





Environmental Health and Societal Wealth Predict Movement Patterns of an Urban Carnivore

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ABSTRACT

How societal, ecological and infrastructural attributes interact to influence wildlife movement is uncertain. We explored whether neighbourhood socioeconomic status and environmental quality were associated with coyote (*Canis latrans*) movement patterns in Los Angeles, California and assessed the performance of integrated social–ecological movement models. We found that coyotes living in more anthropogenically burdened regions (i.e. higher pollution, denser development, etc.) had larger home ranges and showed greater daily displacement and mean step length than coyotes in less burdened regions. Coyotes experiencing differing levels of anthropogenic burdens demonstrated divergent selection for vegetation, pollution, road densities and other habitat conditions. Further, movement models that included societal covariates performed better than models that only assessed ecological features and linear infrastructure. This study provides a unique social–ecological lens examining the anthropogenic drivers of urban wildlife movement, which should be applicable to urban planners and conservationists when building more equitable, healthy and wildlife-friendly cities.

1 | Introduction

Globally, urbanisation is bringing people and wildlife into increasingly closer contact with one another (Jenerette and Potere 2010; Schell et al. 2021; Soulsbury and White 2015). This closer contact can lead to deleterious effects, such as human–wildlife conflicts (Gilleland 2010; Murray, Cembrowski, et al. 2015), biodiversity loss (McDonald et al. 2013) and increased stress and disease susceptibility for wildlife (Murray et al. 2019). These effects are likely to worsen with climate change (Abrahms et al. 2023). Yet some species can exhibit resilience or even thrive in urban landscapes (Rodewald and Gehrt 2014). Within cities, animal movements can

help researchers and managers to understand what constitutes usable habitat and connectivity (Beaujean et al. 2021; Braaker et al. 2017; Kirk et al. 2023; LaPoint et al. 2015), and which anthropogenic barriers and threats may inhibit dispersal, foraging, reproduction and other key behaviours (Byers et al. 2019; Grubbs and Krausman 2009; Kobryn et al. 2022; Voigt et al. 2020). Movement analysis is thus an important tool for approximating the unique needs and survival tactics of urban wildlife (Ryan and Partan 2014). With accelerating global urbanisation, it is critical to examine how wildlife move through cities across scales, and in turn determine how humans and wildlife can successfully coexist in these tightly coupled human–natural ecosystems.

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Most urban wildlife behaviour studies focus on urban-rural comparisons, with the relative proportion of green space to grey space (i.e., the built environment) as the main environmental covariate explaining behavioural divergence in urban taxa (Ditchkoff et al. 2006; Swanwick et al. 2003). These studies have emphasised habitat-driven connectivity between urban green spaces (Coulson et al. 2014; Ignatieva et al. 2011). Additional studies have shown that anthropogenic disturbances—such as linear infrastructure and human activity can disrupt (Doherty et al. 2021; Poessel et al. 2014) or facilitate (Hill et al. 2020; Maclagan et al. 2019; Niesner et al. 2021) animal movements, with additional emerging research into the impacts of human mobility on wildlife activity (Ellis-Soto et al. 2023). However, there have been recent calls to examine how human societal factors may work in tandem with ecology to dictate animal movement and connectivity (Williamson et al. 2023; Wilkinson et al. 2024).

Societal factors that are relevant to urban wildlife extend beyond linear infrastructure and human activity and can include socioeconomics, values, perceptions, political preferences, and anthropogenic pollutants (Dickman 2010; Ditmer, Niemiec, et al. 2022; Murray et al. 2019). Previous research has explored how socioeconomic factors, such as 'luxury effects' (i.e., wealth; Hope et al. 2003) and 'legacy effects' (i.e., redlining; Wilson 2023) influence urban wildlife occupancy and biodiversity due to habitat heterogeneity linked to these effects (Leong et al. 2018; Magle et al. 2021; Schell et al. 2020). Wealth is a dominant predictor of urban black-tailed deer habitat selection due to preferences for landscape features linked to affluence (e.g., house size, green space access; Fisher et al. 2024). Chemical pollution, meanwhile, can alter wildlife movement and social behaviours (Bertram et al. 2022; Saaristo et al. 2018). Evidence also suggests that human perceptions and political leaning dictate wildlife landscape permeability, especially for controversial species (Ditmer, Wittemyer, et al. 2022; Sage et al. 2022; Wilkinson et al. 2024). Despite their importance, we have yet to determine whether integrating societally driven landscape features into animal movement models may yield a better understanding of wildlife decision-making than ecological models alone.

Incorporating societal factors, linear infrastructure and ecological factors together in animal movement models may yield a myriad of benefits. Such integrations may help us to better determine where human-wildlife interactions will most likely occur (Gonzalez-Crespo et al. 2023; Lischka et al. 2018) and to mitigate conflicts accordingly through improved urban design (Hwang and Jain 2021; Kay et al. 2022) and community engagement (Ceausu et al. 2018; Puri et al. 2024; Wilkinson, Caspi, et al. 2023). Recent work has noted that wildlife connectivity planning should consider societal, economic and institutional factors to develop the most effective and long-lasting wildlife connectivity practices (Williamson et al. 2023). Importantly, connectivity is key to fostering biodiversity even within urban areas (LaPoint et al. 2015), and sociocultural factors dictate whether cities may fulfil their potential contributions to biodiversity conservation (Aronson et al. 2017). Building societal factors into urban wildlife movement models can thus advance the transdisciplinary approaches needed to assure biodiverse, wildlife-inclusive cities (Kay et al. 2022; Lambert and Schell 2023).

The coyote (Canis latrans) is a behaviourally flexible carnivore that has expanded its range across North America over the last century (Hody and Kays 2018) and has been the subject of considerable publicity and debate (Draheim et al. 2019; Niesner et al. 2024). Coyotes may serve as bioindicators of urban ecological health, since their residence in highly developed areas and reliance on anthropogenic food correlate with stress and disease (Murray, Edwards, et al. 2015; Raymond et al. 2024; Robertson et al. 2023). Urban coyote movement also differs from their rural and wildland counterparts (Chamberlain et al. 2021; Chamberlain et al. 2000; Holzman et al. 1992; Way et al. 2004), with urban individuals occasionally demonstrating smaller home ranges and shorter travel distances. Further, urban coyotes show greater exploration and boldness relative to rural conspecifics (Breck et al. 2019). Their behavioural flexibility and ability to persist across development gradients (Grinder and Krausman 2001) make this species an ideal candidate for testing the efficacy of integrating societal, linear infrastructure and ecological factors to predict urban wildlife movement.

Here, we addressed the gap in social-ecological wildlife movement analysis using coyotes in Los Angeles County, California. Los Angeles encompasses dramatic gradients of wealth, green space availability and linear infrastructure density, providing an ideal location to test hypotheses oriented around social-ecological systems. We used a coyote movement data set to answer the following questions: (1) How are covote home ranges structured along heterogeneous social-ecological gradients? (2) Which factors best predict coyote movement patterns? and (3) How does coyote movement differ across varying levels of environmental health and vulnerability? We hypothesised that integrating societal (pollution burden, median income, population density, noise pollution, building density, development intensity), linear infrastructure (i.e., features known to serve as distinct barriers and/ or conduits for wildlife: road density, distance to flood channels, distance to railways) and ecological factors (vegetation greenness, distance to freshwater, distance to green spaces) would better predict coyote space use and movement than ecological factors alone (Figure 1), with our detailed hypotheses listed in Table 1.

2 | Methods

2.1 | Study Site

We conducted this study in Los Angeles County (>95% of the study area) and San Bernardino County, California (34.106357, -118.279013). Los Angeles County has a human population density of 952.5 people/km² (United States Census Bureau 2023). Natural spaces within the county are interspersed with intense urbanisation, major freeways and agricultural regions. Los Angeles County has a Mediterranean climate with the driest, hottest periods comprising May-October (i.e., 'drier season') and the coldest, wettest periods comprising November-April (i.e., 'wetter season'). Coyotes

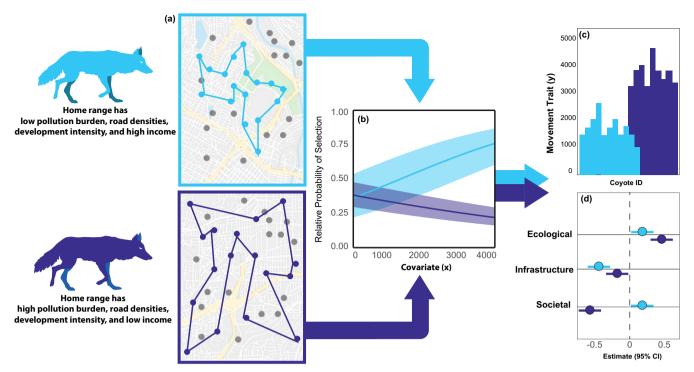


FIGURE 1 | Conceptual figure describing the hypothesised integrated effects of societal, linear infrastructure and ecological factors on urban coyote movement characteristics and habitat selection across differing levels of anthropogenic burden. Coyotes in more anthropogenically burdened regions (i.e., higher pollution burden, road densities, development intensity and lower income) are hypothesised to have larger home ranges (a) with increased movement metrics like daily displacement or step length (c). Individuals across anthropogenic burden gradients may also show divergent selection patterns (b) and strength (d) in response to environmental covariates, whereby more burdened individuals exhibit stronger selection for ecological variables and selection against societal covariates, relative to lower burdened conspecifics.

occur throughout most of the study area, though their county-level populations have not been empirically estimated.

2.2 | Data Collection

2.2.1 | GPS Collars

In October 2019, for a separate study that was later cancelled, we outfitted 20 coyotes (6 females and 14 males) with GPS collars (Ecotone, solar powered, GPS/GSM/UHF), which remained active between 1 and 23 months. All captured coyotes were collared with the intention of achieving an equal sex ratio over time; however, this was not possible. Fix rates varied across coyotes and ranged between 15 min and 2 h to extend collar battery life.

2.2.2 | GIS Data

Geospatial covariates for coyote movement models comprised ecological, linear infrastructure and human socioeconomic and environmental health (hereafter 'societal') variables. All geospatial covariates (see detailed sources in Table S1) were rasterised to 30 m² spatial resolution using ArcGIS Pro v 3.1.1 (ESRI 2023). For the ecological covariates, we considered (1) normalised difference vegetation index (NDVI) from spring 2021 (Landsat 8), (2) distance to rivers and streams (California Department of

Fish and Wildlife 2020), (3) distance to lakes (California State Geoportal 2021) and (4) distance to green spaces, including (a) county parks (County of Los Angeles 2022), (b) golf courses and (c) cemeteries (City of Los Angeles 2023). Importantly, in arid regions, green spaces will not always have a notable vegetation greenness signature.

For the linear infrastructure covariates, we considered (1) road density, (2) distance to storm and flood channels and drains (County of Los Angeles, 2023) and (3) distance to railways (California Rail Network 2022).

Finally, we considered the following societal covariates: (1) human population density (United States Census Bureau 2023), (2) building density (Dao 2020), (3) development intensity (National Land Cover Database (NLCD) 2019), (4) median income (County of Los Angeles, 2023), (5) noise pollution and (6) pollution burden percentile (Cal Enviro Screen 4.0). Population density and building density can describe different aspects of a city's population (i.e., population density is important in residential areas, while building density is relevant across zones). Development intensity was reclassified as 0 = no data, 1 = undeveloped land cover classes, 2 = developed: open space, 3 = developed: low intensity, 4 = developed: medium intensity and 5 = developed: high intensity. Cal Enviro Screen provides a pollution burden index that is calculated from 13 metrics related to drinking water characteristics, groundwater quality, air quality, soil pollutants and hazardous waste.

 TABLE 1
 Hypotheses regarding social-ecological predictors of landscape use and movement of urban coyotes (Canis latrans) in Los Angeles, California.

Question	Hypothesis	Justification
How are coyote home ranges structured along heterogeneous social-	Coyotes in more densely urbanized parts of the city have larger home ranges than those in less densely urbanized locations	Anthropogenic development can deplete prey or access to prey, leading to urban and peri-urban carnivores needing to range further to hunt and forage (Bateman and Fleming 2012; Leighton et al. 2021; Smith et al. 2016)
ecological gradients?	Coyotes whose ranges are adjacent to major highways have smaller home ranges than coyotes whose ranges are farther from major highways	Highways can pose major barriers to both urban and rural wildlife, preventing movement through wildlife fear and through wildlife deaths due to vehicles (Doherty et al. 2021; Murray and St. Clair 2015; Poessel et al. 2014)
	Coyotes that have more flood channels and storm drains within their home ranges have relatively larger home ranges	Flood channels, storm drains and easements for other linear infrastructure can serve as corridors for urban wildlife, increasing connectivity within urban spaces with these features (Fletcher 2009; Maclagan et al. 2019; Niesner et al. 2021)
	Coyotes living in more polluted areas have smaller home ranges than coyotes living in less polluted areas	 Urban pollutants contribute to wildlife stress and disease, which can potentially affect their mobility (Murray et al. 2019; Saaristo et al. 2018) More polluted, underserved regions may provide coyotes with more access to unsecured refuse and associated synanthropic prey animals such as rats (<i>Rattus</i> spp.) (Childs et al. 1991; Dyer et al. 2023; Murray et al. 2024; Promkerd et al. 2008; Traweger et al. 2006) Chemical pollution has been linked to alterations in wildlife behaviours and movement (Bertram et al. 2022; Saaristo et al. 2018)
Which factors—societal, linear infrastructure, ecological or a combination of these—are the best predictors of coyote movement patterns?	Urban coyote movement is best predicted by a combination of societal, linear infrastructure, and ecological variables.	 Human societal factors, such as wealth, perceptions, population density and development intensity, can have cascading impacts on ecology and wildlife landscape use (Aznarez et al. 2023; Ditmer, Niemiec, et al. 2022, Ditmer, Wittemyer, et al. 2022; Ghoddousi et al. 2021; Leong et al. 2018; Magle et al. 2022, Ditmer, Wittemyer, et al. 2022; Ghoddousi et al. 2007) Anthropogenic pollutants, such as environmental pollution and noise pollution, can impact wildlife behaviour, stress, illness and survival (Berkhout et al. 2023; Ditchkoff et al. 2006; Shannon et al. 2015) Linear infrastructure, such as roads, fences, railway easements and flood channels, can serve as barriers or habitats to wildlife or can facilitate movement (Barrientos et al. 2019; Doherty et al. 2021; Fletcher 2009; Hill et al. 2020; Maclagan et al. 2019; Murray and St. Clair 2015; Niesner et al. 2021; Poessel et al. 2014; Popp and Hamr 2018) Despite relatively less 'natural' coyote habitat available in cities versus rural areas, coyotes have been known to den in and generally favour urban green spaces such as parks, cemeteries and golf courses and also seek out urban water sources as a primary need (Baker and Timm 1998; Grubbs and Krausman 2009; Wurth et al. 2020)
	Coyotes on the urban-wildland interface are more likely to select for neighborhoods with higher annual median income	There are preferable ecological resources, such as increased tree cover and more access to green spaces, associated with urban high-income locations; these influence biodiversity and animal movement (Chamberlain et al. 2020; Fisher et al. 2024; Leong et al. 2018; Schell et al. 2020)
		(Continued

TABLE 1 | (Continued)

1. Lower-income areas are more likely than high-income areas to experience a lack of access to quality Linear infrastructure can serve to facilitate wildlife movement through human-dominated landscapes municipal services (i.e., Feigenbaum and Hall 2015), meaning unsecured refuse may be more common synanthropic wildlife that constitute coyote prey, such as rats (Rattus spp.) and raccoons (Procyon spp.) 2. Lower-income urban areas are more likely than high-income areas to have higher densities of (Clarke et al. 2006; Fletcher 2009; Maclagan et al. 2019; Niesner et al. 2021; Popp and Hamr 2018) 2. Urbanisation is correlated with lower quantity and quality of wildlife habitat (Liu et al. 2016) due to access to waste (Bozek et al. 2007; Childs et al. 1991; Dyer et al. 2023; Murray et al. 2024) 1. Both urban and rural coyotes tend to spatiotemporally avoid people (Gehrt et al. 2009; Wang Anthropogenic pollutants affect wildlife stress, behaviour and health (Berkhout et al. 2023; Ditchkoff et al. 2006; Shannon et al. 2015) and are linked to lower habitat quality and resource availability (Scanes 2018) (Sprague et al. 2022) Justification et al. 2015) with lower levels of environmental pollutants Within their home ranges, coyotes use areas Coyotes in densely populated urban areas are less likely to select for neighborhoods for regions with lower population density Within their home ranges, coyotes select Within their home ranges, coyotes select with higher annual median income for flood channels and railways Hypothesis Question

2.3 | Analyses

2.3.1 | Home Ranges and Movement Characteristics

Relevant spatial covariates were summarised at the home range level for each coyote using ArcGIS Prov.3.1.1 (ESRI 2023), and statistical analyses were conducted in R v.4.3.2 (R Core Team 2023). Using the 'adehabitatHR' package, we determined the 50% (core range) and 95% kernel utilisation distribution (KUD) for each coyote and calculated their home range sizes per level. We calculated mean NDVI, pollution burden, median income, road density, development intensity and human population density for each home range and used linear regressions and Mann-Whitney U tests to determine relationships between home range size and socialecological landscape characteristics, including comparing means across levels of anthropogenic burden (i.e., higher vs. lower NDVI, development intensity, median income, pollution burden, population density, development intensity and road density).

To understand the relationship between social-ecological landscape covariates and covote movement characteristics, we used Wilcoxon rank-sum tests to compare means for two key movement metrics-mean daily displacement and step length-across sex, across season and across lower vs. higher anthropogenic burden.

2.3.2 | Resource Selection

To examine coyotes' landscape feature selection, we derived resource selection functions (RSFs) using the 'lme4' package. To reduce autocorrelation, we rarified data to 2-h fixes for a total of 93,670 fixes and generated random points within 95% KUD home ranges, with generated 'available' points equaling three times the number of GPS fixes within each coyote's home range. We tested for collinearity among the covariates using the vif function in the 'car' package (Fox et al. 2007). Using the 'raster' package and base R, we centred and scaled covariates (mean = 0, SD = 1) to facilitate interpretability and model convergence. We assessed resource selection using generalised linear mixed effects models with a logit link, with coyote identity as a random effect to control for individual variation in behaviours (Gillies et al. 2006). We tested the following models: (1) a global model, (2) a model containing only societal covariates, (3) a model containing only ecological covariates and (4) a model containing only linear infrastructure covariates. Data were analysed in aggregate and also subset into the following groups, as indicators of potential anthropogenic burden on coyotes: (1) coyotes with less polluted and more polluted (more burdened) home ranges (i.e., below or above the 50th percentile), (2) coyotes with home ranges consisting of lower or higher (more burdened) human populations than the average across all coyote home ranges and (3) coyotes with home ranges in wealthier or less wealthy (more burdened) regions than the average across all coyote home ranges. We used Akaike's Information Criterion (AIC) to determine the best-performing models (Burnham and Anderson 2002).

2.3.3 | Step-Level Selection

To understand how coyotes move in relation to landscape features at the step scale, we derived step selection functions

(SSFs) using the 'amt' (Signer et al. 2019) and 'survival' packages (Therneau 2015). After creating tracks from the data using the mk_track function, we thinned the data to 2-h fixes for a total of 33,378 steps (mean step length = 414.9 m) and filtered the data so bursts would have at least 3 points (Signer et al. 2019). We chose 2-h fixes since only a smaller subset of our sample individuals had finer fixes available. We generated five random steps per used step using the random_steps function, which uses a gamma distribution fitted to the entire dataset to derive step lengths and derives turn angles from a von Mises distribution (Thurfjell et al. 2014). Covariate scaling and model comparisons reflect our RSF analyses, though for SSFs, we only conducted a global model across all coyotes. To reduce autocorrelation, we used individual coyotes as a cluster term, following the 20 minimum clusters recommended by Prima et al. (2017) and reported on robust standard errors (Nisi et al. 2021; Prima et al. 2017; Roever et al. 2010; Suraci et al. 2020). We estimated coefficients by fitting conditional logistic regressions on covariates. We considered the log of step length (i.e., speed of movement) and cosine of the turning angle (i.e., directionality of movement) as interaction terms with linear infrastructure since linear infrastructure can influence carnivore behavioural states (Abrahms et al. 2016; Thorsen et al. 2022), and with NDVI since we expected coyotes to move more cautiously in places with less vegetative cover. We used the quasi-likelihood independence model criterion (QIC) to determine the best-supported models.

3 | Results

3.1 | Home Range and Movement Characteristics

The mean 95% KUD home range size (Figure 2) was $26.12 \,\mathrm{km^2}$ (95% CI = 13.04, 38.96) and the mean 50% KUD home range size was $4.56 \,\mathrm{km^2}$ (2.11, 6.65) (Table S2). Home ranges with

higher pollution burden were larger than home ranges with lower pollution burden (Figure 3a, Table S4). Human population density was positively correlated with core (50%) home range size (β =0.173, p<0.0001, R^2 =0.94). NDVI was marginally negatively correlated with core home range size (β =-0.002, p=0.001, R^2 =0.14). Road density, income and development intensity were not significantly correlated with home range size.

Home ranges with higher pollution burden had lower mean NDVI and income and higher mean road density, population density and development intensity (Table S2). Males' home ranges had higher mean pollution burden, road density, human population density, development intensity and parks access than did females' (Tables S2 and S3).

Movement characteristics demonstrated impacts of landscape vulnerability on coyote movement (Figure 3; Figure S1). Mean coyote step length was significantly higher during the drier season and for coyotes with home ranges in regions of lower NDVI, lower income, higher population density, higher road density and higher development intensity (Figure 3d, Table S5). There was no significant difference in step length across sex and pollution burden. Mean daily displacement was greater for females and for coyotes in regions of lower NDVI, lower income, higher road density, higher population density, higher pollution burden and higher development intensity.

3.2 | Resource Selection

When assessing multicollinearity among our spatial covariates (Table S6), we found that noise pollution and road density were highly correlated (>0.7) and thus removed noise pollution from our models since roads are ecologically important as both

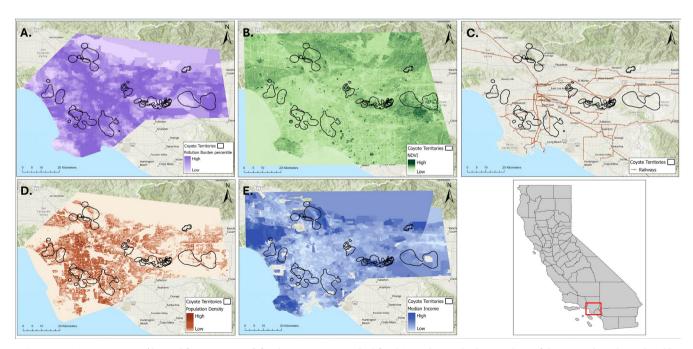


FIGURE 2 | Home ranges (derived from 95% KUD) for the 20 coyotes tracked for this study, overlaid on a subset of the societal, ecological and linear infrastructure covariates considered. The example covariates included here are (a) pollution burden, (b) normalised difference vegetation index (NDVI), (c) railways, (d) population density and (e) median income.

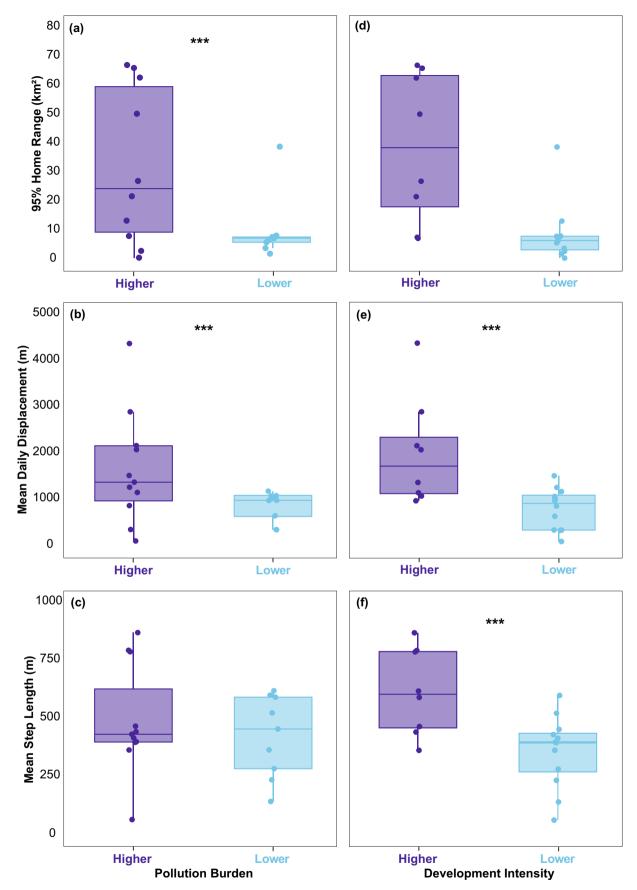


FIGURE 3 | Legend on next page.

FIGURE 3 | Box plots demonstrating coyote home range sizes, mean daily displacement and mean step lengths across levels of anthropogenic burden (higher and lower pollution burden and development intensity), for 20 coyotes tracked in Los Angeles and San Bernardino Counties from 2019 to 2021. Higher pollution burden is calculated as having a 95% kernel utilisation distribution (KUD) home range with a mean pollution burden above the 50th percentile. Higher population density is calculated as having a 95% KUD home range with a mean population density that is above the average for our sample.

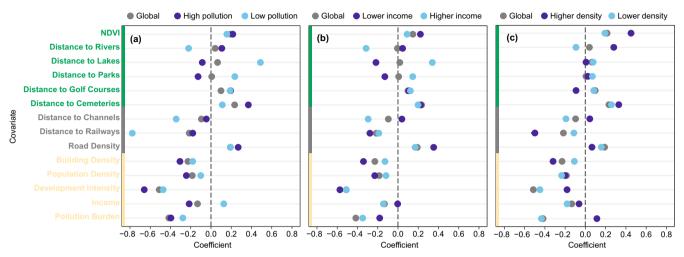


FIGURE 4 | Results from resource selection function random effects models including all covariates for (a) coyotes living in regions of higher or lower pollution burden, (b) coyotes living in regions of higher and lower median income and (c) coyotes living in regions of higher and lower human population densities compared to the estimates from the global model including all sampled coyotes. Ecological covariates are colour-coded green, linear infrastructure covariates are grey, and societal covariates are yellow. 95% confidence intervals were included yet smaller than the coefficient markers and are thus not visible.

barriers and attractants for mammalian carnivores (Poessel et al. 2014).

3.2.1 | Resource Selection for all Sampled Coyotes

The best-performing global models ($\Delta AIC \le 2$) included (1) all covariates and (2) all covariates except distance to cemeteries (Table S7). In the random effects model, including all covariates (Figure 4), coyotes exhibited strong selection for NDVI, road density, rivers, flood channels and railways and against income, building density, population density, lakes, golf courses, cemeteries and development intensity. Of these, the most pronounced effects were selection for railways (β =-0.212, 95% CI=-0.232: -0.192, p<0.0001) and road density (β =0.195, 0.176:0.212, p<0.0001) and against development intensity (β =-0.504, -0.517:-0.491, p<0.0001) and pollution burden (β =-0.412, -0.428: -0.397, p<0.0001).

3.2.2 \mid Resource Selection for Highly Burdened vs. Less Burdened Coyotes

Coyotes with home ranges in locations of higher pollution burden selected against higher income locations and rivers and selected for parks and lakes, while less-burdened coyotes showed the opposite patterns (Figures 4a, 5, Table S7). Selection against human population density, development intensity and pollution burden was stronger for more burdened coyotes, with weaker selection for flood channels and railways compared with less burdened coyotes.

Coyotes with home ranges in locations of lower (i.e., more burdened) median income selected for parks and lakes and selected against rivers and channels, whereas less-burdened coyotes showed opposing patterns (Figures 4b, 5, Table S7). More burdened coyotes also demonstrated stronger selection for NDVI, railways and road density; stronger selection against building density and weaker selection against pollution burden relative to burdened coyotes.

Coyotes with home ranges in locations of higher (i.e., more burdened) human population density selected against rivers and flood channels and selected for golf courses and pollution burden, whereas less-burdened individuals showed the opposite patterns (Figures 4c, 5, Table S7). Selection for NDVI and railways and against building density was stronger for burdened coyotes, with weaker selection against development intensity and median income relative to less-burdened coyotes.

Across all data subsets (including the full data set), the societal model always performed the best among the partitioned ecological, societal and linear infrastructure models (Table S8).

3.3 | Step Selection

The best-performing SSF models included three interaction terms: median income: log(step length), NDVI:log(step length) and development intensity: cosine(turn angle), which we retained for the global model. The most influential covariates within the global model were development intensity (relative

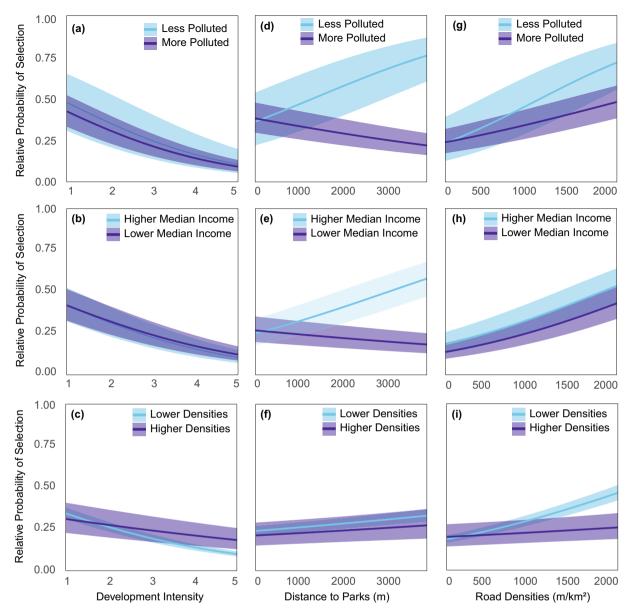


FIGURE 5 | Relative probability of selection for three variables: Development intensity (a-c), distance to parks (d-f), and road density (g-i) for coyotes with home ranges in locations of higher and lower pollution burden (a, d, g), median income (b, e, h) and population density (c, f, i), as derived from resource selection function models.

importance=0.18), pollution burden (0.15) and distance to golf courses (0.09). The global model with interaction terms (Table S9) showed strong selection against pollution burden (β =-0.357, 95% CI=-0.692: -0.022, p=0.037), building density (β =-0.185, -0.289: -0.081, p=0.0004), population density (β =-0.160, -0.268: -0.052, p=0.004) and development intensity (β =-0.434, -0.565: -0.303, p<0.0001). Coyotes' steps were longer in areas with higher NDVI (β =0.032, 0.007:0.057, p=0.012) and shorter in areas with higher median income (β =-0.022, -0.04: -0.004, p=0.022).

4 | Discussion

Our study demonstrated that movements and habitat selection by urban coyotes can best be described by a combination of societal and ecological factors. This runs contrary to prior movement studies that have solely examined ecological landscape features and aligns well with recent studies suggesting that we should consider societal elements when examining and planning for wildlife landscape permeability, connectivity and restoration (Ghoddousi et al. 2021; Williamson et al. 2023; Wilkinson et al. 2024).

4.1 | Home Range and Movement Characteristics

Our analysis of home range and movement characteristics confirmed the influence of anthropogenic burden on urban coyotes. Coyotes living in more polluted, densely populated areas had significantly larger home ranges. Of all measures of burden, human population density was the strongest predictor of coyote home range size. The latter aligns with previous findings that coyote occupancy and behaviour are influenced

by human presence and activity (Gallo et al. 2022; Gehrt et al. 2009; Murray and St. Clair 2015; Nickel et al. 2020). Meanwhile, urban wildlife in more polluted areas may experience more dispersed resources and frequent disturbances (Murray et al. 2019; Soulsbury and White 2015). Daily displacement, a measure of exploration (e.g., Hertel et al. 2019), was significantly higher for coyotes in more burdened areas (i.e., regions of lower NDVI, lower income, and higher population density, pollution burden, development intensity and road density). Mean step length followed the same pattern, with the addition of significantly longer step lengths during the drier season, though the latter difference was small. However, coyotes travelling longer distances per step in the drier season support evidence demonstrating seasonal variation in covote movement due to altered resource availability (Bateman and Fleming 2012; Poessel et al. 2017). Larger home ranges, displacement values and step lengths suggest higher energetic demands for coyotes in more burdened environments. Consuming more human subsidies may be a coping strategy to deal with increased energetic costs, though there may be trade-offs, such as ingesting foods with lower nutritional value or bringing individuals into conflict with people (Murray, Cembrowski, et al. 2015; Murray and St. Clair 2017). Future research quantifying the energetic costs of individuals across social-ecological gradients may provide insight into how divergent stable behavioural strategies can be locally adapted.

4.2 | The Relative Influence of Societal, Infrastructural and Ecological Covariates on Coyote Movement

Overall, models containing only societal covariates tended to perform better than models containing only ecological and linear infrastructure covariates. Urban features linked to societal characteristics, such as pollution, wealth and human population density, thus may be key predictors for urban wildlife movement. This finding builds upon existing evidence of the influences of these societally driven features on wildlife biodiversity, occupancy and survival (Leong et al. 2018; Magle et al. 2021; Saaristo et al. 2018). Additionally, across all data subsets, models that integrated societal, ecological and infrastructural characteristics performed better than siloed models. Together, these findings provide some of the first empirical evidence to support recent frameworks proposing the importance of considering social–ecological landscape suitability for wildlife connectivity (Ghoddousi et al. 2021; Williamson et al. 2023).

4.3 | Social-Ecological Predictors of Coyote Resource and Step Selection

4.3.1 | Selection by all Sampled Coyotes

Across all movement metrics and data subsets, development intensity was the most influential covariate for coyote habitat selection and movement. Overall, coyotes selected for vegetation greenness, road density, rivers, flood channels and railways. Coyotes selected against income, building density, population density, pollution burden, development intensity, lakes, golf courses and cemeteries. The latter two, along with relatively

lower selection for parks in our model, run counter to studies that have shown coyotes and other urban wildlife select for large urban green spaces (Wurth et al. 2020), though this tendency may be reflected in our coyotes' selection for vegetation greenness and railways. In arid regions (e.g., southern California), not all parks are vegetatively green. Additionally, urban spaces can contain many small, ungazetted vegetated areas along with potential habitats alongside railways and rivers (Douglas 2020). However, within our step-selection models, golf courses emerged as an important covariate, indicating potential fine-scale movement preferences towards golf courses, even if coyotes in our study spend relatively little time within these spaces.

Paradoxically, selection for road density and against development intensity showed the strongest effects (Figure 4). While high development intensity is often correlated with more human presence and disturbance for wildlife (i.e., Lendrum et al. 2017), roads may have more nuanced impacts on wildlife by allowing them to move more easily through complex landscapes (Abrahms et al. 2016; Hill et al. 2020). Road-dense areas may also be associated with key resource opportunities, such as roadkill and roadside habitat patches that potentially harbour mammalian prey (e.g., Bellamy et al. 2001; Kent et al. 2021; Meunier et al. 1999).

Contrary to our hypotheses, coyotes select against wealthier areas and move more slowly in less wealthy areas. While wealthier urban areas may have preferable ecological resources like natural prey items and refugia (Leong et al. 2018; Schell et al. 2020), wealthier neighbourhoods also tend to harbour more unfavourable and separationist views on coyotes than others (Niesner et al. 2024; Wilkinson, Caspi, et al. 2023). Covote encounters, human-covote conflicts, hazing and support for lethal control of coyotes have all been found to be more likely in wealthier areas (Draheim et al. 2019; Wilkinson, Caspi, et al. 2023; Wine et al. 2015). Additionally, under California state law, residents can hire a trapper to remove coyotes from their communities, which is not uncommon in southern California. Combined with the wealth-linked tendency towards coyote intolerance, the high costs of hiring a trapper (N. Quinn, pers. comm.) may mean that coyotes are being more frequently trapped in wealthier areas, potentially influencing coyote habitat selection.

4.3.2 | Differences Between More Burdened and Less Burdened Home Ranges

The degree of anthropogenic burden altered habitat selection. Coyotes with more burdened home ranges demonstrated stronger selection against population density, building density, and development. Coyotes in more burdened regions may be more acutely affected by these societal factors, influencing the strength of selection against these features. Unexpectedly, coyotes living in locations of higher human population densities selected for higher pollution burden, and for those living in lower-income areas, selection against pollution burden was weaker than in higher-income areas. In lower-income areas, unsecured refuse may be more common due to reduced quality and quantity of municipal services (Sprague et al. 2022). Underserved regions that are subject to higher pollution burden may also have higher populations of synanthropic rodents and

other prey (Childs et al. 1991; Murray et al. 2024). Additionally, in Los Angeles, higher population densities are correlated with increased trash generation (Liang et al. 2019). Human refuse, synanthropic rodents and outdoor cats are coyote attractants, especially in urban areas where native wild prey may be less accessible (Baker and Timm 1998; Bucklin et al. 2023; Poessel et al. 2017; Sugden et al. 2021).

All burdened coyotes exhibited stronger selection for more vegetated areas (i.e., higher NDVI) and for road densities than did less burdened coyotes. Coyotes in lower-income and more populationdense locations also selected more strongly for railways than did their less-burdened counterparts. Though roads may operate as dispersal and movement barriers for wildlife (Riley et al. 2003), roads, railways and other linear infrastructure may also provide habitat and connectivity for wildlife living in urban and periurban spaces (Barrientos et al. 2019; Fletcher 2009; Maclagan et al. 2019). Our study indicates that vegetated habitat, roads and railways may be particularly important for urban coyotes in places that are more anthropogenically burdened and provides further evidence regarding the diverse effects of societally driven risks and burdens on urban wildlife (e.g., Murray et al. 2019; Schell et al. 2020). These results also point to the potential disproportionate impact of linear infrastructure for improving wildlife landscape permeability in more burdened or complex contexts (Niesner et al. 2021; Popp and Hamr 2018).

Diverging from our global results, coyotes with more polluted home ranges and those with more highly populated home ranges selected for parks, unlike less-burdened coyotes. Because public parks often contain concentrated resources such as potential den sites and prey, urban coyotes are known to frequent public parks regardless of the human activities within (Gehrt et al. 2013; Wilkinson, Caspi, et al. 2023). Coupled with our broader results showing that coyotes typically selected against golf courses and cemeteries, it is possible that coyotes living in more burdened regions are more willing to spend time in parks despite the risks of human activity. Parks may differ from golf courses and cemeteries in two key ways. First, while parks vary in spatiotemporal patterns of human activity, golf courses and cemeteries have constant, predictable human activity due to visitors and staff. Golf courses and cemeteries are also consistently maintained, including landscaping choices that may thin any available bushy vegetation which coyotes can use for cover (i.e., Nooten et al. 2018). Finally, due to variations in management and use, parks are more likely to contain persistent potential anthropogenic resources (i.e., trash) that could be attractive to coyotes and their prey (Sugden et al. 2021). Anthropogenic food removal by urban wildlife in parks also positively correlates with vegetation cover (Morales-Vasquez et al. 2018), which coyotes strongly selected for across all models. Coyotes tend to spatiotemporally partition themselves from human activity (Murray and St. Clair 2015), so in Los Angeles they are likely avoiding exposure to people by also prioritising non-gazetted green spaces, as mentioned earlier.

4.3.3 | Urban Complexity and Coyote Movement

To contextualise our results, it is important to consider that some of the coyote movements we observed may reflect decision-making at a finer spatial scale than our analysis could capture. For example, societal covariates such as pollution burden and income were collected at the census tract level, and our movement data were also collected at an intermediate scale. Further, cities are highly complex landscapes, likely requiring urban coyotes—and other urban wildlife—to thread the needle by selectively navigating areas that minimise risk while capitalising on accessible resources, both anthropogenic and natural. Future research should focus on fine-scale wildlife movement in relation to the myriad localised attractants, deterrents and barriers present in cities to fully understand the nuanced decisions made by urban wildlife in these complex environments.

4.4 | Utility of These Approaches for Improved Urban Wildlife Ecology and Management

Most prior studies regarding the effects of within-city social-ecological heterogeneity on wildlife have focused on species distribution and biodiversity (Magle et al. 2016) and non-linear infrastructure (Haight et al. 2023), leaving a significant gap in our understanding of wildlife movements through these societally driven landscapes. Though behaviourally flexible species can successfully live alongside people, these resilient species may exhibit key across- and within-population divergences in their responses to anthropogenic risks and rewards on the landscape (Breck et al. 2019; Murray and St. Clair 2015; Wilkinson et al. 2024). Our study demonstrates that environmental health, wealth and linear infrastructure are key predictors of urban coyote movement and habitat selection. Further, the effects of these features on coyotes differ depending on variations in the city's social–ecological gradient.

Future studies should make it standard practice to assess the relative importance of societal covariates on wildlife landscape permeability, particularly for wildlife that are more likely to interact with or live alongside people. Social-ecological modelling should reflect species' unique interactions with human-altered environments. For instance, while urban-adapted covotes in our study respond strongly to pollution and development intensity, other species, such as large carnivores in less urbanised settings, may require different societal predictors (e.g., hunting prevalence or political attitudes toward rewilding efforts). Such flexible approaches are especially pressing considering the global spatial overlap of people and wildlife is projected to significantly increase by 2070 due to the intensification of human population densities (Ma et al. 2024). Similarly, scientists and wildlife managers are also increasingly concerned about climate change exacerbating human-wildlife conflicts through societal and ecological pathways (Abrahms et al. 2023). Finally, our study has demonstrated the nuanced influence of linear infrastructure on urban coyotes, confirming previous anecdotal evidence that coyotes utilise linear features for traversing and surviving within urban landscapes (Fletcher 2009; Niesner et al. 2021). In the future, it will be key to reimagine conservation perspectives regarding the potentially positive roles of linear infrastructure for wildlife landscape permeability, especially in places of higher anthropogenic development (Douglas 2020; McInturff et al. 2020; Niesner et al. 2021; Wilkinson, Jones, et al. 2023). Overall, with increasing data availability and collaborative capacity, these integrated approaches will provide the nuanced information needed to design healthy, equitable shared landscapes in an urbanising world.

Author Contributions

C.E.W. conceived the ideas, designed methodology, led analyses and visualisations and led writing. N.Q. coordinated and provided resources for field research, which was aided substantially by C.E. C.J.S. aided in conceiving ideas, aided in creating visualisations and contributed to revisions. All authors discussed, edited and approved the final version.

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Data Availability Statement

Data, metadata and R Code necessary to reproduce model results, analyses and figures are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.15dv41p5j) and Zenodo (https://doi.org/10.5281/zenodo.14597737). See the 'Description of the data and file structure' section of the associated metadata for a full list of data sources.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.