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Cover Photograph: *Columba livia* perched on an ornamental structure in Parque de el Retiro, one of the largest city parks in Madrid, Spain. Photo courtesy of Daisy Lewis.

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Pigeon Density Varies with Environmental Factors Across a European and North American City

Daisy E. Lewis[1*], Jonathan B. Losos[1, 2], and Elizabeth J. Carlen[1,2]

Abstract: Wildlife often modify their movement and space use in response to the dramatic alterations to landscapes resulting from urbanization. One such species, *Columba livia* (also known as the Rock Dove, Rock Pigeon, or the feral pigeon), is found in many cities throughout the world. While pigeon population density is influenced by the built environment, no study has directly compared population dynamics between two different cities. Understanding how urbanization influences pigeon population dynamics in different cities may enlighten how the differences among cities, both presently and historically, affect urban wildlife. In this study we analyze how various factors of urban environments affect pigeon density by performing visual encounter surveys in St. Louis, USA and Madrid, Spain. We conducted surveys along ten 5 km transects in each city with every transect being surveyed twice. Along these transects we recorded observations of pigeons along with environmental factors including: weather conditions, pedestrian density, presence of waste disposal/litter, and restaurants with outdoor tables. When creating our models, we added additional urban environmental factors including: density of roads, parks, population density, and impervious surface, as well as presence of schools, transportation points, and predators. We found that pigeon density was more than 3.5 times greater in Madrid than in St. Louis and that pigeon density was positively correlated with pedestrian density in both cities, positively correlated with restaurants with outdoor seating and population density in Madrid, and positively correlated with impervious surface in St. Louis. These findings corroborate some pigeon space-use findings but contradict others, adding to the growing evidence that wildlife populations respond to different cities in varying ways, probably as a result of their unique histories and cultures.

Introduction

A key goal of landscape ecology is to understand how spatial heterogeneity and environmental variation shape ecological patterns—a question that becomes especially compelling in urban environments. Cities represent highly heterogeneous landscapes, where a mix of native and introduced species, built structures, human culture, and local climate create unique ecological conditions. Yet, the extent to which differences among cities lead to different ecological communities is relatively unexplored.

Differences in urban biodiversity between and within cities can be influenced by the political, economic, or natural histories such as the history of land-use (Elmqvist et al. 2013). For example, the National Urban Park of Stockholm is relatively biodiversity rich because, unlike the rest of the city, the land had historically been used for production of food and feed. Similarly, the city of Istanbul boasts rich biodiversity in semi-natural patches in locations used since the end of the fourteenth century as urban farmlands in times of siege (Barthel et al. 2005, Barthel and Isendahl 2013, Elmqvist et al. 2013, Güneralp et al. 2013).

Along with varied histories, cities have undergone varying processes of urbanization, resulting in different built landscapes. Major urban centers in Europe experienced construction surges

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long before cities in the U.S., resulting in the application of different urban planning techniques. Therefore many cities in Europe have older buildings, higher human densities, and more centralized land-use patterns as opposed to the less compact urban form in the U.S. that consists of dispersed population and greater reliance on cars (Antipova 2018).

These natural, cultural, and political histories have resulted in different urban environments and likely have important consequences for the wildlife that still exist within them. Urban wildlife often exhibit distinct behavioral and ecological patterns compared to their non-urban counterparts; including differences in diet, reproduction, disease resistance, and movement patterns (Ditchkoff et al. 2006). The spatial configuration of urban resources—particularly human-provided food sources—directly influences how wildlife modify their spatial distribution and habitat use within cities, lending importance to space-use analysis of urban populations (Ditchkoff et al. 2006, Jokimäki and Suhonen 1998, Robb et al. 2008). Comparative studies across diverse urban landscapes are therefore essential to understanding how city-specific habitat characteristics shape wildlife spatial distribution patterns.

A common urban dweller is *Columba livia* Gmelin (Pigeon). Pigeons were domesticated 5,000–10,000 years ago as a food and fertilizer source (Johnston and Janiga 1995); however, since domestication, individuals have escaped or were intentionally released, leading to the formation of feral pigeon populations across the globe using buildings as a substitute for their native habitat, cliffs (Blechman 2007, Blechman 2013). Pigeons have a high reproduction rate and participate in group foraging leading to large deposits of feces, thereby solidifying their perception as a nuisance pest species (Glünder 1989, Johnston and Janiga 1995, Skandrani et al. 2014). Pigeon prevalence in cities can also incur economic costs due to the physical deterrence structures added to buildings, with one Italian city spending an estimated 30,000–40,000 euros per 1 km^2, and pharmacological sterilization costing 18–19 euros per pigeon per year (Giunchi et al. 2012). Due to the negative consequences large and uncontrolled pigeon populations can have in urban centers, understanding their population dynamics and interactions with humans is vital to any potential population management. However, population management is not a one-size-fits-all solution as population densities of pigeons vary across cities with different local landscape factors and even historical and cultural differences influencing this relationship (Hetmański et al. 2011, Przybylska et al. 2012, Tang et al. 2018). While many studies have examined pigeon population density in various cities, no study has directly compared landscape factors between two cities.

Here we investigate how environmental factors of the urbanized landscape influence pigeon density. Specifically, we perform a comparative study between Madrid, Spain, and St. Louis, Missouri, USA using the same methods for both cities to identify correlates that are transferable between cities. Previous research has shown that pigeon density is positively correlated with human density, food sources (such as restaurants with outdoor seating), transportation hubs, water sources, litter, non-pigeon birds, parks, and schools (Chace and Walsh 2006, Fuller et al. 2008, Jokimäki and Suhonen 1998, Muscat et al. 2022, Przybylska et al. 2012, Robb et al. 2008, Ryan 2011), and negatively correlated with road density and predator presence (Przybylska et al. 2012, Tang et al. 2018); therefore we predict we will find the same correlates here.

Materials and Methods

Study area

We focused our study on two metropolitan cities Madrid, Spain and St. Louis, Missouri, USA (Fig. 1, map of cities to scale in Supplementary Fig. 1; available online at https://eaglehill.us/urnaonline/suppl-files/urna-079-Lewis-s1.pdf). Both cities are located inland

and have a river (Real de Manzanare and the Mississippi River, respectively) as a central feature. However, culturally, the cities are vastly different.

Madrid is a bustling capital city covering 604.3 km^2 with a population of 3.4 million (Instituto Nacional Estadística 2021). This region has a Mediterranean climate with both continental and semi-arid influences. The city experiences cool winters, with January averaging 6.3º C, and hot summers, with July averaging 25.6º C. Madrid is overall very dry, only receiving 423 mm in rainfall per year. The geographic region of Madrid has been inhabited since the Roman settlements dating back to 200 BCE but urban development began when the Spanish King Philip II moved his court from Toledo to Madrid in 1561, making Madrid the political center of the Iberian Peninsula (Andreu Mediero 2007, Fusi Aizpurúa 1989). During the second half of the 19th century, Madrid's role as a financial and service center was consolidated as the economy modernized and railway construction made the city a transportation center, leading to building developments that expanded urbanization of the area (Ruiz 2011). Madrid experienced a physical and cultural revolution after the 1975 fall of the Francoist dictator regime that influences how humans interact with the city to this day (Stapell 2015). The government undertook revitalization efforts that included repairing historic buildings, cleaning public parks and plazas, placing thousands of trash cans in the city center, expanding the public transportation system, and restricting automobiles from certain parts of the city leaving many streets in the city center to pedestrians (Fig. 2) (Stapell 2015). Along with these structural transformations, "the residents of Madrid were also transformed from subjects of the dictatorship into active participants, engaging in all manner of social activities around the clock and creating traffic jams at 3:00 a.m." (Stapell 2015). Following a brief population decline in 1975 after the fall of the dictatorial Franco regime, the population has been steadily increasing since the 1990s (Fernández 2008) and Madrid remains the most populous city in Spain (Instituto Nacional Estadística 2021).

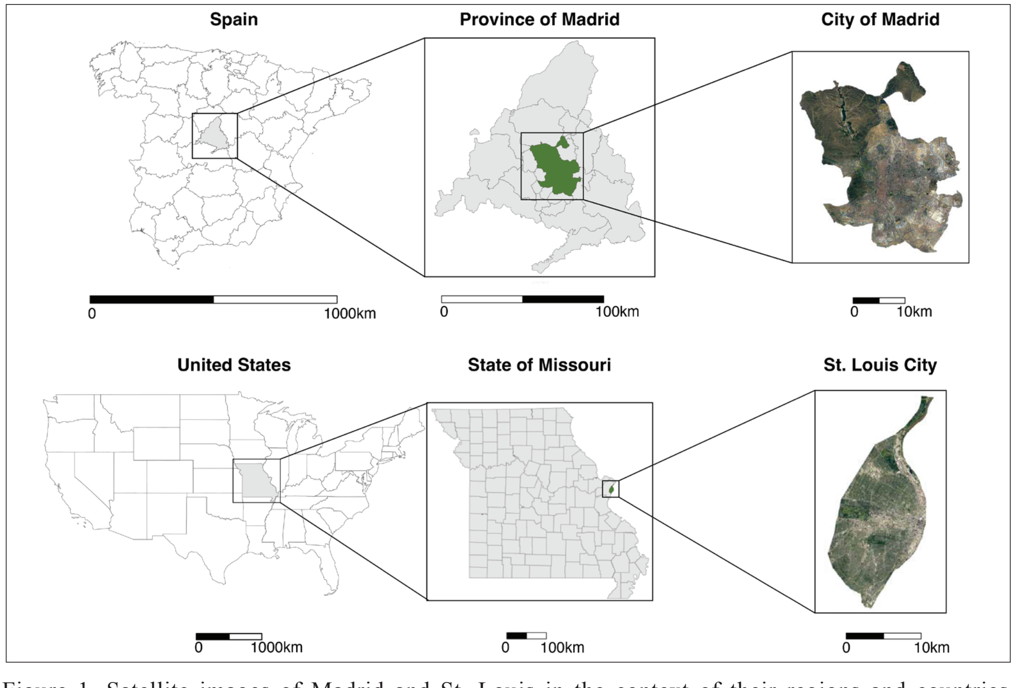

Figure 1. Satellite images of Madrid and St. Louis in the context of their regions and countries. Supplemental Figure 1 shows each city at the same scale.

St. Louis encompasses an area of 172 km^2 and contains a population of 301,508 people in the city proper and a metro area of over 2.8 million (US Census Bureau 2020). St. Louis's climate is temperate with average temperatures ranging from -0.1^o C in January to 26.7^o C in July, and an average yearly rainfall of 1,040 mm. St. Louis has held historical cultural and economic importance in North America for centuries. The geographic area was home to Cahokia, an indigenous city first settled in 600 CE (Hall 1991). Europeans began colonizing the area starting in the 17th century (Primm 1998), and the city of St. Louis as we know it today was founded in 1763 (Fausz 2012). In the late 19th century, industrial production became vital to the St. Louis economy and the city reached its population peak in 1950 (US Census Bureau 2020), but has been experiencing considerable population loss as it undergoes suburbanization (Primm 1998) and white flight (Gibson 1998). This population loss has led to urban decline in the city, changing the dynamics of the city center, leaving it with abandoned houses and boarded up storefronts (Gordon 2008). Unlike Madrid, city revitalization efforts resulted in building more highways and parking spaces, as opposed to more public transportation, and also focused on luring suburban dwellers back to city center, rather than investing in renewal in the current tenants (Gordon 2008). The urban renewal efforts in St. Louis often involved clearing blighted areas (e.g. areas with vacant homes or factories) for new commercial or industrial development which perpetuated population loss and the replacement of older architecture with newer buildings (Fig. 2) (Gordon 2008).

Transect selection and conduct

We conducted surveys in Madrid from February–June, 2022 and in St. Louis from September–December 2022. Surveys were conducted by one person (D.E.L.) walking 5 km transects that covered the central area of each city. Half the transects ran east–west while the other half ran north–south (see Fig. 3A and 3E in results for a map of the transects) lead-

Figure 2. Images of two distinct environmental survey points from each city; downtown city center (red point on map) and one from outside downtown (blue point on map). Each location has a difference in the number of pedestrians, width of road, structure height, architecture style, and building use.

ing to a grid pattern that was selected to maximize geographic distribution. Eight transects were used to cover the geographic area of the city and an additional two transects in the city center were added to obtain data from the most central areas of the city which were not covered in the grid pattern transects. Each transect was surveyed either west to east or north to south. Because we were interested in how humans influenced pigeon density, we used two sample periods to cover human working hours and after work hours. Therefore, each transect was surveyed twice, once during a typical 9am–5pm workday (day surveys) and once after 5pm (evening surveys) to include movements of the human population as an environmental variable. The order of the surveys in each city was determined using a random number generator. All surveys were conducted on weekdays, during daylight hours, and on days without active precipitation or high wind (i.e. wind was never above 5 on the Beaufort Wind Scale). Because pigeons are not migratory, and urbanization is known to lead to year-round breeding (Dunmore and Davis 1963, Häkkinen et al. 1973, Johnston and Janiga 1995, Lees 1946, Murton et al. 1972), we expect the difference in survey periods to have negligible influence on our results.

Pigeon surveys

We performed continuous visual encounter surveys for pigeons for the whole survey length, while also stopping every 500 meters to collect environmental variables, standardizing across cities using the same transect length (5 km) across 10 transects for a total of 50 km in each city. For every individual or group of pigeons observed, the coordinates and time were recorded using Gaia GPS (https://www.gaiagps.com/). We also recorded the number of pigeons and categorized the substrate the pigeons were observed on as: building, phone line, streetlight, ground, flying overhead (pigeon was observed flying above the tallest building), flying closer to the ground, tree, or other (typically another smaller structure such as a car or statue).

Environmental survey

We recorded environmental variable surveys every 500 m along each transect with the first survey point occurring at the starting point of each transect. On the second survey of each transect, the first survey point occurred 250 m into the transect before continuing every 500 m pattern. By alternating the starting points of the first and second survey, we were able to build a map of survey points that occurred every ~250 m on the transects. At every data collection point, we noted the temperature (º C), percent cloud cover (estimated out of 100), presence of restaurants with outdoor tables, number of tables occupied with people (if applicable), presence of waste disposal receptacles and type (e.g. dumpster, trash can, compost can), presence and type of water source (e.g. puddle, fountain), litter (on a scale of 0–4), presence and number of birds that were not pigeons, and number of pedestrians.

Human-provided food sources have been shown to positively correlate with pigeon density across many studies (Chace and Walsh 2006, Fuller et al. 2008, Jokimäki and Suhonen 1998, Marzluff 2001, Przybylska et al. 2012, Robb et al. 2008). Therefore, in our study, we used restaurants with outdoor seating, presence of waste disposal, and litter to quantify human-provided resources (sources for all environmental variables in Supplementary Table 1, available online at https://eaglehill.us/urnaonline/suppl-files/urna-079-Lewis-s2.pdf). We also recorded water sources because pigeons were observed drinking and bathing in public water features in Madrid and studies have shown pigeons forage for water sources within several hundred meters of their nesting sites (Johnston and Janiga 1995).

Pedestrian density has been shown to be positively correlated with pigeon density (Jokimäki and Suhonen 1998, Muscat et al. 2022, Przybylska et al. 2012, Ryan 2011); therefore in addition to our own measure of pedestrian density, we decided to include transportation stops (bus stops) which typically have high pedestrian traffic. To account for human density beyond pedestrian density, we also incorporated population density into our models. Schools have also been shown to be positively correlated with pigeon density (Przybylska et al. 2012); therefore, we included the presence/absence of schools in our model.

Predator presence has been shown to be negatively correlated with pigeon density (Cade et al. 1996, Johnston and Janiga 1995, Przybylska et al. 2012, Tang et al. 2018); thus we surveyed the literature to determine which local species preyed upon pigeons and included these species in our models. Predators included in the Madrid model were: *Aquila fasciata* Vieillot (Bonelli's Eagle), *Hieraaetus pennatus* Gmelin (Booted Eagle), *Buteo buteo* L. (Common Buzzard), *Falco tinnunculus* L. (Eurasian Kestrel), *Circus aeruginosus* L. (Eurasian Marsh Harrier), *Accipiter nisus* L. (Eurasian SparrowHawk), *Aquila chrysaetos* L. (Golden Eagle), *Falco peregrinus* Tunstall (Peregrine Falcon), and *Milvus milvus* L. (Red Kite). Predators included in the St. Louis model were: *Haliaeetus leucocephalus* L. (Bald Eagle), *Falco peregrinus* Tunstall (Peregrine Falcon), *Accipiter cooperii* Bonaparte (Cooper's Hawk), *Accipiter striatus* Vieillot (Sharp-Shinned Hawk), *Buteo jamaicensis* Gmelin (Red-Tailed Hawk), and *Buteo lineatus* Gmelin (Red-Shouldered Hawk). We downloaded all observations of these predators (through January 2023) in each city using eBird and clipped these data to the buffer for each environmental survey location. We then used these observations to estimate predator density along the transect (Sullivan et al. 2009). We combined all raptor observations into one "predators" variable and included a binary predator presence variable.

Finally, green space and density of impervious surfaces have been shown to be positively correlated with pigeon density (Przybylska et al. 2012), while density of roads has been shown to be negatively correlated with pigeon presence (Przybylska et al. 2012, Tang et al. 2018), therefore we included these variables in our analysis.

Statistical analysis

We examined potential covariates of pigeon observations including: date (as a sequential integer by day starting 1 January 2022 and ending 31 December 2022), observation time (as fractional time), time of day (day vs. evening survey), cloud cover, temperature (^{o}C), transect length, and total number of environmental survey points. We then tested for multicollinearity among our covariates using the function 'vif' in the R package *car* (Fox et al. 2023).

Landscape analysis

We conducted our statistical analysis in R v.4.2.0 (R Core Team 2022). To assess the influence of environmental variables, we created spatial buffers around each environmental survey point using the function "st_buffer" from package *sf* (Pebesma et al. 2024). The radius of each buffer was set to 125 m, half of the ~250 m distance between environmental survey points, so the buffers would adjoin but not overlap. We summed the number of pigeons encountered in each buffer and attached this number to the buffer using the "st_intersects" function in the package *sf*. Because pigeon counts of 11 or more were recorded categorically (11–20, 21–50, 51–100, <100) we created three estimates for pigeon counts that encompassed the endpoints and midpoint of the ranges: low (11, 21, 51, 101), mid (15, 35, 75, 125), and high (20, 50, 100, 150). Each of these estimates (low, mid, high) were used to build three separate models for each city. Similarly, as the number of people was recorded categorically (11–20, 21–50, 51–100, <100), we used the mid estimate (15, 35, 75) for all analyses. We decided to treat higher pigeon counts as a categorical variable because we could not accurately assess the number of pigeons at high densities but wanted to account for these differences in our model. We counted the number of people categorically as well for the same reason as the number of large flocks of pigeons– we were unable to quickly count large crowds but wanted to account for differences in crowd size. We added all listed environmental variables to the model along with our covariates

To capture the heterogeneity of urban landscape we considered 6 landscape factors for both cities: parks, bus stops, road density, impervious surface, schools, and predators. We transformed all spatial data sets into a shapefile by first converting to data frames using the "as.data.frame" function from base R, followed by converting to shapefiles using the "st_as_sf" function in the *sf* package. We then ensured each shapefile was in the same projection (i.e. World Geodetic System 1984). Several environmental variable maps were downloaded as Tiff files (impervious surfaces for both cities) and were transformed to raster files using the package *terra* (Hijmans et al. 2024). The process of transforming these Tiff files into shapefiles resulted in point geometry which we grouped with the other point environmental variables. For the environmental variables with point geometry, we performed the same technique as with the pigeon counts, using "st_intersects" from the *sf* package to identify and sum the number of points that fell within each buffer. For linestring and polygon environmental variables, "st_intersection" from the *sf* package was used to find the length of road within the buffer (linestring) and area of parks within the buffer (polygon).

Statistical models

For each city we investigated how pigeon count varied across the environmental landscape by fitting a linear model of pigeon count by environmental variables and our covariates. We then performed a backwards stepwise regression selection using the function 'step' in the base *stats* package in R. A backwards stepwise regression starts with the most complex model which includes all variables of interest, and then systematically removes variables, simplifying the model. The simplification process involves removing the variable with the highest *p*-value (therefore least significant in the model), and then reevaluating the model with the variable removed. This step is repeated until removing variables no longer improves the model's performance according to Akaike information criterion.

Results

Climate variation

Temperature was higher in St. Louis compared to Madrid, 19.6° C vs. 17.2° C, respectively. St. Louis also had a larger temperature range of -1.1° C–34.4° C, compared to Madrid's range of 7.2° C–31.1° C. Cloud cover averaged 43.6 % and 29.2 % in Madrid and St. Louis, respectively.

Confounding variables

We fit a single linear model of pigeon presence and found cloud cover to be correlated with pigeon presence in Madrid (cloud cover: $\beta = 0.080$, t_{152}: 2.100, $P = 0.037$). We found no covariates for St. Louis. All covariates were the same across the low, mid, and high pigeon estimate models for each city. Our one covariate for Madrid (cloud cover) had an inflation factor of 1.608. As the calculated inflation factor of our covariate was not over 5, we concluded that multicollinearity was not a concern.

City-specific pigeon density findings

Madrid, Spain. We observed 2294 pigeons across 20 surveys (2 surveys of 10 transects) and collected 163 environmental survey points (Fig. 3B). On average, we observed groups of pigeons containing 5 individuals. We observed more pigeons during the evening surveys (n =11 30) than the day surveys (n = 842), but this difference was not statistically significant (p = 0.18). During our surveys, we observed the majority of pigeons on the ground (50.7 %), followed by on a building (17.8 %), flying closer to the ground (10.2 %), flying overhead (10.0 %), in a tree (4.2 %), other (3.8 %), on a phone line (2.2 %), on a streetlight (1.2 %) (Fig. 4). For Madrid, pedestrian density (Fig. 3C; p < 0.05 for low model, p < 0.01 for mid model, p < 0.001 for high model) and restaurants with outdoor seating (Fig. 3D; p <0.05 for low and mid models), population density (p <0.001 for all models) were statistically significant in our environmental analysis models.

St. Louis, Missouri, USA. We observed 644 pigeons across 20 surveys (2 surveys of 10 transects) and collected 156 environmental survey points (Fig. 3F). We observed fewer pigeons in the evenings (n = 232) than the day surveys (n = 262), but this difference was not statistically significant (p = 0.58). We observed a plurality of pigeons on buildings (41.3 %) followed by flying overhead (25.4 %), phone lines (20.6 %), flying closer to ground (7.9 %), and finally on streetlights (4.8 %; Fig. 4). For St. Louis, pe-

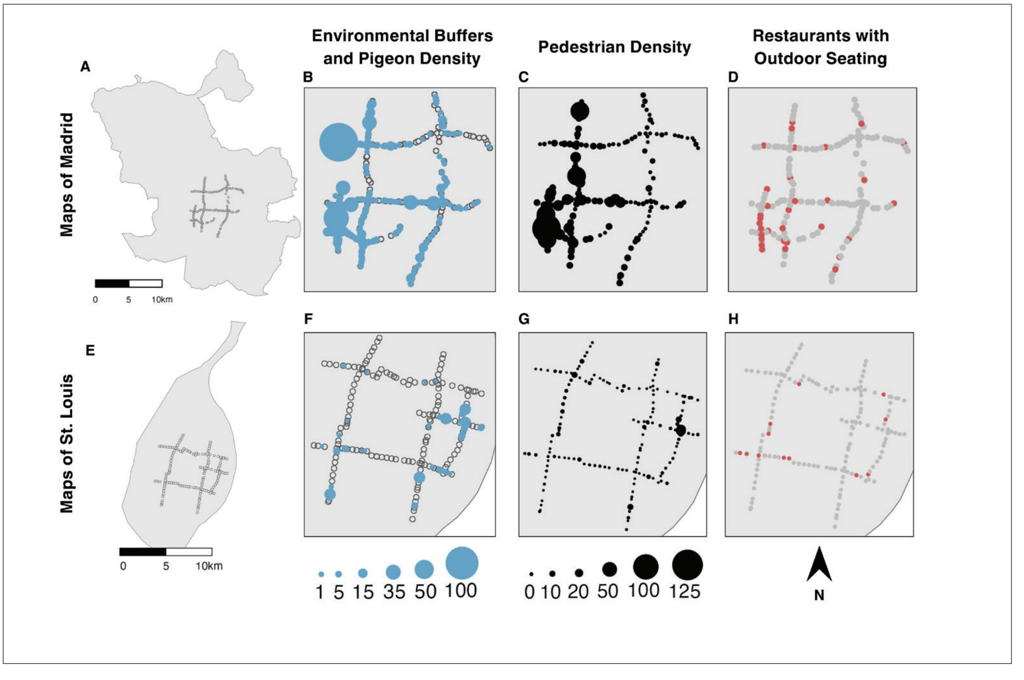

Figure 3. Pigeon presence in Madrid, Spain and St. Louis, Missouri, USA. B, F depict the area sampled (black circles) and observed presence of pigeons (blue dots). C, G depict pedestrian density with point size correlating to the number of pedestrians observed (larger points have more observed pedestrians). D, H displays the presence of restaurants with outdoor seating; red dots indicating presence and gray dots indicating absence. Supplementary Figure 1 shows B and F at the same scale.

destrian density (Fig. 3G; $p < 0.001$ for all models) and impervious surface ($p < 0.001$ for all models) were statistically significant in our environmental analysis models.

Discussion

Our research indicates that human density strongly influences pigeon density in both St. Louis and Madrid, and that urban pigeons exhibit fine-scale spatial patterns that reflect the built environment and location of humans. Our findings strongly or partially supported three of our hypotheses: that pigeon population density would increase with (1) human density, (2) prevalence of food resources, and (3) impervious surfaces. Specifically, we found pigeon population density to be positively correlated with pedestrian density across both cities; with population density and restaurants with outdoor seating in Madrid; and with impervious surface in St. Louis. Our results corroborate previous studies that show positive correlations between pigeon and human density (Hetmański et al. 2011, Jokimäki and Suhonen 1998, Muscat et al. 2022, Przybylska et al. 2012, Ryan 2011). In Madrid, we found that pigeon density increased in areas with restaurants with outdoor seating corroborating multiple studies (Chace and Walsh 2006, Fuller et al. 2008, Jokimäki and Suhonen 1998, Marzluff 2001, Przybylska et al. 2012, Robb et al. 2008). Finally, in St. Louis we found that pigeon density increased with impervious surfaces, consistent with a previous study conducted in Poznań, Poland (Przybylska et al. 2012).

Our results did not support four of our hypotheses: (1) pigeon density is negatively correlated with predator presence, (2) pigeon density is negatively correlated with road density, (3) pigeon density is positively correlated parks, and (4) pigeon density is positively correlated with water sources. First, we predicted that pigeon density would be negatively correlated with predator density as pigeons are a food source for raptors (Cade et al. 1996, Johnston and Janiga 1995). However, our models found no correlation between raptor presence and pigeon presence in either city. Second, we predicted pigeon density would be negatively correlated with road density (Przybylska et al. 2012, Rose et al. 2006) but found no correlation. However, this lack of correlation may be a result of differences in our

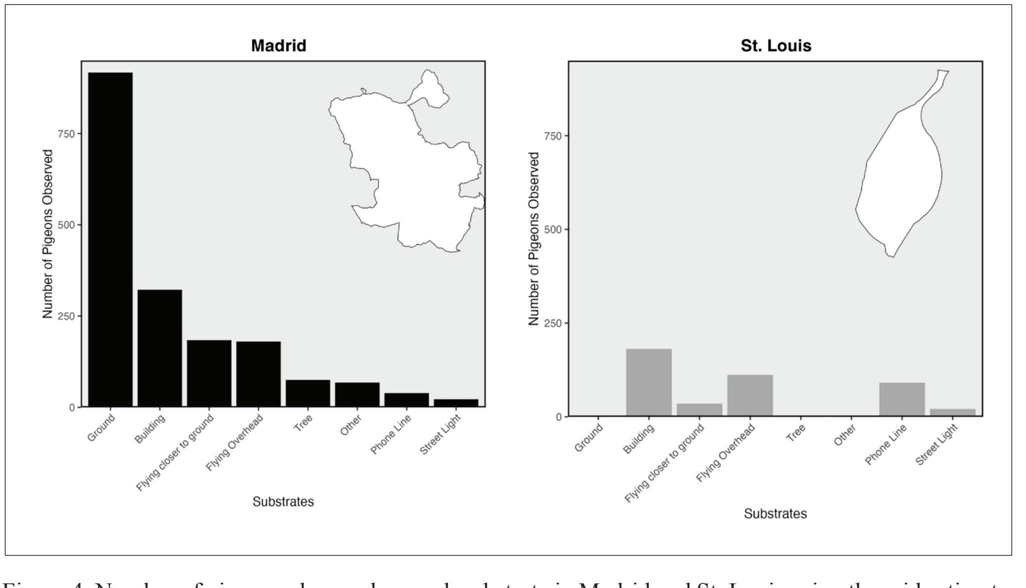

Figure 4. Number of pigeons observed on each substrate in Madrid and St. Louis using the mid estimate.

data collection methods. Previous studies performed surveys in randomly selected plots (Przybylska et al. 2012) or attached GPS monitors to individual pigeons (Rose et al. 2006), while we performed our surveys walking along roads. Therefore, every one of our buffers captures some section of road, meaning our model may be too homogenous for road density to be able to observe any correlations. Third, previous research has also shown positive correlations between urban bird populations and parks (Chace and Walsh 2006, Maciusik et al. 2010, Przybylska et al. 2012); however, our models found no correlation with these landscape features. Finally, we predicted that pigeon density would increase with the number of water sources, but our models did not identify their presence as a significant correlate.

Given that our results from Madrid and St. Louis were inconsistent, and often did not match previous studies, we hypothesize that the political and cultural histories of each city impact pigeon abundance and distribution. For example, we found that pigeon density was significantly higher in Madrid, which is likely a reflection of the significantly higher density of pedestrians we observed. We propose that St. Louis' historical policies neglecting the revitalization of downtown areas has discouraged more human use of the spaces, and that this lower human use of the downtown area of St. Louis has led to fewer pigeons in these spaces (Gordon 2008). Additionally, we found that pigeon presence increased with the number of restaurants with outdoor seating in Madrid but not St. Louis. Similar to pedestrian density, we think this may also be a reflection of cultural differences between Madrid and St. Louis. For example, in Spain there is a "terraza" culture where people will meet at outdoor cafes for wine, coffee, and tapas. This tradition means that it is very common to eat at outdoor tables as opposed to dining indoors, creating human food waste that may be used as food sources by pigeons. We also found that pigeon density was positively correlated with impervious surface density in St. Louis but not Madrid. This difference may be the result of St. Louis prioritizing building new highways and parking lots (Gordon 2008, Stapell 2015) leading to an increase in impervious surface density throughout the city. Previous studies have shown that the highest pigeon densities occur in areas where human density and impervious surface density are also at their highest (Hetmański et al. 2011, Przybylska et al. 2012, Sacchi et al. 2002). In a city like St. Louis where human density is comparatively lower and impervious surface is comparatively higher it is reasonable that impervious surface would emerge as a more significant factor in this context.

Our proposal that political and cultural histories influence current pigeon spatial distribution can also be supported by the unsupported hypotheses. While we found no correlation between pigeon density and park density in either city, Madrid has a much larger area of parks (85,000 m² and 46,000 m² respectively) which could be a factor influencing the greater number of pigeons we found in Madrid. We also did not find a correlation between pigeon density and water source, but 15 of the 20 recorded water sources in Madrid were permanent (fountains or water features as opposed to rain puddles), while in St. Louis, only 5 of the water sources were permanent. The greater number of permanent water sources could be another factor causing significantly more pigeons in Madrid than St. Louis. Both landscape features– parks and fountains– resulted from the revitalization undertaken in Madrid in the late 1970s (Stapell 2015). Revitalization that was not undertaken in St. Louis, leaving the city with fewer parks and permanent water sources and therefore, fewer pigeons. However, further studies are needed to confirm a statistically significant correlation between these landscape features and pigeon density.

Beyond the historical differences pertaining to our specific hypotheses regarding pigeon density, our findings support previous studies relating pigeon population dynamics to city infrastructure and antiquity. Studies have found that pigeon presence is associated with building features including building age and height (Ali et al. 2014; Przybylska et al. 2012; Sacchi et al., 2002) because older and taller buildings provide more roosting and shelter opportunities (Haag-Wackernagel and Geigenfeind 2008). We found that there was a higher density of pigeons in Madrid which has older architecture than St. Louis (St. Louis Civic League 1907, Thomas 2013). Finally, the timing of the colonization of each city in and of itself could be a factor influencing greater pigeon density as this has been shown to influence population density of other urban birds (Møller et al. 2012). Our findings serve to support this pattern as we found a stark difference in the total number of pigeons observed between cities.

This research builds on a growing body of literature that describes how the individual social history of a city, and even neighborhoods within a city, can shape urban wildlife patterns and ecosystem dynamics. For example, Cocroft et al. (2024) found that human ethnicity and the average income of neighborhoods in Phoenix, Arizona, USA are associated with the activity patterns and occupancy of urban mammals. Additionally, Kinnunen et al. (2025) found that commuting time, which varies by city age and suburban sprawl, is correlated with migratory bird species richness in U.S. cities. Taken collectively, this growing body of research reinforces the central tenet of landscape ecology that spatial heterogeneity—in this case shaped by human history, culture, and policy—creates diverse ecological responses in urban wildlife. Understanding these city-specific patterns is not only theoretically important but has practical implications for urban wildlife management, suggesting that management strategies may need to be tailored to the unique landscape characteristics and human-wildlife dynamics of each urban environment.

Data Availability Statement

All code for this manuscript can be found at: https://github.com/daisylew01/Pigeon-Population-Dynamics.

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