

4-13-2018

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Ripp, Jake; Omar T. Eldakar; Andrew C. Gallup; and Paul T. Arena. 2018. "The Successful Exploitation of Urban Environments by the Golden Silk Spider, *Nephila clavipes* (Araneae, Nephilidae)." *Journal of Urban Ecology* 4, (1): 1-6. doi:10.1093/jue/juy005.

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SHORT NOTE

The successful exploitation of urban environments by the golden silk spider, *Nephila clavipes* (Araneae, Nephilidae)

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Submitted: 6 July 2017; Received (in revised form): 12 March 2018; Accepted: 15 March 2018

Abstract

Urbanization typically leads to habitat destruction producing negative effects for native species, but some species may exploit these settings. This concept was investigated in the golden silk spider (*Nephila clavipes*), a large, formidable spider that commonly inhabits forest edges as well as open spaces in urban environments throughout its vast geographic range. Here, we compared variation of *N. clavipes* success as measured by body size, web size and web positioning along an urban–rural gradient in southern Florida. From morphological measurements collected in the field, urban spiders had 60% longer legs and 35% longer bodies than both park and rural spiders. Furthermore, webs of urban spiders were considerably larger and constructed significantly further from the ground than those of park and rural habitats. The combined observations of body size, web measurements and prominent web placement suggest that *N. clavipes* are successful exploiters of urban environments relative to park and rural settings in southern Florida. Although previous research has generally focused on the negative aspects of urbanization on animal welfare, this study provides evidence suggesting *N. clavipes* might benefit from these environmental changes.

Key words: urbanization, disturbance, urban-rural gradient, edge effects, South Florida

Introduction

Urbanization has profound impacts on local ecology and native species success (Sih et al. 2011; Sih 2013; Sol et al. 2013). Resulting anthropogenic modifications to natural environments alter habitats and threaten overall biodiversity (Foley et al. 2005). Human-induced environmental changes result in fragmentation and replacement of natural habitats with artificial structures (Sih et al. 2011). These alterations often push animal inhabitants beyond their limits of flexibility and tolerance, yet some species appear to benefit from the ecological opportunities that urbanization provides (Kotze et al. 2011; Sol et al. 2013).

Introduced ant species, such as longhorn crazy ants *Paratrechina longicornis* (Wetterer 2008), pharaoh ants *Monomorium pharaonis* (Wetterer 2010) and ghost ants *Tapinoma melanocephalum* (Wetterer 2009), along with the infamous German cockroach *Blatta germanica* (Berenbaum 1989) come standard with urban construction. Spiders, such as the common house spider *Parasteatoda tepidariorum* (Levi 1967; Levi and Randolph 1975) and longbodied cellar spider *Pholcus phalangoides* (Schäfer et al. 2001), also readily inhabit human dwellings, while the golden silk spider *Nephila clavipes* regularly adorns artificial structures in tropical and subtropical environments from North to South America and the Caribbean (Vargas 1997).

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Although it might seem that spiders in general should benefit from urbanization due to the increased attraction of insects to urban light sources (Heiling 1999; Eisenbeis et al. 2009), success is not universal (Johnson et al. 2012; Argañaraz et al. 2017). Recent multi-species comparisons of web-building spiders suggest a general loss of biodiversity with increased urbanization, yet also mention that not all species are negatively affected (Argañaraz et al. 2017; Lowe et al. 2018). Urbanization selects for particular ecological traits (Blair 2001) due to the more exposed structure that these environments provide (Varet et al. 2011), and thus is expected to favor open habitat species. More generally, the successful exploitation of urban environments is related to the degree of match/mismatch between the focal organism's natural environment and the novel human-altered environment (Sih et al. 2013). Magura et al. (2010) reported that the abundance of open habitat ground-dwelling spiders increased compared to their forest-adapted counterparts in urban settings.

It has also been suggested that generalist species are favored in urban environments due to their flexibility (Sih et al. 2011; Sih 2013). For example, the successful colonization of the bridge spider *Larinioides sclopetarius* in urban areas throughout the Holarctic has been attributed to their extraordinary behavioral plasticity (Kralj-Fišer and Schneider 2012). Horváth et al. (2012) investigated multiple hypotheses surrounding the relationship between species diversity of terrestrial arthropods and urbanization in Hungary. Results from pitfall traps revealed that both open habitat adapted and generalist spider species increased in abundance with urbanization. Furthermore, the percentage of generalist spiders caught significantly increased with urbanization in Greece (Kaltsas et al. 2014); however, these spiders were also associated with open habitats.

Although the diversity and richness of web-building spiders might show an overall decline with urbanization (Argañaraz et al. 2017; Lowe et al. 2018), a recent report suggests that the spider *Nephila plumipes*, which is known as both a generalist predator and one that naturally utilizes open habitats, might individually benefit (Lowe et al. 2014). Specifically, the presence of hard surfaces and the extent of anthropogenic disturbance was positively associated with female body size and fecundity. Given this backdrop, we investigated whether a closely related spider, *N. clavipes*, is also a successful exploiter of urban environments in southern Florida (see Fig. 1).

N. clavipes is particularly well positioned to benefit from urbanization. Similar in morphology, behavior and ecological niche to its congener *N. plumipes*, *N. clavipes* are naturally found along forest edges and trails (Robinson and Mirick 1971) where they build prominent webs to intersect the flight path of insects. Webs can reach a few meters across connecting trees and shrubs as well as crossing over flowing water courses often at heights >5 m (Robinson and Mirick 1971; Moore 1977). In urban habitats, *N. clavipes* readily construct webs in large open spaces at similar heights over roads, drainage ditches, walkways, as well as connecting buildings to the surrounding vegetation, suggesting comparable habitat usage/overlap between their natural and artificial environments. These open space webs generally improve foraging success as they provide corridors in which spiders may exploit (Blamires et al. 2007). Furthermore, these high-positioned webs may coincidentally take advantage of increased prey abundance near sources of artificial lighting (Heiling 1999; Eisenbeis et al. 2009). Populations of these spiders from Florida are also known to possess adaptations that counteract thermal stress by orienting the tip of the abdomen toward the sun as well as employing evaporative cooling through



Figure 1. Example of an adult female golden silk spider, *N. clavipes*. Members of this species can reach sizes over 40 mm.

manipulating a droplet of fluid with the chelicerae (Krakauer 1972). This allows these spiders to better exploit a wide range of thermal conditions, including high heat that accompanies life in the city (i.e. heat-island effect; Santamouris 2001, 2013). Overall, the natural history of *N. clavipes* appears ideally suited for the successful exploitation of urban environments.

Moreover, *N. clavipes* is an ideal subject for measuring success across environments. Body size is a reliable predictor of fecundity in this species (Higgins 1992), and spider body size overall is strongly influenced by the environment (Li and Jackson 1996; Higgins and Goodnight 2011; Lowe et al. 2014). Also, once mature, *N. clavipes* build conspicuous semi-permanent webs on which they remain for the duration of their life, thus their webs serve as an *extended phenotype* that reliably reflects variation in spider physiology, fitness and stress across environments (Blamires 2010; Nakata 2012; DiRienzo and Montiglio 2016; Blamires et al. 2017).

To explore whether *N. clavipes* benefit from urbanization, field measurements of mature female body size and metrics of web size and location were compared across sites categorized by the extent of urbanization (rural, park and urban). Overall, we predicted that urban spiders would (i) be physically larger than those inhabiting rural locations and parks and (ii) construct webs that were both larger and positioned higher off the ground.

Methods

Study sites

Several study sites in southern Florida along an urbanization gradient were used in this study. Specific sites were placed into

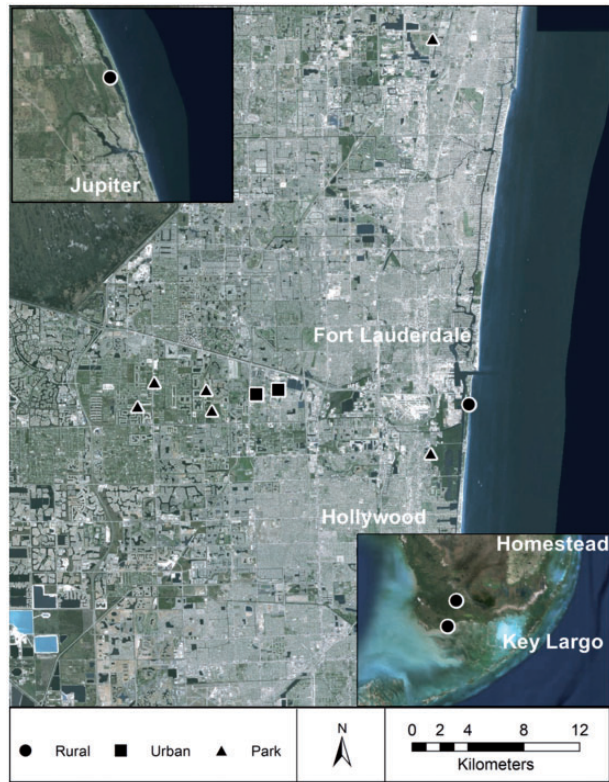


Figure 2. Satellite imagery of sample locations in southern Florida. Cities are labelled for reference. The main image contains all urban and park sample locations which were within the Miami metropolitan area. Rural locations were more widespread, extending 70 km to the northern most limit of the main image (upper inset image) and 95 km to the south of the southernmost boundary of the main image (lower inset image). GPS data for individual samples within sites are available in an online data repository (see Data availability section).

three different environmental categories: urban, parks and rural. Urban locations ($n=4$) were characterized as small areas of highly developed land dominated by residential homes and commercial buildings with garden beds and little to no native vegetation. Overall, urban locations of southern Florida were samples that contained <12% green cover. Park locations ($n=8$) were fragmented patches of native vegetation (0.41–0.99 km²), which were isolated from other patches by extensive urban development. Rural locations ($n=3$) were characterized by large continuous natural habitats, dominated by native species and minimally impacted by humans and development within Everglades National Park or well-within coastal parks (see Fig. 2). In all, parks and rural locations were similar in having >90% green cover, yet were distinguished from each other based on the nature of the immediate surrounding environment.

Field measurements

Field measurements of 187 mature females ($n=52$ urban, $n=103$ parks and $n=32$ rural) took place over the course of 1 year from February 2015 to February 2016. Field measurements included the following variables: web height (distance from web hub to the ground), web diameter (width of main prey capture web), GPS location, as well as female leg and body length. Total leg length (coxa to tarsus) of the first leg served as a proxy of hard body size (Jakob et al. 1996; Lowe et al. 2014), while body length (cephalothorax length + abdomen length)

represented a measure of soft body size (Lowe et al. 2014). Leg and body length were measured using the open source software *ImageJ*© on photos taken in the field of females with a ruler held directly next to the spider. Although body weight is predictive of fecundity, and therefore success, this variable was not measured since it varies dramatically based on time since feeding or reproductive state (Jakob et al. 1996; Lowe et al. 2014) and these factors are difficult to control for when assessing field populations. Metrics of hard body components provide more reliable and consistent proxies of the general size and state of the individual (Higgins 1992; Jakob et al. 1996; Lowe et al. 2014). Since females in areas experiencing low seasonality may reproduce year-round (Higgins 2000), which we have observed in our study populations, study sites were visited in a random order. The sample order of individuals did not correlate with metrics of body size (leg length, Spearman $r=0.05$, $P=0.455$; body length Spearman $r=0.064$, $P=0.38$) such that differences between sites cannot be attributed to age.

Statistical analysis

Multivariate analysis of variance (ANOVAs) were conducted to test whether the spider-associated dependent variables (web height, web diameter and measures of female leg length and body length) were influenced by environmental category. Tukey Honesty Significant Difference (HSD) post hoc tests were then used to assess differences between the three respective environmental types. Regression analyses were performed to assess the linear relationships between metrics of female body size and the diameter and placement (distance from ground) of corresponding webs.

Results

For a complete summary of all variables across the three environmental categories along with ANOVA output statistics, see Table 1. Morphological measures differed significantly based on location. Overall, urban spiders had ~60% longer legs and ~35% longer bodies compared with spiders inhabiting rural and park habitats. There were no significant differences in either leg or body length between park and rural habitats, supporting the notion that the immediate microhabitat is the relevant scale to observe physiological effects. Web size and placement also varied significantly between environments. On average, urban settings had both the largest webs and those furthest from the ground, with rural webs the smallest and closest to the ground, and parks falling in the middle for both metrics.

A series of simple regressions revealed that across all environments, web diameter positively predicted both components of body size (leg length, $R^2=0.37$, $F_{1,84}=106.98$, $P<0.001$; body length, $R^2=0.38$, $F_{1,84}=113.75$, $P<0.001$). Overall, these results suggest that spiders attain greater body size and therefore increased reproductive potential through their exploitation of urban settings compared to spiders inhabiting either parks or rural environments. This advantage is presumably achieved through the construction of larger and more optimally placed webs that exploit the anthropogenic modifications of urban settings.

Discussion

While urbanization is exceedingly detrimental to overall biodiversity, some species actually thrive within ecological settings characterized by human habitat modification. Here we have

Table 1. Summary of the variables measured across the three environment types ($M \pm SD$)

Variable	Urban (n = 52)	Park (n = 103)	Rural (N = 32)	F	η^2	P
Female measurements						
Leg length (cm)	6.03 (± 1.25)a	3.89 (± 1.57)b	3.63 (± 1.41)b	48.92	0.347	<0.001
Body length (cm)	2.71 (± 0.57)a	1.97 (± 0.86)b	1.92 (± 0.72)b	18.97	0.171	<0.001
Web measurements						
Web diameter (cm)	70.41 (± 28.71)a	51.93 (± 20.78)a	42.80 (± 20.32)b	15.15	0.143	<0.001
Web distance from ground (cm)	278.62 (± 95.00)a	206.27 (± 74.60)b	153.88 (± 64.78)c	48.94	0.348	<0.001

ANOVA F and P values, as well as effect sizes (partial eta, η^2) are displayed in the respective columns. When present, letters (a, b, c) following measurements represent statistically discrete categories as determined by Tukey HSD post hoc tests ($P < 0.05$).

shown that within southern Florida, *N. clavipes* residing in urban environments were substantially larger and thus presumably more successful than their counterparts residing in the nearby parks or rural settings. Many factors might contribute to why *N. clavipes*, in particular, would thrive in cities. *N. clavipes* naturally occupies forest edges, so fragmentation and the proliferation of edge space that typifies urbanization only serves to increase their preferred habitat. Moreover, *N. clavipes* naturally build expansive webs reaching across open areas in effort to ensnare flying insects, and our data show that both the placement and construction of webs from our samples varied by environment type. Urban spiders built webs that were both considerably larger and more elevated from the ground which emulate the placement of webs in their natural environment along forest edges (Robinson and Mirick 1971). Therefore, *N. clavipes* seemed to be able to readily exploit human-made structures, which ground-dwelling or forest-interior species may be unwilling or unable to capitalize on. These findings are consistent with those of the closely related *N. plumipes*, which responded favorably as natural vegetation decreased and presence of artificial structures increased (Lowe et al. 2014).

While *N. clavipes* individuals of urban populations were significantly larger than those inhabiting either parks or rural settings, no measurable difference in body size existed between individuals from the latter habitat types. This supports the notion that the local microhabitat was a principle driver of these effects in *N. plumipes* (Lowe et al. 2014). Since parks are simply small patches of natural vegetation within an urban setting, they might essentially share the same immediate microhabitat. This view is also supported by the relative similarity of webs in park and rural settings compared to urban webs, suggesting that at least with regards to overall web construction, our samples of *N. clavipes* respond more similarly to parks and rural areas than to urban sites.

Interestingly, urban spiders appear to have disproportionately longer legs than park and rural spiders. However, including body size as a covariate in our analysis revealed no interaction with environment type. Therefore, we suggest that this relationship is driven by allometry as opposed to a result of local adaptation, especially considering spiders need to first reach larger sizes for this effect to occur. This is not to say that developmental byproducts do not provide any benefit. Spider leg length has been shown to influence running speed across species (Moya-Laraño et al. 2008), and longer legs have been shown to decrease running speed on horizontal surfaces while increasing speed on inclines in the congener of our study species, *N. plumipes* (Prenter et al. 2012). These effects indeed might be beneficial in vertically structured urban habitats due to the prevalence of man-made structures such as buildings, poles and railings. Furthermore, a recent report on the garden spider

Araneus diadematus suggests that body size also imposes constraints on web-building behavior (Dahirel et al. 2017). However, despite this limitation, smaller urban individuals remained remarkably plastic in their ability to adjust their web-building behavior to compensate for changes in food availability. Thus, while we attribute the substantially larger bodies of urban spiders to greater foraging success, if this yields disproportionately longer legs and modified web-building behavior, it could feed-back on body size, further complicating the relationship between urbanization and *N. clavipes* body size and web architecture.

Additional factors that were not sampled here but could contribute to the differences found in urban locations might include increased overall prey abundance, and decreased top-down trophic pressures. Heiling (1999) found a significantly higher abundance of available prey for bridge spiders *L. scopeptarius* in lit habitats compared to unlit habitats. Higher temperatures provided by cities also effect prey availability as warmer conditions can hasten arthropod developmental rates (Li and Jackson 1996; Briere et al. 1999; Huffaker et al. 1999) and increase their relative abundance (Meineke et al. 2013). While these conditions would seemingly also favor potential predators of *N. clavipes*, such as bats, many potential predators seem to avoid urban locations to avoid predation themselves (Rydell and Racey 1995; Stone et al. 2009). Also, despite their conspicuous web locations, *N. clavipes* appear less vulnerable to predation than other spiders, due in part to their willingness to form colonial webs (Hodge and Uetz 1992) although colonial individuals were uncommon in our sample populations and excluded from our study. It has also been suggested that *N. clavipes* construct barrier webs to thwart potential predators and therefore might indicate local predation pressure (Higgins 1992); however, barrier web size was not assessed in our study. Furthermore, sample sites varied considerably in their proximity to one another, thus an element of spatial autocorrelation might have contributed to our results. For example, urban sites were relatively clumped whereas rural sites were largely spaced. However, the similarity of findings between sites within each environmental category suggest these effects were minimal if not non-existent.

In conclusion, previous assessments of spiders along the urban-rural gradient have generally supported the notion that open habitat generalists are more likely to move into and benefit from urban environments. Building upon the findings of the closely related congener *N. plumipes* (Lowe et al. 2014), we provide preliminary evidence of the successful exploitation of urban environments by *N. clavipes*. While *N. clavipes* appear to benefit from the ecological conditions of urbanization, recent research suggests this is atypical for web-building spiders (Argañaraz et al. 2017; Lowe et al. 2018). Therefore, more research is needed to reveal the factors and potential feedbacks

contributing to the differences in response to urbanization observed across spider species.

Data availability

Data is stored and publicly available through the data repository provider Open Science Framework (<https://osf.io/m5v8s/>).

Acknowledgements

We thank Cassandra Corrigan and Brice Schrenkel for assistance in the field. We also thank the editor and anonymous reviewers for the helpful feedback.

Conflict of interest statement. None declared.

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