Urbanization affects web abundance and aggregation of a funnel-weaving spider, *Agelenopsis pennsylvanica* (Agelenidae)

Brandi J. Pessman[1] · Madison Hays[1] · Earl Agpawa[2] · Eileen A. Hebets[1]

Abstract

Animals distribute themselves within habitats based on a variety of environmental conditions, including those impacted by urbanization. Suspected global declines in urban arthropod biodiversity have required that we examine how urban conditions affect the distribution of this ecologically important group. Throughout North America, funnel-weaving spiders (Agelenidae) are prevalent across urban habitats and actively choose sites to build webs. We compared *Agelenopsis pennsylvanica* abundance and distribution between two distinct urban habitats: an urban center (university campus) and an urban forest (city park). These urban habitats differed significantly in features like plant diversity and proximity to roads and highways. We searched along paths from randomly selected start sites in each habitat until we found the first occupied (focal) web. Within a ten-meter radius of the focal web, we found that both (i) webs and (ii) spiders were more abundant in the urban center than in the urban forest. We also found (iii) shorter distances between webs and (iv) lower web heights in the urban center. Generally, spiders were more abundant and aggregated at sites that had lower plant diversity. Abundance decreased with increased road-traffic impact. Thus, *A. pennsylvanica* exhibits different spatial patterns across distinct urban habitats, which relates, in part, to differences in environmental conditions. The suggested importance of road and highway impacts on *A. pennsylvanica* distribution may signify that vibratory noise plays an essential role in this system. Since vibratory information use is ubiquitous across arthropods, future research should further address how vibratory noise may impact urban arthropod spatial patterns.

Keywords Arthropods · Environmental predictors · Human-Induced Rapid Environmental Change (HIREC) · Nearest neighbor · Spatial distribution

Introduction

Animal abundance and distribution are influenced by combinations of environmental factors, intra- and interspecific interactions, and dispersal capacity (Diez and Pulliam 2007; Svamberkova and Leps 2020). Environmental factors, including climatic conditions, land cover, habitat heterogeneity, and access to certain resources (like water and shelter), are suspected to relate to physiological constraints that limit the fundamental niche (Chase and Leibold 2003). Interactions within species (between conspecific competitors and mates) and across species (with predators, prey, and heterospecific competitors) further shape animal spatial patterns (Anderson 2017; Boulangeat et al. 2012). While dispersal capacity can determine a species' range, barriers can limit dispersal and prevent animals from reaching suitable habitats (Amundrud et al. 2018; Boulangeat et al. 2012).

Aggregations can form when suitable conditions and resources are not evenly distributed, leading to higher-quality patches (Churchill et al. 2020). For example, gaps in the tree canopy allow more sunlight to reach the understory – thus, increasing plant height and soil moisture and decreasing leaf litter – causing some invertebrate families to become more abundant in these patches (Perry et al. 2018). Clumping can also result from incomplete dispersal that occurs when barriers, often due to habitat structure, prevent adequate dispersal (Riechert 1974a). Scientists have found differences in the relative importance of different spatial predictors based on the type of taxon-specific spatial

✉ Brandi J. Pessman
  bjpessman@gmail.com

1 Department of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE, USA

2 Department of Entomology, University of Nebraska-Lincoln, Lincoln, NE, USA

information collected – *i.e.,* presence, abundance, aggregation, or vertical position (Boulangeat et al. 2012).

Due to intense habitat disturbance and dense human presence, urbanization has drastically modified the land (Alberti et al. 2020; McDonnell and Pickett 1990; Pickett et al. 2001). These land changes lead to altered environmental conditions, community dynamics, and dispersal capability (Piano et al. 2020). Urban environments are characterized by decreased biodiversity (McKinney 2002), increased impervious cover (compacted soil from buildings and pavement, Nowak and Greenfield 2020), habitat patchiness (Cadenasso et al. 2007), pollution (air, water, and light, Grimm et al. 2008; Hopkins et al. 2018), and noise (air-, water-, and substrate-borne, Barber et al. 2010; Slabbekoorn et al. 2010; Wu and Elias 2014). These conditions can contribute to changes in local climatic conditions, such as when impervious cover traps heat and increases the average temperatures in cities compared to surrounding areas — *i.e.,* the Urban Heat Island Effect (Morabito et al. 2021). Growing evidence shows that urbanization changes species interactions, even reshaping whole food webs (Start et al. 2020) and altering the landscape of parasite and disease transmission (Bradley and Altizer 2007). As many of these conditions and dynamics determine animal spatial patterns, it is likely that urbanized landscapes have changed how animals spatially distribute themselves.

Urban ecosystems can also be extremely heterogeneous, with unique and diverse habitats nested within (Rivkin et al. 2019). For example, habitats within urban ecosystems can differ considerably in landscape features (e.g., tree and building cover), weather conditions (e.g., temperature, humidity, and wind speed), and disturbance (e.g., fragmentation and air, light, and sound pollution), resulting in variable access and distributions of resources and opportunities for certain species to thrive. These factors can also differentially drive animal spatial patterns (Murray et al. 2019; Trubl et al. 2012), sometimes leading to higher degrees of aggregation for urban animals (Johnson and Munshi-South 2017).

Variations in the abundance and distribution of urban arthropods can have implications for ecosystem function due to the essential ecosystem services that arthropods provide, like pest control (Otoshi et al. 2015) and pollination (Ivers et al. 2022). Arthropods are considered critical bioindicators of ecosystem health as their short generation time requires them to respond rapidly to human-induced change (McIntyre 2000). However, the impact of urbanization on arthropod ecology is still understudied (Fenoglio et al. 2020; but see Kotze et al. 2011), and the relationship between urban habitats and arthropod abundance and diversity remains controversial, with different data indicating distinct relationships (Dale and Frank 2018; Gippet et al. 2017). Such discrepancies are most likely due to abundance and distributions being species- (Gippet et al. 2017), habitat- (Bennett and Lovell 2014), and scale-dependent (Philpott et al. 2014).

While some animals benefit from urban conditions (Guenard et al. 2015), many cannot survive the disturbance and change associated with cities (Wagner 2020). Thus, it is important to determine how urban factors contribute to variation in arthropod abundance and spatial patterns for the conservation of arthropods and their essential services.

Spiders, specifically, play an important role in pest control. They are predicted to collectively consume up to 800 million tons of arthropods each year (Nyffeler and Birkhofer 2017). Previous studies have found that factors that vary across urban habitats may drive differences in spider spatial distribution, including prey abundance (Riechert and Tracy 1975; Trubl et al. 2012), noise (Bunkley et al. 2017; Gomes et al. 2020), pollution (Żmudzki and Laskowski 2012), fragmentation (Stefani and Del-Claro 2015), microclimate conditions (Riechert and Tracy 1975), vegetation structure (Peng et al. 2020), and suitable web substrates (Chan et al. 2009). Random spacing in solitary spiders is typically maintained by territoriality and aggression over resources like prey and mates (Riechert 1974a), but occasionally, conditions arise that allow solitary spiders to become more tolerant of neighbors. The mechanisms behind non-social spider aggregations—especially in urban habitats—are unclear. Nonetheless, there are reports of aggregations of spiders in urban habitats, such as the web-building spiders *Lactrodectus hesperus* and *Brigittea civica* (Johnson et al. 2012; Mammola et al. 2018). A more thorough understanding of how and why various species of spiders might distribute themselves differently in urban settings is important, as urban spider aggregations can have medical and aesthetic consequences, as well as implications for urban pest control services.

Funnel-weaving spiders (otherwise known as grass spiders) in the genus *Agelenopsis* (Agelenidae) are found across North America and can be locally very common. Typical web substrates include grasses, bushes, rocks, and buildings (Whitman-Zai et al. 2015). They actively select web locations based on experience of perceived quality of the site (Riechert 1976) and are thus likely impacted by environmental conditions resulting from urbanization. Abundant prey, protective web substrates (especially crevices and shrubs), and preferred thermal conditions (21 to 35 °C) have been shown to be indicators of a quality web site in a desert habitat for *A. aperta* (Riechert et al. 1973; Riechert 1974b; Riechert and Tracy 1975). *Agelenopsis pennsylvanica* (Koch 1843) is a non-desert dwelling relative that similarly builds webs consisting of a sheet that functions as a prey capture area and a retreat to escape from predators and unfavorable conditions (Fig. 1), such as direct sunlight (Riechert and Tracy 1975). The horizontal sheet is not sticky, and the web is used solely for its vibratory properties to rapidly and accurately alert the spider to prey that fall upon or walk across the web (Singer et al. 2000). Although the natural
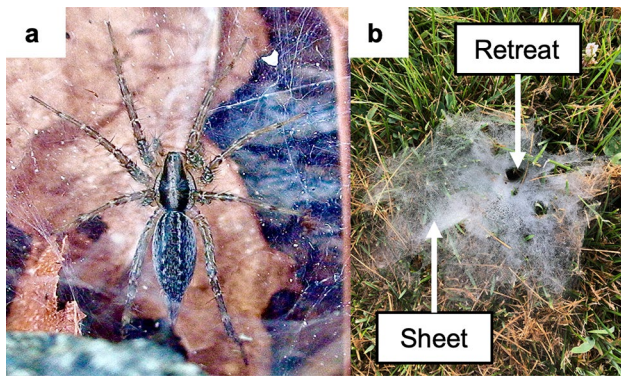
Fig. 1 Study System—*Agelenopsis pennsylvanica* (**a**). The web consists of a retreat where the spider waits for prey to land, fall, or walk on the web sheet (**b**)

habitat of the species is unclear, they are thought to have originated in Pennsylvania – a region of primarily forested landscape – but have since spread across North America and are described as opportunistic (Whitman-Zai et al. 2015). Still, Whitman-Zai et al. (2015) suggest that the genus tends to build webs in tall and short grass prairies.

To understand habitat characteristics that might influence the distribution of *A. pennsylvanica* across urban environments, we compared *A. pennsylvanica* spatial patterns between two urban habitats (an urban center and an urban forest). In particular, we asked the following three questions: (*i*) How do environmental conditions vary between two urban habitats? (*ii*) How does *A. pennsylvanica* web abundance, aggregation, and position vary between these two urban habitats? (*iii*) What environmental variables help predict spider spatial patterns in distinct urban habitats? Here, we define aggregation (according to Clark and Evans (1954)) as the clumping of webs in space – taking the web density into account. Aggregations in this study do not suggest contact between webs or interactions between neighbors, as contact between web sheets was never observed. Based on preliminary observations, we predicted that *A. pennsylvanica* would be more abundant and aggregated in the urban center than the urban forest. We further expected that specific environmental conditions that vary between the two habitats (e.g., tree cover, plant species richness, and disturbance from roads) would be correlated with the variation in the spatial patterns of *A. pennsylvanica*.

Material and methods

We conducted our study in September and October of 2020 in Lincoln, Nebraska, USA. Lincoln – with a population of about 300,000 people (QuickFacts 2020) – has diverse urban habitats that vary in the degree of disturbance, management,

and plant cover. We compared the abundance, aggregation, and position of funnel webs of the spider *Agelenopsis pennsylvanica* between two urban habitats: the University of Nebraska-Lincoln (UNL) City Campus (an urban center) and Wilderness Park (an urban forest) (Fig. 2, Fig. S1). These two habitats were selected due to their distinctive characteristics (described below), preliminary observations of potential differences in funnel-weaving spider abundance and aggregation (Fig. S2), and ease of access.

Urban Center—We defined the study boundaries of UNL City Campus as Salt Creek Roadway, North Antelope Valley Parkway, North 10th Street, and Q Street (1.12 km^2, Fig. 2, Fig. S1). UNL City Campus is adjacent to, and just north of, downtown Lincoln (253.73 km^2). Lawns are maintained by frequent mowing, and gardens and landscaping are regularly pruned. There was heavy foot traffic from UNL's 20,286 undergraduates enrolled in the 2020–2021 academic year, 37% of which lived in college-owned, -operated, or -affiliated housing (UNL Office of Institutional Effectiveness and Analytics 2021).

Urban Forest—Wilderness Park is a stretch of forested land (6.44 km^2, Fig. 2, Fig. S1) starting about 3.58 km southwest of UNL City Campus and downtown Lincoln, extending south and along Lincoln city limits. Wilderness Park has about 18 km of dirt trails, dense deciduous tree growth, and variable undergrowth. The trails are open for recreational walking, running, biking, and horse riding. While we found no public records of the number of visitors to Wilderness Park, trail-goers were infrequent during data collection.

Survey sites

To select random survey sites in each of the two habitats, we assigned numbers to each intersection of roads and sidewalks that meet from the four cardinal directions in the urban center and to intersections of three or more trails in the urban forest (Fig. S3). We used a random number generator to randomly select 12 intersections in the urban center and 10 intersections in the urban forest as start sites (Table S1). We marked the GPS coordinates of these locations using a GPS receiver (Magellan SporTrak Map, Model 980616–01, Parsippany, New Jersey, USA).

From each start site, we began walking along a path in a randomly selected direction (North, East, South, or West using a random number generator). We conducted a thorough visual search of the edges of the path for *A. pennsylvanica* funnel webs as the GPS receiver tracked our movement (Fig. S4). We walked along pre-existing sidewalks, roads, and trails because paths were a common feature of both habitats, along which we had previously found funnel-weaving spiders. We often found *A. pennsylvanica* in edge habitats in the study region, and this tendency to build webs at a habitat's edge is shared by other spider species (Cobbold
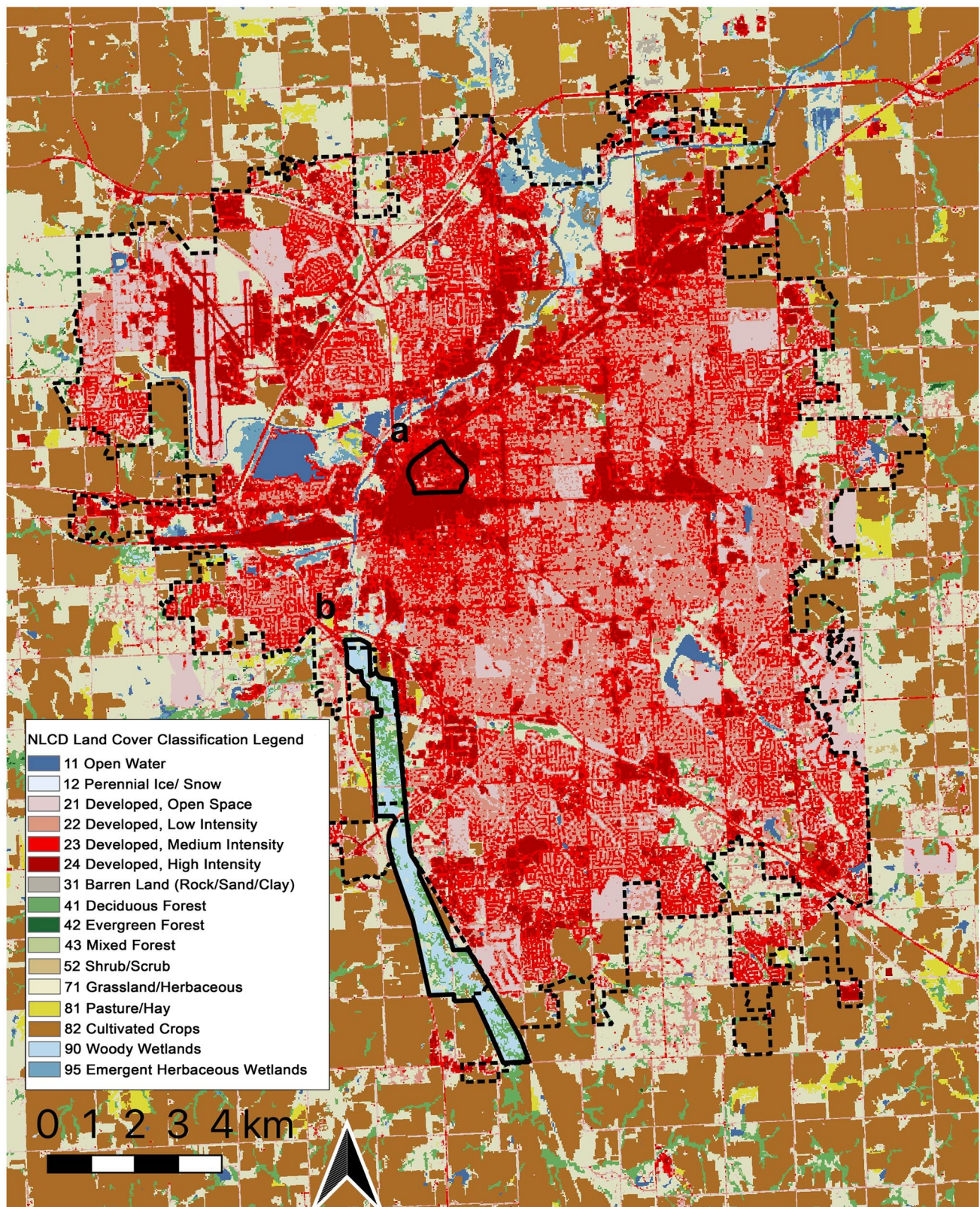
Fig. 2 Land cover raster with borders for Lincoln, Nebraska, USA city limits (dashed border), University of Nebraska-Lincoln (UNL) City Campus (Urban Center, solid border, **a**), and Wilderness Park (Urban Forest, solid border, **b**) using the 2019 National Land Cover Data on Land Cover and QGIS (v. 3.16.3-Hannover, ESRI 102704). For visualization and listing of survey sites, see Fig. S1 and Table S1, respectively

and Supp 2012). Additionally, the thick undergrowth of the urban forest often restricted searches off the trails. To ensure equivalent search efforts, we took more time searching the edge of dense undergrowth in the urban forest.

Focal web – When we reached a funnel web, we checked to see if the web was occupied by a spider. We did this by resting a toothpick secured to the bristled end of a vibrating toothbrush on the sheet of the web. We turned on the electric toothbrush to simulate prey in the web, as the vibrations are at frequencies similar to those produced by prey (Chuang and Riechert 2021). Our preliminary trials and other studies (Frohlich and Buskirk 1982) have demonstrated this to be an effective means of inducing an attack response from a spider. For example, in the lab, 76 out of 99 (76.8%) of *A. pennsylvanica* females attacked the vibrating toothbrush within 30 s every time (from 12 trials, unpublished data). If a spider emerged, we noted this web as the *focal web*. If no spider emerged after 30 s, we continued searching until we found an occupied funnel web. Any unoccupied webs found before the focal web were excluded from the web count when comparing the number of webs between habitats. However, we included these webs when we calculated density in the Clark and Evans aggregation index (Methods: Spider web abundance, patterns, and positions between habitats). We used the GPS receiver to mark the coordinates of the focal web. Although it is possible that other species of *Agelenopsis* are present in Lincoln, we have only found *A. pennsylvanica* during surveys in the area.

We collected data from September 23 to October 14, 2020. During these dates, all *A. pennsylvanica* had reached maturity (personal observation; Guarisco 2014).

Urban habitat characteristics

Environmental conditions at different scales– To explore how conditions at the small scale (habitats) relate to the conditions at the large scale (the city), we first compared differences in environmental conditions across our two selected urban habitats (urban center and urban forest) and Lincoln city limits. We chose impervious cover, tree cover, and land cover class for this initial analysis to capture the degree of variation between the habitats as compared to the entire city. We gathered and analyzed Geographic Information Systems (GIS) data in QGIS (v. 3.16.3-Hannover, ESRI 102704). We obtained impervious cover (building and pavement, U.S. Geological Survey 2019b), tree cover (U.S. Forest Service 2016), and land cover class (U.S. Geological Survey 2019a) from the National Land Cover Database (30-m resolution). We polygonized the tiff files and calculated the average value for each factor by location using the boundaries described above: urban center (UNL City Campus), urban forest (Wilderness Park), and Lincoln city limits (see Figs. 2, S5-S8). We calculated the averages using the following equation:

$$average = \frac{\sum_{i=a}^{b} i * x_i}{100}$$

where i is the value indicated by the pixel (with range a-b) and x_i is the percent of the habitat covered by the $i^{(th)}$ pixel category.

Environmental variables between habitats – To address how environmental conditions vary between the two habitats (urban center and urban forest), we collected nine total environmental predictors from each survey site: (1) impervious cover (percent developed surface), (2) tree cover, (3) thermal conditions (spectral radiance), (4) light at night radiance, (5) plant species richness, (6) patch area (area of continuous vegetation), and estimates of (7) road-traffic impact, (8) highway-traffic impact, and (9) total road length. All measurements except plant species richness were completed in QGIS (v. 3.16.3-Hannover, ESRI 102704).

We recorded (1) the percent impervious cover and (2) tree cover at each site using the polyganized tiff files described above. To collect (3) spectral radiance – a measure of thermal conditions on Earth's surface, we used an image from path 28, row 32 of the Landsat-7 World Reference System-2 (Band 6, 30-m resolution, taken on September 2, 2020). We assessed (4) artificial light at night levels using the 2020 Visible Infrared Imaging Radiometer Suite (VIIRS) from https://www.lightpollutionmap.info/ (500-m resolution). We analyzed these measures in 100-m buffers around each focal web. We used a 100-m buffer to accommodate the resolution of the GIS data. We refrained from including a larger buffer region as the dispersal range of this system is unknown and may be dependent on barriers present in the habitat. Despite the artificial light at night measure having a resolution of larger area than our buffer region, we chose satellite measures for artificial light measures because they exclude variation in light measures due to weather conditions and moonlight levels (Falchi et al. 2016).

We collected (5) plant species richness on-site by recording each unique plant species found in a ten-meter radius of the focal web at each survey site (Fig. S9). To identify plant species, we used the phone application, PictureThis, which has been shown to be about 84% accurate at identifying tree species (Schmidt et al. 2022). We identified many of the plants by morphospecies that were validated by the application. Questionable identifications were repeated by photographing different leaves to confirm the identification. We measured (6) patch area using satellite imagery to define the area of continuous vegetation at each survey site. Roads, sidewalks, and trails were defined as fragment boundaries. To determine the (7) road-traffic impact and (8) highway-traffic impact, we first measured the shortest distance from each focal web to the nearest road (GIS vector from: https://www.nebraskamap.gov/datasets/nebraska::street-centerlines/about) and highway (GIS vector from: https://www.nebraskamap.

gov/datasets/nebraska::highways/about) using the NNJoin Plugin (Tveite 2019) for QGIS. Next, we used the 2021 Average Daily Traffic Volume report (City of Lincoln Transportation and Utilities, 2021) to identify the average daily number of vehicles to travel on each of our identified nearest roads and highways. We then divided the average daily traffic by the shortest distance from the focal web to the nearest road and highway (as in Dooley and Brown 2020) for metrics of road-traffic impact and highway-traffic impact, respectively. Lastly, we measured (9) the total length of all roads within a 100-m buffer of each survey site.

Spider web abundance, patterns, and positions between habitats

To determine differences in spider web abundance, aggregation, and position between the two urban habitats, we completed each of the following measurements at each survey site within a ten-meter radius of the focal web.

Spider Abundance – To quantitatively determine the abundance of webs and spiders near each focal web, we measured a ten-meter radius around the focal web and counted the number of occupied and unoccupied webs. We used the same methods (using the electric toothbrush) as those used for determining the presence/absence of the focal spider. Thus, a web with no response to the electric toothbrush was included in the number of webs but not the number of spiders, and a web with a response was included in both the number of webs and spiders.

Spider Aggregation – Search distance can often be used to estimate density (Buckland et al. 2005). Since our focal spiders were likely less dense in an area where we needed to search further from the path intersection to the focal web, we used search distance as a test for variation in density. We assessed nearest neighbor distances as a measure of aggregation behavior. Starting at the focal web and working outwards, we marked the locations of the two webs (including occupied and unoccupied) nearest to the focal web and within ten meters. We limited our measurements to the nearest two webs because we often found no more than three webs (including the focal web) per site in the urban forest. We measured the shortest distance from the retreat of the focal web to the retreat of the two nearest neighbor webs and used this as our nearest neighbor distances.

To further explore whether nearness of neighbors in the urban center was the result of aggregation specifically or simply increased density from higher abundance, we completed calculations described by Clark and Evans (1954). These calculations compared the observed mean nearest neighbor distance and the expected mean distance (derived from web density) if animals were randomly spaced within an area. For each site, we estimated the total search area by adding (a) the length of the path searched multiplied by four

meters (for searching two meters on either side of the central path line) and (b) the area of the 10-m radius circular site. We subtracted the overlap in the search path and site by subtracting four x 10 m (Fig. S10). To determine the observed web density, we divided the total number of webs identified in search areas by the total area for each habitat (Table S2). For each habitat, we obtained a ratio (R) of observed mean nearest neighbor distance to the expected mean nearest neighbor distance given a random distribution (Table S2). We followed the described calculations to compare this ratio to one of a randomly distributed population (R = 1) and used an F-test to test for differences in spatial patterns between habitats (Table S2).

Web Position – To explore differences in web placement, we measured the web height from the ground to the web retreat for every web within the ten-meter radius. Differences in web height have been shown to vary by environmental factors associated with urbanization (Dahirel et al. 2017).

Environmental predictors of spider spatial patterns

To assess potential environmental influences on variation in abundance, aggregation, and position, we looked for correlations between spider spatial patterns and the nine environmental conditions described earlier. In addition to exploring relationships across the data set overall, we subset the data by habitat to explore within habitats. We reduced the number of environmental predictors by removing variables that had a pairwise correlation above 0.6 using the *caret* package in R (Kuhn 2022). As a result of this analysis, artificial light at night radiance was dropped from all subsequent analyses. Only plant species richness, road-traffic impact, and highway-traffic impact remained for analyses of overall data. The urban center subset includes plant species richness, patch area, spectral radiance, road-traffic and highway-traffic impacts, and road length. We kept tree cover, plant species richness, patch area, and road-traffic and highway-traffic impacts for the urban forest subset.

Statistical analysis

Environmental variables between habitats

To quantify similarities/differences between our habitats with respect to variables we thought might influence spider abundance, distribution, and web height, we first tested whether the nine environmental predictors varied by habitat. Despite being removed from the model selection of the predictors, we maintained artificial light at night radiance for this test because our goal was to describe environmental differences between habitats, and variables were tested in separate models. Each predictor was tested by habitat using negative binomial generalized linear models (MASS package in

R, Venables and Ripley 2002) because the predictors were positive, not normally distributed, and over dispersed.

Spider web abundance, patterns, and positions between habitats

For the second set of models, we focused on whether web abundance, aggregation, and/or position differed between the two habitats (the urban center and urban forest). We used negative binomial generalized linear models for the response variables: number of webs, number of spiders, and search distance. We used negative binomial generalized linear mixed effect models (*lme4* package in R, Bates et al. 2015) with site as a random effect for the response variables: nearest neighbor distance and web height. For each site, we collected a single instance for the number of webs and spiders and search distance. However, we collected multiple instances for nearest neighbor distance (the first and second neighbor) and web height (all webs at a site), so we performed mixed-effect models with site as a random factor for these measures. For the model with nearest neighbor distance, we also included neighbor number (nearest and second nearest web) and its interaction with habitat. We used negative binomial distributions because the response variables were not normally distributed according to Shapiro–Wilk Normality Tests. Also, all data were strictly positive with no upper limit, and the data were over dispersed for a Poisson distribution.

Model selection for environmental predictors of spider spatial patterns

Since we found significant variation in distribution measures between habitats (see Results: Urban habitat characteristics), we wanted to explore environmental correlations with our findings. Specifically, we used the habitat subsets and the selected (non-correlated) environmental predictor variables to assess relationships between predictor variables and spatial pattern measures. In the global models, we included the predictors (without interactions) that remained after removal for collinearity with the response variables: web and spider abundance, nearest neighbor distance, and web height for the complete data and habitat subsets. We excluded search distance as a response variable because the predictors were collected from the site of the focal web and may vary along the search path.

Several predictors (plant species richness, patch area, and road-traffic and highway-traffic impacts) were highly right-skewed, so we used a natural log-transformation prior to model selection. We used negative binomial generalized linear models for the number of webs and spiders and nearest neighbor distance. We excluded the second nearest neighbor distance (leaving only the first neighbor distance) to simplify the model (no random effect) given that both neighbors differed

by habitat (see Results: Spider web abundance, patterns, and positions between habitats). We used negative binomial generalized linear mixed-effect models for web height with site as a random effect, as multiple web heights were measured at each site. From these global models, we performed Akaike Information Criterion (AIC) model selection with the *MuMIn* package in R (Bartoń, 2020), which ranks models produced from every combination of the predictors in the global model. We reported the results of each top model, as well as a model average of models within 2 delta AICc points of the top model. We reported the estimates and standard error from the models without back-transformations for the log-transformed variables. We checked that the Variance of Inflation (VIF) stayed at or below a score of two for predictors in each top model using the *car* package in R (Fox and Weisberg 2019).

We also explored how land cover may affect web abundance, aggregation, and position using the National Land Cover Database and QGIS to record the category of the land cover class for the pixel that each site was located. We tested negative binomial generalized linear models for each response variable (mixed effects model for web height with site as a random factor) with land cover as the only predictor. We used the *Anova()* function in the *car* package (Fox and Weisberg 2019) to get the Likelihood Ratio Chi-Squared values, then used the *glht()* function in the *multcomp* package (Hothorn et al. 2008) to perform pairwise comparisons among categories. We include these results in supplemental material (Fig. S11, Table S3) as the sample sizes were small (deciduous forest=7, woody wetlands=3, urban high-intensity=4, urban medium-intensity=6, urban low-intensity=2).

We completed statistics and visualization using R 4.0.0 (R Core Team 2022) and RStudio 2022.07.2 (RStudio Team 2022). All graphs show raw data and (top) model estimates (*broom* package, Robinson et al. 2021; *emmeans* package, Lenth 2022). We used the *tidyverse* (Wickham et al. 2019), *ggpubr* (Kassambara 2020), and *broom.mixed* (Bolker and Robinson 2022) packages in R to produce and customize the graphs. The *flextable* package (Gohel and Skintzos 2022) was used to produce the tables. For negative binomial generalized linear mixed effect models, we determined the standard error of the model estimates by completing 1000 bootstrap iterations using the function *bootMer()* in R package *lme4* (Bates et al. 2015). All R code and data are available in a GitHub repository at: https://github.com/brandipessman/Agelenopsis_aggregation.

Results

Urban habitat characteristics

Urban Center – Impervious cover – in the form of buildings and pavement – dominated the urban center, considerably more

than impervious cover across the city of Lincoln (Table 1, Fig. S5). Tree cover in the urban center and in Lincoln overall was low (<6%, Table 1, Fig. S6). Over half of the urban center was high-intensity urban cover compared to only 13.16% for Lincoln overall. Further, the urban center exhibited heighten spectral radiance (thermal conditions, Fig. S7) and artificial light at night radiance (Fig. S8), even above that of Lincoln as a whole.

Urban Forest – We found about two-fifths of the urban forest was shrouded in trees (Table 1, Fig. S6), with less than 2% of its land imperviously covered (Table 1, Fig. S5). Over three-quarters of the urban forest was categorized as forested land with only 5.44% labeled as urban (Table 1, Fig. 2). The urban forest showed greatly reduced spectral radiance

(Fig. S7) and artificial light at night radiance (Fig. S8) than the city of Lincoln.

All environmental predictors assessed within a 100-m radius of the focal web varied by habitat (Table 2). The urban center sites had higher (1) impervious cover, with all but four sites being zero in the urban forest ($z_{21} = 14.49$, $P < 0.001$). Site (2) tree cover was lower in the urban center than the urban forest, with five urban center sites measuring zero tree cover ($z_{21} = -13.77$, $P < 0.001$). The urban center sites also had higher (3) spectral radiance ($z_{21} = 3.08$, $P = 0.002$) and (4) artificial light at night radiance ($z_{21} = 17.17$, $P < 0.001$). Overall, (5) plant species richness was lower in the urban center than the urban forest ($z_{21} = -6.61$, $P < 0.001$). Similarly, spiders used a lower diversity of plants

Table 1 Landscape variables for the urban center (UNL City Campus), the urban forest (Wilderness Park), and Lincoln (Nebraska, USA) city limits, collected from the National Land Cover Database (2016 Tree Cover, 2019 Impervious Cover, 2019 Land Cover) using QGIS (v. 3.16.3-Hannover, ESRI 102704). The National Land Cover Data-base assigned the intensity of urban cover based on percent impervious cover (High=80–100%, Medium=50–79%, Low=20–49%, Open Space=0–19% (https://www.mrlc.gov/data/legends/national-land-cover-database-class-legend-and-description)

	Urban Center (UNL City Campus)	Urban Forest (Wilderness Park)	Lincoln City Limits
Area (sq. km)	1.12	6.44	253.73
Impervious Cover (%)	78.32	1.73	40.97
Tree Cover (%)	0.79	40.32	5.97
Urban Cover (%)	100.00	5.44	79.42
Urban, High Intensity (%)	58.19	0.04	13.16
Urban, Medium Intensity (%)	33.28	0.95	28.49
Urban, Low Intensity (%)	7.33	2.92	27.61
Urban, Open Space (%)	1.20	1.53	10.15
Forest Cover (%)	0.00	78.29	1.58
Deciduous Forest (%)	0.00	26.91	1.01
Mixed Forest (%)	0.00	0.26	0.05
Evergreen Forest (%)	0.00	0.07	0.01
Woody Wetlands (%)	0.00	51.05	0.51
Other Cover (%)	0.00	16.26	18.99
Herbaceous Wetlands (%)	0.00	0.31	0.90
Grassland Herbaceous (%)	0.00	13.07	9.46
Pasture (%)	0.00	0.26	0.52
Cultivated Crop (%)	0.00	2.22	6.48
Open Water (%)	0.00	0.41	1.56

Table 2 Mean and standard error of the collected environmental predictors by habitat. Percent impervious and tree cover, spectral radiance, artificial night sky radiance, and total road length were collected in a 100-m buffer of each focal web, while plant species richness was recorded in a 10-m buffer of each focal web. We used the nearest road or highway for traffic impact measures. Patch area was defined as the area of continuous vegetation that includes the focal web

	Mean ± Std. Error	
	Urban Center (UNL City Campus)	**Urban Forest (Wilderness Park)**
Percent Impervious Cover [%]	76.52 ± 2.63	1.27 ± 0.36
Percent Tree Cover [%]	1.58 ± 0.37	47.15 ± 3.46
Spectral Radiance [Watts/(m² * sr * μm)]	153.39 ± 3.58	137.44 ± 3.71
Artificial Night Sky Radiance [mcd/m²]	116.90 ± 9.39	5.89 ± 0.91
Plant Species Richness	3.33 ± 0.58	13.30 ± 1.56
Patch Area [m²]	654 ± 144	46,295 ± 11,128
Road-Traffic Impact [vehicles/day/m]	398 ± 125	104 ± 36
Highway-Traffic Impact [vehicles/day/m]	65.0 ± 9.82	35.6 ± 6.04
Total Road Length [m]	93.03 ± 40.60	15.67 ± 7.54

as substrates in the urban center (mean $\pm$ se $= 1.42 \pm 0.34$ species) than the urban forest (mean $\pm$ se $= 2.7 \pm 0.52$ species, $z_{21} = -2.08$, $P = 0.037$). Site (6) patch area was smaller in the urban center ($z_{21} = -13.08$, $P < 0.001$). (7) Road-traffic impact ($z_{21} = 2.87$, $P = 0.004$), (8) highway-traffic impact ($z_{21} = 2.64$, $P = 0.008$), and (9) road length ($z_{21} = 2.741$, $P = 0.006$) were higher for urban center sites than sites in the urban forest.

Spider web abundance, patterns, and positions between habitats

Over the course of the study, we identified 131 funnel webs as being occupied or unoccupied. The 67 unoccupied webs could be those once owned by males, abandoned by females, or inhabited by spiders not responsive to the toothbrush. While webs were found on many of the same plant types between sites in the urban center and urban forest in varying proportions, 15% of webs in urban center sites were built on non-plant substrates (Fig. S12).

All abundance, aggregation, and position metrics (except search distance) – the number of webs and spiders within 10 m of the focal web, the distance from the focal web to the two nearest neighbor webs, and web height – varied by habitat (Fig. 3).

Within a 10-m radius of the focal web, we counted significantly more webs ($z_{20} = 4.45$, $P < 0.001$, Fig. 3a) and spiders ($z_{20} = 3.13$, $P = 0.002$, Fig. 3b) in the urban center than the urban forest. There was no difference in the distance we searched from the start site to the focal web in the urban center and the urban forest ($z_{20} = -1.15$, $P = 0.251$, Fig. 3c,

Fig. S4). We also found that the distances between the focal web and the two nearest neighbors were significantly shorter in the urban center than the urban forest ($z_{34} = -5.02$, $P < 0.001$, Fig. 3d). By definition, the second nearest web was further from the focal web than the nearest neighbor ($z_{34} = 2.83$, $P = 0.005$). There was not a significant interaction between neighbor number and habitat ($z_{34} = 1.09$, $P = 0.276$, Fig. 3d). Lastly, webs were built lower in the urban center than the urban forest ($z_{128} = -2.44$, $P = 0.015$, Fig. 3e). This difference was not due to differences in substrate height because we found no difference in substrate height between habitats ($z_{128} = -1.13$, $P = 0.259$).

We computed Clark and Evans' (1954) aggregation index that determined whether aggregation was due to increased density or clumping of individuals. A ratio value significantly below 1 suggests clumping, while values that do not significantly differ from 1 indicate random spacing. We found that web distribution in the urban center significantly varied from a random distribution, suggesting aggregation (c = -4.13, R = 0.349, $P < 0.001$, Table S2). However, webs in the urban forest did not significantly vary from a random distribution (c = -1.03, R = 0.830, $P = 0.303$, Table S2). There was a significant difference in web spatial patterns between habitats – urban center webs were more aggregated than urban forest webs ($F_{1,19} = 4.605$, $P < 0.05$, Table S2). We concluded that aggregations formed for reasons other than increased spider density.

Environmental predictors of spider spatial patterns

To explore potential environmental factors that might influence our observed variation in spatial patterns, we looked
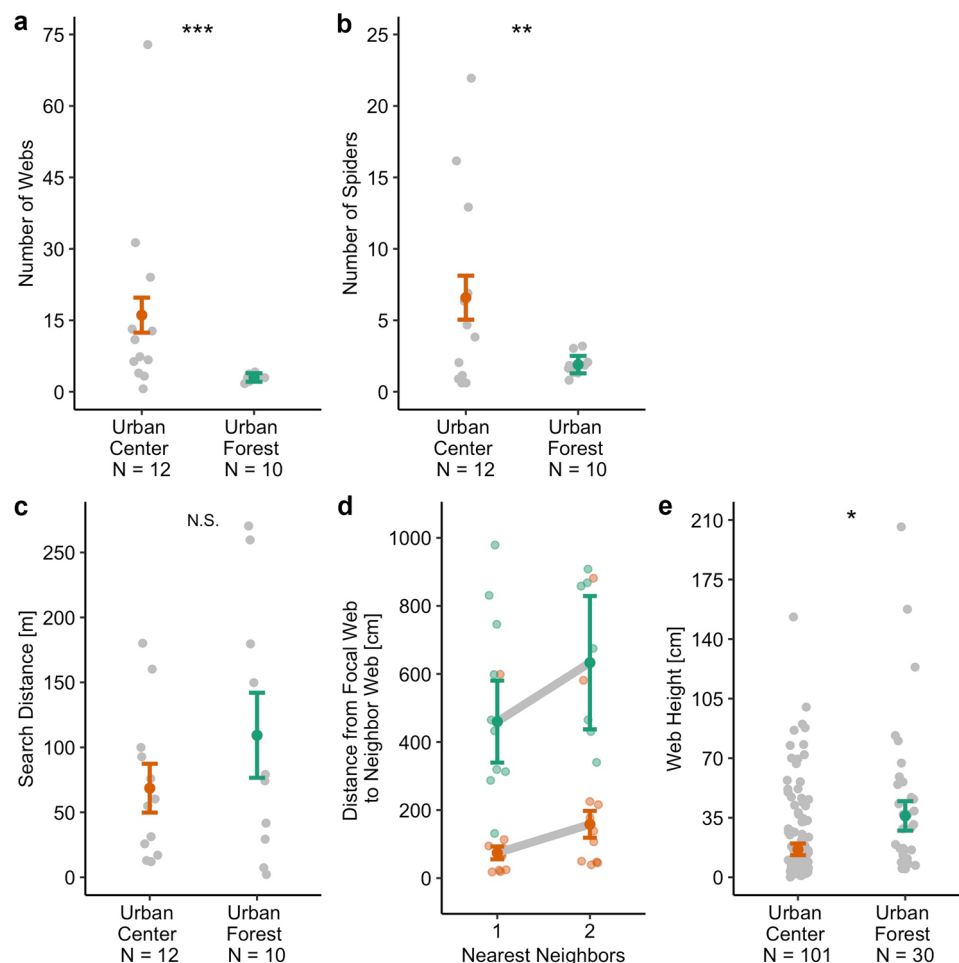
Fig. 3 Comparison of the number of webs (**a**) and spiders (**b**) in a 10-m radius of the focal web, search distance (**c**), the distance from the focal web to the first and second (**d**) nearest neighbors, and web height (**e**) by habitat—urban center vs. urban forest. Grey jittered points (and faded colored points by habitat in **d**) represent the raw data, while colored points (orange = urban center, green = urban forest) and error bars represent the mean and standard error, respectively, from model predictions. Models were either negative binomial generalized linear models (**a–c**) or negative binomial generalized linear mixed effect models with site as a random factor (**d–e**). Asterisks indicate significance level (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$, N.S. = not significant). We found more webs (**a**) and spiders (**b**) in a 10-m radius of the focal web in the urban center than the urban forest. Search distance did not differ between habitats (**c**), but we measured shorter distances between the focal web and the two nearest neighbors (**d**), and recorded shorter web heights (**e**) in the urban center than the urban forest

for correlations between response variables (number of webs, number of spiders, nearest neighbor distance, and web height) and environmental predictors overall and within each habitat (Tables 3, S4, Figs. 4–5).

Abundance – The top models for the number of webs and the number of spiders yielded similar results (Table 3, Figs. 4–5). Plant species richness had a negative relationship with the number of webs and spiders for the overall data set (Table 3, Fig. 4). For both measures of abundance, the urban center subset and overall data set showed a decrease in abundance with increasing highway-traffic impact (Table 3, Fig. 5), while the urban forest subset retained no predictors (Table 3). For the urban center subset, the model average for the number of webs and spiders suggested similar results, although the number of spiders also negatively correlated with plant species richness (Table S4). Total road length was

also retained in the model average for the number of spiders in the urban center subset, but the effect was not significant (Table S4).

Aggregation – Spiders were closer together across habitats when plant species richness was low (Table 3, Fig. 4). Spiders were more aggregated at urban center sites that had more roads (Table 3, Fig. 5), while no predictors were retained for the urban forest subset (Table 3). The model average for the nearest neighbor distance in the overall and urban center subsets corroborated the findings of the top model and added that webs were clumped as spectral radiance increased in the urban center (Table S4). The model average kept road-traffic impact for the overall data, but did not suggest a significant relationship (Table S4).

Web Height – Webs were built higher when the number of plant species was higher overall (Table 3, Fig. 4) and as
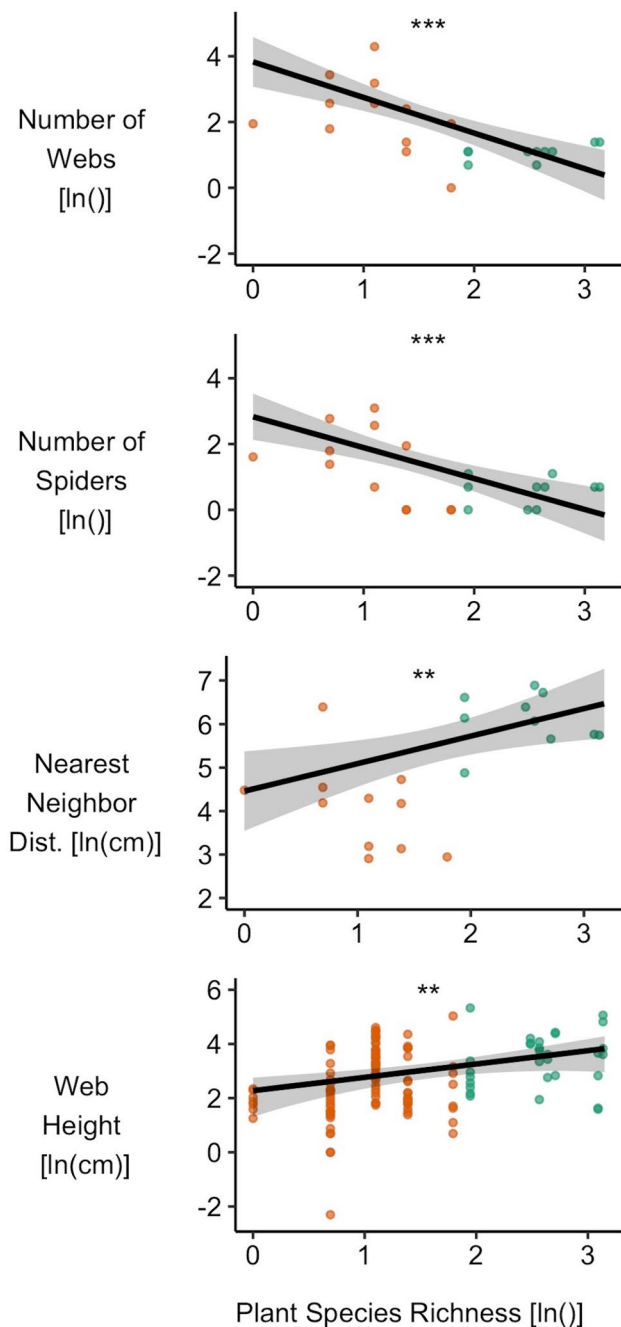
Fig. 4 Significant correlations between measures of abundance, aggregation, and position, and plant species richness for the overall data. The regression lines and shaded regions represent the predictions and 95% confidence intervals (respectively) from the top negative binomial generalized linear model after AIC selection. The points represent the raw data (orange = urban center, green = urban forest). Asterisks indicate significance level (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$)

a trend for the urban center subset (Table 3). Trends also suggested that lower webs were associated with higher road-traffic impacts overall and fewer roads in the urban center, although these results were not significant (Table 3, Fig. 5).

In the urban forest, web height was positively related to tree cover (Table 3). We see similar results from the model averages for web height (Table S4). Despite the addition of predictors under the model averages, none of the added predictors varied by web height in their respective data sets (Table S4).

For statistical analysis and figures of response variables by land cover class, see supplemental material (Table S3, Fig. S11). Following Likelihood Ratio tests, we found that all response variables, except for search distance (Fig. S11c), significantly varied by land cover class (Table S3). The number of webs only varied by habitat—urban low-, medium-, and high-intensity had more webs than deciduous forest or woody wetland (Fig. S11a). There were no significant pairwise comparisons for the number of spiders (Table S3, Fig. S11b). Nearest neighbor distance also varied by habitat – urban intensities were more clumped than deciduous forest and woody wetland (Table S3, Fig. S11d). For the urban intensities, webs were closer at low intensities than medium intensities (Table S3, Fig. S11d). Lastly, web height only differed between medium urban intensities and deciduous forest, building higher in the latter (Table S3, Fig. S11e).

Discussion

The two urban habitats that we studied here – an urban center and an urban forest – significantly differed by the selected environmental conditions. The urban center exhibited higher impervious cover, light at night, surface temperature, road-traffic and highway-traffic impact, and total road length than the urban forest. On the other hand, the urban forest sites had higher tree cover, plant diversity, and patch area than the urban center. These urban habitats each host *Agelenopsis pennsylvanica*, but the spatial patterns displayed by this funnel-weaving spider vary considerably across the two habitat types. The spiders were more abundant, aggregated, and built lower webs at sites in the urban center as compared to the urban forest. We hypothesized that many of the environmental conditions that were distinct between the habitats may be influencing these differences. In particular, we found that spatial patterns were often related to plant species richness and impacts from road and highway traffic.

Spiders were more abundant and aggregated with lower webs in the urban center

Both webs and spiders of *A. pennsylvanica* were more abundant and aggregated at sites in the urban center than the urban forest. Aggregations in the urban center were likely not the result of increased density as the Clark and Evans (1954) aggregation index showed that webs were clumped in the urban center but not the urban forest (while controlling

Fig. 5 Significant correlations between abundance, aggregation, and position measures and the environmental predictors relating to traffic impacts for the data overall (black outline) and the urban center subset (orange outline). Grey boxes represent environmental predictors that were dropped from models after AIC model selection. The regression lines and shaded regions represent the predictions and 95% confidence intervals (respectively) from the top negative binomial generalized linear model after AIC selection. The points represent the raw data (orange = urban center, green = urban forest). Road length for web height was scaled without centering. Asterisks indicate significance level (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$, N. S. = not significant)
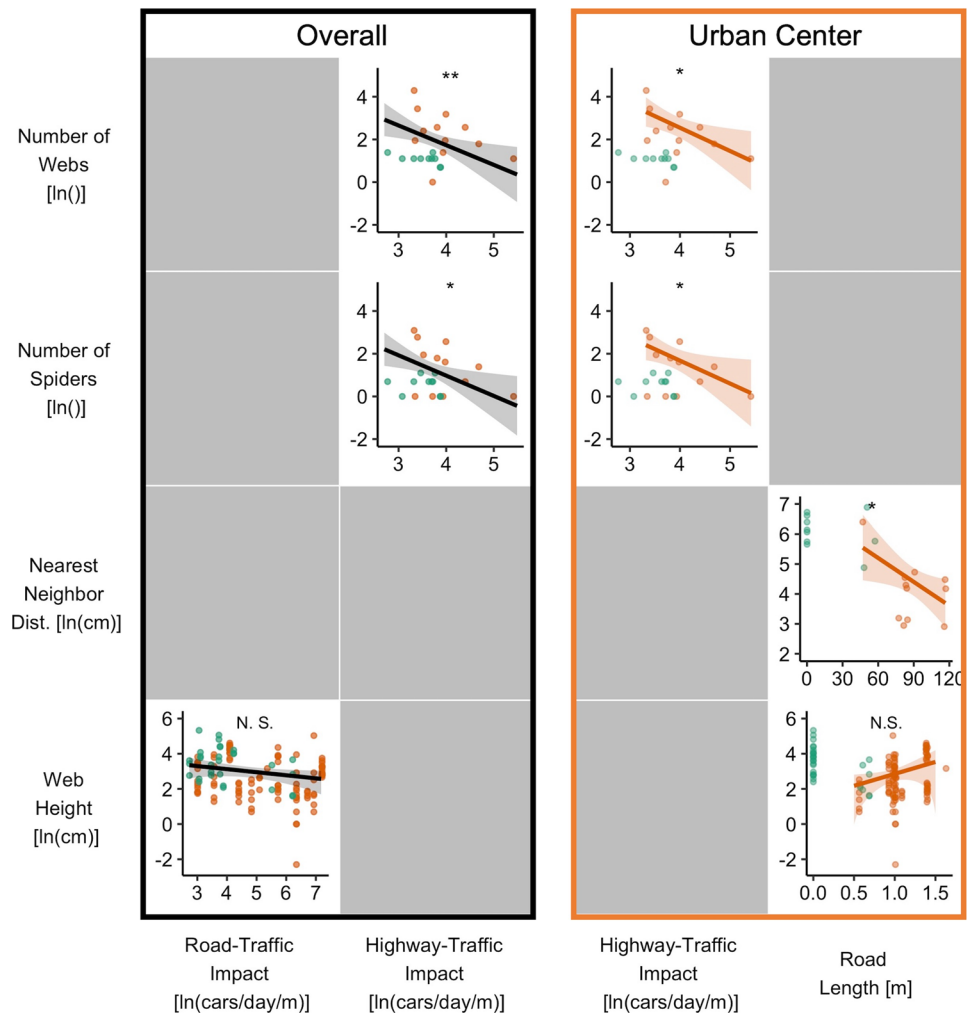
for density). Further support of this comes from our finding that the nearness of neighbors was not due to increased density of webs in the urban center, as we observed no difference in search distances to the focal web between habitats, and previous studies have used search distance as an estimate of density (Kral et al. 2018).

Animal abundance and spatial distributions across urban habitats might reflect differential resource distributions and/or spatial patterns of survival risk. For example, urban ecosystems tend to differ from surrounding areas in terms of the prey and predators that are present (Start et al. 2020). In terms of prey, an animal's characteristics – such as being a generalist consumer (Bang and Faeth 2011; Sol et al. 2013) – may allow them to more readily adjust to urban ecosystems. Most spiders, including *Agelenopsis* spiders, are generalist predators (Riechert 1974b; personal observations). While arthropods are generally found to decline in urban environments (Piano et al. 2020; Wagner 2020), generalists are more likely to be urban exploiters than specialists (Callaghan et al. 2021). For example, *Nephila plumipes*, a generalist predator, was found to abundantly occupy urban

habitats where prey abundance supported greater numbers of spiders (Lowe et al. 2016). Prey abundance has been repeatedly found to be a strong predictor of spider abundance (Harwood et al. 2001; Parkinson et al. 2020; Trubl et al. 2012). Unfortunately, we do not have data on prey abundance across our focal habitat types, but this would be a good avenue for future research.

Although we might hypothesize higher prey availability in the urban forest, we observed far greater potential for competition from other spider species in the urban forest than the urban center. In the urban center, *A. pennsylvanica* appeared to dominate spider communities whereas we observed many other spiders, notably web-building spiders, in the urban forest. These differences were not quantified and would require additional data collection, but it is interesting to think about why certain spiders, despite most being generalists, are able to successfully inhabit more urbanized environments over others. One obvious possibility is that humans might be more likely to physically remove large, conspicuous orb webs, potentially preventing the colonization of some orb-weaving species. *Agelenopsis pennsylvanica* tends to build

Table 3 Results of the top models after AIC model selection from negative binomial generalized linear models with the environmental predictors for data overall and subset by habitat (urban center and urban forest). Asterisks indicate significance level (*** $P<0.001$; ** $P<0.01$; * $P<0.05$; $P<0.10$)

Variable	Model	Predictor	Estimate	Standard Error	Z-Value	P-Value	McFadden's R²	AICc Weight
Number of Webs	Overall	Plant Species Richness[a]	-1.083	0.22	-4.912	< 0.001 ***	0.575	0.660
		Highway-Traffic Impact[a]	-0.922	0.356	-2.589	0.010 **		
	Center	Highway-Traffic Impact[a]	-1.088	0.437	-2.487	0.013 *	0.342	0.336
	Forest	Null						0.578
Number of Spiders	Overall	Plant Species Richness[a]	-0.94	0.217	-4.325	< 0.001 ***	0.55	0.678
		Highway-Traffic Impact[a]	-0.95	0.376	-2.528	0.012 *		
	Center	Highway-Traffic Impact[a]	-1.072	0.486	-2.205	0.027 *	0.304	0.202
	Forest	Null						0.590
Nearest Neighbor Distance	Overall	Plant Species Richness[a]	0.633	0.242	2.621	0.009 **	0.222	0.414
	Center	Total Road Length	-0.027	0.012	-2.216	0.027 *	0.427	0.250
	Forest	Null						0.602
Web Height	Overall	Plant Species Richness[a]	0.492	0.168	2.938	0.003 **	0.181	0.344
		Road-Traffic Impact[a]	-0.174	0.102	-1.715	0.086 .		
	Center	Plant Species Richness[a]	0.701	0.369	1.899	0.058 .	0.135	0.051
		Total Road Length (Scaled)[b]	1.362	0.767	1.776	0.076 .		
	Forest	Proportion Tree Cover[c]	4.846	1.711	2.831	0.005 **	0.239	0.217

[a]Predictors that were natural log-transformed prior to model evaluation. Estimate and standard errors were not back transformed.

[b]Total road length was scaled (without centering) by dividing each value of road length by the root mean square prior to model evaluation to avoid model convergence issues.

[c]Tree cover was assessed as proportion (value from 0 to 1) rather than a percent (values 0 to 100) to avoid model convergence issues.

their webs low to the ground and in unobtrusive places to humans, thereby potentially escaping removal. Additionally, since *A. pennsylvanica* can quickly disappear into their retreats, removal of their sheet web may not be sufficient to eradicate them. All of these ideas require further study.

Higher abundance of particular animals in urban habitats may also reflect a higher tolerance of urban conditions and disturbances. As traffic impacts appear to play an important role in *A. pennsylvanica* spatial patterns, we propose that vibratory noise impacts the spatial distribution of *A. pennsylvanica*. Despite this likely impact, we simultaneously hypothesize that urban *A. pennsylvanica* may be equipped to cope with heightened levels of vibratory noise. The web of spiders represents an extended phenotype – a trait beyond the physical body. Many spiders are considered plastic in their webs' structure and tuning with respect to prey availability (Blamires 2010; Mortimer et al. 2016), and urban exploiters are often fast to adjust to changing conditions (Kralj-Fišer et al. 2017). Research is currently underway exploring the impact of noise on prey detection in urban center versus rural *A. pennsylvanica* and any potential plasticity associated with web structure. We expand on our discussion of the potential impacts of vibratory noise below when we address correlations between road-traffic and highway-traffic impacts and the spatial measures.

Multiple reports have found spider aggregations in urban habitats (Mammola et al. 2018; Trubl et al. 2012), another spatial measure that is often related directly or indirectly to the abundance of prey. Territoriality, especially over prey resources, often drives regular (and non-random) spacing of solitary species (Riechert 1974a), but aggregations can form when abundant resources allow for increased tolerance of neighbors (Gillespie 1987). Light at night in cities attracts insects, creating pockets of increased prey abundance for spiders, possibly leading to spiders aggregating under such light sources (Davies et al. 2012). Although we did not measure microhabitat levels of light at night or prey abundance, *A. pennsylvanica* were more aggregated in the urban center where light at night radiance was higher than the urban forest. Our observed aggregations, however, were not directly underneath lights (e.g. of campus buildings) as has been observed in other web-building spiders (Mammola et al. 2018). As such, we suspect that light at night is not one of the primary drivers of *A. pennsylvanica* aggregations in our urban center, though this remains to be empirically tested.

We also found that the webs of urban center spiders were built lower than webs in the urban forest, and this result was independent of the height of the substrate. One possible explanation for this pattern is that vibratory noise

might promote lower web heights. Vibratory noise might, for example, be dampened on a plant nearer to the ground. We did find a trend that showed lower web heights overall at sites with higher road-traffic impact, but this idea requires further testing. Another potential explanation is that webs may vary in height based on the type of prey being ensnared. We have observed *Agelenopsis* spiders capture flying, hopping, and crawling insects. Arthropod community structure can be highly variable between urban habitats (Bang and Faeth 2011), and urban centers and urban forests may support different types of prey items for *A. pennsylvanica*. Lower webs in the urban center may be ideal for more crawling prey, while higher webs in the urban forest may intercept more flying insects. Alternatively, webs in different habitats may experience different levels of disturbance. In the urban center, where lawns are mowed frequently and ornamental plants are regularly pruned, spiders could maintain lower webs to conserve energy from frequent rebuilding. Additionally, urban forests likely support (and act as a refuge for) many ground-dwelling vertebrates, whose movement along the forest floor could frequently damage lower webs. Greater tree coverage in the urban forest predicted higher webs, which may further suggest that small mammal movement could destroy low webs as areas with greater tree cover may provide protection and food resources for small mammals (Sarkar and Bhadra 2022). Future research should assess the prey types available and small animal abundance and movement between these two habitats.

Several environmental predictors relate to spider spatial patterns

We found that webs and spiders, overall, were more abundant and more aggregated as plant species richness decreased. The urban center sites were covered in grass lawns and managed landscaping that usually had few plant species present but in high abundance. Sites with lower plant diversity may have few plant species that are highly preferred, leading to higher spider abundance. Research has shown mixed but often positive effects of plant diversity on spider abundance (Koricheva et al. 2000; Malumbres-Olarte et al. 2013), suggesting that plant community composition may play a vital, yet context-specific role in spider spatial patterns. To better understand the role that plant species play in abundance would require comparing plant communities between patches used by spiders versus those devoid of spiders. We speculate that greater aggregation on less diverse plant communities may suggest that *A. pennsylvanica* prefers a certain plant or type of plant, especially in the urban center where we observed similar plants clumped in space. Spiders in this study appeared to have chosen different web substrates between habitats (Fig. S12) – the largest proportion of urban center spiders (~ 39%) built webs

on shrubs, whereas urban forest spiders preferred herbs (~ 66%). A close relative, *A. aperta*, also exemplifies different substrate choices in different habitats—depressions were important in mixed grasslands, shrubs in lava beds, and tall grasses in rangeland (Riechert et al. 1973).

Road-traffic and highway-traffic impacts also seemed to play an important role in spider spatial patterns. We showed that webs and spiders were more abundant overall and in urban center sites that have lower highway-traffic impact. Living in close proximity to high-traffic roads and highways is likely to affect the vibratory environment that the spider is exposed to because vehicles introduce vibrations to the ground through contact with their tires. Vibrations can propagate through the ground at low frequencies for meters to kilometers. For example, elephants communicate by sending low-frequency vibrations (20–40 Hz) through the ground for up to six kilometers (Mortimer et al. 2021). In the current study, the nearest road to a site varied from three to 735 m.

Environmental noise, especially from road traffic, has been shown to affect habitat use across broad taxonomic groups (e.g., birds, frogs, fishes, aquatic and terrestrial mammals, invertebrates, etc.; Shannon et al. 2016). Specifically, vibratory information is used widely across all animal taxa, and arthropods are particularly known for their reliance on vibratory signals and cues (Hill and Wessel 2016). *Agelenopsis pennsylvanica* rely heavily on vibrations to capture prey (Riechert and Maupin 1998), court potential mates (Singer et al. 2000), and potentially evade predators (Riechert and Hedrick 1990). Thus, we suspect that vibratory noise may impact web structure (as discussed earlier) and/or web site selection, with spiders choosing sites that mitigate these effects. Also, selective spiders in urban habitats may choose plants as web substrates that reduce vibratory noise since various plants transmit vibrations differently (Cocroft et al. 2006). Although most research on the effects of noise on arthropod behavior has focused on acoustic rather than vibratory noise (Roberts and Howard 2022), some studies have found strong negative effects of acoustic and vibratory noise on arthropod behavior (Bunkley et al. 2017; Carosi et al. 2019). A recent study showed that the orb-weaving spider, *Larinioides sclopetarius,* is able to detect airborne sound that induces vibrations in the web (Zhou et al. 2022).

More roads in the 100-m radius correlated with more aggregated urban center webs. Total road length could be another indirect measure of vibratory noise and/or represent dispersal barriers. High-traffic roads may increase mortality of dispersing spiders via collisions with vehicles, or passing cars may influence wind currents making aerial dispersal difficult (Martin et al. 2019). Higher spider abundance in smaller patches may be more evidence for the role of environmental barriers. Furthermore, small patch areas may be a preferred habitat of edge specialists (Martinson and Fagan 2014), as we suspect *A. pennsylvanica* may be.

The trend that urban center webs were built higher at sites with more roads could also suggest that areas fragmented by roads may encourage spiders to spread vertically rather than horizontally.

We note that urban forest web and spider abundance did not correlate with any of the selected environmental conditions, potentially due to low variation. For example, only two to four webs and one to three spiders were found per site in the urban forest compared to one to 73 webs and one to 22 spiders in the urban center. Alternatively, urban forest abundance may be better predicted by factors not assessed here, such as prey and predator abundance or dispersal limitation (Bonte et al. 2003; Harwood et al. 2001).

Lastly, spiders in the urban center were more aggregated at sites with higher spectral radiance (a measure of surface temperature). However, spectral radiance was not included in the top model, but was found to have a significant effect from the model average. Urban centers tend to be warmer on average compared to surrounding areas due to heat-trapping via pavement in a phenomenon called the Urban Heat Island Effect (Johnson et al. 2020). Aggregation formation in warmer sites could be the result of preference for or acclimation to warmer areas (Meineke et al. 2013), or perhaps aggregation occurs at limited thermal refuges (Riechert 1974a).

Conclusions

We have shown that human-caused environmental changes correlate with spider spatial patterns. We found that a solitary, generalist predator (*A. pennsylvanica*) was more abundant and aggregated with lower web height in an urban center compared to an urban forest – habitats that vary significantly in environmental conditions. Plant species richness and traffic impacts appear to play an especially important role in the spatial patterns of *A. pennsylvanica*. Traffic impacts and road presence likely introduce vibrations to the ground that could disrupt vibratory information acquisition of this species. The use of vibratory information is widespread among many other urban-dwelling arthropods, and future research is needed to determine if vibratory noise could play a role in the global decline of urban arthropod biodiversity. Our variables that estimate the potential for vibratory noise negatively affected spider abundance while promoting lower web heights, potentially to reduce interference from vibratory noise. We hypothesize that *A. pennsylvanica* may exhibit plasticity in their web – an extended phenotype – to cope with heightened levels of vibratory noise. Plasticity in web structure in response to variation in background noise levels may be shared among other web builders and may help explain why some web-builders can live in noisy habitats while others cannot. We emphasize that elucidating the complex relationship between arthropod abundance and the impacts of urbanization is essential for our understanding of how urbanization affects ecosystem services and food web interactions.

Declarations

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