



Impacts of urban heterogeneity in environmental and societal characteristics on coyote survival

Emily Zepeda¹ · Andrew Sih² · Christopher J. Schell³ · Stanley Gehrt¹

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Abstract

Survival links individual-level responses to population, community, and ecosystem dynamics. Thus, understanding species' survival responses to environmental change in urban areas is critical for gaining insights into the ecology and management of wildlife in these rapidly expanding environments. Despite existing research on the broadscale effects of urbanization on wildlife survival, the impacts of heterogeneity within urban areas remain largely unexplored. We identified environmental and societal characteristics evidenced to influence the distribution of resources and risks important for urban wildlife ecology. Using Cox proportional hazards models, we examined the association between these characteristics and the survival of coyotes (*Canis latrans*) living in the Chicago metropolitan area. We found a significant interaction between income and human population density, such that survival was negatively associated with income in densely populated areas. Notably, no environmental characteristics were significantly associated with survival. This study adds to the growing literature demonstrating the significance of ecological heterogeneity in wildlife responses to urbanization and highlights society's influence on wildlife survival in cities.

Keywords Social-ecological systems · Urban wildlife ecology · Wildlife responses to urbanization · Urban wildlife survival · Urban wildlife mortality · Coyote (*Canis latrans*)

Introduction

Given the central role of survival in ecological and evolutionary dynamics, disturbances to survival patterns can have profound effects on populations, communities, and ecosystems. These disturbances are exceedingly apparent in urban ecosystems where extensive landscape changes, the introduction of novel species, the presence of pollutants, and high levels of human activity have devastating impacts on some species while creating ecological niches for others (Blouin et al. 2019; Groffman et al. 2014; McKinney 2006). These changes reduce biodiversity and nature's contributions to

people (i.e., ecosystem services) in urban areas whose positive interactions with nature can be rare (Des Roches et al. 2021; Soulsbury and White 2015). The separation of urban residents from nature can reduce people's motivation to advocate for conservation initiatives that mitigate and halt the biodiversity crisis (Dearborn and Kark 2010; Dunn et al. 2006). Thus, understanding species' survival responses to urbanization is connected to larger discourses on establishing wildlife-friendly cities and bolstering conservation efforts that reconnect people with nature and regenerate ecosystem services (Kay et al. 2022). Previous research has examined the effect of urbanization intensity (e.g. urban vs. rural) on wildlife survival (Brearley et al. 2013; Halfwerk et al. 2018; Prange et al. 2003). However, there are few studies that explore the relationship between survival and social-ecological variation in urban ecosystems.

Survival is largely dependent on an animal's ability to acquire resources and avoid risks; therefore, environmental features that shape the distribution of resources and risks have direct implications for wildlife survival. Many urban species require some natural food or habitat to survive (Krausman et al. 2011; Magle et al. 2021; McKinney 2002).

✉ Emily Zepeda
zepeda.31@osu.edu

¹ School of Environment and Natural Resources, The Ohio State University, Columbus, OH, USA

² Department of Environmental Science and Policy, University of California, Davis, CA, USA

³ Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA, USA

Areas with high vegetation cover and low impervious surface cover can provide opportunities for urban wildlife to forage as well as structures for burrowing, denning, etc. (Fidino et al. 2021). These areas can also serve as refuge where many of the risks urban wildlife face, including vehicle collisions, conflict with humans, and exposure to pollutants, can be avoided (Adams et al. 2005; Markevych et al. 2017; Rodewald and Gehrt 2014; Sepp et al. 2019).

Often, urban green spaces like nature preserves, city parks, or golf courses are cited as important habitats for urban wildlife due to their typically higher productivity and lower levels of human activity compared to the surrounding urban matrix (Gallo et al. 2017; Wurth et al. 2020). Despite the potential benefits of green space for urban wildlife, these areas comprise a relatively small proportion of urban landscapes, which limits wildlife's access to these resources. When access to green space is low, wildlife can use 'disturbed habitat', areas that are altered by humans but are still relatively low in human activity with some unmanaged vegetation growth (Fernandez-Juricic 2001; Rodewald and Gehrt 2014). These disturbed habitats often consist of areas surrounding transportation and utility infrastructure or vacant land and have been shown to provide resources and refuge for some wildlife species (Anderson and Minor 2017; Rega-Brotsky and Nilon 2016; Riley et al. 2018; Zúñiga-Palacios et al. 2020).

Cities are a type of social-ecological system – systems shaped by complex interactions between society and nature – where humans are the dominant driver of ecological patterns and processes (Des Roches et al. 2021; McPhearson et al. 2016; Schell et al. 2020). Therefore, evaluating the role of societal characteristics is a key part of identifying the mechanisms behind wildlife responses to urbanization. In the United States, cities are structured, in part, by societal systems which result in the inequitable distribution of resources amongst urban residents. These systems, including classism and racism, tend to shape cities such that more privileged communities have more resources like green space, tree cover, and plant species diversity (Gerrish and Watkins 2018; Locke et al. 2021; Mennis 2006). These relationships result from the ability of wealthy and/or white communities' to influence institutional policies affecting urban planning decisions, their economic and social power to settle in more environmentally desirable areas, and the resources wealthy homeowners have for managing large residential lots (Chamberlain et al. 2020; Cubino et al. 2020; Pickett and Grove 2020). Social systems also affect the distribution of risks. For instance, noise and chemical pollution occur at higher levels in communities that experience discrimination and exclusion (i.e., minoritized communities; Dionisio et al. 2010; Estien et al. 2024; Evans and Kantrowitz 2002; Jesdale et al. 2013; Schuyler and Wenzel 2023;

Tonne et al. 2018). Even vehicle collisions, a major risk for urban wildlife, are negatively associated with wealth (Cottrill and Thakuriah 2010; Morency et al. 2012).

The impacts of inequitable social systems permeate throughout urban ecosystems affecting wildlife. For instance, McKinnon et al. (1976) found that gray squirrels (*Sciurus carolinensis*) living in lower income areas had significantly higher concentrations of lead, a highly toxic metal, in their kidneys. In contrast, 'the luxury effect' describes the positive association between biodiversity and wealth that has been observed in cities across the globe (De la Barrera et al. 2016; Gupta et al. 2016; Leong et al. 2018; Magle et al. 2021; Romero et al. 2012). Studies examining the relationship between redlining – the racially discriminatory housing policies that furthered segregation in major cities – and avian ecology have found that these areas had poorer-quality habitat and lower bird abundance (Ellis-Soto et al. 2023; Wood et al. 2023). Similarly, a study by Schmidt and Garroway (2022) found that population-level genetic diversity was higher in neighborhoods with predominantly white residents across the United States. Their study suggests a potential mechanism behind patterns like the luxury effect: forcing minoritized people to live in areas with more environmental risks, while preferentially investing in environmental quality in privileged communities, results in reduced connectivity, genetic diversity, and, consequently, biodiversity of wildlife in minoritized communities.

Human presence is another societal characteristic that poses a major risk to urban wildlife (Corsini et al. 2019; Lasky and Bombaci 2023; Reilly et al. 2017; Woodroffe et al. 2005). The extensive impact of human activity on wildlife survival is evidenced by the extirpation of many native species from major cities (Lokatis and Jeschke 2022; McCleery et al. 2014). Directly, humans kill urban wildlife through lethal management and vehicle collisions (Bateman and Fleming 2012). Indirectly, humans can negatively impact wildlife survival by negatively impacting their physiology and behavior (Berkhout et al. 2023; Gaynor et al. 2018; Sievers et al. 2019; Wilson et al. 2020). For example, as human population density intensifies, permeable surface and vegetation cover decrease, reducing the availability of natural resources while high levels of human activity reduce opportunities for foraging temporally (Fardell et al. 2022; Sun et al. 2019).

Coyotes (*Canis latrans*) are an especially compelling model species to address how survivorship is attenuated to social-ecological factors in cities. Despite the major risk of human-related mortality either due to direct persecution or vehicle collisions, coyotes have established growing populations in all major urban areas in North America (Hody and Kays 2018). Their proliferation may be attributed, in part, to their adaptability in avoiding these risks. Coyotes readily

adjust their activity patterns to avoid humans temporally and spatially (Ellington and Gehrt 2019; Riley et al. 2010). They prefer natural habitat patches, but in highly developed areas they will use disturbed habitats that are low in human activity – e.g., areas like railroads or cemeteries (Wurth et al. 2020; S Gehrt, unpublished data). In addition to providing refuge, urban coyotes use natural and disturbed habitats to forage for natural resources like fruit, insects, and small mammals (Newsome et al. 2015; Sugden et al. 2021). Coyotes living in urban environments, where natural resources are limited, often consume anthropogenic resources, such as refuse, pet food, and bird seed, which can negatively impact their health (Murray et al. 2015; Newsome et al. 2015; Sugden et al. 2021). Additionally, there is evidence that distribution of urban coyotes is associated with wealth. Income is associated with coyote occurrence in some urban areas and may influence coyote survival through its effect on vegetation cover and resource availability (Magle et al. 2016, 2021).

To understand the role of environmental and societal factors in shaping urban coyote survival, we analyzed the space use and a survival time proxy (i.e., tracking duration) of 214 coyotes living in the Chicago metropolitan area (CMA). Like other urban areas, some resources and risks important for coyote survival are associated with societal characteristics in the CMA. Tree cover, green space, and avian density, potential indicators of resource availability, are higher in areas with higher median income (Iverson and Cook 2000; Liu et al. 2021; Loss et al. 2009). Risks like environmental pollution and waste treatment plants tend to be concentrated in racially minoritized communities (Pellow 2004). A negative association between pedestrian-vehicle collisions and community-level wealth has also been observed in the region, which could be particularly impactful for coyotes as they are susceptible to vehicle collisions (Cottrill and Thakuriah 2010; Margenau et al. 2023; Robertson et al. 2023).

We hypothesized that habitat availability, road density, median income, race, and human population density would affect survival via their effects on the distribution of resources and risks important for coyote ecology. We predicted that habitat availability, median income, and the proportion of white residents would positively affect survival, largely because the racial composition of neighborhoods is frequently a strong predictor of habitat quality (Klomp maker et al. 2023; Pickett and Grove 2020; Watkins and Gerrish 2018). We also predicted that human population density and road density would have a negative effect on survival due to the risks associated with anthropogenic activities, especially vehicle collisions. Finally, we predicted that there would be an interaction between population density and the other

societal characteristics due to a weakening of their effects at low population densities.

Methods

Study area

This study is part of a long-term research program, the Urban Coyote Research Project, exploring coyote ecology in the CMA. The region is one of the largest metropolitan areas in North America and has a robust coyote population of over 4,000 individuals (S Gehrt, unpublished data). It is made up of diverse land uses including nature preserves which are areas protected against development and other human activities that are disruptive to plant and animal life.

Animal captures and monitoring

Animals included in this study were captured and monitored between 2013 and 2021. Captures were carried out using foot-hold traps or cable restraints which were set in nature preserves and private properties throughout the CMA. After animals were captured, they were transported to a laboratory where they were immobilized with Telazol (2.5 mg/kg, intramuscular injection; Zoetis Manufacturing & Research) and fitted with VHF ($n = 198$; Advanced Telemetry Systems and Lotek Wireless) or GPS ($n = 16$; Lotek Wireless) collars. Each coyote was weighed and sexed. Of the 214 individuals in the study, 96 were female and 118 were male. Animals were released at the trap site on the day of capture after recovering from the effects of the anesthetic – i.e., once the animal regained consciousness and complete control of its movements. All procedures were approved by Ohio State University's Institutional Animal Care and Use Committee (Protocol Nos. 2006A0245, 2010A00000113, 2013A00000012).

VHF collared coyotes were located using triangulation with a truck mounted antenna or by visual observations. Triangulations were recorded using a minimum of three bearings with a maximum of twenty minutes between first and final bearings. Coordinates were recorded with the program LOCATE II (Pacer). Coyotes were located once during the day, typically two or three times per week, and at night during tracking shifts in which we focused on a group of coyotes and obtained sequential locations at 60–120-minute intervals for 5–6 h during the night. GPS collars were programmed to collect data at several fix rates including every 7.25 h, 2 h, and every 15 min at different intervals for various projects. All fixes were included in this study. After GPS functionality ceased, GPS collared animals were

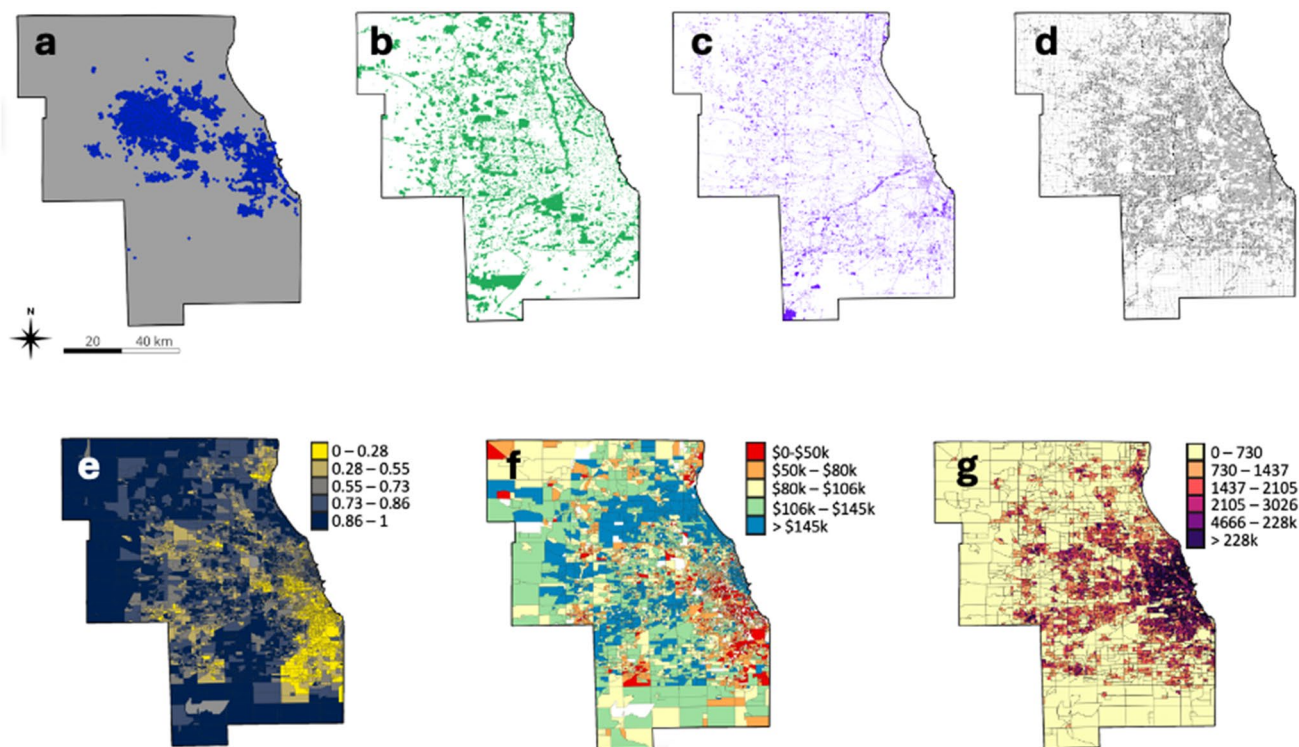


Fig. 1 Spatial distributions of environmental and societal characteristics in the CMA. Recorded locations (a) show where collared coyotes were tracked. Natural habitat (b), disturbed habitat (c), and roads (d) geospatial data were collected from the CMAP (2015). The proportion

tracked using the collars' VHF beacons. The median number of recorded locations for individuals was 119 locations (25% IQ: 59, 75% IQ: 368) and the median tracking duration was 382 days (25% IQ: 104, 75% IQ: 865).

We did not conduct systematic telemetry error testing for this study. However, previous work conducted by the project involving the triangulation and then visual identification of resting animals using the same equipment resulted in an average error of 49.1 m. This is within the average error range of 42.9 m reported by Bartolommei et al. (2012). A previous study demonstrated a mean location error of 15.4 m (SD: 10.1 m) for similar GPS collars from the same manufacturer (Forin-Wiart et al. 2015).

When collared coyotes could not be located by vehicle, we conducted flights with a helicopter or fixed-wing aircraft to locate signals and then confirmed their location on the ground. Such flights were deployed opportunistically in most years and covered northeastern Illinois and parts of Wisconsin and Indiana. Animals recovered postmortem were usually located using their VHF beacons but were occasionally located by residents who notified technicians.

of white residents (e), median household income (f), and population density (residents per km²) (g) in Census block groups were collected from the American Community Survey (United States Census Bureau 2017)

Table 1 CMAP land use categories included in each habitat type (Chicago Metropolitan Agency for Planning 2022)

Habitat type	Land use categories
Natural habitat	Nature preserves, open space (e.g., urban parks, golf courses), cemeteries
Disturbed habitat	Rail rows, communication infrastructure, utility infrastructure, vacant land

Environmental and societal characteristics

To determine the environmental and societal characteristics experienced by each coyote, we created rasters (resolution = 10 m²) using the geographic information systems software, QGIS (QGIS.org 2023; Fig. 1). Natural habitat, disturbed habitat, and road density rasters were generated using data from the Chicago Metropolitan Agency for Planning which inventories land use types across the CMA at the parcel level (Chicago Metropolitan Agency for Planning 2022). Natural habitat is mostly made up of nature preserves and parks, but also includes cemeteries and golf courses – land types selected for by coyotes in urban areas (Table 1; Wurth et al. 2020). Disturbed habitat encompasses areas affected by human activities but with less human traffic than developed and residential areas and some natural features like unmanaged vegetation growth. These areas include

lands used for transportation and utility infrastructure and vacant lots (Table 1). We chose to calculate the proportion of natural habitat, disturbed habitat, and roadways within three spatial scales of each recorded location: 250 m, 1 km, and 2 km. This allowed us to explore which spatial scale best explains variation in survival.

Societal characteristic data (i.e., median income, the proportion of white residents, and human population density) were extracted from American Community Survey data (ACS; United States Census Bureau 2017) using the R package *tidycensus* (R Core Team 2024; Walker et al. 2021). The ACS collects data on an array of sociodemographic characteristics in areas across the country that are designated by the United States Census Bureau. We used data from census block groups because they are the smallest designated area for data on income and race thus providing the highest resolution data for our study. Census block groups are established based on population and housing densities, resulting in substantial variation in block group area across the CMA (median = 0.48 km², range = 0–96 km²). However, due to the association between population density and sociodemographic heterogeneity, variation in sampling intensity by the ACS across block groups is not expected to change the reliability of their estimates. After rasterizing the societal data, we calculated the median values of societal variables at the previously mentioned spatial scales.

There were disparities in the distributions of the environmental and societal values in the study region and the distribution of values in our sample of recorded coyote locations (Supplementary Information S2). It is possible that this discrepancy was a result of the distribution of coyotes in the region. For example, high values of the proportion of natural habitat are overrepresented in the sample which may reflect coyotes' preference for natural habitat. However, the accessibility of trapping sites across the region likely plays an important role. While efforts have been made to trap animals in highly urbanized areas and in predominantly Black communities, it was difficult to gain access to suitable trapping sites in these areas. While there is still significant

information to be extracted from a limited sample, care should be taken when generalizing these results especially to lower income areas (< \$50k) and communities with low proportions of white residents (< 0.30) which are particularly underrepresented in this study.

Territorial status

There are two main patterns of territorial space use in coyotes (Webster et al. 2022). Residents, who belong to a mated pair or a pack, defend a territory where they exhibit high levels of site fidelity. Transients are solitary individuals who tend to range across large areas exhibiting low site fidelity. Residents tend to have longer survival times than transients likely due to their increased familiarity with rewards and risks within their territory and access to higher quality habitats (Margenau et al. 2023; Ward et al. 2018).

We determined the territorial status of these animals by calculating the mean squared displacement (MSD), the mean displacement of all relocations relative to the center of movement, and the linearity (LI) of their movement, the linear distance between movement endpoints divided by the total distance traveled (Wolfe and Lowe 2015). We calculated these site-fidelity metrics using the *amt* package in R (R Core Team 2024; Signer et al. 2019). If there was a gap between locations of more than 14 days, a new set of metrics were calculated for the group of locations collected after the gap to account for potential changes in territorial status. The MSD and LI of each group of locations were compared to the distributions of MSDs and LIs of 1000 simulated random paths. If both metrics fell below 95% of those randomized paths, individuals were categorized as residents, otherwise they were considered transients. The final sample included 36 resident coyotes, 93 transient coyotes, and 85 animals who exhibited both space use patterns at different periods.

Survival analysis

We evaluated three Cox proportional hazards models with time-varying covariates (Table 2). These models estimate the effects of time-varying predictor variables by comparing hazard rates at different levels of each variable to produce hazard ratios, i.e., the ratio of mortality probabilities between different levels of a categorical variable or with a 1 unit increase of a continuous variable. By including time-varying covariates, we were able to account for changes in the environmental and societal factors experienced by the animals as they moved across the landscape. We also assessed territorial status across time to account for changes in the animal's social status while they were tracked. Of the 214 animals in the study 114 were recovered postmortem. Individuals who had a location rate of less than 1 location

Table 2 Models evaluated at three spatial scales: 250 m, 1 km, and 2 km. All models included the individual-level attributes sex and territorial status

Model	Predictors
Environmental	Natural habitat + Disturbed habitat + Road density
Societal	Proportion white residents + Median income + Population density + Proportion white residents x Population density + Median income x Population density
Environmental + Societal	Natural habitat + Disturbed habitat + Road density + Proportion white residents + Median income + Population density + Proportion white residents x Population density + Median income x Population density

per week, had fewer than 10 total locations, or whose last location was recorded more than 30 days before they were recovered postmortem were excluded from the study (total excluded = 654).

For the 114 animals recovered postmortem, the time between their first recorded location and postmortem recovery was used as a proxy for survival time. This allowed us to include individuals with unknown birth years in the study, substantially increasing the sample size. Data from VHF collared individuals with known birth years and postmortem recoveries indicated that tracking duration is a strong predictor of age (correlation = 0.87, 95% CI [0.73, 0.94]; Supplementary Information S1). Animals who were not recovered postmortem were considered censored and were assigned a “survival” time equal to the difference between their first and last recorded location. We adjusted for right-censoring with the R package *survival* (R Core Team 2024; Therneau and Grambsch 2015). The date of the animals’ first recorded locations represented time zero for the time-varying component of the model. All continuous, independent variables were scaled and centered.

The assumption of proportional hazards was assessed using a chi-square significance test. We assessed model fit using Akaike information criterion (AIC). We used the *MuMIn* package in R (Barton 2024; R Core Team 2024) to conduct model averaging with competing models ($\Delta\text{AIC} < 4$). The package uses an information criterion framework to determine model weights and average model parameters. We interpreted the results for full model averaging where predictor coefficients are set to zero in top-fitting models if they were not included in the original model.

Independent variables in the model were tested for multicollinearity using variance inflation factors (VIF). VIFs for variables in all models were within the acceptable range (S4; Gareth et al. 2013). However, we observed some estimation issues with the inclusion of road density in the “Environmental + Societal” models. Road density exhibited the highest VIF among all variables and was highly correlated with natural habitat (-0.80) and population density (0.86) (Supplementary Information S3; Supplementary Information S4). Thus, road density was removed from those models revealing a significant effect of population density. The interaction between the proportion of white residents and population density was removed due to its non-significant estimate.

Results

AIC scores indicated that the 2 km scale “Environmental + Societal” model was the best-fitting model (Table 3). The 2 km scale “Societal” model was also a top-fitting

Table 3 Model fit for models evaluating the effect of environmental and societal characteristics on survival for 214 coyotes at three spatial scales (250 m, 1 km, and 2 km) from recorded locations. The number of predictors (k), Akaike information criterion score (AIC), and the change in model fit relative to the top model (ΔAIC) are included

Model	Scale	k	AIC	ΔAIC
Environmental + Societal	2 km	8	961.7	0.0
Societal	2 km	6	963.4	1.7
Environmental + Societal	1 km	8	966.5	4.8
Environmental	2 km	5	968.0	6.3
Environmental	1 km	5	968.0	6.3
Societal	250 m	6	968.2	6.5
Societal	1 km	6	969.6	7.9
Environmental + Societal	250 m	8	970.9	9.2
Environmental	250 m	5	973.3	11.6

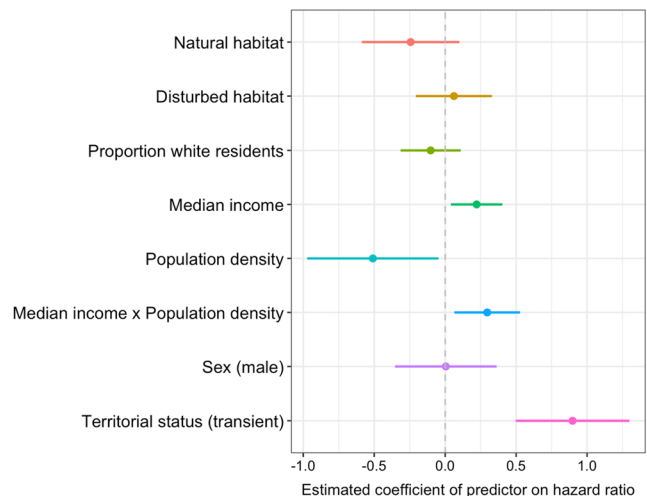


Fig. 2 Model-averaged coefficients of environmental and societal characteristics on hazard ratios and 95% confidence intervals

model ($\Delta\text{AIC} < 4$; Table 3). Fine-scale models, i.e., 250 m, tended to have larger AIC scores suggesting that large-scale metrics of the animal’s environmental and societal experience better predict their survival response.

After model averaging, the results indicated that neither natural habitat nor disturbed habitat were significant predictors of coyote survival (Fig. 2). Median income and population density had significant main effects and a significant interaction effect (Fig. 2). The interaction between median income and population density indicated that at low human population densities, coyote survival was generally low, and median income had no significant relationship with survival (Fig. 3a). However, in densely populated areas (5,000 people/km²), coyotes in lower income areas (\$50,000) were 1.5 times more likely than coyotes in high-income areas (\$150,000) to survive to 2-years old – the age at which most resident animals begin reproducing (Fig. 3c). There was no significant association between the proportion of white residents and survival.

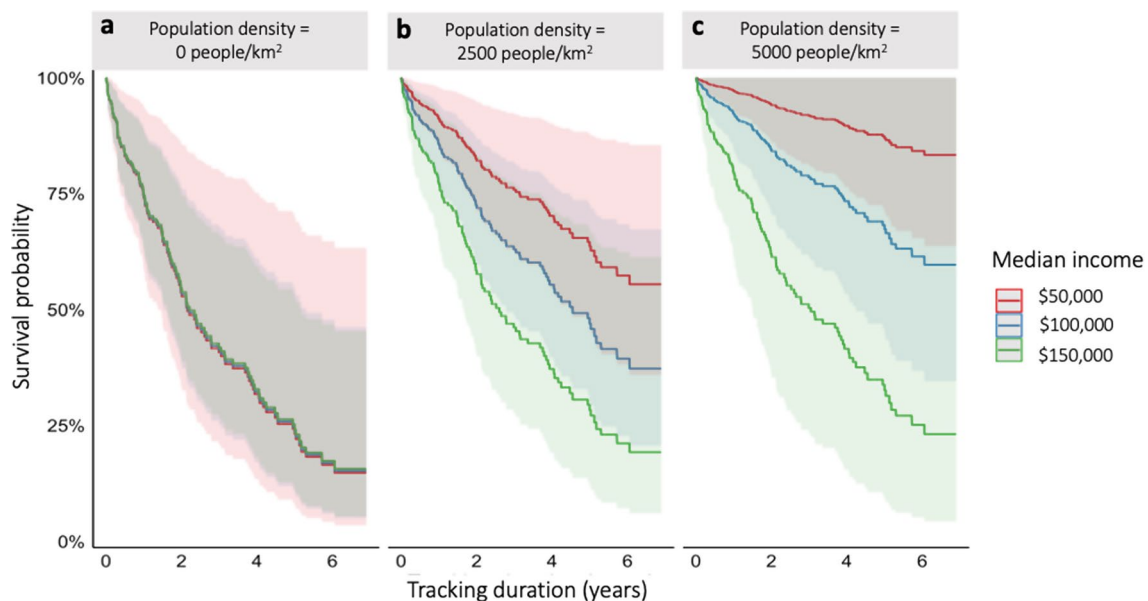


Fig. 3 Model predicted survival probability curves generated at (a) low population density, (b) median population density, and (c) high population density and three levels of median income: \$50k (red), \$100k (blue), and \$150k (green). Shading is 95% CI. Predictions were made

for resident females with mean values of the proportion of natural habitat, the proportion of disturbed habitat and the proportion of white residents using model-averaged coefficients

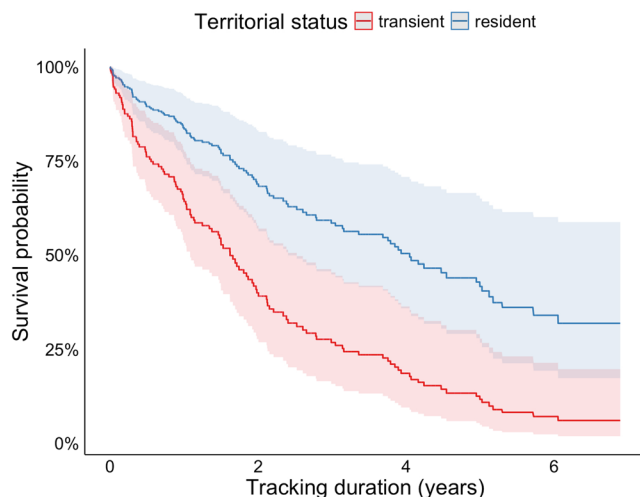


Fig. 4 Model predicted survival probability curves for transient (red) and resident (blue) coyotes. Shading is 95% CI. Predictions were made for females with mean values of the proportion of natural habitat, the proportion of disturbed habitat, the proportion of white residents, median income, and human population density using model-averaged coefficients

Territorial status had a significant relationship with survival. Transients had a higher hazard rate than residents, i.e., they tended to have lower survival probabilities than residents (Fig. 4). Model-averaged predictions indicated that residents were 1.7 times more likely to survive to 2-years old than transients. Sex was not significantly associated with survival.

Discussion

Understanding wildlife survival responses within cities is becoming increasingly important as urban expansion progresses. We explored the effects of environmental and societal characteristics on coyote survival in the CMA. Our results indicated that – along with territorial status – median income, and human population density were significant predictors of urban coyote survival. However, contrary to our predictions, survival was positively associated with population density and negatively associated with median income. Natural habitat, disturbed habitat, and the proportion of white residents did not have a significant relationship with survival. Our results add to the growing literature illuminating society's role in shaping urban ecology.

In studies exploring wildlife responses to humans, human presence and infrastructure tend to have detrimental effects (Ceballos et al. 2015; IUCN 2023; Lasky and Bombaci 2023; Rodewald and Gehrt 2014). We predicted that coyote survival would follow this trend. However, our results revealed a positive relationship between survival rate and human population density. Importantly, the bulk of our data comes from the suburban areas surrounding the city of Chicago where the landscape ranges from small, low density agricultural areas to large villages with populations of more than 75,000 and population densities rivaling some areas of Chicago (Chicago Metropolitan Agency for Planning 2022). In less densely populated areas, the hunting and trapping of coyotes is a significant cause of mortality and a

reduction in hunting activity may lead to increased survival rates in higher density areas (Gehrt et al. 2011; Margenau et al. 2023). Mange is also an important mortality factor for coyotes, especially in the CMA where winter temperatures can quickly kill animals that are unable to thermoregulate due to fur loss (Gehrt et al. 2011). Anthropogenic structures may increase survival in animals with severe infestations by providing them refuge from extreme temperatures (Murray and St. Clair 2017; Wilson 2012). Additionally, anthropogenic food (e.g., compost, pet food) may offer animals the resource subsidies needed to survive disease, injury, or periods of low food availability (Becker et al. 2015; Murray et al. 2015; Reddell et al. 2023). While unexpected, the result suggests that high survival probability in densely populated areas may be one of the processes facilitating coyote's colonization of cities.

Further research on the relationship between human presence and survival may benefit from evaluating different aspects of human presence. For instance, a study by Nickel et al. (2020) found that some mammalian species differed in their responses to human activity versus building density. Identifying the specific aspects of human presence (e.g., human foot traffic, traffic volume, structure of built environment, food subsidies) that impact coyote survival would provide a mechanistic understanding of the relationship we observed and may be informative for the management of urban coyote populations.

Wealth is emerging as an important factor shaping urban wildlife ecology (Leong et al. 2018; Schell et al. 2020). Contrary to our hypothesis, we found that survival rates declined with income in more densely populated areas. Interestingly, coyote occupancy and human-coyote encounters tend to be higher in wealthier areas (Fidino et al. 2022; Magle et al. 2016, 2021; Raymond and St. Clair 2023; Wilkinson et al. 2023; Wine et al. 2015). High-income areas may act as ecological traps, where an increase in resources and reduction in risks like pollution in wealthy areas may increase coyote population density through birth and immigration rates while simultaneously reducing survival rate due to density-dependent factors like disease or intraspecific competition (Becker et al. 2015; Murray et al. 2019). Human behavior may also contribute to this relationship. In San Francisco, California, human-coyote conflict reports were more likely in areas with higher median income, which also coincided with higher vegetation cover (Wilkinson et al. 2023). Similarly, in Edmonton, Canada, wealthy households are more likely to have resources like compost piles on their property which are associated with higher levels of ectoparasites and poorer condition in the coyotes who frequent them (Murray et al. 2016; Raymond and St. Clair 2023).

Coyotes in cities exhibit strong selection for natural areas indicating that these habitats provide resources or refuge

that developed areas do not (Grubbs and Krausman 2009; Poessel et al. 2016; Thompson et al. 2021). The positive relationship between urbanization and coyote home range size found in some studies further emphasizes the role natural habitat plays in coyote ecology as individuals living in more developed areas are forced to increase their range to meet their needs (Ellington and Gehrt 2019; Gese et al. 2012; Riley et al. 2003). Despite coyote's selection for natural habitat features, there was no significant association between their use of either natural or disturbed habitats and survival in our study. This may be due to a mismatch between the habitat classification methods used in our study and the environmental features that benefit coyotes. For instance, urban parks considered "recreational open space" by CMAP may vary in their level of refuge (e.g., unmanaged vegetation growth) and risks (e.g., human activity) such that the land use category is meaningless for coyote ecology. A study of vacant lots as habitat for songbirds in Baltimore found that habitat quality in a lot was dependent on shrub density, highlighting the importance of measuring finer-scale environmental features within natural and disturbed habitat categories (Rega-Brodsky and Nilon 2016). If natural habitat features do impact survival, identifying the features of these habitats (e.g., vegetation structure, anthropogenic resource availability) selected for by urban coyotes may help elucidate their relationship with survival.

Coyotes are a highly territorial species (Gese 2001). Thus, it is not surprising that resident, territorial animals survived better than transient animals. Higher site fidelity allows animals to forage more efficiently, avoid risks more effectively, and minimize movement costs (Pietersen et al. 2010; Piper 2011). Resident coyotes also tend to occupy higher quality habitat due to their ability to fend off competitors from these preferred areas (Thompson et al. 2021). In addition to the survival benefits of occupying stable, higher quality territories, the characteristics that allow coyotes to defend territories may directly contribute to their longer survival times. For instance, in Capricorn silvereyes (*Zosterops lateralis chlorocephalus*) body size is positively associated with success in intraspecific competitions and over-winter survival (Robinson-Wolrath and Owens 2003). This suggests that exploring the effect of other individual-level traits (e.g., condition, behavior) on coyote survival is worthwhile. Incorporating behavioral traits into survival studies (e.g., boldness, innovation, neophobia) could be especially useful for the management of species like the coyote whose behavior often dictates its level of conflict with humans (Caspi et al. 2022; Lee and Thornton 2021; Schell et al. 2021; Wilkinson et al. 2023).

There are limitations to our study. First, the sample consists of coyotes whose minimum weight requirements for collaring excluded very young animals. While our study

includes individuals at the onset of reproductive maturity, juvenile recruitment can be an important factor contributing to population dynamics and our study cannot detect effects at the juvenile stage (Chandler et al. 2018). Furthermore, the limited access to trapping locations, especially in highly urbanized areas, resulted in a sample biased towards coyotes in higher income areas with low-to-moderate human population densities and higher proportions of white residents. The limited range of values in the proportion of white residents may have prevented us from detecting an effect of this variable. While the sample was somewhat more representative of the distribution of median income values in the region, missing data in the extremities of the median income range may change the strength of the relationship. In addition to reducing the generalizability of our results, these limitations highlight the exclusion of racially and ethnically minoritized people from ecological and environmental research and remind us that – even with improving efforts made to equitably engage and coproduce with historically disenfranchised communities – more work is needed to overcome these inequities (Chapman et al. 2024; Carlen et al. 2024; Lambert and Schell 2023; Schell et al. 2020).

As rapid urbanization continues, understanding wildlife survival responses to urbanization is critical to maintaining biodiversity and managing human-wildlife interactions. This study adds to the growing literature demonstrating the significance of within city, or metropolitan area, heterogeneity in wildlife responses to urbanization. The significant, unexpected effects of population density and median income emphasize the importance of exploring the effects of society on urban ecology – and that these effects are likely to vary across scales, species, and the process of interest.

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Author contributions S.G. designed the telemetry data collection. E.Z., C.J.S., A.S., and S.G. devised the study design. E.Z. wrote the first draft of the manuscript and C.J.S. and A.S. commented on all versions. All authors read and approved the final manuscript.

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Data availability Analyses reported in this article can be reproduced using the data provided by Zepeda et al. 2024 (link will be provided once manuscript number is generated).

Declarations

Competing interests The authors declare no competing interests.

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