either urban or desert habitat. Cannibalism diet supplementation for these laboratory-reared black widows lowered C: P and N: P ratios, but not C: N ratios, to levels comparable to that seen in field-caught spiders. Here, we consider the implications of intraspecific variation in stoichiometry as an adaptive response in urban exploiters to disturbance following human-induced rapid environmental change (HIREC).

4.1. Spatial variation in C: N ratios of black widows and crickets in urban field habitats

We found significant C: N variation for both black widow and cricket populations across urban-localities. Previous work suggests that terrestrial arthropods exhibit extensive intraspecific variation in nutrient composition (Bertram et al., 2008). Bertram et al. (2008) found the most variation in P composition with a four-fold (0.32–1.27%) difference in field crickets and three-fold (0.38–0.97%) difference in Weevils. Moreover, El-Sabaawi et al. (2012a,b, 2014) found that intraspecific variation in nutrient composition is strongly linked to spatial variability in elemental availability moreso than ontogeny, body size, and morphology. We found that site strongly influenced C: N ratios, but other factors that were variable between subpopulations (i.e. spider mass, spider subpopulation density, and prey abundance; see Trubl et al., 2012) were poor predictors of C: N. Intraspecific variation in nutrient composition may result due to an organism's ability to locate and assimilate nutrients from their diet (Bertram et al., 2008). This variation in nutrient composition among species can influence condition-dependent behaviors (Bertram et al., 2006) and condition-dependent signals such as the black widow's red hourglass (Johnson et al., 2017). For example, male crickets that assimilate more P into their tissues spend more time signaling for mates (Bertram et al., 2006, 2009). Future work should explore intraspecific variation in nutrient composition on condition-dependent behaviors (e.g. precopulatory sexual cannibalism) in novel environments.

4.2. Arthropod stoichiometry from field- urban and field -desert habitats

Black widows from urban habitats were not more N limited than desert black widows (Fig. 4), despite the fact that arthropod prey

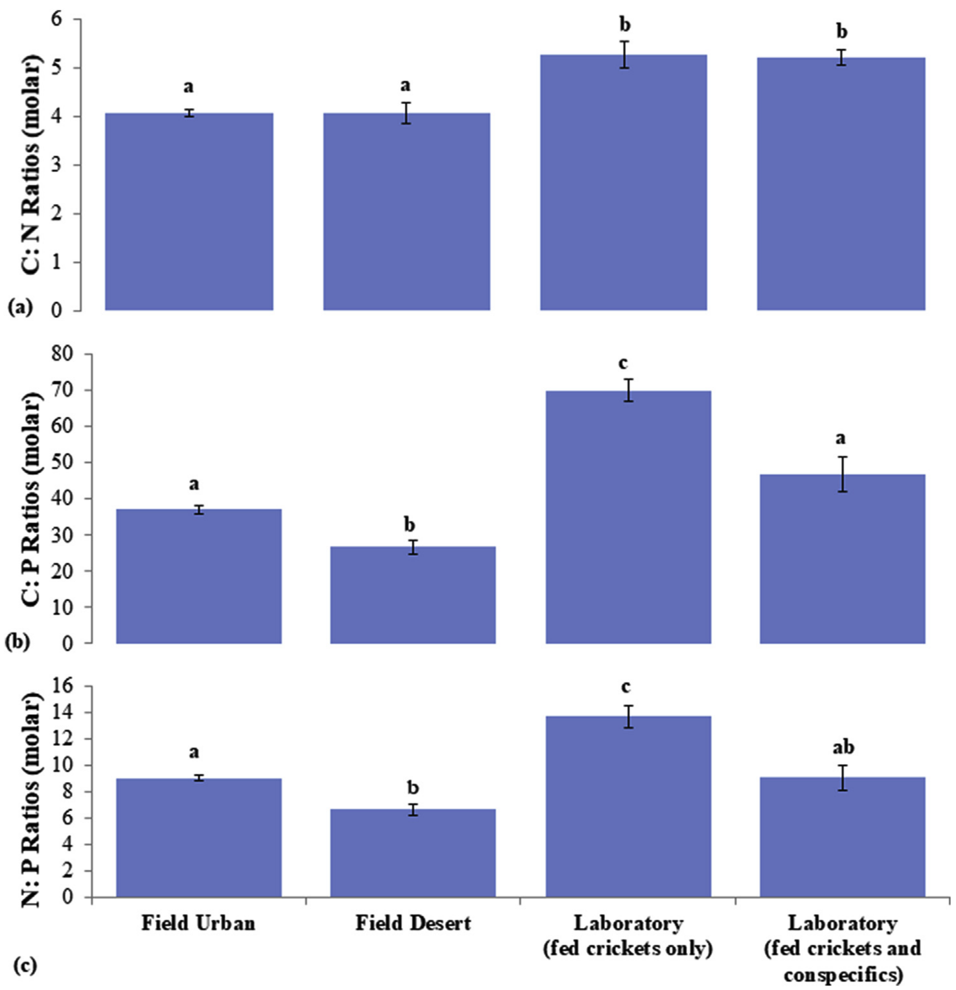

Fig. 3. Urban black widow spiders contain lower (a) C: N (t = 2.67; d.f. = 9; P = 0.013), (b) C: P (t = 17.2; d.f. = 9; $P < 0.001$) and (c) N: P (t = 17.0; d.f. = 9; $P < 0.001$) ratios than cricket prey collected across the greater metropolitian Phoenix area. Laboratory black widows fed a diet of laboratory crickets were similar in their (d) C: N (t = 1.502; d.f. = 8; P = 0.086), (e) C: P (t = 0.393; d.f. = 8; P = 0.353), and (f) N: P (t = 0.762; d.f. = 9; P = 0.2325) ratios to cricket prey. Values represent mean ± se. Asterisk above columns denote significant (P = 0.001) differences between treatment groups.

diversity is reported to be higher in Sonoran Desert habitat relative to urban Phoenix habitat (Bang and Faeth, 2011). It is conceivable that the diversity of arthropod prey available to urban black widows may be greater than previously thought. Indeed, our censuses revealed only a slight, non-significant increase in prey diversity for desert subpopulations relative to urban subpopulations. One prey type that is much more readily available for urban spiders than desert spiders is conspecifics (Johnson et al., 2012). Indeed, cannibalism is thought to offer predators a high-quality meal that is ideally composed of all nutrients required for successful growth and reproduction (Wise, 2006). Our data from the laboratory experiment suggests that cannibalism among black widows does not relax N imbalances, but instead involves a transfer of high levels of P (see below).

Alternatively, abiotic disturbances unique to the urban ecosystem could be affecting this comparison. We have shown that Phoenix's urban heat island creates a microclimate that is 6 °C hotter for urban black widows, and that this has profound influences on both black widow development and behavior (Johnson et al., unpubl. data). Such a profound urban abiotic stressor could have a dramatic impact on physiology and stoichiometry as well. Alternatively, anthropogenic N

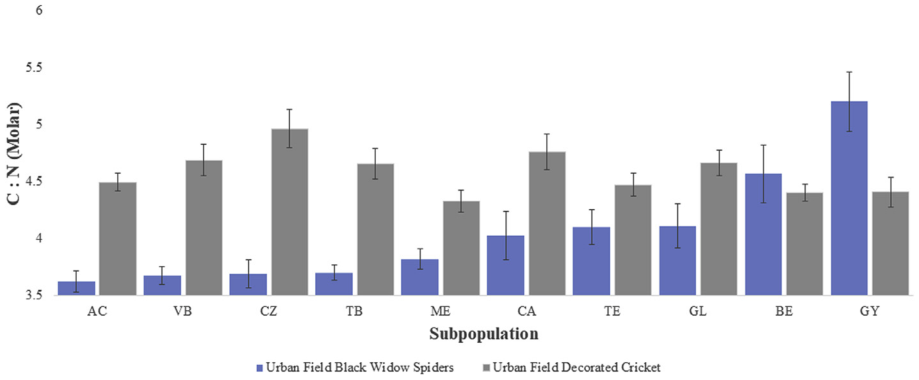

Fig. 4. Mean (and SE) nutrient ratios, (a) C: N ($F_{3,160}$ = 12.333; $P < 0.001$), (b) C: P ($F_{3,159}$ = 26.242; $P < 0.001$), (c) N: P ($F_{3,163}$ = 19.523; $P < 0.001$) of black widow spiders on diets from the field or laboratory. Different letters (above bars) indicate significant differences among diet treatments ($P < 0.001$ with a Bonferroni correction).

deposition in urban environments can cause a shift from N to P limitation (Vitousek et al., 2010) which could explain why urban spiders (and their prey) were no more N limited than desert arthropods. For example, in an aquatic system, human-mediated nutrient inputs increased consumer nutrient composition (Singer and Battin, 2007). Human-mediated N inputs are an order of magnitude higher within urban Phoenix than N inputs in surrounding Sonoran Desert habitat (Baker et al., 2001). Thus, in urban environments black widow subpopulations may not be constrained by N imbalances (see Fig. 4).

Interestingly, across urban habitat, some outlier subpopulations harbored twice the prey diversity seen at other subpopulations of the same habitat type. This latter finding suggests spatial variation within urban habitat (perhaps caused by differential water or N supplementation across city municipalities) may be greater than variation among urban and desert habitats. Such ideas that emphasize the ecological complexity that can arise from urban habitat fragmentation are replacing antiquated notions that urban habitats are somehow less complex than pristine regions (Grimm et al., 2008; Trubl et al., 2012).

While desert spiders were not more N limited than urban spiders, we did find that urban spiders were more P limited than their desert counterparts. Phosphorus is a limiting element that is essential in juveniles for growth (Elser et al., 2001; Huberty and Denno, 2006) and adults for reproduction (Visanuvimol and Bertram, 2010). European house crickets (*Acheta domesticus*) fed P-rich diets gained more weight, were in better condition at maturity, and contained more P in their bodies than crickets fed a P-poor diet (Visanuvimol and Bertram, 2011). In line with this thinking, Johnson et al. (2012) found desert black widows to be in better condition and to produce denser eggs than urban black widows. Recently, dietary P availability has been linked with reproduction in *Daphnia* with low P diets causing reduced egg size and egg survival (Urabe and Sterner, 2001). These results suggest that P imbalances in urban environments could impact black widow fitness. Recent data suggests that spiders face higher risk of P limitation due to large P imbalances between trophic levels and that trophic specialization may further increase P imbalances (González et al., 2011; Ludwig et al., 2018). However, black widows flourish in urban environments where infestations are influenced, in part, by high levels of prey abundance (Trubl et al., 2012). Future studies should examine black widow P requirements, as well as the hypothesis that cannibalism offers urban black widows an opportunity to relax P imbalances (see below).

4.3. Laboratory results of diet influences on black widow and cricket stoichiometry

Crickets reared in the laboratory were similar in their C: N, C: P, and N: P stoichiometry to crickets from urban environments. In contrast, Bertram et al. (2006, 2008) found that crickets reared in the laboratory, on a monotonous diet, exhibited less variation in N and P than crickets collected from the field. This difference may be explained simply by habitat differences.

The crickets from Bertram et al. (2008) were collected from a relatively high productivity urban habitat (golf course), whereas the urban crickets from our study were collected from relatively xeric locales that are likely restricted in productivity and prey availability (Cook and Faeth, 2006). It would be interesting to target the urban spatial patchiness described above, for example contrasting the stoichiometry of urban arthropods collected from yards/neighborhoods employing different levels of supplemental water in the urban desert.

Our laboratory population of black widows fed a single-species diet of crickets had significantly higher N: P and C: P, but not C: N ratios than laboratory widows fed a mixed diet of crickets and conspecifics (Fig. 4). Generalist predators on a single-species diet experience reduced survival and reproduction compared to mixed diets (Evans et al., 1999; Toft and Wise, 1999). A single prey species diet like the one we provided for spiders in the laboratory, and which many arthropod ecologists rely upon for their laboratory populations, may not provide adequate nutrients required for optimal growth and reproduction for generalist predators (Toft and Wise, 1999) and may therefore interfere with our understanding of the ecology of urban arthropods.

4.4. Laboratory and field comparisons of black widow and cricket stoichiometry

Our laboratory population of black widows fed a single-species diet of crickets were significantly more nutrient limited than black widows captured from urban and desert field subpopulations (Fig. 4). Despite the presumed lack of prey diversity in urban habitat (Bang and Faeth, 2011), urban black widows had lower C: N, N: P, and C: P than laboratory-raised spiders fed on a single prey type. Indeed, our laboratory spiders were not only more nutrient limited than field spiders, but they also did not vary in C: N, C: P, and N: P ratios from their food source, laboratory-raised crickets! We recognize that there are several ecological and evolutionary factors that can affect an organism's stoichiometry in the field such as spatial variability in elemental availability (El-Sabaawi et al., 2012a, b, 2014). However, our comparative approach in utilizing laboratory experiments combined with field (urban and desert) observations may shed insight into how variation from a strict nutrient homeostasis may serve as an adaptation for species that thrive in rapidly changing environments. For example, cannibalism in black widows may result as a behavioral adaptation to alleviate P imbalances in areas of reduced prey diversity and due to increased densities of conspecifics seen within urban habitat (Trubl et al., 2012). Thus, more controlled studies in the field are needed to investigate the link between behavioral adaptations and stoichiometry of urban pest species.

5. Conclusion

We have shown that black widows exhibit extensive stoichiometric variation within urban field habitats. Black widows may thrive in urban habitats, in part, by their ability to deviate from a strict elemental composition when restricted to a single-species diet. Furthermore, in comparison to our laboratory experiment, cannibalism may be a behavioral mechanism for black widows to cope with P imbalances in urban field subpopulations that house fewer prey species. Future work should study how shifts from elemental homeostasis influence black widow performance and reproduction across urban subpopulations. This work can lead to better management strategies in controlling urban exploiter populations to maintain or even increase biodiversity. The integration of population dynamics and ES is an area that can identify the mechanisms that drive urban exploiter populations and ultimately shape biodiversity patterns in urban ecosystems. We suggest the high levels of nutrient variation and intraspecific variation shown here may help urban pests to thrive following HIREC.

Statement of authorship

PT and JCJ designed the experiment. PT collected the data. PT wrote the first draft of the manuscript. PT and JCJ contributed substantially to the revisions.

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