

## Research article

### Home range and core area characteristics of urban and rural coyotes and red foxes in southern Wisconsin

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#### Wildlife Biology

2024: e01321

doi: [10.1002/wlb3.01321](https://doi.org/10.1002/wlb3.01321)

Subject Editor:

Jean-Francois Robitaille

Editor-in-Chief: Ilse Storch

Accepted 14 October 2024



Second-order habitat selection is influenced by a variety of factors, including individual- and species-specific traits and resource requirements, as well as landscape characteristics. By comparing home range characteristics across individuals, species, and landscapes, we can draw conclusions regarding whether and how different factors influence home range selection. Our objectives were to quantify home range characteristics of VHF- and GPS-collared coyotes and red foxes in urban and rural areas of southern Wisconsin, including home range size and shape, home range stability, and inter- and intraspecific overlap. On average, urban coyotes had smaller home ranges with apparently greater intraspecific overlap between neighboring individuals than rural coyotes. Similarly, urban red foxes had smaller home ranges with apparently greater intraspecific overlap between neighboring individuals than urban coyotes. We found no difference in home range boundary complexity or stability between urban coyotes and red foxes or between urban and rural coyotes. We did identify greater interspecific overlap between urban coyotes and red foxes than has been previously reported. Our results provide further evidence that intrinsic and extrinsic factors, such as species characteristics, resource predictability and availability, and the physical environment, influence home range selection of coyotes and red foxes.

Keywords: *Canis latrans*, core area, home range, perimeter–area ratio, spatial overlap, *Vulpes vulpes*

#### Introduction

Many factors, including individual- and species-specific traits and resource requirements, as well as landscape characteristics, influence second order habitat selection (i.e. home range selection) of wildlife species (Walton et al. 2017, Ofstad et al. 2019, Dickie et al. 2022). By establishing a home range, or an area used by an individual for resource acquisition, mating, and raising young, individuals learn where and when resources and risks occur by continuously updating their cognitive maps, to allow



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optimization of energy and reproduction and likely increase individual fitness (Powell and Mitchell 2012). The idea of home range selection as an opportunity to optimize benefits while reducing costs applies in both urban and non-urban landscapes despite vastly different landscape characteristics (O'Donnell and delBarco-Trillo 2020). Identifying intrinsic or extrinsic factors that influence wildlife home range selection in urban and rural areas provides a fundamental understanding of wildlife behavior and niche breadth in areas with different physical characteristics and varying human population densities.

Home range characteristics, such as size, shape, stability, inter- and intrasexual overlap, and inter- and intraspecific overlap, are a result of optimization, which often is influenced by resource availability and distribution (Nelson et al. 2007, Bino et al. 2010, Duncan et al. 2015). In resource rich areas, home range sizes tend to be smaller because less area is required to meet an individual's nutritional requirements (Prange et al. 2004, Walton et al. 2017). Similarly, inter- and intrasexual and inter- and intraspecific overlap will likely be greater in resource rich areas due to decreased territoriality or species clumping (Doncaster and Macdonald 1991, Atwood and Weeks 2003, Prange et al. 2004, Ruprecht et al. 2021). Further, resource predictability or homogeneity can result in stable home ranges as individuals need not shift their space-use to follow seasonal resources or in more circular home ranges, which are the most energetically efficient home range shape in terms of travel and defense costs (Ables 1969, Prange et al. 2004). Resource availability and distribution, as well as the physical environment, can influence home range characteristics. Land cover and use can constrain the shape of home ranges and may promote home range stability if features serve as barriers that prevent or deter movement, such as with some roads (Doncaster and Macdonald 1991).

Species that colonize urban areas tend to be behaviorally flexible, which allows them to take advantage of the benefits of urban habitat (Bateman and Fleming 2012). Resources such as food and water have relatively greater availability and predictability in urban areas (Bateman and Fleming 2012, Evans and Gawlik 2020, Hansen et al. 2020), and urban areas have increased heterogeneity in land cover and use (Angel et al. 2012, Zipperer et al. 2012). These factors, in addition to the presence of humans, can contribute to the variety of differences between urban and non-urban populations (Gaynor et al. 2018, O'Donnell and delBarco-Trillo 2020, Ritzel and Gallo 2020). For example, coyotes *Canis latrans* and red foxes *Vulpes vulpes* successfully establish home ranges from rural to urban areas, likely due to generalist tendencies and behavioral flexibility (Gehrt et al. 2010, Bateman and Fleming 2012). Typically, overlap between coyotes and red foxes in non-urban areas is generally low, and red fox home ranges are often situated between or along the boundaries of coyote home ranges and rarely overlap with the core areas of coyote ranges (Major and Sherburne 1987, Sargeant et al. 1987, Harrison et al. 1989). However, despite urban coyotes and red foxes selecting for different land cover types, there can be greater interspecific overlap between

coyotes and foxes in urban areas than expected compared to competitive interactions between rural coyotes and red foxes (Mueller et al. 2018).

Urban coyotes have smaller average home ranges than their rural counterparts, though coyote home range sizes in both urban and rural areas vary widely, as values from 1.1 km<sup>2</sup> (100% minimum convex polygon – MCP) (Turner et al. 2011) to 634 km<sup>2</sup> (95% MCP) (Mosnier et al. 2008) have been reported (Atwood et al. 2004, Gehrt and McGraw 2007, Šálek et al. 2015). There is minimal consistency in how researchers define seasonal home ranges and no study to our knowledge has compared seasonal home ranges of urban and rural coyotes. In general, however, home ranges for coyotes tend to be smaller during spring and summer while caring for young and larger during fall and winter during the breeding season (Bowen 1982, Springer 1982, Person and Hirth 1991, Kitchen et al. 1999, Gehrt and Prange 2007, Gese et al. 2012, Mueller et al. 2018). Resource distribution as well as land cover and use can affect urban coyote home range shape (Gehrt et al. 2009), though little is known about factors influencing home range shape of rural coyotes. Coyotes can exhibit flexible sociality, so inter- and intrasexual and intraspecific home range overlap varies widely, including across seasons; however, there is some evidence of higher overlap in urban populations (Chamberlain et al. 2000, Moorcroft et al. 2006, Webster et al. 2022). Typically, mated pairs of coyotes have higher spatial overlap than non-mated pairs (Schrecengost et al. 2009, Hennessy et al. 2012).

Similar to the differences between urban and rural coyotes, urban red foxes have smaller home ranges than rural red foxes (Šálek et al. 2015, O'Donnell and delBarco-Trillo 2020), and, in general, the average annual red fox home range size can extend from 0.1 km<sup>2</sup> (75% harmonic mean) (White et al. 2006) to 44.6 km<sup>2</sup> (95% MCP) (Towerton et al. 2016). Unlike coyotes, there is no clear trend for fluctuations in red fox home range size across calendar seasons, and minimal information on home range size based on biological seasons (Cavallini 1996, Saunders et al. 2002, Van Etten et al. 2007, Holmala and Kauhala 2009, Rosatte and Allan 2009, Drygala and Zoller 2013, Mueller et al. 2018), and currently, little is known about the factors affecting red fox home range shape. The topography of urban red fox home ranges (i.e. their location relative to each other) can be stable even across generations; however, the spatial location of the home ranges may drift continuously while it is unknown whether rural red fox home ranges exhibit drift (Doncaster and Macdonald 1991, Adkins and Stott 1998). Like coyotes, red foxes can exhibit flexible sociality and wide variation in inter- and intrasexual and intraspecific home range overlap with higher overlap in urban populations (Adkins and Stott 1998, Macdonald et al. 1999, Gosselink 2002).

Our objectives were to quantify home range characteristics of coyotes and red foxes in southern Wisconsin, including home range size and shape, home range stability, and inter- and intraspecific overlap in addition to modeling coyote home range and core area size to compare urban and rural populations. If coyotes and red foxes adhere to optimal

foraging theory and home range characteristics are dependent on resource availability, the physical environment, and minimizing aggressive encounters with conspecifics, we expected urban coyotes to have less circular home ranges with greater intraspecific overlap and home range stability than non-urban coyotes. Similarly, we expected urban red foxes to have smaller and less circular home ranges with greater intraspecific overlap and greater home range stability than urban coyotes or reported values for non-urban red foxes (Ables 1969). Due to the abundance and predictability of resources in urban areas, we predicted that urban coyotes and red foxes would have greater interspecific overlap than expected based on current canid interaction literature. Finally, we predicted that home range size and core area would be smaller in urban relative to rural coyotes and that sex would not influence home range or core area size (Henry et al. 2005, Drygala and Zoller 2013, Poessel et al. 2016).

## Material and methods

### Study area

Our urban study area included the city of Madison, Wisconsin (USA) and surrounding contiguous suburbs (Fig. 1a, b). Madison, located in Dane County, Wisconsin, had an estimated population of 259 680 people (2019, US Census) and a population density of 988 people per square kilometer. Madison was comprised of a mosaic of residential and commercial properties along with the University of Wisconsin – Madison campus and a multitude of variably sized public natural areas. These public areas ranged from small, manicured neighborhood parks (i.e. period gardens, 0.001 km<sup>2</sup>) to large, natural preserves (i.e. University of Wisconsin arboretum, approximately 5 km<sup>2</sup>). Available habitats aside from urban development included oak savanna, upland broadleaf deciduous forest, restored tallgrass prairie, planted coniferous forest, and wetlands (Mueller et al. 2019).

Our rural study area included Iowa County, Wisconsin, where coyote captures occurred, and several surrounding counties, where many coyotes dispersed and established home ranges (Fig. 1c). Iowa County was directly west of Dane County, with an estimated population of 23 678 (2019, US Census) and a population density of 12 people per square kilometer. The study area included various villages, towns, and unincorporated communities, was primarily rural and consisted mostly of privately owned land. Public lands included state parks, such as Blue Mound State Park (6.34 km<sup>2</sup>) and Governor Dodge State Park (21.33 km<sup>2</sup>), as well as several Natural Areas and County Parks. Available habitats included forest, mostly consisting of broad-leaved deciduous forest, agriculture, mostly consisting of corn and soybean crop rotation, and grassland, including forage and idle grassland.

Wisconsin had a humid continental climate with warm, humid summers and cold, snowy winters (1991–2020). During summer (June, July, and August) in Madison, temperatures averaged 21°C, with an average minimum

temperature of 15.2°C and an average maximum temperature of 26.9°C. Monthly precipitation during summer averaged 12.3 cm. During winter (December, January, and February), the temperature averaged –5.3°C, with an average minimum temperature of –9.8°C and an average maximum temperature of –0.7°C. Precipitation typically fell as snow during winter and averaged 4.6 cm per month (Wisconsin State Climatology Office 2020).

### Data collection – urban study area

We captured and placed very high frequency (VHF) or global positioning system (GPS) collars on urban coyotes and red foxes beginning with a pilot study in 2014 as part of the University of Wisconsin Urban Canid Project (UCP). We captured coyotes and red foxes in our urban study area annually between October and March using cable restraints while following trapping best management practices (Mueller et al. 2018).

We selected trap sites based on landscape characteristics, such as greenspace and sightings reported to the project's iNaturalist page ('UW Urban Canid Project iNaturalist Project'), and we used bait including carcasses of road-killed deer for coyotes and nuisance-trapped beavers for red foxes to attract canids to a site, especially when there was minimal snow cover. We chemically immobilized captured canids with an intramuscular injection of 4–10 mg kg<sup>-1</sup> ketamine and 2–4 mg kg<sup>-1</sup> xylazine based on the estimated weight of the individual. We then determined weight and physical condition, collected biological samples, and fitted the animal with either a VHF radio collar (2014 and 2015 capture seasons; Advanced Telemetry Systems, Isanti, MN; model M1950 for red foxes and M2220B for coyotes) or a Lotek LiteTrack Iridium GPS collar (2016 through 2022 capture seasons; model no. 360 for coyotes and no. 150 for red foxes). After handling, we reversed the immobilization with an intramuscular injection of either yohimbine (0.1 mg kg<sup>-1</sup>) or antisedan (0.6–0.7 mg kg<sup>-1</sup>). We then released the animal at the capture site.

Location schedules varied with collar type (VHF or GPS). For individuals with VHF collars, we located each radio-collared individual weekly using a five-hour bout, with a triangulated location recorded once every hour, during each bout, for as long as the VHF collar was active and the individual was alive. We rotated tracking bouts across the entire diel cycle to capture variation in temporal activity (Mueller et al. 2018). For individuals with GPS collars, we programmed each collar to collect GPS fixes every hour only between 9:00 and 4:00 h for coyotes and 1:00 and 4:00 h for red foxes. Species-specific time periods were selected to maximize locations during periods of high activity in urban areas and optimize battery life of the telemetry collars (Gaynor et al. 2018, Farmer and Allen 2019). Individuals were tracked until death or the end of the collar's battery life.

### Data collection – rural study area

The Wisconsin Department of Natural Resources (WDNR) collected GPS data from coyotes captured in Iowa County



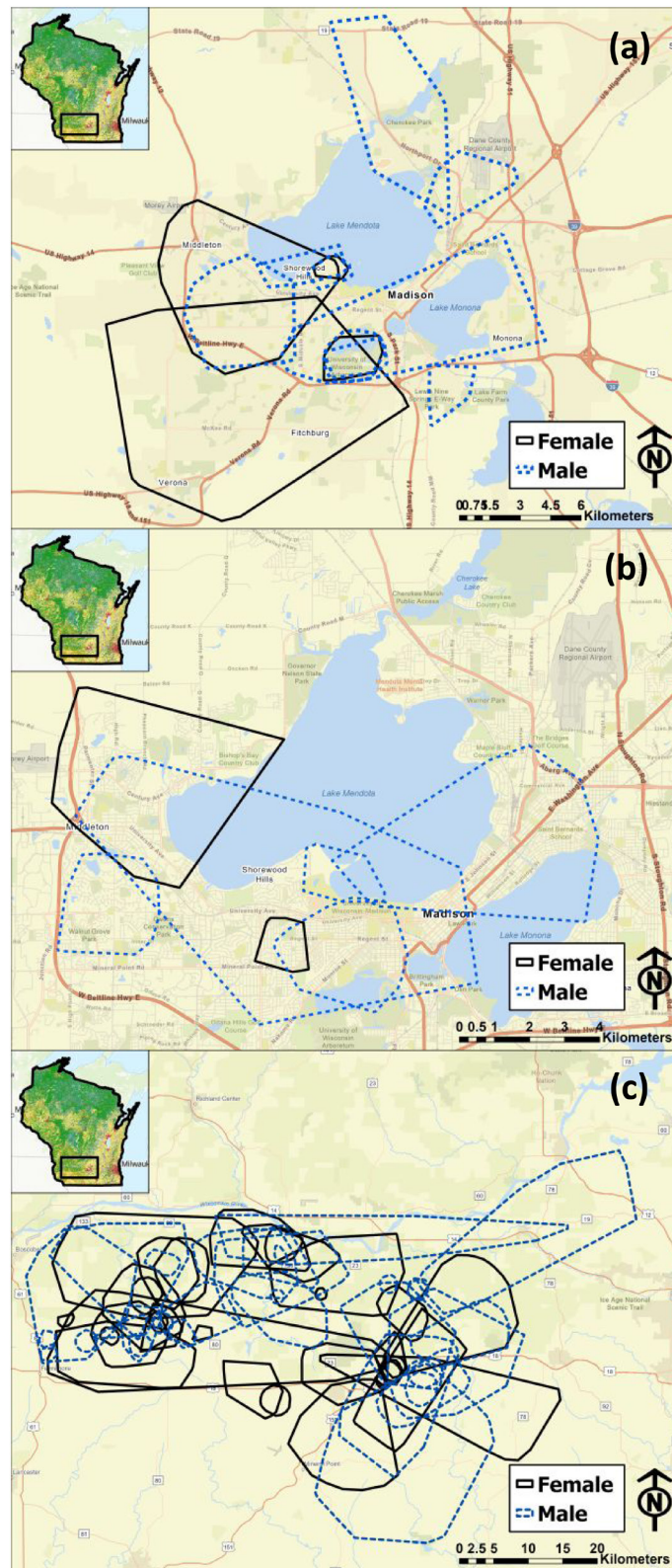


Figure 1. 95% Minimum convex polygon home ranges for male and female (a) urban coyotes, (b) urban red foxes in Madison, Wisconsin, USA, and (c) rural coyotes in southern Wisconsin, USA, based on location data collected from January 2015 to November 2021.

as part of an independent research project on deer and their predators (Fig. 1c). The WDNR started this project in the fall of 2016. Coyotes were captured using cable restraints or foothold traps either through collaboration with trappers and landowners who would voluntarily report a captured coyote or through traps set by WDNR staff. Captured coyotes were anesthetized via an injection of ketamine-dexmedetomidine-butorphanol (4 mg kg<sup>-1</sup> ketamine, 0.2 mg kg<sup>-1</sup> dexmedetomidine, and 0.4 mg kg<sup>-1</sup> butorphanol) based on estimated weight. Staff then weighed and fitted each animal with a Lotek LiteTrack GPS collar (model no. 360) which they programmed to collect a GPS fix every three hours throughout the 24-hour diel cycle. Individuals were tracked until death or the end of the collar's battery life.

## Statistical analysis

We performed all statistical analyses using R ver. 4.3.2 ([www.r-project.org](http://www.r-project.org)) and ArcGIS Pro ver. 3.2.1 (Environmental Systems Research Institute 2023). For analyses, we considered  $p < 0.05$  to be significant.

Using radio-location data from both study sites, we calculated home range (95%) and core area (50%) size for individual coyotes and red foxes using minimum convex polygons (MCP) and fixed kernel density estimators (KDE), and 95% home range size using local convex hull (LoCoH) home range estimators with the 'amt' package (Signer et al. 2019). The MCP home range estimator can suffer from several issues, including sensitivity to sampling frequency, sample size, and outlying locations (Burgman and Fox 2003, Mills et al. 2006, Huck et al. 2008). For example, the MCP estimator can systematically overestimate home range area, although evidence is mixed on whether this effect is always present (Burgman and Fox 2003, Nilsen et al. 2008). However, MCP home ranges are relatively simple to construct and interpret and can still provide value through comparison, so we report home range areas calculated using MCP to facilitate comparison with earlier studies that often used only MCP to estimate home range areas (Tétreault and Franke 2017). KDE is a flexible, non-parametric home range estimator that builds bounded utilization distributions and can have relatively low bias (Silva-Opps and Opps 2011, Tétreault and Franke 2017). It also allows for disjunct activity areas, which may provide a more accurate depiction of a home range in fragmented landscapes, such as urban areas (Atwood et al. 2004). LoCoH is also a non-parametric kernel method, but it builds isopleths by merging local convex polygons (Tétreault and Franke 2017). We included LoCoH because it is consistent even under different sampling protocols and is often recommended for cases where inaccessible areas or hard boundaries are present in or around the home ranges. Our urban study site includes a variety of landscape factors that may have presented hard boundaries such as large, high-traffic roads and a chain of lakes, which are relatively inaccessible during the ice-free portion of the year (Huck et al. 2008). Similar to MCP, KDE and LoCoH are both relatively common methods for calculating and reporting home ranges. By reporting multiple

home range estimators, we can enable the comparison of relative differences between previous studies, which typically report only a single home range metric (Signer et al. 2015).

We chose to retain all locations for each individual rather than thinning data to standardize the tracking schedules between urban and rural individuals and VHF-collared and GPS-collared individuals. Thinning the data would have resulted in a significant decrease in information, and previous studies have provided evidence that while home range size is not significantly influenced by tracking schedule (Huck et al. 2008), it can be influenced by number of locations used in the home range estimator calculations (Girard et al. 2002, Gula and Theuerkauf 2013).

There were several individuals in the dataset with relatively few location points ( $n \leq 50$ ), so we used area-observation curves to determine whether each individual had sufficient data to reach an asymptote, and excluded individuals with too few locations (Gosselink et al. 2003, Riley et al. 2003, Gehrt and Prange 2007, Nelson et al. 2007, Rosatte and Allan 2009, Walton et al. 2017). Similarly, to ensure that dispersing individuals and transients did not artificially inflate average home range sizes, we excluded individuals with large data sets whose home range area also failed to reach a stable asymptote as determined by area-observation curves (Atwood et al. 2004, Van Etten et al. 2007, Poessel et al. 2016, Walton et al. 2017, Zepeda et al. 2021). Fourteen individuals were excluded due to insufficient data or transient behavior.

We used generalized linear mixed effects models in R to identify demographic and study design factors that influenced home range and core area size of coyotes. We evaluated the three home range (95% MCP, KDE, and LoCoH) and two core area (50% MCP and KDE) metrics as dependent variables in separate models to avoid including multiple measures of the same home range or core area. Because there was complete separation with regard to the source (i.e. DNR or UCP) and species and method because the DNR did not collar any red foxes or use any VHF collars, we evaluated only location data from GPS-collared coyotes. Dependent variables included home ranges and core areas from all coyotes, with covariates including source, sex, body mass at capture (kg), and the number of locations needed to reach an asymptote (KDE home range model only). We tested our dependent variables for normality using a Shapiro–Wilkes test, and because all dependent variables tested had  $p$ -values less than 0.05, we used a gamma distribution and a log link (Chamberlain et al. 2000, Zepeda et al. 2021). We also tested correlation between all possible combinations of categorical variables using chi square tests and found no significant correlation between any variables (Skotarczak et al. 2019). We used Akaike's information criterion corrected for small sample size ( $AIC_c$ ) to identify the top models as those with a cumulative  $AIC_c$  weight of 0.90 (Burnham and Anderson 2002).

We also identified whether each possible pair of individuals tracked during the same period were from the same family group by determining whether more than ten percent of their locations were within 100 m of each other – a continuous proximity that would be highly unlikely between individuals

that were unrelated or not mated (Schrecengost et al. 2009). We then calculated volumetric overlap between all pairs of individuals that overlapped both temporally and spatially using 95 and 50% kernel density estimates and classified the overlap as within or between family groups. We estimated home range stability as the percent overlap between subsequent monthly home ranges for each individual. Based on this method, a value of 0 would indicate complete replacement of an individual's monthly home range while a value of 1 would indicate no change in home range between months.

Because an individual's home range and core area may vary based on reproductive status, we also calculated home ranges and overlap for each individual coyote and red fox during breeding (November–February for red fox and December–March for coyote), pup-rearing (March–June for red fox and April–July for coyote), and non-breeding seasons (July–October for red fox and August–November for coyote) (Mueller et al. 2018). Similarly, an individual's home range and core area may vary based on age. However, all but five individuals were captured as adults, primarily due to our capture protocols. One red fox, ID 23, was captured opportunistically as a pup, while three coyotes (ID 7, 81900, and 81915) and one red fox (ID 11), were captured as young-of-the-year during the scheduled fall and winter captures. Due to the minimal sample size of non-adult individuals, we excluded the five juveniles from the analysis. Finally, we calculated a perimeter-area ratio for each annual MCP and KDE home range where higher values indicated greater complexity of home range boundaries; although, it is important to note this metric is not scale independent.

## Results

Over the eight-year study period, we tracked 80 individuals that met our criteria for home range calculations, including 73 coyotes and seven red foxes. Of the coyotes tracked, 61 individuals were from the rural site, which included 31 GPS-collared male coyotes and 30 GPS-collared female coyotes, and 12 individuals were from the urban site, which included five VHF-collared male coyotes, three GPS-collared male coyotes, two VHF-collared female coyotes, and two GPS-collared female coyotes. All seven red foxes were tracked at the urban site and included two VHF-collared male foxes, three GPS-collared male foxes, one VHF-collared female fox, and one GPS-collared female fox. In total, we collected an average of 1623 locations per individual (minimum: 59 locations, maximum: 6874 locations). More specifically, we collected an average of 1818 locations per female coyote (minimum: 147 locations, maximum: 6874 locations), 59 locations per male coyote (minimum: 59 locations, maximum: 4443 locations), 242 locations per female red fox (minimum: 148 locations, maximum: 337 locations), and 486 locations per male red fox (minimum: 253 locations, maximum: 959 locations).

Canid home range sizes varied widely between species and among individuals and home range estimators. Average coyote home range ( $n=73$ ) was 84.23 km<sup>2</sup> (95% MCP,

minimum: 1.35 km<sup>2</sup>, maximum: 483.96 km<sup>2</sup>), 103.95 km<sup>2</sup> (95% FKDE, minimum: 1.84 km<sup>2</sup>, maximum: 984.99 km<sup>2</sup>), and 32.52 km<sup>2</sup> (95% LoCoH, minimum: 0.79 km<sup>2</sup>, maximum: 189.22 km<sup>2</sup>) (Supporting information). Average coyote core area was 20.31 km<sup>2</sup> (50% MCP, minimum: 0.22 km<sup>2</sup>, maximum: 160.93 km<sup>2</sup>) and 19.31 km<sup>2</sup> (50% FKDE, minimum: 0.41 km<sup>2</sup>, maximum: 222.92 km<sup>2</sup>) (Supporting information). Urban coyotes, on average, had smaller home ranges than rural coyotes; however, there was some overlap in home range size between individuals living in urban compared to rural areas. Average urban coyote home range ( $n=12$ ) was 30.64 km<sup>2</sup> (95% FKDE, minimum: 1.84 km<sup>2</sup>, maximum: 165.12 km<sup>2</sup>) while average rural coyote home range ( $n=61$ ) was 118.38 km<sup>2</sup> (95% FKDE, minimum: 2.04 km<sup>2</sup>, maximum: 984.99 km<sup>2</sup>) (Supporting information). Body mass at capture was the best model for all home range estimators; however, body mass was only a statistically significant predictor for MCP core area, which decreased by about 14.2% for each unit increase of body mass (Table 1).

Average coyote home ranges and core areas were larger than average red fox home ranges and core areas. Average urban red fox home range ( $n=7$ ) was 17.16 km<sup>2</sup> (95% MCP, minimum: 1.79 km<sup>2</sup>, maximum: 52.03 km<sup>2</sup>), 18.34 km<sup>2</sup> (95% FKDE, minimum: 2.82 km<sup>2</sup>, maximum: 49.37 km<sup>2</sup>), and 8.24 km<sup>2</sup> (95% LoCoH, minimum: 1.29 km<sup>2</sup>, maximum: 21.84 km<sup>2</sup>) (Supporting information). Average red fox core area was 2.49 km<sup>2</sup> (50% MCP, minimum: 0.14 km<sup>2</sup>, maximum: 5.39 km<sup>2</sup>) and 3.12 km<sup>2</sup> (50% FKDE, minimum: 0.34 km<sup>2</sup>, maximum: 6.38 km<sup>2</sup>). Across species and landscape types, average home ranges typically were largest during the breeding season, intermediate during the non-breeding season and smallest during the young-rearing season (Table 2).

Based on our criteria to identify related or mated pairs of canids, none of the individuals that we tracked concurrently were from the same family group based on continuous proximity (percent of concurrent locations within 100 m, minimum: 0.005%, average: 0.65%, maximum 8.80%). As such, our overlap results are between individuals from different, but neighboring groups. Overlap varied considerably between and within species and with land cover, but not between or within sex. Overlap between red foxes was, on average, higher than between coyotes or between coyotes and red foxes (Table 3). Within species, there was little difference in inter- or intra-sexual overlap. Average overlap was much higher in urban coyotes than in rural coyotes for both home ranges and core areas.

Home range stability averaged 0.60 (minimum=0.00, maximum=0.99) across all individuals. Though individual home range stability varied widely, average home range stability across months varied little (Fig. 2a), and there was no statistically significant difference in stability between species or between urban and rural coyotes (Wilcoxon rank-sum test,  $p=0.71$  and  $p=0.21$ , respectively) (Fig. 2b, c). Urban coyotes had an average perimeter-area ratio of 1.50 (minimum=0.37, maximum=3.30), and rural coyotes had an average perimeter-area ratio of 0.84 (minimum=0.17, maximum=2.54). Urban red foxes had an average perimeter-area



Table 1. Generalized linear mixed effects model results for average home range and core area size of coyotes in southern Wisconsin, USA, based on location data collected from January 2015 to November 2021. Metrics include minimum convex polygon (MCP), fixed kernel density estimator (FKDE), and local convex hulls (LoCoH). Model variables include source (urban, rural), sex (male, female), and asymptote (the number of locations needed for an individual's area-observation curve to reach an asymptote). Global models include all variables for each metric, and significant p-values are bolded.

Metric	Model	AIC <sub>c</sub>	AIC <sub>c</sub> <i>w</i>	Reference	Coefficient	p-value
95% MCP	Mass	647.83	0.85	NA	−0.058	0.478
	Global	651.33	0.15	Rural	−0.554	0.381
				Female	0.239	0.505
				NA (Mass)	−0.094	0.303
50% MCP	Source	725.68	0.00	Rural	−0.646	0.258
	Sex	726.75	0.00	Female	0.003	0.992
	Mass	480.36	0.81	NA	−0.153	<b>0.049</b>
	Global	483.31	0.19	Rural	−0.478	0.470
Female				0.369	0.332	
NA (Mass)				−0.195	<b>0.026</b>	
95% KDE	Source	532.41	0.00	Rural	−0.770	0.199
	Sex	533.69	0.00	Female	−0.072	0.822
	Mass	675.32	0.96	NA	0.0388	0.593
	Global	681.51	0.04	Rural	−0.544	0.423
Female				0.201	0.641	
NA (Asymptote)				0.001	0.591	
NA (Mass)				−0.009	0.924	
50% KDE	Source	749.88	0.00	Rural	−0.654	0.268
	Sex	750.55	0.00	Female	0.185	0.556
	Asymptote	750.73	0.00	NA	0.001	0.402
	Mass	478.97	0.85	NA	0.014	0.833
95% LoCoH	Global	482.42	0.15	Rural	−0.531	0.425
				Female	0.288	0.490
				NA (Mass)	−0.026	0.760
	Source	528.71	0.00	Rural	−0.706	0.227
95% LoCoH	Sex	529.56	0.00	Female	0.183	0.555
	Mass	545.32	0.84	NA	−0.044	0.538
	Global	548.71	0.16	Rural	−0.562	0.329
				Female	0.193	0.569
NA (Mass)				−0.079	0.349	
95% LoCoH	Source	607.56	0.00	Rural	−0.519	0.304
	Sex	608.37	0.00	Female	0.083	0.758

ratio of 1.46 (minimum=0.58, maximum=2.90). Similar to home range stability, there was no statistically significant differences in perimeter-area ratio between urban coyotes and red foxes (two sample t-test,  $p=0.36$ ) (Fig. 3a) or between urban coyotes and rural coyotes (two sample t-test,  $p=0.78$ ) (Fig. 3b).

## Discussion

As predicted, urban coyotes had smaller home ranges than rural coyotes, and urban red foxes had smaller home ranges than urban coyotes in our study, regardless of the home range estimator used (Atwood et al. 2004, Walton et al. 2017, Mueller et al. 2018). This supports the idea that urban areas are relatively resource rich, which would permit individuals to use a smaller area to meet their nutritional requirements (Prange et al. 2004, Bateman and Fleming 2012, Evans and Gawlik 2020, Hansen et al. 2020). Likewise, because red foxes have a smaller body size and therefore lower nutritional needs than coyotes, it is unsurprising that the red foxes had smaller home ranges (Duncan et al. 2015).

Home range and core area sizes in urban and rural landscapes also varied throughout the year based on biological seasons as behavior and resource availability fluctuated (Bekoff and Gese 2003, Randa et al. 2009, Mueller et al. 2018). Even though relative home range and core area size trends were consistent among all of the included estimators, trends across seasonal home ranges were not always consistent between home range estimators. For example, rearing was the largest seasonal home range for VHF-collared, urban, female coyotes when using 95% MCP, but breeding was the largest when using 95% KDE. As such, we recommend caution when comparing results based on different home range estimators, even when considering only relative trends. Home ranges were typically largest during breeding seasons, when individuals may be searching for potential mates or may increase territorial defense (Gese 2001). This period also coincides with the coldest weather and lowest food availability in Wisconsin and in many areas across the Northern Hemisphere, resulting in several factors that may induce larger home ranges during the breeding season (Randa et al. 2009).

Average intraspecific overlap was higher between urban coyotes than between rural coyotes and higher between

Table 2. Average seasonal home range (95% minimum convex polygon (MCP) and fixed kernel density estimate (FKDE)) size of coyote and red fox in southern Wisconsin, USA, based on location data collected from January 2015 to November 2021, where sample size is the number of individuals used to calculate the average values.

Species	Urban	Sex	Tracking method	Sample size	Season	Home range metric	Home range size (km <sup>2</sup> )
Coyote	Yes	F	VHF	2	Breeding	95% MCP	2.04
						95% FKDE	4.91
				2	Rearing	95% MCP	2.21
						95% FKDE	4.36
				2	Non-breeding	95% MCP	1.11
						95% FKDE	4.13
Coyote	Yes	F	GPS	2	Breeding	95% MCP	27.69
						95% FKDE	43.21
				1	Rearing	95% MCP	13.84
						95% FKDE	31.62
				2	Non-breeding	95% MCP	53.52
						95% FKDE	96.11
Coyote	Yes	M	VHF	5	Breeding	95% MCP	7.89
						95% FKDE	25.08
				4	Rearing	95% MCP	2.29
						95% FKDE	5.51
				4	Non-breeding	95% MCP	4.63
						95% FKDE	9.20
Coyote	Yes	M	GPS	2	Breeding	95% MCP	4.72
						95% FKDE	15.36
				3	Rearing	95% MCP	6.64
						95% FKDE	9.63
				2	Non-breeding	95% MCP	58.77
						95% FKDE	82.96
Coyote	No	F	GPS	29	Breeding	95% MCP	55.02
						95% FKDE	82.75
				18	Rearing	95% MCP	31.93
						95% FKDE	41.49
				26	Non-breeding	95% MCP	21.42
						95% FKDE	43.65
Coyote	No	M	GPS	31	Breeding	95% MCP	100.26
						95% FKDE	184.69
				23	Rearing	95% MCP	23.46
						95% FKDE	31.23
				32	Non-breeding	95% MCP	28.29
						95% FKDE	40.98
Red fox	Yes	F	VHF	1	Breeding	95% MCP	0.33
						95% FKDE	1.45
				1	Rearing	95% MCP	2.07
						95% FKDE	4.28
				1	Non-breeding	95% MCP	0.87
						95% FKDE	2.96
Red fox	Yes	F	GPS	1	Breeding	95% MCP	2.01
						95% FKDE	4.30
				1	Rearing	95% MCP	23.80
						95% FKDE	25.87
				0	Non-breeding	95% MCP	NA
						95% FKDE	NA
Red fox	Yes	M	VHF	2	Breeding	95% MCP	5.31
						95% FKDE	13.83
				2	Rearing	95% MCP	4.43
						95% FKDE	8.35
				2	Non-breeding	95% MCP	4.95
						95% FKDE	11.00
Red fox	Yes	M	GPS	2	Breeding	95% MCP	26.79
						95% FKDE	50.64
				2	Rearing	95% MCP	5.68
						95% FKDE	8.51
				2	Non-breeding	95% MCP	3.99
						95% FKDE	6.95



urban red foxes than between urban coyotes, providing insight into conspecific social structure. Both coyotes and red foxes can exhibit varied social structure depending on resource availability, among other factors, ranging from strict mated pair territoriality to loose-knit groups with various male to female ratios (Macdonald et al. 1999, Bateman and Fleming 2012, Hennessy et al. 2012). Higher intraspecific overlap could suggest either reduced territoriality or larger group sizes, both of which could result from abundant resources (e.g. an urban subsidy) and the resulting decrease in competition (Bateman and Fleming 2012). Alternatively, coyotes in rural areas may have lower overlap due to relatively high population turnover in rural areas, potentially allowing coyotes to more easily maintain exclusive territories (Margenau et al. 2023). The urban subsidy concept is further supported by the greater interspecific overlap between urban coyotes and red foxes that we identified relative to reported overlap for non-urban coyotes and red foxes (Major and Sherburne 1987, Sargeant et al. 1987, Harrison et al. 1989). Because coyote and red fox populations also typically reach higher densities in urban areas, it is likely that food and shelter resources are not limiting and that competition is reduced relative to non-urban areas (Bateman and Fleming 2012). As it is highly unlikely that

we captured and tracked all individual coyotes and red foxes within our study areas, it is possible that there were individuals with space use that overlapped more or less than our results reflect. Regardless, urban-specific research and management strategies are potentially even more essential as species face fewer constraints on their populations and the proportion of urban area continues to increase.

In contrast to our predictions, we found no difference between monthly home range stability of urban coyotes and red foxes or between urban and rural coyotes. The lack of a difference in home range stability of urban coyotes and red foxes could reflect the predictability of resources or permanence of features of the physical environment that constrain animal movement within urban areas, resulting in similar stability between the two species (Doncaster and Macdonald 1991, Prange et al. 2004, Bateman and Fleming 2012, Evans and Gawlik 2020, Hansen et al. 2020). Home range stability for urban red foxes in our study was greater than values reported for rural red foxes, providing support that aspects of the urban environment could constrain home range selection (Dekker et al. 2001, Henry et al. 2005). As for coyotes, the lack of difference in home range stability between urban and rural coyotes could be a reflection of a high degree of home range fidelity by resident coyotes regardless of resource

Table 3. Overlap using the volumetric index between 95% and 50% fixed kernel density home ranges and core areas of red foxes and coyotes in southern Wisconsin, USA, based on location data collected from January 2015 to November 2021. The volumetric index ranges from 0 for a pair of individuals with kernel density distributions with no overlap to 1 for a pair of individuals with identical kernel density distributions or complete overlap. Sample size indicates the number of pairs included in the average value. Overlap values are for individuals from adjacent groups based on lack of continued proximity.

Species overlap						
Species		Metric	Sample size	Average overlap	Minimum	Maximum
Coyote – Coyote		95%	300	0.12	< 0.01	0.91
		50%	300	0.04	0	0.90
Coyote – Red fox		95%	18	0.11	< 0.01	0.35
		50%	18	0.01	0	0.23
Red fox – Red fox		95%	3	0.10	< 0.01	0.25
		50%	3	0	0	0
Sexual overlap						
Species	Sex	Metric	Sample size	Average overlap	Minimum	Maximum
Coyote	M-M	95%	71	0.12	< 0.01	0.91
		50%	71	0.05	0	0.82
	F-F	95%	74	0.12	< 0.01	0.77
		50%	74	0.04	0	0.58
	M-F	95%	155	0.10	< 0.01	0.90
		50%	155	0.05	0	0.90
Red fox	M-M	95%	2	0.03	< 0.01	0.05
		50%	2	0	0	0
	M-F	95%	1	0.25	0.25	0.25
		50%	1	0	0	0
Landscape						
Species	Urban	Metric	Sample size	Average overlap	Minimum	Maximum
Coyote – Coyote	Y	95%	11	0.44	0.02	0.91
		50%	11	0.28	0	0.90
	N	95%	289	0.10	< 0.01	0.88
		50%	289	0.03	0	0.82

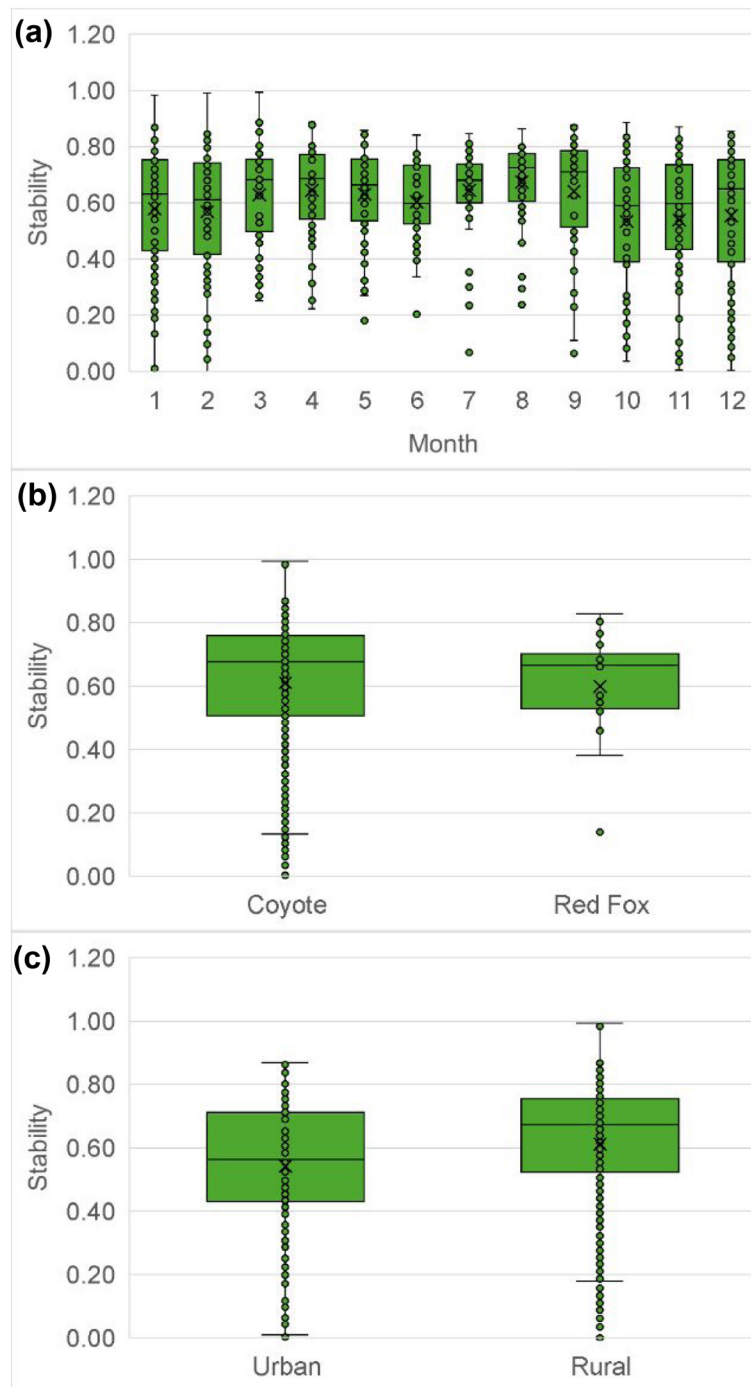


Figure 2. (a) Average individual home range stability by month, (b) average individual home range stability by species, and (c) average individual home range stability for coyotes in rural and urban areas in southern Wisconsin, USA, based on location data collected from January 2015 to November 2021.

availability or turnover of adjacent individuals (Young et al. 2008, Morin and Kelly 2017).

Perimeter-area ratio was not significantly different in urban coyotes relative to rural coyotes or in urban coyotes relative to urban red foxes, indicating no average difference in home range boundary complexity. Because urban areas tend to have increased heterogeneity in land cover and use, we had

expected that urban coyotes would have greater home range boundary complexity than rural coyotes (Doncaster and Macdonald 1991, Angel et al. 2012, Zipperer et al. 2012). Similarly, because coyotes in Madison, WI tended to inhabit larger greenspaces with home range boundaries that aligned closely with those greenspaces, while red foxes selected for medium and open development, we had expected red foxes

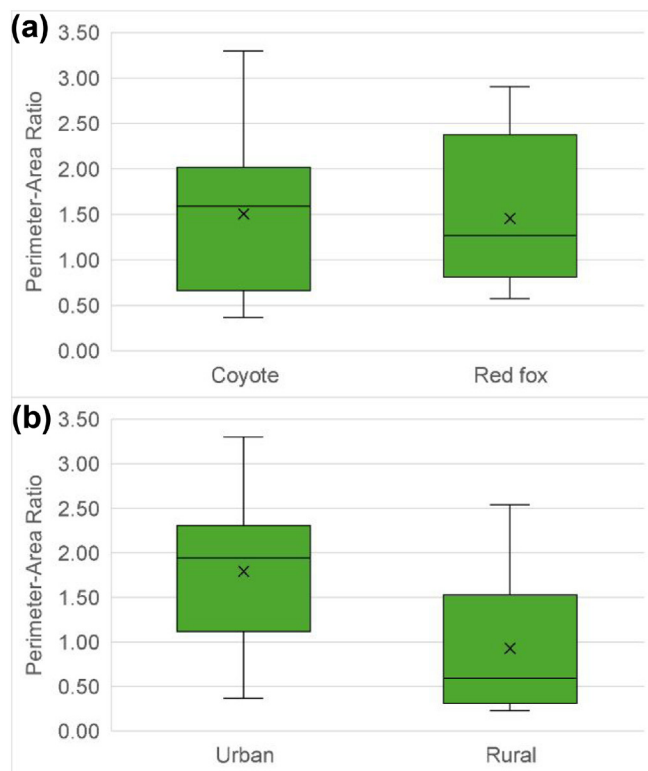


Figure 3. Perimeter-area ratio from 95% minimum convex polygon home ranges of (a) urban coyotes and red foxes in Madison, Wisconsin, USA and (b) urban and rural coyotes in southern Wisconsin, USA, based on location data collected from January 2015 to November 2021.

to have greater home range boundary complexity than urban coyotes (Mueller et al. 2018). Instead, the lack of difference in home range boundary complexity between urban and rural coyotes and between urban coyotes and red foxes could be due to the extensive behavioral flexibility that coyotes and red foxes often exhibit, which may allow them to maintain similar home range boundary complexity irrespective of the physical landscape.

Our results provide further evidence that aspects of urban environments, such as resource predictability and availability and the physical environment, influence space use of coyotes and red foxes. Currently, research on urban red foxes is sparse, especially in North America, and research on the relationship between urban coyotes and red foxes is even more limited. In addition to providing insight into the interactions between coyotes and red foxes, this research also expands our knowledge of coyote and red fox space use across seasons and the urban–rural gradient. The current body of literature on canid spatial ecology uses varied methods and metrics, rendering comparison across species and regions difficult, if not impossible. Since new methods are continuing to be developed in spatial ecology, we recommend reporting methods (e.g. fix rate and schedule) and results (e.g. multiple home range estimators) to facilitate comparison with previous studies when possible. Since urban wildlife tend to be behaviorally flexible and because

coyotes and red foxes are likely permanent inhabitants of urban areas, research specific to urban wildlife across a wide geographic expanse is necessary for effective management of both people and urban wildlife. Further research could focus on determining whether resources in urban areas are measurably more abundant and predictable, how different landscape features influence home range characteristics across the urban to rural gradient, and whether these results vary between urban regions.

*Acknowledgements* – We are grateful to the many students and members of the public who provided property access or assisted with canid captures and fieldwork and to the City of Madison and Dane County for allowing us to capture canids on park properties. We are also grateful for the collaboration of the Wisconsin Department of Natural Resources through the sharing of canid location data.

*Funding* – The work of MJF and DD was supported by the USDA Hatch Act Formula Funds (award no. MSN201473).

*Permits* – Our animal handling protocol was approved by the University of Wisconsin Institutional Animal Care and Use Committee (protocol A005905-R01), and we had all necessary permits through the Wisconsin Department of Natural Resources (permit SRLR-22-27) in addition to following trapping best management practices. All animal handling of rural coyote by the Wisconsin Department of Natural Resources was conducted based on WDNR and American Society of Mammologist guidelines.

## Author contributions

**Morgan J. Farmer:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Software (lead); Writing – original draft (lead); Writing – review and editing (lead). **Timothy R. Van Deelen:** Conceptualization (supporting); Methodology (supporting); Supervision (equal); Validation (equal); Writing – review and editing (equal). **Daniel J. Storm:** Data curation (supporting); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal). **Marcus A. Mueller:** Data curation (supporting); Investigation (equal); Project administration (supporting); Resources (supporting); Writing – review and editing (supporting). **David Drake:** Conceptualization (supporting); Funding acquisition (equal); Investigation (equal); Methodology (supporting); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Writing – review and editing (equal).

## Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/wlb3.01321>.

## Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.d7wm37q9j> (Farmer et al. 2024).

## Supporting information

The Supporting information associated with this article is available with the online version.

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