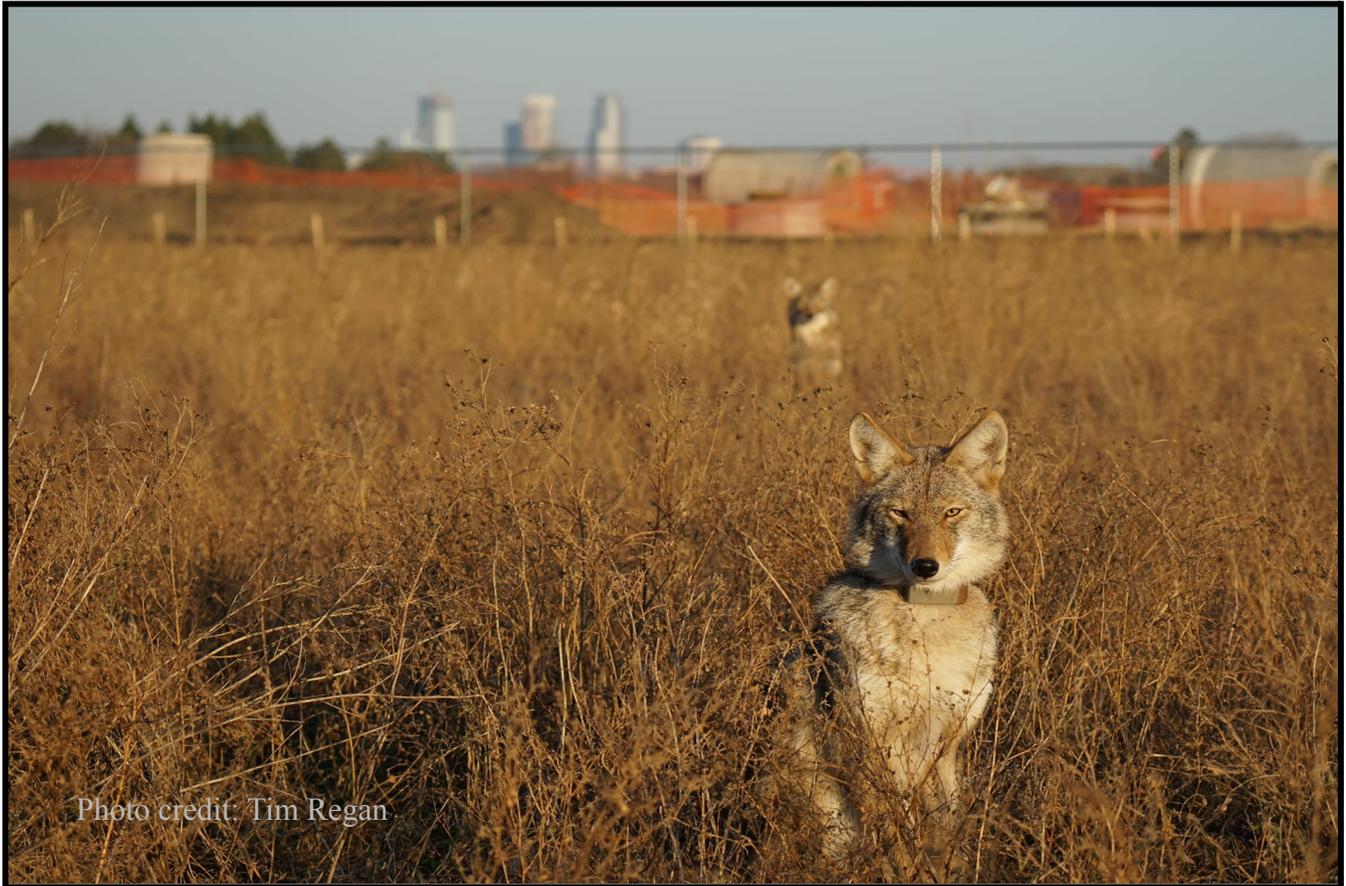


# Mapping habitat use and disease of urban carnivores



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## Abstract

1. Wildlife is an important part of many urban landscapes. Coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and gray foxes (*Urocyon cinereoargenteus*) occupy rural and urban landscapes but urban research is infrequent, and no study has occurred in the Minneapolis-Saint Paul Metropolitan Area (hereafter the Twin Cities Metro Area; TCMA). In this study, we captured, GPS collared and collected samples (hair, blood, and scat) from 17 coyotes, 16 red foxes, and two gray foxes across the TCMA's urban-rural gradient to assess space-use, survival, diet, and disease.
2. We found that coyotes survival was greater than for red foxes, suggesting higher population growth for coyotes than for red foxes. Coyote and free-roaming dog attacks caused at least 20% of red fox mortalities, which was more than we expected, and likely reflects expansion of coyotes into areas previously occupied by foxes and also the presence of free-roaming dogs in residential areas.
3. Diets of coyotes and foxes consisted of primarily natural foods, with only 8% of individuals exhibiting corn-rich diets associated with human foods found in refuse. Wide dietary breadths show that coyotes and foxes relied on diverse food resources, with wider dietary breadth for coyotes.
4. The positive relationship we found between serological pathogen richness and non-moving water bodies (e.g., ponds) appears to be partly explained by the interaction between vectors of pathogen transmission and habitat selection, as *Toxoplasmosis gondii* (transmitted via cat feces) was one of the most prevalent pathogens we detected in coyotes and foxes. *T. gondii* was especially frequent in red foxes, potentially due to red fox selection of residential areas where free-roaming domestic cats are more common.
5. Elevated heavy metal content in the hair of coyotes that selected impervious surfaces is likely a result of coyotes using industrial and commercial areas more than foxes, the latter of which selected residential areas that were less affected by heavy metal contamination.
6. Home range size suggests greater resource availability for coyotes than for red foxes. Coyote home ranges were similar to other urban studies but red fox home ranges were much larger than has been reported. Because abundant resources result in smaller home ranges (and vice-versa), our results suggest that coyotes found resources more easily than red foxes.
7. Variation in den sites selected by foxes and coyotes reflected the more general differences in space-use: coyotes denned in non-residential areas, whereas most fox dens were in residential areas.
8. Across all seasons, coyotes established home ranges in areas with low human use (with more wetlands and low road density), while red foxes were found in home ranges with more residential areas and high road density. Each of the habitat variables selected for by coyotes and red foxes within the home range suggest selection for areas of the landscape associated with low human use. The downtown and industrial areas of Minneapolis and St. Paul appear to lack the necessary resources to support resident red foxes, as are the areas that contain the most large, natural green spaces; the downtown areas and much of the residential areas of the Twin Cities appear to lack the resources necessary to support resident coyotes. Increases in the most urban coyotes' selection for non-residential areas and wetlands during the pup-rearing season highlights the importance of urban wetlands for mitigating risk of human-wildlife conflict during the pup-rearing season. Differences in how coyotes and foxes select home ranges and in what parts of the home ranges that they use the most suggests that minimizing the likelihood of encountering coyotes may

be a primary driver of habitat suitability for foxes, and that residential areas are one of the most important variables allowing for the coexistence of coyotes and red foxes in the TCMA.

9. Coyote and fox densities appear to be relatively low. RSF-based density estimates were 0.27 coyotes/km<sup>2</sup> and 0.21 red foxes/km<sup>2</sup>, which is lower than in other urban settings and corresponds with estimates based on home range size ( $\leq 3$  foxes/km<sup>2</sup>).
10. Our results support the anecdotal observation that coyotes expanded into areas once occupied by red foxes. Fortunately, coyotes and foxes rarely became nuisances; 0 collared coyotes were reported as being in conflict with people and the only reported red fox conflict was due to foxes leaving prey carcasses near a den.
11. Outreach stressing the importance of leashing pets and keeping cats inside is likely to improve the health of pets, coyotes, and foxes. Communicating the smaller-than-expected weight of coyotes (males: 14.3 kg [31.5 lbs.]; females: 11.9 kg [26.2 lbs.]) and low risk of conflict is likely to reduce negative perceptions of this species. Management activities that improve natural habitat in residential greenspaces are likely to benefit red foxes. Whereas coyotes occupied many of the large greenspaces, red foxes often selected green spaces in residential areas.
12. This study's results provide much-needed information to Minnesota residents and wildlife managers, and also provide a foundation for future studies that extend into other areas in and beyond the TCMA.

## Introduction

Wildlife species are an important part of urban landscapes. Although urban wildlife studies have increased in frequency, they remain only a small proportion of the wildlife literature (Magle et al. 2012). A recent review summarizing the benefits and costs of urban wildlife for people found that wildlife provides important ecological services (e.g., as predators of pest species) and improve the wellbeing of city residents (Soulsbury and White 2016). Evidence suggests that viewing wildlife improves physical and mental health, and that the presence of wildlife may increase the value of green spaces (Soulsbury and White 2016). In addition to these benefits, urban wildlife also present challenges. Negative human-wildlife interactions can range in severity from damage to gardens to attacks on pets and people (White and Gehrt 2009). Whereas benefits of urban wildlife are difficult to quantify (Soulsbury and White 2016), costs are often more obvious and thus have garnered more attention. Severe human-wildlife conflicts draw media attention (White and Gehrt 2009) and may lead to negative misperceptions about wildlife (Gompper 2002). Perceptions of urban wildlife will likely be influential in how people prioritize conservation efforts as human populations grow and become more urbanized.

The presence of wildlife in urban areas has increased recently (Gompper 2002, Gehrt 2007, Gehrt et al. 2009) and research that elucidates how these growing wildlife populations interact with the urban landscape and the people that reside there is critical (Riley 2006). Studies have shown that the behavior and demographics of urban wildlife differ between urban and rural settings (Harrison 1997, Riley 2006) and have also shed light on why human-wildlife conflicts occur (Miller 2015, Poessel et al. 2017). To better understand these conflicts, it is also important to understand human behavior because people in cities use “green spaces” (areas of natural vegetation within otherwise urban environments) primarily during the day and tend to use public parks at higher rates than privately owned green spaces (e.g., railroads or industrial sites). This

can result in spatial and temporal concentrations of human outdoor activity that are independent of land cover. Understanding where and when human and wildlife activity patterns overlap will help managers reduce the probability of human-wildlife conflicts (Breck et al. 2017).

Mapping animal space use provides important information to wildlife managers about resource selection (McCann and Moen 2011) and human-wildlife conflict (Miller 2015). It is possible to map space use in multiple ways, including by collecting locational data using game cameras, scent stations, and Global Positioning System (GPS) collars (Gompper et al. 2006, Mueller et al. 2018). Tracking animals with GPS collars is a powerful way to assess animal space use (Cagnacci et al. 2010) because it allows researchers to consider variations caused by individual, age, and sex that are difficult or impossible to account for using other methods. Advancements in GPS collar battery life and location accuracy have expanded opportunities to track wildlife for long durations at fine temporal and spatial scales.

Recent advances in availability of fine-scale human mobility data provide an additional opportunity to explore the role of human movement in wildlife conflict, and in shaping animal movement patterns (Corradini et al. 2021). The ability to track fine-scale, spatial recreational activity data through exercise apps, such as Strava, allows for the ability to investigate how wildlife interact with human outdoor activity at wide spatial extents (Corradini et al. 2021, Thorsen et al. 2022). These advancements will be particularly useful for understanding urban wildlife, because they will allow researchers to track how animals move among the patchy resources typical of urban landscapes, and how human use of those resources affects habitat selection (Gehrt et al. 2009, Corradini et al. 2021).

Coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and gray foxes (*Urocyon cinereoargenteus*) are mesocarnivores that occupy rural and urban landscapes. The three species can be important predators in some cities and their presence can improve the quality of life for human residents there (Gehrt and Riley 2010; Soulsbury et al. 2010). Although coyotes and foxes are relatively well-studied in rural landscapes, urban research is less common (Gehrt and Riley 2010). Urban gray fox research is especially rare and most urban red fox research is from Europe and Australia (Soulsbury et al. 2010). This is unfortunate as behavior of urban canids can differ from that of rural canids (Gehrt and Riley 2010), so extending results from rural research to urban landscapes is questionable.

Some urban canid populations have increased in recent decades, creating interest and concern for city residents (e.g., coyotes: Gompper 2002, Gehrt et al. 2007; red foxes: Reperant et al. 2007). Studies from multiple cities have improved our understanding of urban canid ecology, including in Chicago (Illinois; Gehrt et al. 2009), Madison (Wisconsin; Mueller et al. 2018), Denver (Colorado; Poessel et al. 2016), Geneva (Switzerland), near San Francisco (California; Riley 2006), and elsewhere (reviewed by Gehrt and Riley 2010 and Soulsbury et al. 2010). These studies have revealed consistent patterns of how urban canids navigate urban landscapes. Coyote nocturnality and red fox density, for example, are positively correlated with urbanization, and vehicle strikes are the most important cause of mortality for both species in multiple urban areas (Gehrt and Riley 2010, Soulsbury et al. 2010). Such research has elucidated how canids use cities and interact with people, and how canid behavior changes across the urban-rural gradient.

Results that differ among cities highlight the necessity for city-specific research. For example, coyotes consumed 18-times more anthropogenic food in Tucson (Arizona) than in Chicago (reviewed by Gehrt 2007) and gray fox home range sizes were more than five-times larger in a residential area in New Mexico than near San Francisco (Harrison 1997, Riley 2006). Patterns of disease prevalence also differ among cities. Red foxes had 2.5-times more tapeworms (*Taenia* spp.) in Geneva than in Zurich (Switzerland; Hofer 2000, Reperant et al. 2007) and both positive (Soulsbury et al. 2010) and negative (Reperant et al. 2007) correlations of disease with urbanization have been reported. Different human population densities may partially explain why results differ among cities (Gehrt 2007); however, location-specific species assemblages, landscape compositions, and ecological interactions likely also influence study results.

Here, we report on the first study of coyote and fox ecology in the Minneapolis-Saint Paul Metropolitan Area (hereafter the Twin Cities Metro Area; TCMA). Coyotes, red foxes, and gray foxes occur in the TCMA, but no published research exists to inform managers about TCMA coyote and fox resource requirements, disease, and demographics. Residents have reported human-coyote conflicts, which range from sightings to pet killings (M. Lunaris, Saint Paul Animal Control, Pers. Comm.). Apparent sarcoptic mange (*Sarcoptes scabiei*) has been found in coyotes (A. Shoemaker, Minnesota Trappers Association, Pers. Comm.), but these disease insights were based on opportunistic events and a baseline study of disease prevalence had not been conducted. The overarching purpose of this study was to understand how coyotes, red foxes, and gray foxes use the TCMA, thereby providing valuable information to residents and managers. Our project addressed three main research goals:

#### 1) Resource selection

H1: Coyotes, red foxes, and gray foxes select resources at multiple spatial scales (e.g., where to establish a territory and then how to use the resources within it; Johnson 1980's second and third orders of selection).

#### 2) Disease

H2: Diseases that are found in other coyote, red fox, and gray fox populations are present in the TCMA and will vary in prevalence across the urban-rural gradient. Because we expect to find that patterns of space use and disease prevalence differ for coyotes, red foxes, and gray foxes, we expect that disease transmission risk—among wildlife species and to people and pets—will also be heterogeneous across the landscape.

#### 3) Diet

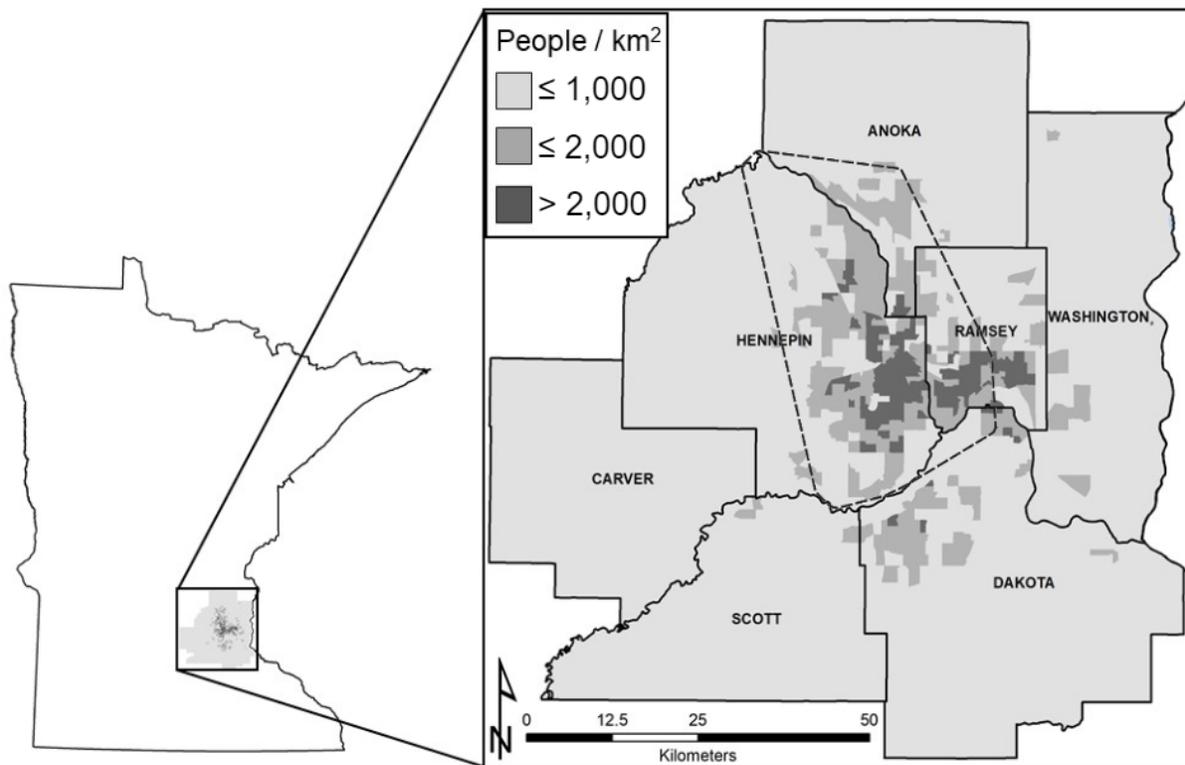
H3: Diets for each species will differ across the urban-rural gradient, with a greater prevalence of anthropogenic foods found in urban areas.

## Methods

### Study area

We studied coyotes, red foxes, and gray foxes in the TCMA, a 7,705 km<sup>2</sup> area in Anoka, Carver, Dakota, Hennepin, Ramsey, Scott, and Washington counties (Figure 1). The mean temperature is -7 °C during winter (Dec–Feb) and 22 °C during summer (June–Aug; National Climate Data Center 2010). Annual liquid precipitation is 82 cm. Common tree species include green ash (*Fraxinus americana*), American elm (*Ulmus americana*), and boxelder (*Acer negundo*; Nowak

et al. 2006). Human density varies widely across the study area. Urban centers of Minneapolis and Saint Paul are occupied by  $> 8,000$  people/ $\text{km}^2$ . Outlying areas are typically occupied by  $< 1,000$  people/ $\text{km}^2$  (US Census Bureau 2010).



**Figure 1.** The seven-county Twin Cities Metro Area (TCMA) where we studied coyotes, red foxes, and gray foxes across a range of human densities. Darker gray shading corresponds with greater human density (people /  $\text{km}^2$ ; US Census Bureau 2010). Inset depicts the Minnesota border. The dashed outline is the study area within the TCMA where we captured study animals; a 100% minimum convex polygon of locations of non-dispersing individuals.

## Capturing and handling

We captured coyotes, red foxes, and gray foxes across the range of human densities in the TCMA (Figure 1) using cable restraint and laminated foothold live traps that we set and checked daily Nov 28, 2019–Feb 28, 2020, Sep 15, 2020–Feb 28, 2021, and Sep 15–Nov 15, 2021. Each cable restraint included a “relaxing lock” that released pressure on a captured animal’s neck when the animal relaxed and “stops” that minimized the risk of capturing white-tailed deer. Foothold traps had springs and multiple swivels to reduce the risk of leg injury, and we only used footholds when temperatures precluded risk of damaging a study animal’s foot by constraining blood flow. To locate study animals, we scouted, and used reports from the public (e.g., iNaturalist.org) and wildlife managers (e.g., Three Rivers Park District and USFWS). We focused efforts in a  $1205 \text{ km}^2$  area that intersected 52 municipalities to facilitate fieldwork with limited staff (Figure 1; dashed outline).

We chemically immobilized captured foxes and coyotes using ketamine (10 mg/kg for coyotes, 4 mg/kg for foxes) and xylazine (2 mg/kg; Mueller et al. 2018). For each coyote and fox, we recorded mass, presence of fleas and ticks, collected biological samples (hair, blood, and feces), and equipped a GPS collar that transmitted locational data to us by satellite (Telonics, Inc., Mesa, AZ; model TGW-4177-4 for foxes and model TGW-4277-4 for coyotes; Figure 2) while monitoring body temperature and respiratory rate. We also examined study animals for apparent sarcoptic mange; irritated bald patches on the animal's pelage. After collecting samples and fitting a GPS collar, we administered Atipamezole (1 mg / 10 mg xylazine; intramuscular) to reverse Xylazine and released study animals once they appeared fully recovered from the effects of immobilization drugs. Capture and handling will follow guidelines from the American Society of Mammalogists (Sikes et al. 2016) and the University of Minnesota (Institutional Animal Care and Use Committee; 1906-37119A; 23 Sep 2019).



**Figure 2.** Female red fox (F9) being fitted with a GPS tracking collar. We immobilized this fox for processing and released it unharmed thereafter.

## GPS fixes

We programmed GPS collars to record and relay location fixes for 1 yr (battery life limited deployment duration), with locational fixes scheduled at three temporal scales: a coarse scale (11-hr intervals), intermediate scale (5.5-hr intervals), and fine scale (2.5-hr bursts of 10 min fixes every 33 hr). Coarse and intermediate scales provided information about daily and seasonal space use, while fine-scale locational data provided information about local movement paths (e.g., near trails). We increased fine scale fix attempts during periods with greater human-coyote conflict (pup-rearing).

GPS locations were filtered to exclude GPS fixes that were acquired with fewer than four satellites and with horizontal dilution of precision greater than 10. Additionally, any locations with a speed > 5 km/hr between locations were examined manually for plausibility based on the context of the previous and following GPS locations, and eliminated accordingly.

## Causes of mortality

The GPS collars we used contained a sensor designed to notify us when a study animal mortality occurred. Upon receiving a mortality notification, we located the general location of the study animal (using GPS locations), navigated to it in the field (using radio signals emitted by the collar's VHF transmitter, while respecting private property boundaries), and when possible we used evidence at the site (tracks and scat) and wounding patterns on the carcass to assign a cause of death. We ascribed the cause of death as “unknown” when we did not find evidence sufficient to make a reliable determination. This usually occurred when collars did not send a mortality signal.

## Den site data collection

We collected data at den sites during spring (Mar–June) 2020–2022. Dens were located where GPS locations indicated a study animal spent more than 1 hr in an area (location clusters less than 20 m apart) during a single 2.5 hr burst of 10-min locations. We found other dens by investigating areas where TCMA residents reported frequent GPS-collared coyote and fox activity. Once a den was located, we confirmed the presence of offspring by direct observation, scat, tracks, and by placing a motion-sensitive trail camera trap within approximately 20 m of the den entrance. We then classified the den structure (subterranean, log, culvert, or non-culvert human structure) and its surroundings (in a residential yard or in a nonresidential green space). Dens were only visited once to confirm active status during the denning season to reduce disturbance. If we did not confirm denning activity within 15 min of visiting the site, we set trail cameras and left the area, and retrieved cameras after June 20 to assess denning activity.



**Figure 3.** Examples of a subterranean coyote den (A), a coyote culvert den (B) and a red fox den under a house. Active status of a den was confirmed either visually (D; coyote pup in culvert den), through observation of offspring sign (E; coyote pup scat at subterranean den mouth) or through observation of pups or kits with trail cameras (F; adult red fox with three kits).

## Data analysis

### Survival

We estimated annual survival for each species using the Kaplan-Meier Method, which allows for staggered entry and censoring of missing study animals (Pollock et al. 1989). To align with capture activities and maximize statistical power of our data, we began the annual period on Sep 15 and combined data across study years. We staggered entry of study animals that were captured after the annual start date and right censored animals that went missing without a known mortality before the end date (e.g., collar battery drained).

### Diet

We assessed coyote and fox diets using stable isotope analysis. We sent hair samples collected from each captured study animal (Murray et al. 2017) to the Cornell COIL Lab for processing. Stable isotope ratios of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  are recorded by comparing values of those isotopes in a sample to isotope levels found in reference materials— $\text{N}_2$  in air and Vienna Pee Dee Belemnite (VPDB), respectively. Resulting  $\delta^{13}\text{C}$  stable isotope ratio data were assessed for the contribution of corn-rich foods in coyote and fox diets, and whether there were differences in consumption between the species (Murray et al. 2015, Newsome et al. 2015). Corn is present in nearly all processed foods and livestock feed. Corn-rich foraging by coyotes and foxes suggest dependence on human food sources, like refuse. In a previous study of urban coyote diets,  $\delta^{13}\text{C}$  ratios above  $-20.5$  parts per thousand were considered to indicate elevated consumption of corn-rich foods (Newsome et al. 2015). As an additional metric, we examined  $\delta^{15}\text{N}$  stable isotope ratios to assess diet overlap between coyotes and foxes (Newsome et al. 2015).

We used linear regression to test for the correlation of percent impervious surface within an individual's annual home range (independent variable; reflects urbanization) with  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (dependent variables) in two separate tests. To assess diet overlap by species,  $\delta^{15}\text{N}$  ratios and  $\delta^{13}\text{C}$  ratios in coyotes and red foxes were compared between species using a two one-way analyses of variance (ANOVA); gray foxes were excluded due to small sample size. All analyses were conducted using R statistical software (version 4.1.2, R Core Team 2021). We set  $\alpha = 0.05$  for all statistical tests; adjusted to  $\alpha = 0.01$  to control for experimentwise error when multiple tests were conducted with the same data.

### Disease prevalence

We used sucrose and zinc sulfate fecal flotation methods to test rectum-collected fecal samples for the presence of parasites (e.g., *Echinococcus* spp., *Taenia* spp., etc.). In separate tests using each flotation solution, we combined 1 g of feces with 5 mL of the flotation solution, which was mixed thoroughly and strained through a tea strainer. That mixture was poured into a 15 mL centrifuge tube, which was filled to the top with additional flotation solution. The mixture was then centrifuged at 1,500 rpm for 5 min, which causes debris to sink and parasite cysts and eggs

to float to the top. After centrifugation, the solution rested for 10 min while covered by a microscope slide to collect parasites that floated to the top. To identify protozoan parasites such as *Giardia* in the zinc sulfate flotation, two drops of Lugol's iodine were added as a staining agent to the microscope slide after removal from the top of the centrifuge tube. Microscope slides were then covered with a coverslip after removal from the flotation solution, and examined under  $\times 100$  magnification with a light microscope.

We transported blood samples collected from coyotes and foxes to be processed  $< 4$  hr after collection in 7.5 mL BD Tiger Top Vacutainer vials (Becton, Dickinson and Company, Franklin Lakes, NJ), centrifuged samples at 2,000 rpm for 10 min, and collected the serum supernatant (stored at  $-80^{\circ}\text{C}$ ) for testing at the University of Illinois Veterinary Diagnostic Laboratory for antibodies to: canine distemper virus, canine parvovirus, *Toxoplasma gondii*, *Leptospira* spp., *Ehrlichia* spp., *Anaplasma* spp. and Lyme disease (*Borrelia burgdorferi*). The laboratory also tested serum samples for infection by *Dirofilaria immitis*, which is the causative agent for canine heartworm.

We used linear regressions to test whether fecal parasite richness (the number of species detected) and serum pathogen richness (dependent variables) were correlated with the following factors at the scale of the annual home range: proportion impervious surface, proportion covered by non-moving bodies of water (i.e., lakes and swamps), and whether the home range intersected the Minnesota River, Mississippi River, or both (downstream of the Minnesota and Mississippi River confluence). Additionally, we used logistic regression to test whether the presence or absence of any fecal or serum pathogens (dependent variable) could be predicted by the same predictor variables in separate models for each pathogen.

## Metals

We submitted coyote and fox hair samples to the University of Minnesota's Snell-Rood Lab to quantify the following metals: sodium, magnesium, aluminum, plutonium, potassium, calcium, viridium, chromium, manganese, iron, cobalt, nickel, copper, zinc, arsenic, selenium, cadmium, and lead. We then used linear regressions to assess the correlation between each heavy metal concentration (parts per million [ppm]; dependent variable) with the same independent variables as in disease prevalence (home range percent impervious surfaces, proportion covered by non-moving water bodies, and proximity to the Minnesota or Mississippi Rivers).

## Home range analysis

We estimated coyote, red fox, and gray fox home ranges by plotting coarse (11-hr fix intervals) and intermediate (5.5-hr and) temporal scale locations from GPS collars in a Geographic Information System (GIS) and calculating 95% kernel density estimates (KDE; Gehrt et al. 2009, Mueller et al. 2018). We fit an anisotropic, area-corrected 95% kernel density estimate ( $\text{KDE}_c$ ) to each set of GPS locations in R (*amt* package; Signer et al. 2019, and Fleming et al. 2014, Calabrese et al. 2016).  $\text{KDE}_c$  allows for variation in two spatial dimensions and reduced overestimation of home ranges when locations are along linear features (e.g., river corridors). To avoid temporal autocorrelation, we thinned locational data to 11-hr intervals. The suitability of thinning to 11 hr was visually confirmed by examining the leveling time of semivariance function (SVF) variograms; leveling occurred before a lag of 12 hr (*ctmm* packaged; Calabrese et al. 2016, Fleming et al. 2014). SVF variograms plot the displacement between GPS locations at

different lag times between locations. Presence of a horizontal asymptote in a variogram indicated constrained movement distances and low displacement within a defined area (Fleming et al. 2014). The 11-hr lag is also biologically reasonable because our study animals traversed home ranges within 11 hr.

For comparison with other studies, we also developed 95% minimum convex polygon home range estimates (MCPs) using the *amt* package in R (Thompson et al. 2021, Gehrt et al 2009, Signer et al. 2019).

We developed home ranges after dividing locational data into distinct four-month biological seasons: dispersal (Nov–Feb for foxes; Dec–Mar for coyotes); pup-rearing (Mar–June for foxes; Apr–July for coyotes); and the non-reproductive (July–Oct for foxes; Aug–Nov for coyotes; Mueller et al. 2017). We required home ranges to have > 30 d of locational data. Additional multi-season (annual) home ranges were fit for the entirety of the tracking period of the animal.

To test whether an individual displayed territoriality, we examined SVF variograms. Presence of a horizontal asymptote in a variogram indicated constrained movement distances and low displacement within a defined area (Fleming et al. 2014). Such behavior would suggest that the individual did not have a stable home range, and was displaying dispersing or transient behavior. Near-linear increases in the SVF variogram indicated dispersal (increasing displacement). After visually examining variograms, we mapped the locations of all study animals with non-asymptotic variograms in QGIS GIS software (version 3.23.0) to visually determine what type of non-resident behaviors lead to the variogram pattern.

When study animals had periods of transiency, we estimated a separate home range for each period to avoid the overly-smoothed home ranges that would have resulted from pooled locations. Transiency caused non-asymptotic or weakly asymptotic SVFs that corresponded with apparent exploratory behavior, returns to the previous home range, and eventual establishment of a new home range. Resulting SVFs had a high-value, weakly asymptotic semi-variance during periods of transience. To determine when transiency started, we identified the start of exploratory behavior (with returns to the original home range). From 30 d beyond the start of transiency, we decreased the end date for the variogram by 5 d until it stabilized (clear asymptote). To determine when transiency ended, we identified when the animal localized into the area in which it established a new home range without returning to the previous home range.

Dispersal periods occurred when a study animal moved out of its home range, without returning or localizing in another area for more than 30 d. The start of dispersal was the first location out of a home range (without return) and the end of dispersal (start of territory establishment) was the first location within the home range the individual eventually established. Dispersal periods were visually confirmed as having approximately linearly increasing variograms, and home ranges that they dispersed out of or colonized were confirmed as having asymptomatic SVF variograms.

## **Resource selection**

We developed case-control logistic regression resource selection functions (RSFs) using the *amt* package in R (Signer et al. 2019) to assess habitat selection at two scales: the home range (second-order selection) and within home range (third-order selection; Johnson 1980).

Second-order RSFs compared random locations within a study animal's home range to random locations within the study area (100% MCP of resident locations; Figure 1). Third-order RSFs compared habitat at observed (used) locations recorded for the animal to random available locations within the animal's home range. We fit RSFs to individual animals before averaging coefficients across individuals to make population-level conclusions (variance weighted approach; Fieberg et al. 2021).

All RSFs were for seasonal home ranges, with data thinned to 5.5 and 11-hr locations to reduce temporal autocorrelation. For second-order (home range) RSFs, we generated a number of random locations within the 95% KDE<sub>C</sub> home range that was equal to the mean number of species-specific observed locations per individual for that season (hereafter referred to as used locations). We then generated 10 random locations (hereafter referred to as available locations) within the study area for every random "used" location within the home range for second-order RSFs, and 10 available locations within the home range for every observed location for third-order RSFs. We chose 10 available locations for each used location after fitting models with more random locations to examine model sensitivity.

We developed global RSFs (containing all independent variables) to test for preferences at both scales of selection using seven independent variables: proportion canopy cover, proportion buildings, proportion wetland habitat (emergent, shrub and swamp), proportion residential area, cumulative outdoor activity index (COI), slope, and road density (km/km<sup>2</sup>). Each dataset was a raster geospatial dataset that we resampled and aligned at a 30 m<sup>2</sup> pixel resolution. After preliminary examination, we excluded two additional variables (open habitat and size of largest area of natural vegetation intersecting the pixel) from analysis because increases in variance inflation factor (VIF) values indicated correlation with those variables and others.

Proportions of canopy cover, buildings, and wetland habitat were generated from the TCMA landcover classification (1-m Land Cover Classification, Minnesota Geospatial Commons) using QGIS. Proportional raster datasets were calculated by converting the respective landcover category into a binary dataset of ones and zeros at a 1-m scale indicating presence or absence of that habitat type, and averaging within a 30-m<sup>2</sup> pixel to create the final dataset. Proportion of residential areas was generated by querying the TCMA ownership plat dataset (Metro Regional Parcel Dataset, Minnesota Geospatial Commons) for residentially owned parcels, classifying the query as a binary dataset (with results coded as one), and converting the resulting polygon dataset to a raster map that averaged the underlying data into proportion within a 30 m<sup>2</sup> pixel.

We developed COI from the Strava tracking application's publicly available Global Heatmap (<https://www.strava.com/heatmap>; Corradini et al. 2021). The Global Heatmap aggregates user locations over 1 yr as they engage in outdoor activities (Corradini et al. 2021). We developed this into a raster dataset by zooming in to the finest scale allowed for viewing, converting the color to blue, and taking screenshots of the resulting study areas. These screenshots were converted to PNG images, which can then be imported into QGIS. We used nine control points (obvious features like trail intersections) to georeference each image. The color values were then resampled as a color stretch from zero to one to create the COI dataset, and the resulting 22 m<sup>2</sup> resolution dataset was interpolated to 30 m<sup>2</sup> by averaging COI.

We calculated slope using 1-m LiDAR-derived digital elevation model (DEM) rasters for Minnesota (MnTOPO; Minnesota Department of Natural Resources) using the Slope tool in QGIS. This dataset was generated as a percent slope, which was then averaged within 30 m<sup>2</sup> pixels. Road density was from the OpenStreetMaps ([www.openstreetmap.org](http://www.openstreetmap.org)) road dataset. To create a raster dataset with a resolution of 30 m<sup>2</sup>, we calculated the length of road features within a circular buffer of the pixel with an area of 1 km<sup>2</sup>, yielding road density (km/km<sup>2</sup>).

To create second- and third-order coyote and red fox resource selection maps, we combined the average seasonal species-specific RSF coefficients (from each global model) with study-area-wide rasters, resulting in a heatmap that reflected relative resource selection (once exponentiated; DeCesare et al. 2012). We applied a linear stretch to second- and third-order rasters so that minimum selection probabilities corresponded to zero, and maximum values to one (DeCesare et al. 2012, Johnson et al. 2004). The maps we generated represent the relative probability of raster pixels being selected by a coyote or fox across the study area at each order of selection.

After developing second- and third-order maps, we developed a scale-integrated selection map that estimates the relative probability of encountering a coyote or red fox across both scales simultaneously (DeCesare et al. 2012, Johnson et al. 2004). This approach takes advantage of the nested approach of fitting RSFs at multiple scales. Since our study area is within the known range of all three species, first-order selection (the scale of a species' range) is one and the integrated relative probability of a location (i.e., a raster pixel) being selected given home range (second-order) and within home range (third-order) selection simplifies to the product of second- and third-order relative selection probabilities (DeCesare et al. 2012). We reported coefficients for which 95% confidence intervals of fitted coefficients (before back-transformation) did not intersect 0.

## **Distribution and abundance**

To estimate abundances of coyotes and foxes within the study area, we used breeding season home ranges sizes and compositions to approximate the number of coyotes that could be supported. We used the breeding season home ranges because juvenile coyotes and foxes typically disperse before or during that season (fall–winter; Bekoff & Gese 2003, Trehwella et al. 1988). Those left after this period could be considered territorial individuals. Scale-integrated selection maps were used as a proxy for habitat suitability within the study area. We used the QGIS Moving Average tool with a circular moving window the same size as the respective species' median breeding season home range size to average values in the scale-integrated selection score raster. This created a habitat suitability raster dataset in which each pixel indicates the average scale-integrated selection score surrounding that pixel in an area the size of that species' median home range.

We then calculated average scale-integrated selection scores within breeding home ranges for each study animal. We chose the minimum average selection score value within the home range of any observed study animal during the breeding season as a threshold defining the minimum habitat selection score that could support a territorial individual. This threshold was used to define areas of the habitat suitability raster that could support home ranges of a given species. This area was then divided by the median area of home range estimates for the species to estimate the number of home ranges that the species could establish within the study area.

Resident red fox populations were estimated by taking the number of home ranges that could be supported in the study area and multiplying by two to account for mated pairs occupying the home range. This estimate does not account for springtime estimates of kit abundance, and assumes no social structure beyond mated pairs. We then multiplied that number by the proportion of study animals displaying transient behaviors to estimate the number of non-territorial individuals that could reside in the study area (Breck et al. 2017).

Coyote packs vary in size (two–four, Cape Cod, MA, Way et al. 2002; four–six, Chicago, IL, Gehrt & Riley 2010). Since we did not attempt to estimate pack sizes across the study area, we calculated a range of estimates based on a range of possible pack sizes. Pack size was multiplied by the number of median home ranges that could be supported in the study area to estimate the number of territorial individuals. Transient individuals were estimated as the percentage of observed transients multiplied by the number of estimated territorial individuals.

## Results

### General

We captured 18 coyotes, 17 red foxes, and two gray foxes. Of these, we did not collar one coyote because we wanted to maximize the independence of our data (it was captured near an apparent packmate) and one red fox because it was killed (likely by a coyote). We monitored the remaining 35 coyotes and foxes for an average of 244 d ( $SD = 146$ ; Table 1). Coyotes weighed 13.3 kg ( $SD = 2.4$  kg,  $N = 18$ ), with females averaging 11.9 kg ( $SD = 1.3$  kg,  $N = 7$ ) and males averaging 14.3 kg ( $SD = 2.5$  kg,  $N = 11$ ). Average weights of the two fox species were the same, with red foxes weighing 4.8 kg ( $SD = 1.1$  kg,  $N = 17$ ) and gray foxes weighing 4.8 kg ( $SD = 1.0$  kg,  $N = 2$ ). As was the case for coyotes, the average weight of red fox males (5.1 kg,  $SD = 0.8$ ,  $N = 10$ ) was greater than for females (4.3 kg,  $SD = 1.2$  kg,  $N = 7$ ). The one female gray fox that we captured, however, weighed more than the one male (female: 5.6 kg; male: 4.1 kg), though our small sample size limits inference.

Apparent mange was detected on one coyote (6% of captures) and three red foxes (18% of captures), but was not detected for either gray fox (Table 1). Fleas were detected on about half of the red (41%) and gray foxes (50%) we processed but were not observed on any coyotes.

| ID              | Sex | Weight (kg) | Age class <sup>‡</sup> | Ectoparasites | Date processed | Days monitored | Residency |
|-----------------|-----|-------------|------------------------|---------------|----------------|----------------|-----------|
| <u>Coyote</u>   |     |             |                        |               |                |                |           |
| C1.1            | F   | 12.91       | A                      | None          | 02/25/2020     | 338            | Resident  |
| C12             | F   | 12.15       | A                      | None          | 01/04/2021     | 380            | Resident  |
| C13             | F   | 12.85       | A                      | None          | 02/28/2021     | 225            | Resident  |
| C4              | F   | 11.75       | A                      | None          | 01/07/2020     | 368            | Resident  |
| C5              | F   | 9.68        | A                      | None          | 02/27/2020     | 183            | Resident  |
| C8              | F   | 13.23       | A                      | None          | 10/08/2020     | 366            | Resident  |
| C9              | F   | 10.75       | A                      | None          | 10/15/2020     | 365            | Resident  |
| C1              | M   | 9.85        | A                      | None          | 11/23/2019     | 72             | Disperser |
| C10             | M   | 16.93       | A                      | None          | 12/13/2020     | 366            | Resident  |
| C11             | M   | 14.47       | A                      | None          | 12/16/2020     | 381            | Resident  |
| C14             | M   | 9.85        | A                      | None          | 10/20/2021     | 100            | Disperser |
| C15             | M   | 13.60       | A                      | None          | 11/09/2021     | 143            | Resident  |
| C2              | M   | 16.61       | A                      | None          | 12/18/2019     | 366            | Resident  |
| C3              | M   | 13.25       | A                      | None          | 01/03/2020     | 375            | Resident  |
| C5.1            | M   | 14.75       | A                      | Mange         | 11/10/2021     | 142            | Resident  |
| C6              | M   | 15.64       | A                      | None          | 02/17/2020     | 357            | Resident  |
| C7              | M   | 17.00       | A                      | None          | 02/03/2020     | 249            | Resident  |
| CU1             | M   | 14.86       | A                      | None          | 02/03/2020     | --*            | Resident  |
| <u>Gray fox</u> |     |             |                        |               |                |                |           |
| F10             | F   | 5.55        | A                      | Fleas         | 10/03/2020     | 531            | Resident  |
| F18             | M   | 4.10        | A                      | None          | 10/14/2021     | 169            | Resident  |
| <u>Red fox</u>  |     |             |                        |               |                |                |           |
| F12             | F   | 5.05        | A                      | Fleas         | 10/14/2020     | 164            | Resident  |
| F13             | F   | 5.89        | A                      | Fleas         | 10/09/2020     | 48             | Resident  |
| F5              | F   | 4.20        | A                      | None          | 10/12/2021     | 14             | Resident  |
| F6              | F   | 4.85        | A                      | Mange         | 10/3/2020      | 162            | Resident  |
| F8              | F   | 4.46        | A                      | None          | 02/28/2020     | 344            | Resident  |
| F9              | F   | 1.93        | A                      | None          | 09/30/2020     | 136            | Resident  |
| MortF1          | F   | 3.80        | J                      | NA            | --**           | --             | Unknown   |
| F14             | M   | 4.10        | A                      | None          | 11/01/2020     | 29             | Disperser |
| F15             | M   | 5.95        | A                      | Fleas         | 11/19/2020     | 171            | Resident  |
| F16             | M   | 4.35        | A                      | Fleas         | 12/05/2020     | 90             | Resident  |
| F17             | M   | 5.25        | A                      | None          | 12/23/2020     | 338            | Resident  |
| F2              | M   | 6.68        | A                      | Fleas & mange | 02/29/2020     | 118            | Resident  |
| F3              | M   | 5.56        | A                      | None          | 11/27/2019     | 174            | Resident  |
| F4              | M   | 4.40        | A                      | Fleas         | 09/22/2020     | 144            | Resident  |
| F1              | M   | 5.45        | J                      | None          | 01/30/2020     | 628            | Resident  |
| F11             | M   | 5.00        | J                      | None          | 10/09/2020     | 134            | Resident  |
| F7              | M   | 4.70        | J                      | Fleas & mange | 09/23/2020     | 363            | Resident  |

<sup>‡</sup>A=adult/subadult; J=juvenile.

\*Did not collar this individual because captured another coyote nearby.

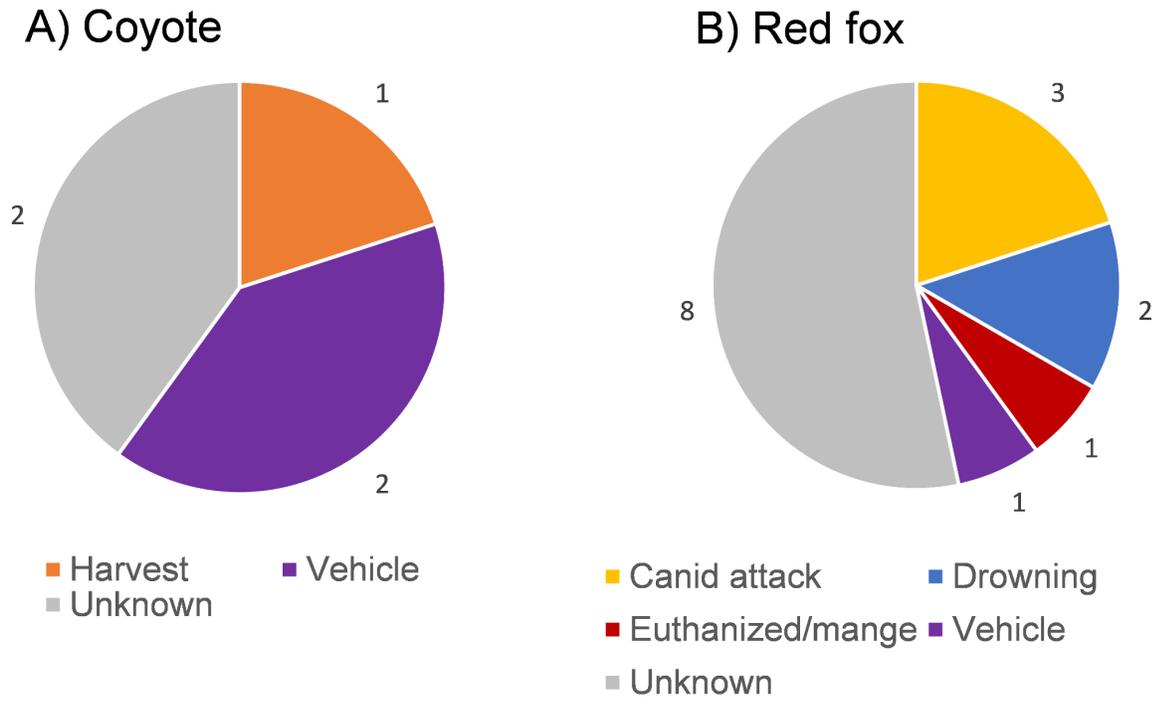
\*\*Did not collar because found dead in livetraps; coyote attack.

**Table 1.** Information about coyotes, gray foxes, and red foxes captured in the Twin Cities Metro Area.

## Survival

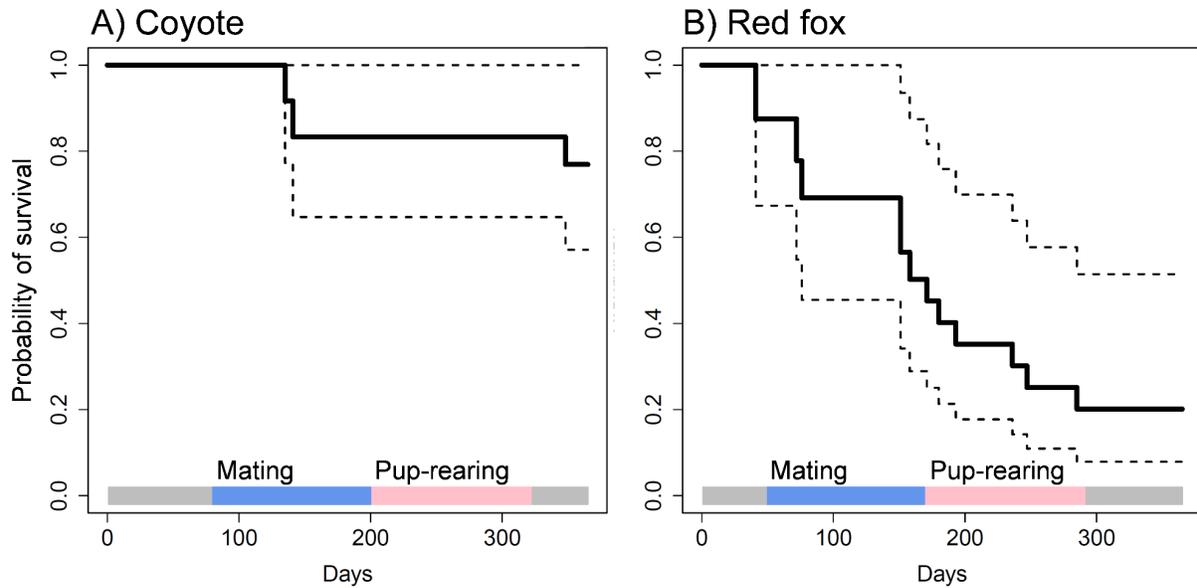
Five coyotes and 15 red foxes died during monitoring but neither of the two gray foxes we studied died (Figure 4). The cause of mortality was unknown for 40% of coyote and 53% of red fox mortalities. For mortalities with known causes, vehicle strikes killed the most coyotes (67%), while canid attacks (43%) killed the most red foxes.

Coyotes were suspected in the three red fox mortalities caused by canid attacks. One additional red fox mortality occurred after local residents reported seeing the fox being chased by a free-roaming dog (*Canis familiaris*). We classified this additional mortality as unknown because we did not observe trauma during necropsy. Although canids killed the most red foxes, 27% of red fox mortalities for which we were able to ascribe a cause were drownings. These drownings occurred in a lake in winter (Feb) and an uncovered pool in spring (May).



**Figure 4.** Causes of mortality for coyotes (A) and red foxes (B) in the Twin Cities Metro Area.

Survival was high and varied minimally across biological seasons for coyotes, with the greatest decline occurring during the mating season (Figure 5). Red fox survival was lower, with sharp declines during mating (40% decline) and pup-rearing (30% decline).



**Figure 5.** Daily survival for coyote (A) and red fox (B) in the Twin Cities Metro Area 2019–2022. Mating season was from Nov–Feb and Dec–Mar for red foxes and coyotes, respectively. Pup-rearing was from Mar–June and Apr–July, respectively.

## Diet

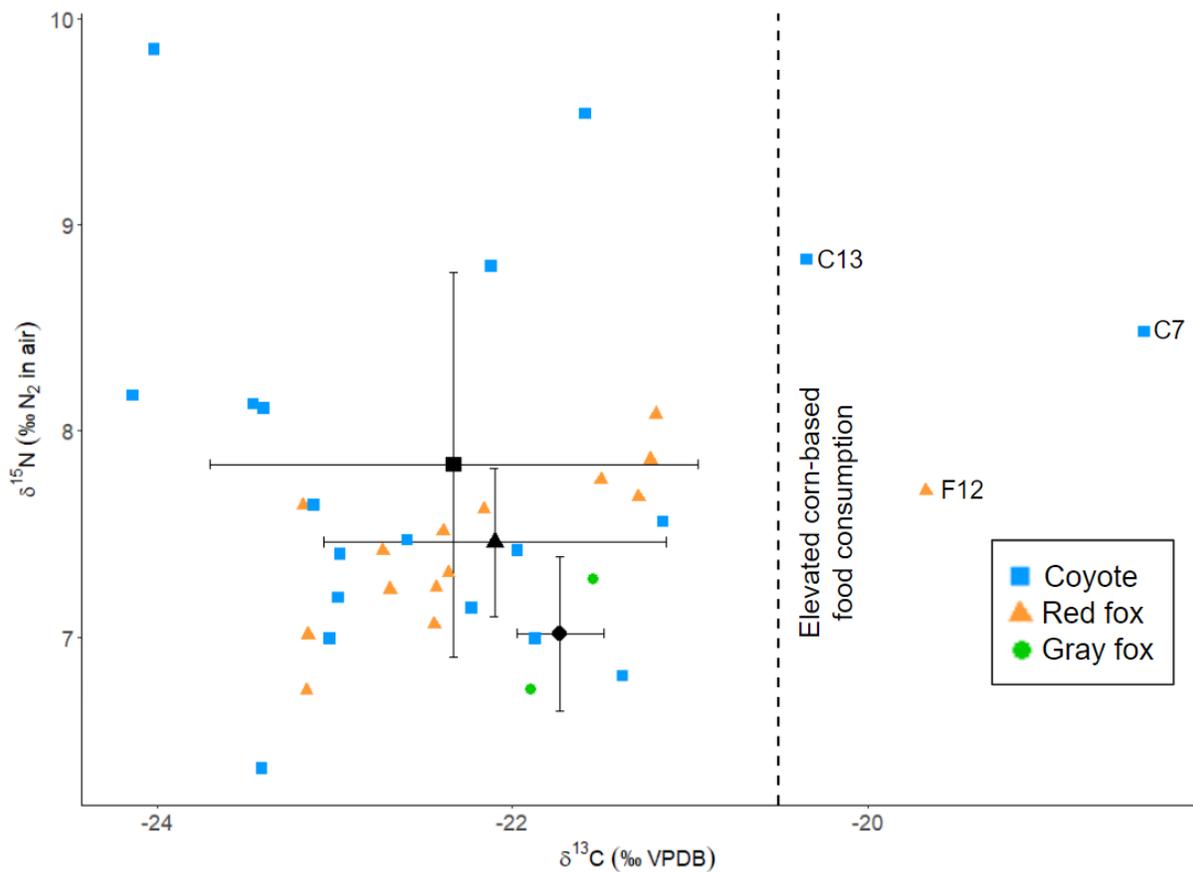
Coyotes and foxes displayed high variability in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  stable isotope ratios found in their hair (Figure 6) but variability was not explained by the percentage of impervious surface within the study animal’s home range in coyotes or red foxes ( $\delta^{13}\text{C}$ :  $F_{1,10} = 1.9$ ,  $p = 0.195$ , red foxes;  $F_{1,16} = 0.4$ ,  $p = 0.536$ , coyotes;  $\delta^{15}\text{N}$ :  $F_{1,10} = 0.4$ ,  $p = 0.551$ , red foxes;  $F_{1,16} = 0.003$ ,  $p = 0.955$ , coyotes).

Coyotes were found to have an average  $\delta^{13}\text{C}$  ratio of  $-22.3$  parts per thousand (‰;  $SD = 1.4$ ,  $N = 19$ ) difference from the reference, and a  $\delta^{15}\text{N}$  ratio of  $7.8$ ‰ ( $SD = 0.9$ ,  $N = 19$ ). Red foxes displayed similar values, with a  $\delta^{13}\text{C}$  ratio of  $-22.1$ ‰ ( $SD = 1.0$ ,  $N = 15$ ) and a  $\delta^{15}\text{N}$  ratio of  $7.5$ ‰ ( $SD = 0.4$ ,  $N = 15$ ). The two gray foxes averaged a  $\delta^{13}\text{C}$  ratio of  $-21.7$ ‰ ( $SD = 0.25$ ) and a  $\delta^{15}\text{N}$  ratio of  $7.0$ ‰ ( $SD = 0.4$ ,  $N = 2$ ).

Ratios of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  did not differ between coyotes and red foxes ( $\delta^{13}\text{C}$ :  $F_{1,32} = 0.2$ ,  $p = 0.599$ ;  $\delta^{15}\text{N}$ :  $F_{1,32} = 2.2$ ,  $p = 0.149$ ; Figure 6). All three species exhibited variability in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Gray foxes exhibited the least variation in  $\delta^{13}\text{C}$  (coefficient of variation [ $CV$ ] = 0.01) and intermediate variation in  $\delta^{15}\text{N}$  ( $CV = 0.06$ ). Red foxes exhibited intermediate variation in  $\delta^{13}\text{C}$  ( $CV = 0.04$ ) and the least variation in  $\delta^{15}\text{N}$  ( $CV = 0.05$ ). Relative to red foxes, coyotes exhibited 1.5-times greater variation in  $\delta^{13}\text{C}$  ( $CV = 0.06$ ) and two-times greater variation in  $\delta^{15}\text{N}$  ( $CV = 0.12$ ).

Corn-rich diets were uncommon for coyotes and foxes. Only 11% of coyotes, 7% of red foxes, and 0% of gray foxes had corn-rich diets (above a threshold considered high;  $\delta^{13}\text{C} > -20.5$ ). Of the two coyotes with corn-rich diets, C13 and C7 had 5% and 25% impervious surfaces in their home ranges, and the only red fox with a corn-rich diet (F12) had 50% impervious surface

(Figure 6). The ranges of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope ratios for both species of fox were within the range of coyotes. Although there was high overlap in  $\delta^{15}\text{N}$  ratios between coyotes and red foxes, 42% of coyotes ( $N = 8$ ) had  $\delta^{15}\text{N}$  ratios higher than the maximum recorded for red foxes.



**Figure 6.** Stable isotope ratios ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) for coyotes, red foxes, and gray foxes in the Twin Cities Metro Area. Black shapes represent mean ( $\pm$  SD; error bars)  $\delta^{15}\text{N}$ ‰ and  $\delta^{13}\text{C}$ ‰ pooled by species. The dashed line is the threshold for a high consumption of corn-rich food.

## Disease prevalence

We detected a total of eight pathogens in serum of the 17 coyotes, 12 red foxes, and one gray fox we sampled (Table 2); indicating previous or current pathogen exposure. All 30 of these study animals had canine parvovirus antigens, while canine distemper antigens were present in 94% of coyotes, 75% of red foxes, and in the one gray fox. We detected Lyme disease, *Leptospira*, and *Toxoplasma gondii* antigens in coyotes and red foxes, while *T. gondii* was the only additional antigen detected in the gray fox. *T. gondii* was detected in 2.8- to 2.9-times more red foxes (50% [IgG] and 83% [IgM] of foxes) than coyotes (18% [IgG] and 29% [IgM] of coyotes). Overall, we detected 3.4 ( $SD = 0.9$ ,  $N = 17$ ) pathogen antigens in coyotes, 2.3 ( $SD = 0.7$ ,  $N = 12$ ) in red foxes, and three in the one gray fox.

|                                                       | Coyote    | Red fox   | Gray fox |
|-------------------------------------------------------|-----------|-----------|----------|
| <u>Serological pathogens</u>                          |           |           |          |
| N individuals                                         | 17        | 12        | 1        |
| Heartworm ( <i>Dirofilaria immitis</i> ) antigen      | 0         | 0         | 0        |
| <i>Ehrlichia</i> antibody                             | 0         | 0         | 0        |
| Lyme disease ( <i>Borrelia burgdorferi</i> ) antibody | 4         | 7         | 0        |
| Anaplasmosis ( <i>Anaplasma</i> sp.)                  | 0         | 0         | 0        |
| <i>Leptospira atumnalis</i>                           | 2         | 3         | 0        |
| <i>Leptospira bratislavis</i>                         | 1         | 2         | 0        |
| <i>Leptospira canicola</i>                            | 0         | 0         | 0        |
| <i>Leptospira grippotyphosa</i>                       | 1         | 2         | 0        |
| <i>Leptospira hardjo</i>                              | 0         | 0         | 0        |
| <i>Leptospira icterohaemorrhagiae</i>                 | 0         | 0         | 0        |
| <i>Leptospira pomona</i>                              | 0         | 0         | 0        |
| Toxoplasmosis ( <i>Toxoplasma gondii</i> ) IgG        | 5         | 10        | 1        |
| Toxoplasmosis ( <i>Toxoplasma gondii</i> ) IgM        | 3         | 6         | 0        |
| Canine parvovirus                                     | 17        | 12        | 1        |
| Canine distemper                                      | 16        | 9         | 1        |
| Serology pathogen richness (mean ± SD)                | 3.4 ± 0.9 | 2.3 ± 0.7 | 3*       |
| <u>Fecal pathogens (sucrose fecal float)</u>          |           |           |          |
| N individuals                                         | 7         | 1         | 0        |
| <i>Toxocara canis</i>                                 | 3         | 0         | —        |
| <i>Toxocara leonia</i>                                | 1         | 0         | —        |
| Coccidea                                              | 5         | 0         | —        |
| <i>Echinococcus</i> sp.                               | 1         | 0         | —        |
| <i>Toxoplasma gondii</i>                              | 1         | 0         | —        |
| <i>Chyptosporidium</i> sp.                            | 1         | 0         | —        |
| <i>Capillaria</i> sp.                                 | 0         | 1         | —        |
| <i>Isospora</i> sp.                                   | 0         | 1         | —        |
| <i>Tricharis vulpis</i>                               | 0         | 1         | —        |
| <i>Diphyllobothrium latum</i>                         | 0         | 1         | —        |
| <u>Fecal pathogens (zinc sulfate fecal float)</u>     |           |           |          |
| N individuals                                         | 6         | 1         | 0        |
| <i>Giardia intestinalis</i>                           | 1         | 0         | —        |
| Strongylidae                                          | 1         | 1         | —        |
| <i>Toxoplasma gondii</i>                              | 1         | 0         | —        |
| Coccidea                                              | 1         | 0         | —        |
| <i>Isospora</i> sp.                                   | 1         | 1         | —        |
| <i>Acylostoma caninum</i>                             | 0         | 1         | —        |
| <i>Tricharis vulpis</i>                               | 0         | 1         | —        |
| Fecal pathogen richness (mean ± SD)                   | 2.4 ± 1.4 | 6*        | —        |

\*Richness values without SD result from single observations of a host species.

**Table 2.** Pathogen antigens and parasites detected in coyotes and foxes in the Twin Cities Metro Area. Pathogen richness is the number of pathogens detected per individual.

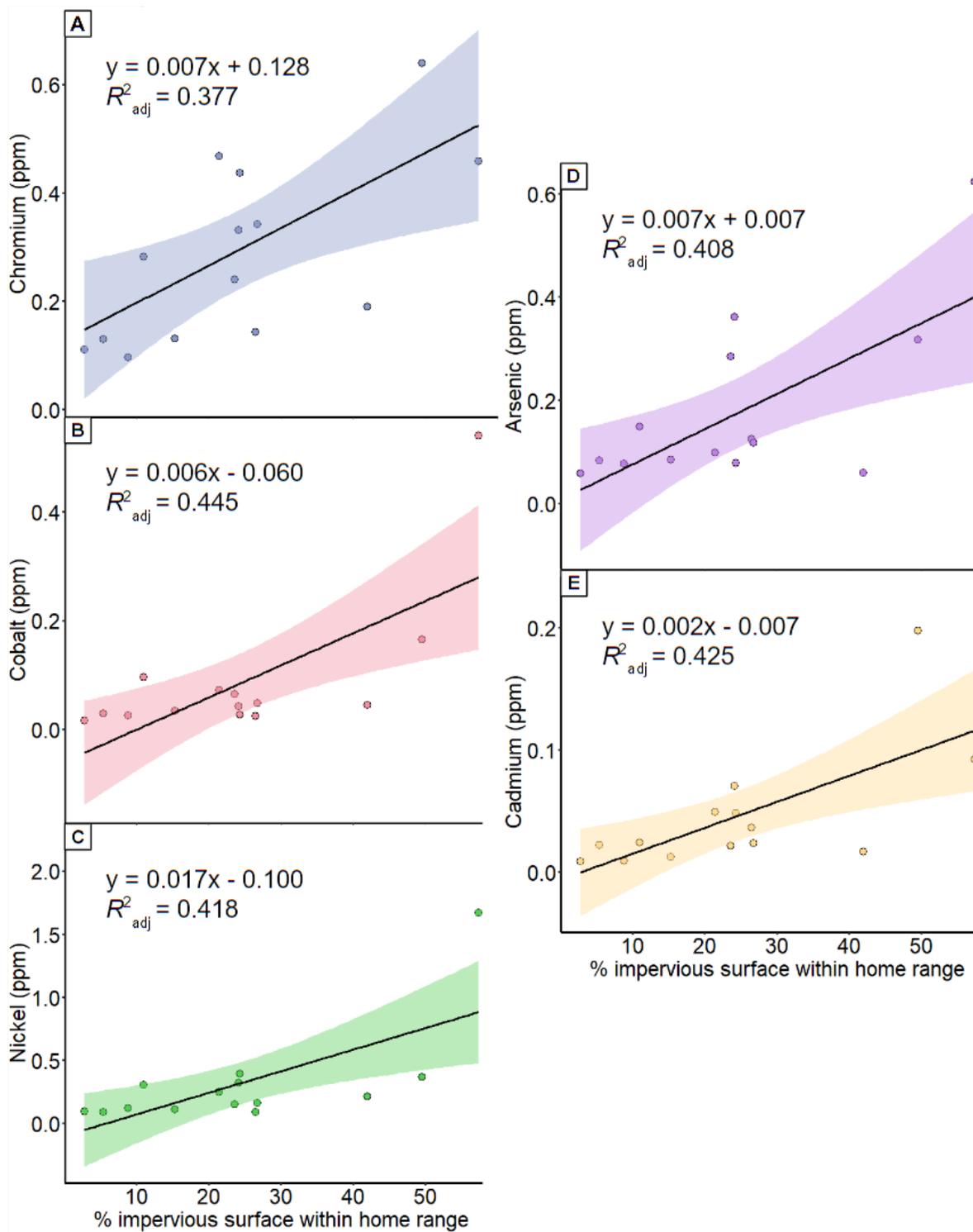
We identified 14 fecal parasites (Table 2) from rectal fecal samples of seven coyotes and one red fox, but were unable to collect samples from other study animals (fecal matter was absent). We identified *Coccidia* most frequently in coyotes ( $N = 5$  individuals). Coyotes had an average fecal

parasite richness of 2.4 ( $SD = 1.4$ ,  $N = 7$  individuals) while the single red fox had 2.5-times greater fecal parasite richness.

Fecal parasite richness, presence of pathogens, and presence of parasites were not correlated with any landcover variables we tested (all  $p > 0.01$ ), but serological pathogen richness was positively correlated with the proportion of annual home range covered by non-moving water bodies ( $\beta_1 = 10.1$ ,  $R^2_{\text{adj}} = 0.39$ ,  $F_{1,14} = 10.6$ ,  $p = 0.006$ ).

## Metals

Impervious surface was positively correlated with levels of chromium ( $F_{1,13} = 9.5$ ,  $p = 0.009$ ; Figure 7A), cobalt ( $F_{1,13} = 12.2$ ,  $p = 0.004$ ; Figure 7B), nickel ( $F_{1,13} = 11.0$ ,  $p = 0.006$ ; Figure 7C), arsenic ( $F_{1,13} = 10.7$ ,  $p = 0.006$ ; Figure 7D), and cadmium in coyote hair ( $F_{1,13} = 11.4$ ,  $p = 0.005$ ; Figure 7E). No other metals were found to correlate with percent impervious surfaces with  $p$ -values adjusted to  $\alpha = 0.01$  for experimentwise error (i.e., all  $p > 0.01$ ). Non-moving water bodies and proximity to the Minnesota and Mississippi Rivers were not correlated with the content of any metals found in coyote or fox hair (all  $p > 0.01$ ).



**Figure 7.** Linear regression lines (with 95% confidence intervals) showing correlations between chromium (A), cobalt (B), nickel (C), arsenic (D) and cadmium levels (E) found in coyote hair across impervious surfaces.

## Home range analysis

We developed multi-season (annual) 95% KDE<sub>C</sub> home ranges for 33 coyotes and foxes ( $N_{\text{coyote}} = 17$ ,  $N_{\text{gray fox}} = 2$ ,  $N_{\text{red fox}} = 14$ ; Table 3, Figure 8). Two red foxes were excluded because they were classified as having an unknown life history (< 30 d of tracking data) or dispersed without establishing a home range.

The average number of locations used to generate annual KDE<sub>C</sub> home ranges for coyotes, red foxes, and gray foxes were 457.1 ( $SD = 225.7$ ,  $N = 17$ ), 195.1 ( $SD = 158.5$ ,  $N = 13$ ) and 306.0 ( $SD = 330.9$ ,  $N = 2$ ), respectively. Coyotes, red foxes, and gray foxes had respective average KDE<sub>C</sub> home ranges of 8.8 km<sup>2</sup> ( $SD = 5.9$ ,  $N = 17$ ), 8.9 km<sup>2</sup> ( $SD = 5.6$ ,  $N = 13$ ) and 2.4 km<sup>2</sup> ( $SD = 0.3$ ,  $N = 2$ ).

We developed breeding season 95% KDE<sub>C</sub> home ranges for 29 individuals ( $N_{\text{coyote}} = 15$ ,  $N_{\text{gray fox}} = 2$ ,  $N_{\text{red fox}} = 12$ ), pup-rearing ranges for 21 individuals ( $N_{\text{coyote}} = 13$ ,  $N_{\text{gray fox}} = 1$ ,  $N_{\text{red fox}} = 7$ ) and non-reproductive ranges for 17 individuals ( $N_{\text{coyote}} = 13$ ,  $N_{\text{gray fox}} = 1$ ,  $N_{\text{red fox}} = 3$ ; Table 3).

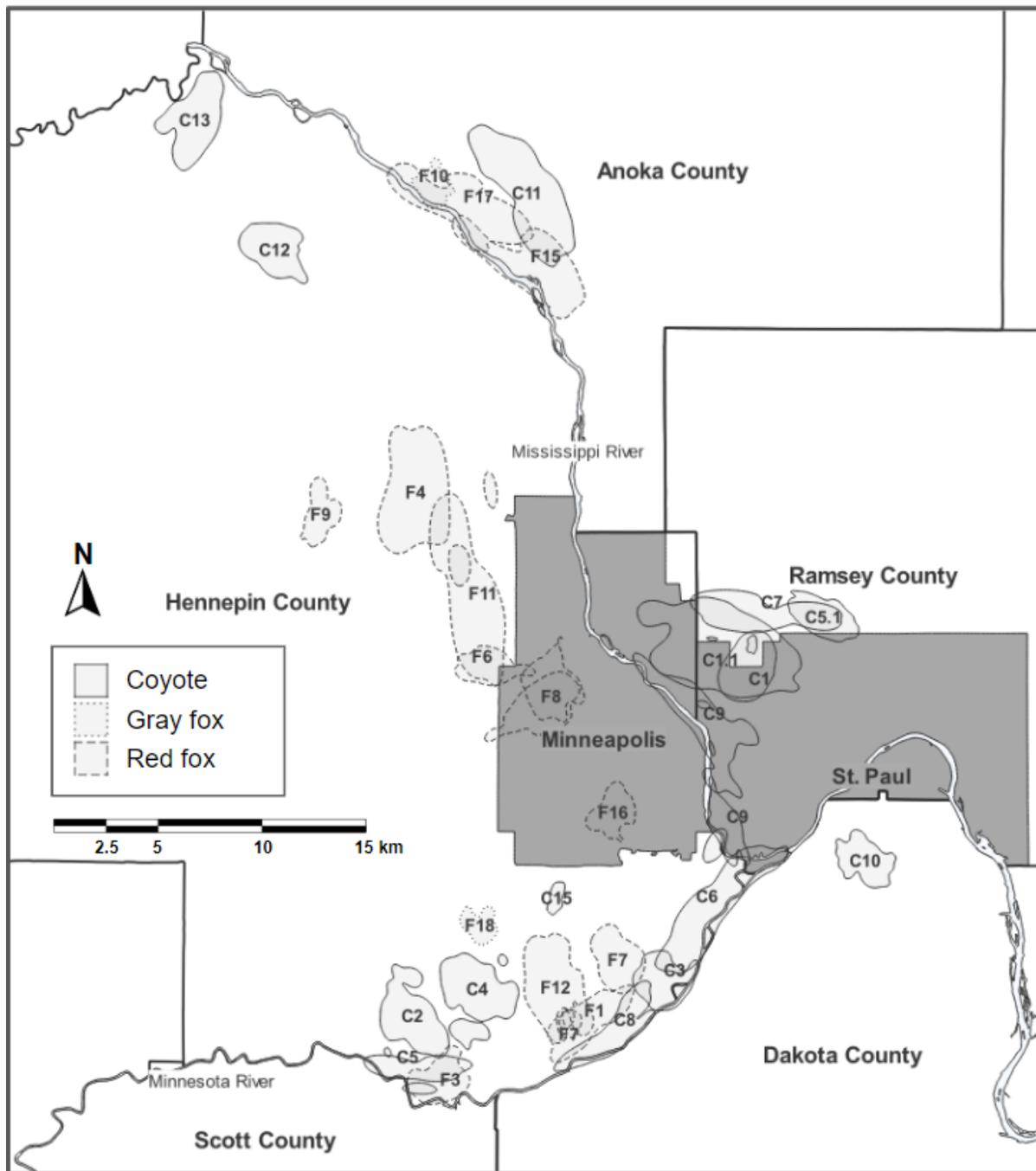
One coyote and one red fox each had two distinct multi-season home ranges (SVF variogram asymptotes absent when pooled to include transiency period included and asymptotic when separated). Periods of transiency were identified in four individuals ( $N_{\text{coyote}} = 2$ ,  $N_{\text{red fox}} = 2$ ).

Three individuals ( $N_{\text{coyote}} = 2$ ,  $N_{\text{red fox}} = 1$ ) dispersed out of a home range and never colonized a new home range before ceasing transmission of GPS locations ( $N_{\text{coyote}} = 1$ ) or dying ( $N_{\text{red fox}} = 1$ ,  $N_{\text{coyote}} = 1$ ). Two individuals ( $N_{\text{gray fox}} = 1$ ,  $N_{\text{red fox}} = 1$ ) dispersed < 30 d from the start of the tracking period, and home ranges could not be fit for them at the start of the tracking period.

|                  | Duration (d)  | Locations (n) | KDE (sq. km) | MCP (sq. km) | Home ranges (n) | Individuals (n) |
|------------------|---------------|---------------|--------------|--------------|-----------------|-----------------|
| <u>Coyote</u>    |               |               |              |              |                 |                 |
| Breeding         |               |               |              |              |                 |                 |
| Male             | 76.1 ± 33.4   | 149.6 ± 67.5  | 9.6 ± 6.5    | 6.7 ± 5.0    | 12              | 9               |
| Female           | 60.3 ± 28.8   | 118.4 ± 53.8  | 12.1 ± 9.6   | 8.3 ± 7.0    | 10              | 6               |
| Pooled           | 68.9 ± 31.6   | 135.4 ± 62.3  | 10.8 ± 8.0   | 7.5 ± 5.9    | 22              | 15              |
| Pup-rearing      |               |               |              |              |                 |                 |
| Male             | 121.2 ± 5     | 205.2 ± 22.2  | 9.6 ± 3.8    | 8.0 ± 3.9    | 6               | 6               |
| Female           | 120.7 ± 1.8   | 193.6 ± 26.2  | 7.8 ± 2.8    | 6.8 ± 2.6    | 8               | 7               |
| Pooled           | 120.9 ± 1.4   | 198.6 ± 24.4  | 8.6 ± 3.2    | 7.3 ± 3.1    | 14              | 13              |
| Non-reproductive |               |               |              |              |                 |                 |
| Male             | 100.6 ± 36.9  | 175.9 ± 76.8  | 8.7 ± 5.9    | 6.7 ± 4.6    | 7               | 7               |
| Female           | 87.9 ± 32.9   | 161.6 ± 80.0  | 10.4 ± 7.7   | 8.2 ± 7.7    | 9               | 6               |
| Pooled           | 93.5 ± 34.1   | 167.8 ± 76.3  | 9.6 ± 6.8    | 7.6 ± 6.4    | 16              | 13              |
| Annual           |               |               |              |              |                 |                 |
| Male             | 245.3 ± 136.8 | 439.6 ± 265.4 | 7.5 ± 5.3    | 7.1 ± 6.1    | 10              | 10              |
| Female           | 269.5 ± 93.1  | 476.6 ± 186.1 | 10.1 ± 6.6   | 10.0 ± 6.6   | 9               | 7               |
| Pooled           | 256.8 ± 115.6 | 457.1 ± 225.7 | 8.8 ± 5.9    | 8.5 ± 6.3    | 19              | 17              |
| <u>Red fox</u>   |               |               |              |              |                 |                 |
| Breeding         |               |               |              |              |                 |                 |
| Male             | 80.4 ± 23.4   | 94.8 ± 41.4   | 13.0 ± 10.1  | 7.8 ± 5.5    | 8               | 8               |
| Female           | 100.9 ± 10.4  | 103.3 ± 44.2  | 7.0 ± 3.9    | 4.8 ± 3.3    | 4               | 4               |
| Pooled           | 87.3 ± 21.9   | 97.6 ± 40.5   | 11.0 ± 8.8   | 6.8 ± 5.0    | 12              | 12              |
| Pup-rearing      |               |               |              |              |                 |                 |
| Male             | 84.8 ± 30.2   | 122.9 ± 43.6  | 5.6 ± 2.6    | 3.8 ± 2.1    | 8               | 6               |
| Female           | 115.0         | 144.0         | 7.2          | 4.5          | 1               | 1               |
| Pooled           | 88.2 ± 30.0   | 125.2 ± 41.4  | 5.7 ± 2.5    | 3.9 ± 2.0    | 9               | 7               |
| Non-reproductive |               |               |              |              |                 |                 |
| Male             | 100.9 ± 19.3  | 131.7 ± 35.1  | 7.0 ± 3.8    | 4.9 ± 2.5    | 3               | 3               |
| Annual           |               |               |              |              |                 |                 |
| Male             | 182.1 ± 169.0 | 215.8 ± 181.2 | 9.7 ± 6.2    | 7.0 ± 4.7    | 10              | 9               |
| Female           | 172.8 ± 109.2 | 143.5 ± 50.7  | 7.0 ± 3.7    | 5.2 ± 3.2    | 4               | 4               |
| Pooled           | 179.4 ± 150.1 | 195.1 ± 156.5 | 8.9 ± 5.6    | 6.5 ± 4.3    | 14              | 13              |
| <u>Gray fox</u>  |               |               |              |              |                 |                 |
| Breeding         |               |               |              |              |                 |                 |
| Male             | 62.3          | 72.0          | 2.3          | 1.1          | 1               | 1               |
| Female           | 118.7 ± .6    | 105.0 ± 33.9  | 2.7 ± .0     | 1.8 ± .4     | 2               | 1               |
| Pooled           | 99.9 ± 32.6   | 94.0 ± 30.6   | 2.6 ± .3     | 1.6 ± .5     | 3               | 2               |
| Pup-rearing      |               |               |              |              |                 |                 |
| Female           | 119.6         | 130.0         | 1.3          | .9           | 1               | 1               |
| Non-reproductive |               |               |              |              |                 |                 |
| Female           | 122.8         | 200.0         | 2.8          | 2.0          | 1               | 1               |
| Annual           |               |               |              |              |                 |                 |
| Male             | 62.3          | 72.0          | 2.3          | 1.1          | 1               | 1               |
| Female           | 484.5         | 540.0         | 2.6          | 2.2          | 1               | 1               |
| Pooled           | 273.4 ± 298.5 | 306.0 ± 330.9 | 2.4 ± .3     | 1.7 ± .8     | 2               | 2               |

Values are given as mean ± SD.

**Table 3.** Summary of 95% KDE<sub>C</sub> and 95% MCP home range estimates. Duration of tracking period, number of locations recorded, home range area, number of home ranges, and number of individual animals are given for each species, sex and season.



**Figure 8.** Annual 95% KDE<sub>C</sub> home range estimates for coyotes, gray foxes, and red foxes in the TCMA.

## Resource selection

Coyotes were found to select home ranges composed of average of 36.3% habitat with canopy cover, 15.4% wetland cover types, road densities of 6.6 km/km<sup>2</sup>, 29.2% residential areas, 8.5 % slope grade, 6.7% cover of buildings and COI values of 0.24. Red foxes selected 36.6% habitat with canopy cover, 3.9% wetland cover types, road densities of 10.3 km/km<sup>2</sup>, 47.2% residential

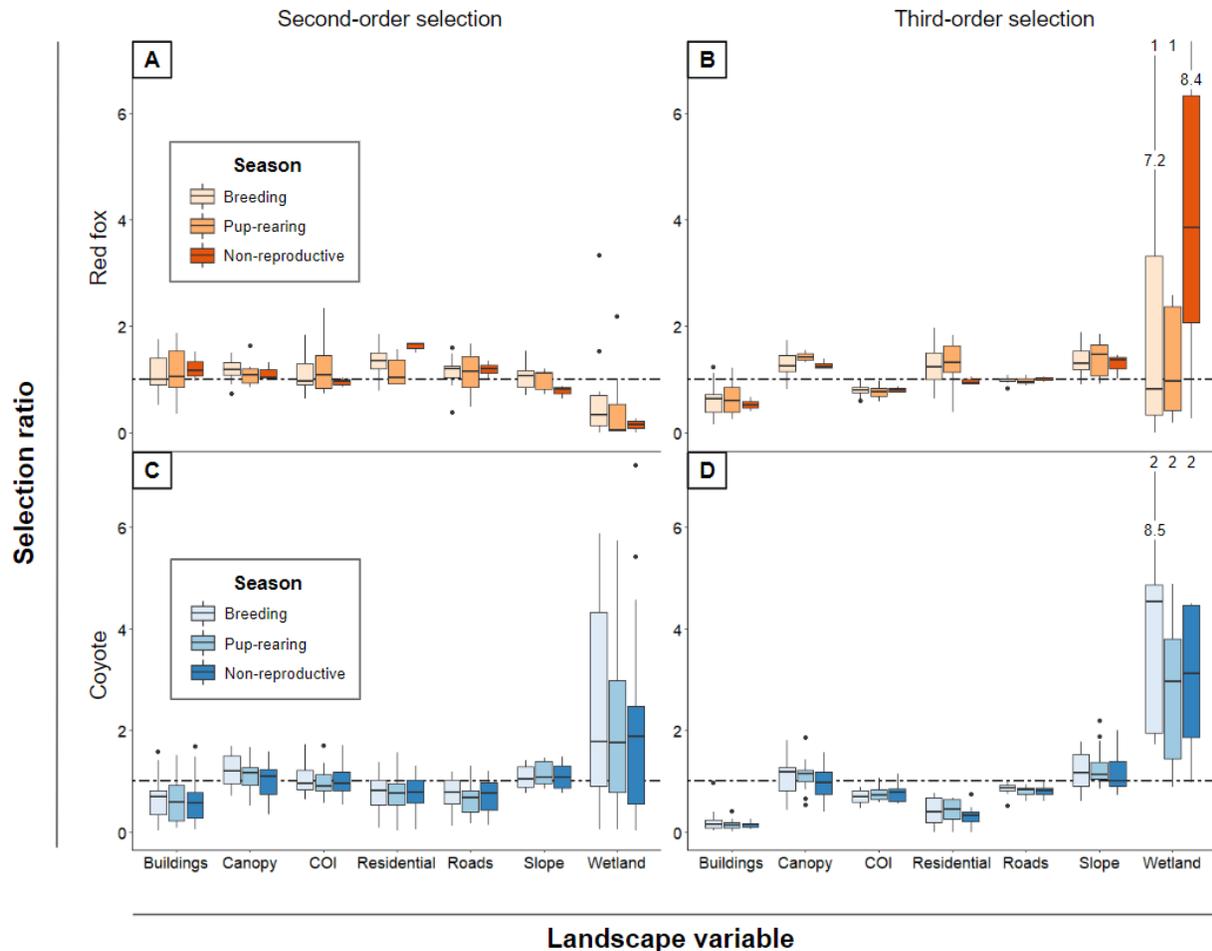
areas, 7.4% slope grade, 10.9% cover of buildings and COI values of 0.28. The two gray foxes selected home ranges with 30.6% habitat with canopy cover, 1.1% wetland cover types, road densities of 9.5 km/km<sup>2</sup>, 50.2% residential areas, 5.7% slope grade, 13.8% cover of buildings and COI values of 0.26. The study area was composed of 32.7% habitat with canopy cover, 7.2% wetland cover types, has road densities of 9.1 km/km<sup>2</sup>, is 37.5% residential areas, has an average of 7.6% slope grade, 10.3% cover of buildings and COI value of 0.24.

RSF models were fit to every individual for which a KDE<sub>C</sub> home range was estimated (see *Results: Home range analysis*). At the home range scale (second-order selection), coyotes were 1.43 times more likely to have home ranges in areas with low road density, and 1.16 times more likely to select areas with high wetland habitat relative to what was available in the study area across all seasons (Figure 9C). Averaged across seasons, red foxes were 1.41 times more likely to choose home ranges in areas with more residential areas available, and 1.36 times more likely to choose areas with high road density (Figure 9A). Gray foxes were 1.68 times more likely to choose home ranges with high residential areas and 1.90 times more likely to select home ranges with low slopes across all seasons.

Seasonally, areas with canopy cover were 1.17 times more likely to be selected by coyotes as home ranges in the breeding season, areas with high COI 1.14 times more likely in the non-reproductive season, and areas with high slopes 1.17 times more likely in the pup-rearing and non-reproductive seasons (Figure 9C). Red foxes were an average of 1.20 times more likely to establish home ranges in areas with high COI in the breeding and pup-rearing seasons, while in the non-reproductive seasons they were 1.8 times more likely to select home ranges with low slopes and 1.48 times more likely to select areas with low available wetland habitat (Figure 9A). From both gray foxes, we determined that gray foxes were 1.48 times more likely to establish home ranges with high amounts of wetland during the breeding season. Individual second-order selection results are summarized in Appendix 1 (Table A1).

Within home ranges, coyotes were on average 1.72 times more likely to select areas with low building density, 1.43 times to select low COI, 1.41 times to select low residential areas, 1.24 times to select steep slopes and 1.38 times more likely to select wetlands across all seasons (Figure 9D). Red foxes were shown to be an average of 1.30 times more likely to select areas of their home ranges with steep slopes, 1.37 times more likely to select areas with low COI, and 1.50 times more likely to choose areas with low building density (Figure 9B). Across seasons, gray foxes were on average 2.85 times more likely to select wetlands, 1.98 times more likely to select areas with canopy and 1.78 times more likely to select home ranges with low building density.

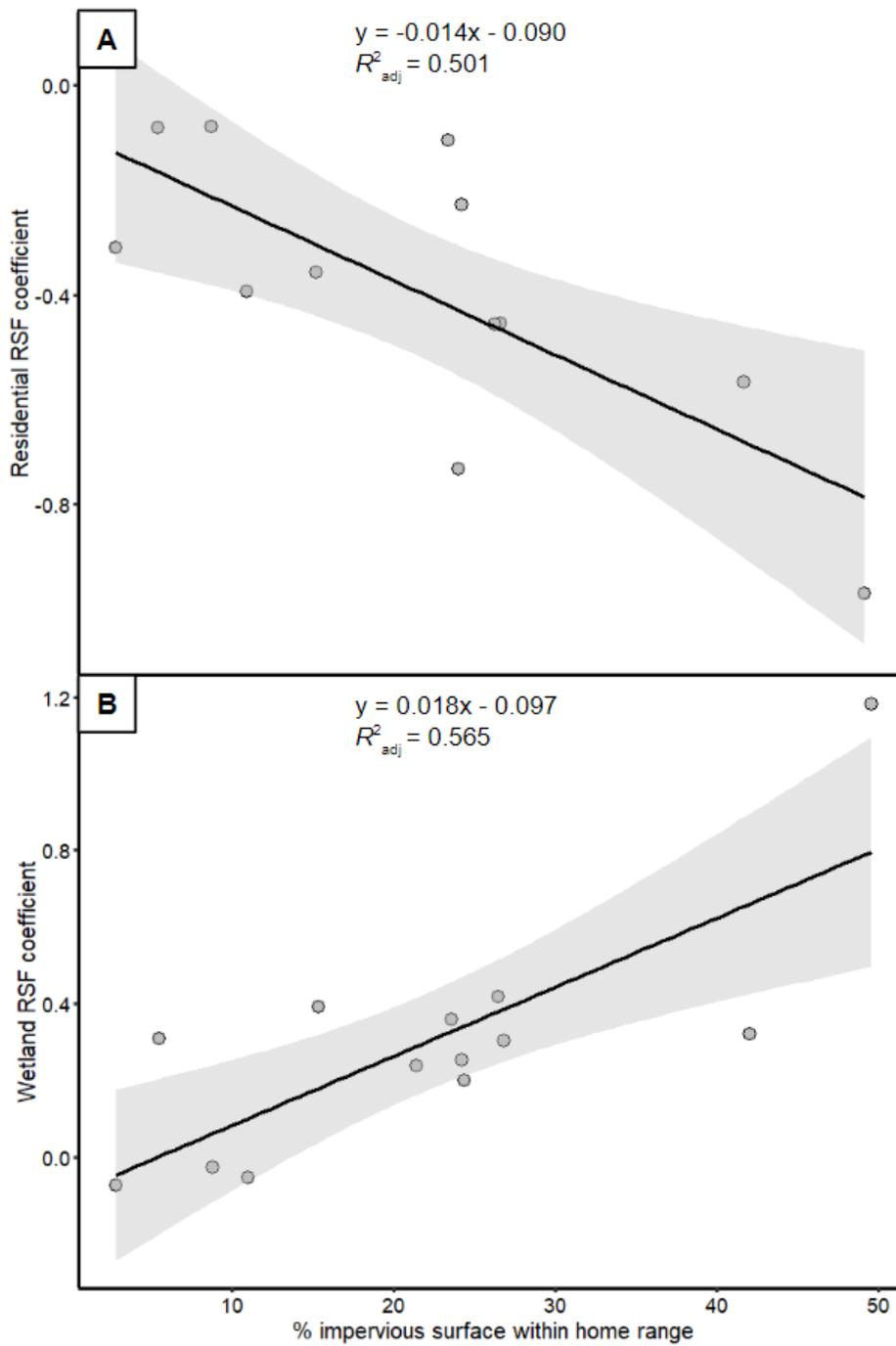
Coyotes were 1.39 times more likely to choose areas with low road density during the pup-rearing and non-reproductive seasons. Red foxes were 1.55 times more likely to select areas with high canopy cover during the pup-rearing and non-breeding seasons, and 1.38 times more likely to select residential areas in the breeding season. During the breeding season, gray foxes were 2.05 times more likely to select areas with high COI. Individual third-order selection results are summarized in Appendix 1 (Table A2).



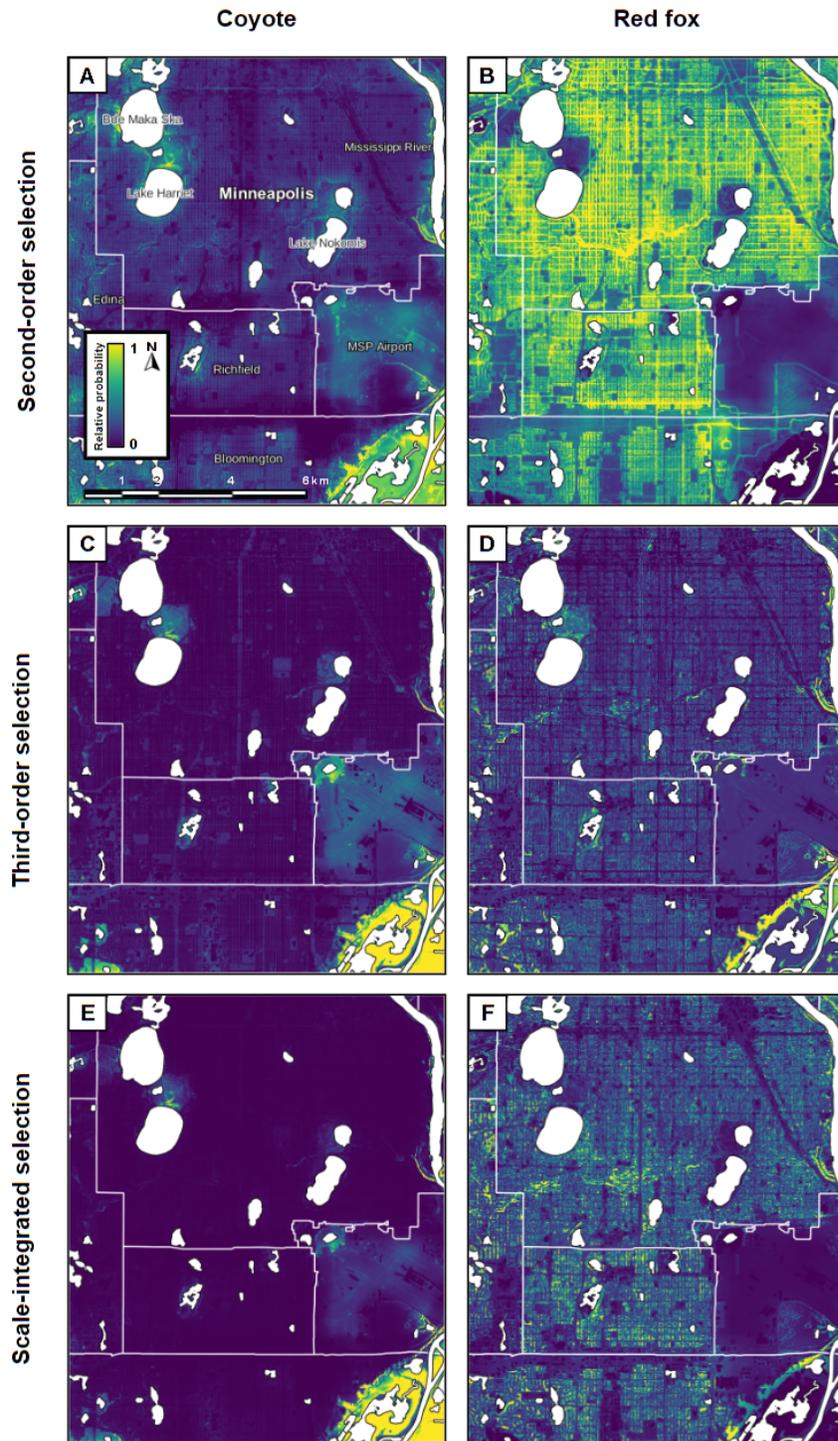
**Figure 9.** Box plots of per-animal selection ratios (i.e., mean landcover variable an individual selected/mean available) for each landcover variable at each order of selection for red foxes (A–B) and coyotes (C–D) summarized by biological season. Selection ratios > 1 (dashed line) indicate selection of a variable. Points above or below box plots indicate outliers, while numbers above box plots indicate the number of outliers beyond the extent of the y-axis range. Numbers within the box plot indicate whisker extent if beyond y-axis range.

During the pup-rearing season, selection of non-residential areas within the home range increased as percent impervious surface increases ( $\beta_1 = -0.014$ ,  $R^2_{\text{adj}} = 0.50$ ,  $F_{1,10} = 12.0$ ,  $p = 0.006$ ; Figure 10A), while selection for wetland habitat increased ( $\beta_1 = 0.018$ ,  $R^2_{\text{adj}} = 0.56$ ,  $F_{1,11} = 16.6$ ,  $p = 0.002$ ; Figure 10B). No other coefficients were found to change with percent impervious surfaces in any species.

Using the second- and third-order selection RSF models developed for coyotes and red foxes, we developed second-order, third-order and scale-integrated selection maps depicting the probability that an area (represented by a raster pixel) will be selected by a coyote or red fox in the study area (Figures 11–13).



**Figure 10.** Linear regression lines (with 95% confidence intervals) showing changes in individual coyote third-order selection coefficients for residential areas (A) and wetlands (B) as percent impervious surfaces within their home range increases during the pup-rearing season.



**Figure 11.** Examples of relative selection maps developed for coyotes (A, C, E) and red foxes (B, D, F) in the area west of the MSP Airport in the TCMA. Second order maps depict the relative probability of a pixel being selected within a home range (A–B), third order maps depict the relative probability of being selected within an individual’s home range (C–D), and scale-integrated maps indicate the relative probability of a pixel being selected within a home range, given the probability that the pixel is within a home range (E–F).

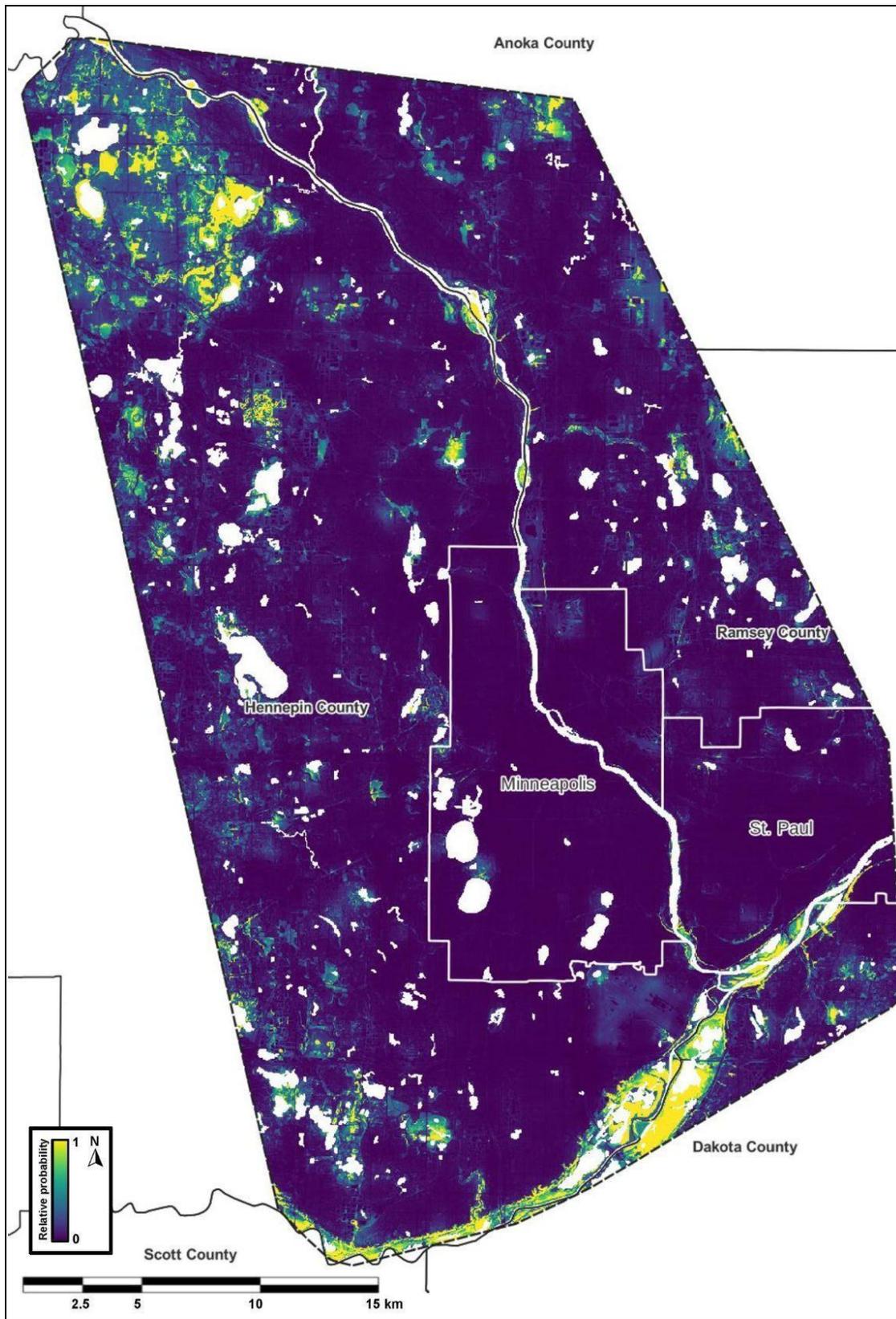


Figure 12. Coyote scale-integrated selection map for the pup-rearing season across the study area.

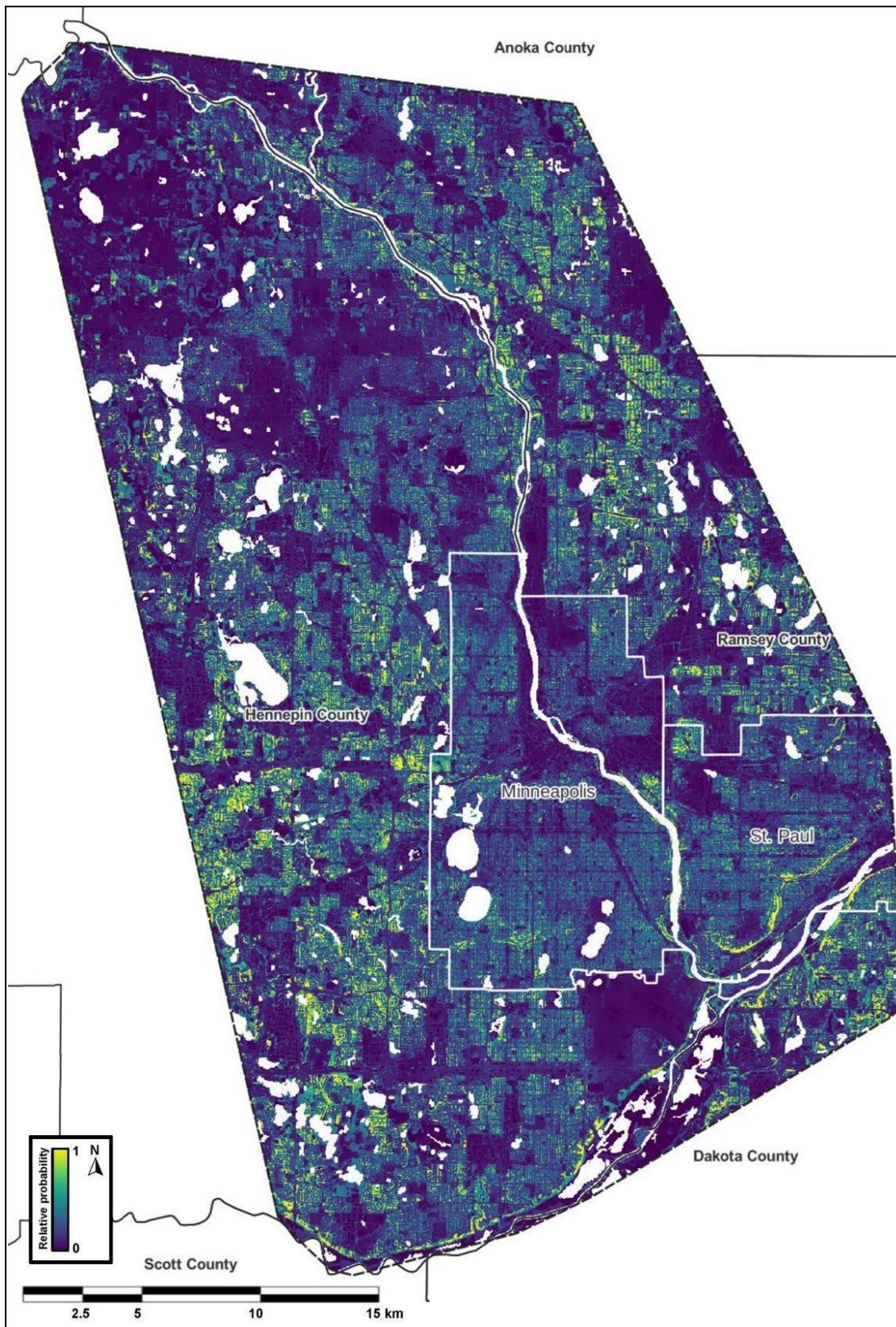


Figure 13. Red fox scale-integrated selection map in the pup-rearing season across the study area.

## Distribution and abundance

We found 82% of the study area (985 km<sup>2</sup>) contained suitable habitat for coyote territories (Figure 14A). This area could support 116 median-sized home ranges. Based on varying the number of possible pack members from two to six, we estimate the population to be 261–783 coyotes, with 29–87 of those being transient (13%,  $N = 2$ ; Table 4). Coyote density was estimated to be 0.26–0.79 coyotes/km<sup>2</sup> (one coyote per 1.3–3.8 km<sup>2</sup>) within the areas suitable for home ranges, and 0.22–0.65 coyotes/km<sup>2</sup> (one coyote per 1.5–4.5 km<sup>2</sup>) in the entire study area.

Sixty-seven percent (803 km<sup>2</sup>) of the study area had habitat suitable for 123 red fox home ranges (246 individuals in mated pairs, Figure 14B). We estimated that there were 31 transient red foxes from observations of collared red foxes (12% of collared red foxes were transient;  $N = 2$ ) for a total estimated population of 277 individuals.

Of the area suitable for red fox home ranges, 80% overlapped with the areas suitable for coyote home ranges (646 km<sup>2</sup>, Figure 14C). Since we expect coyotes to exclude red foxes from heavily used areas of their home range (i.e., home range core areas), we calculated the number of possible coyote home ranges in that area ( $N = 76$ ), used 50% KDE<sub>C</sub> isopleths of coyote breeding season home range estimates to approximate the area of coyote home range core areas, and subtracted the product of the number of home ranges and the median area 50% KDE<sub>C</sub> isopleth (131 km<sup>2</sup>) from the available area. This left a total of 672 km<sup>2</sup> of habitat suitable for red fox home ranges, which could support 103 home ranges. A lower estimate of red fox abundance from this available area—accounting for overlap with suitable coyote habitat—would be 230 individuals (206 territorial, 24 transient).

From these estimates, we predict red fox density across the study area to be of 0.29–0.34 (one red fox per 2.9–3.4 km<sup>2</sup>) in areas with compatible habitat, and 0.19–0.23 (one red fox per 4.5–5.3 km<sup>2</sup>) across the study area.

Gray fox populations were not estimated due to small sample size ( $N = 2$ ).

|                         | <i>n</i> home ranges | <i>n</i> territorial | <i>n</i> transient | <i>n</i> total | Density (km <sup>-2</sup> ) |
|-------------------------|----------------------|----------------------|--------------------|----------------|-----------------------------|
| <u>Coyote</u>           |                      |                      |                    |                |                             |
| Mated pair              | 116                  | 232                  | 29                 | 261            | 0.22                        |
| Pack size = 3           | 116                  | 348                  | 44                 | 392            | 0.32                        |
| Pack size = 4           | 116                  | 464                  | 58                 | 522            | 0.43                        |
| Pack size = 5           | 116                  | 580                  | 73                 | 653            | 0.54                        |
| Pack size = 6           | 116                  | 696                  | 87                 | 783            | 0.65                        |
| <u>Red fox</u>          |                      |                      |                    |                |                             |
| Upper estimate          | 123                  | 246                  | 29                 | 275            | 0.23                        |
| Adj. for coyote overlap | 103                  | 206                  | 24                 | 230            | 0.19                        |

**Table 4.** Abundance estimates of coyotes and red foxes in the study area, with predicted density across the entire study area.



**Figure 14.** Map depicting predicted suitable habitat for establishing territories in coyotes (A) and red foxes (B), and areas in which they overlap (C).

## Den sites

We located 20 active coyote dens, 19 red fox dens, and one gray fox den (Table 5). All 20 coyote dens were located in non-residential areas with natural vegetation; 15 were subterranean, four dens were located in culverts, and one was in a hollow log.

Of the 19 red fox dens, 11 (58%) in residential areas and eight (42%) were in non-residential areas. Most dens (58%) were under a manmade structure, and of these 53% were associated with dwellings (under a deck, shed, or house) while the remainder (47%) were subterranean. The one gray fox den we found was in a residential area under a deck. A pair of dens in Theodore Wirth Park were occupied by red foxes in 2021 (Unknown 5) and occupied by coyotes (Unknown 1) in spring 2022.

| Coyote    |              |             | Red fox   |              |             | Gray fox |           |             |
|-----------|--------------|-------------|-----------|--------------|-------------|----------|-----------|-------------|
| ID        | Structure    | Residential | ID        | Structure    | Residential | ID       | Structure | Residential |
| C11       | Subterranean | N           | F1        | Subterranean | Y           | F10      | Structure | Y           |
| C1.1      | Subterranean | N           | F3        | Structure    | Y           |          |           |             |
| C1.1      | Subterranean | N           | F6        | Structure    | Y           |          |           |             |
| C1.1      | Subterranean | N           | F7        | Structure    | Y           |          |           |             |
| C1.1      | Culvert      | N           | F8        | Structure    | Y           |          |           |             |
| C3        | Subterranean | N           | F12       | Subterranean | N           |          |           |             |
| C3        | Log          | N           | F12       | Subterranean | N           |          |           |             |
| C8        | Subterranean | N           | Unknown 1 | Subterranean | N           |          |           |             |
| C8        | Subterranean | N           | Unknown 1 | Subterranean | N           |          |           |             |
| C4        | Subterranean | N           | Unknown 2 | Structure    | Y           |          |           |             |
| C4        | Subterranean | N           | Unknown 2 | Culvert      | N           |          |           |             |
| C5        | Subterranean | N           | Unknown 3 | Structure    | Y           |          |           |             |
| C9        | Culvert      | N           | Unknown 4 | Structure    | Y           |          |           |             |
| C9        | Culvert      | N           | Unknown 5 | Subterranean | N           |          |           |             |
| C9        | Culvert      | N           | Unknown 5 | Subterranean | N           |          |           |             |
| C10       | Subterranean | N           | Unknown 6 | Structure    | Y           |          |           |             |
| C15       | Subterranean | N           | Unknown 7 | Structure    | Y           |          |           |             |
| C15       | Subterranean | N           | Unknown 8 | Structure    | Y           |          |           |             |
| Unknown 1 | Subterranean | N           | Unknown 8 | Subterranean | N           |          |           |             |
| Unknown 1 | Subterranean | N           |           |              |             |          |           |             |

**Table 5.** Coyote and fox den locations in the Twin Cities Metro Area. Alphanumeric IDs were study animals with GPS collars. IDs beginning with unknown were from uncollared coyotes and foxes. A structure was made by humans and associated with a dwelling (e.g., deck, shed, house). Non-residential was a public or private green space not associated with human dwellings (residential neighborhoods).

## Discussion

### Survival

Variable annual survival suggests higher population growth for coyotes than for red foxes in the TCMA. Coyote survival was similar to other urban studies of established populations but red fox survival was lower than in other studies, with other urban studies reporting 1.4 to 2.1 times higher red fox survival (Table 6). These results, in combination with numerous anecdotal reports made by local residents of coyotes occupying areas once used by red foxes, suggest better demographics for coyotes than for foxes in the TCMA. Notably, inferential strength is limited due to wide confidence intervals that overlapped with results from other urban canid survival studies (Table 6); likely a result of modest sample sizes across studies.

| Author (year)               | Location                          | Sex              | Survival    | Lower CL*   | Upper CL*   |
|-----------------------------|-----------------------------------|------------------|-------------|-------------|-------------|
| <b>Coyote</b>               |                                   |                  |             |             |             |
| Grinder & Kraussman (2001)  | Tucson, AZ                        | M                | 0.86        | 0.62        | 1.10        |
| Soulsbury (2008)            | Santa Monica, CA                  | F & M            | 0.86        | --          | --          |
| Riley et al. (2003)         | Santa Monica, CA                  | F & M            | 0.83        | --          | --          |
| Riley et al. (2003)         | Santa Monica, CA                  | M                | 0.77        | --          | --          |
| <i>Current study (2022)</i> | <i>Minneapolis-Saint Paul, MN</i> | <i>F &amp; M</i> | <i>0.77</i> | <i>0.57</i> | <i>1.00</i> |
| Riley et al. (2003)         | Santa Monica, CA                  | F & M            | 0.74        | --          | --          |
| Riley et al. (2003)         | Santa Monica, CA                  | F                | 0.73        | --          | --          |
| Grinder & Kraussman (2001)  | Tucson, AZ                        | F & M            | 0.72        | 0.50        | 0.95        |
| Gehrt et al. (2011)         | Chicago, IL                       | F                | 0.70        | 0.57        | 0.83        |
| Gehrt et al. (2011)         | Chicago, IL                       | M                | 0.59        | 0.48        | 0.70        |
| <b>Red fox</b>              |                                   |                  |             |             |             |
| Soulsbury et al. (2008)     | Bristol, UK                       | M                | 0.43        | 0.26        | 0.60        |
| Gosselink et al. (2006)     | Champaign, IL                     | F & M            | 0.42        | 0.26        | 0.60        |
| Soulsbury et al. (2008)     | Bristol, UK                       | F                | 0.27        | 0.19        | 0.35        |
| <i>Current study (2022)</i> | <i>Minneapolis-Saint Paul, MN</i> | <i>F &amp; M</i> | <i>0.20</i> | <i>0.08</i> | <i>0.52</i> |

\*95% Confidence Limit

**Table 6.** Annual survival for coyotes and red foxes from urban studies of primarily adult study animals. The current study is italicized to facilitate comparison with other studies.

Canid attacks caused more red fox mortalities in the TCMA than we expected. In previous studies the combination of canid attacks and predation accounted for 8% ( $SD = 4\%$ ,  $N = 3$  studies) of urban red fox mortalities (Soulsbury et al. 2010). By comparison, the percentage of mortalities caused by canid attacks was 2.4-times greater in the TCMA (20%). We speculate that higher than expected canid attack mortalities in the TCMA was due to red fox interaction with an apparently expanding coyote population combined with free-roaming domestic dogs (*Canis familiaris*). Although coyotes have been observed in the TCMA for  $> 10$  yr (A. Shoemaker, Minnesota Trappers Association, Pers. Comm.), local residents have often reported coyotes in neighborhoods previously occupied by red foxes, and coyotes are known to attack and kill red foxes (likely due to territoriality; Soulsbury et al. 2010). In addition to coyotes, domestic dogs also kill red foxes (Soulsbury et al. 2010). Local residents reported to us that free-roaming domestic dogs chased a collared red fox that we found dead soon thereafter (but without apparent trauma) and trail cameras we deployed frequently recorded images of free-roaming dogs and red foxes, thereby showing overlap in dog–fox space-use.

## Diet

Coyotes and foxes consumed primarily natural foods in the TCMA, with only 8% of individuals exhibiting  $\delta^{13}C$  and  $\delta^{15}N$  values consistent with corn-rich diets (Newsome et al. 2015). This finding is consistent with other coyote studies that reported  $< 20\%$  of scats contained human-associated foods, including only 5% trash ( $SD = 6\%$ ,  $N = 9$  study areas) and 0.3% pet food ( $SD = 0.7\%$ ,  $N = 8$  study areas; Gehrt and Ridey 2010).

Wide dietary breadths show that coyotes and foxes relied on diverse food resources in the TCMA, which is consistent with research elsewhere that showed coyotes and foxes to be generalist foragers (Gehrt and Riley 2010). Wider dietary breadth suggests coyotes had more

flexible eating habits than red foxes in the TCMA but the reason for this is unclear. We speculate that TCMA coyotes had more flexible foraging habits. In this study, for example, we often encountered coyote scats rich in domestic apples (*Malus* spp.) during fall and early winter but we did not observe this for foxes, suggesting foxes did not forage on apples as frequently in the TCMA (though foxes consume fruits; Soulsbury et al. 2010). Another explanation is that greater dietary breadth mirrored larger coyote home ranges; coyotes may have encountered a broader range of food resources while traveling a larger area relative to foxes.

## Disease

The positive relationship between serological pathogen richness and non-moving water bodies appears to be partly explained by the interaction between vectors of pathogen transmission and habitat selection. *T. gondii* was one of the most prevalent pathogens we detected in blood serum. *T. gondii* infection can result in attraction to cat odors (urine), neuropsychiatric conditions, and aberrant behavior (e.g., Dopey Fox Syndrome; Milne et al. 2020) but its full effect on animal populations remains unclear (Milne et al. 2020b). Domestic cats (*Felis catus*) are the only definitive host of *T. gondii*, the oocysts of which are spread via cat feces that contaminate soil, crops, and water sources, including surface water contaminated by cat feces via runoff (Milne et al. 2020b, Lass et al. 2022). Hence, cat-feces-contamination of surface water used by coyotes and foxes may explain the link between *T. gondii* infection and non-moving water bodies. The greater prevalence of *T. gondii* in red foxes than in coyotes supports this conclusion because foxes selected residential areas, where cats are likely to be most abundant (and where we observed them most frequently), whereas coyotes did not. Hence, we hypothesize that selection of residential areas by foxes increased their risk of encountering surface waters contaminated by cat feces with *T. gondii* oocysts, resulting in greater prevalence of *T. gondii* in red foxes. In contrast, coyotes had lower prevalence of *T. gondii* because they selected non-residential areas where surface waters contaminated by cat feces with *T. gondii* oocysts were less frequent.

Our results suggest localized sarcoptic mange events rather than a widespread outbreak. Apparent mange was detected on only 6% of coyotes and 18% of red foxes. These percentages are low compared to mange outbreaks. In Bristol, UK, for example, the red fox population was reduced by > 95% in only 2 yr (Soulsbury et al. 2010).

## Metals

Our data provide reference levels for coyotes and foxes in the TCMA that improve understanding of how each species interacts with their environment. Establishing TCMA-specific reference levels is important because they vary between studies due to complex factors (Hough et al. 2020, Solademi and Thompson 2020). Elevated heavy metal content in TCMA coyotes that selected impervious surfaces is likely to be a result of using industrial areas more than foxes. Although RSFs did not differentiate between industrial and non-industrial non-residential areas, coyotes often used railroad yards and industrial parks. We expect that coyotes selecting areas with more industrial pollutants consumed (and bioaccumulated) hazardous metals more than foxes by foraging on small mammals and vegetation (e.g., fruits) and through contact with soil at den sites. For red foxes, impervious surfaces corresponded with residential areas that were less affected by industrial pollutants; residential areas have less heavy metal contamination than industrial, roadside, and commercial areas (Solademi and Thompson

2020). Consequently, foxes were less likely than coyotes to consume forage and den in areas polluted with heavy metals.

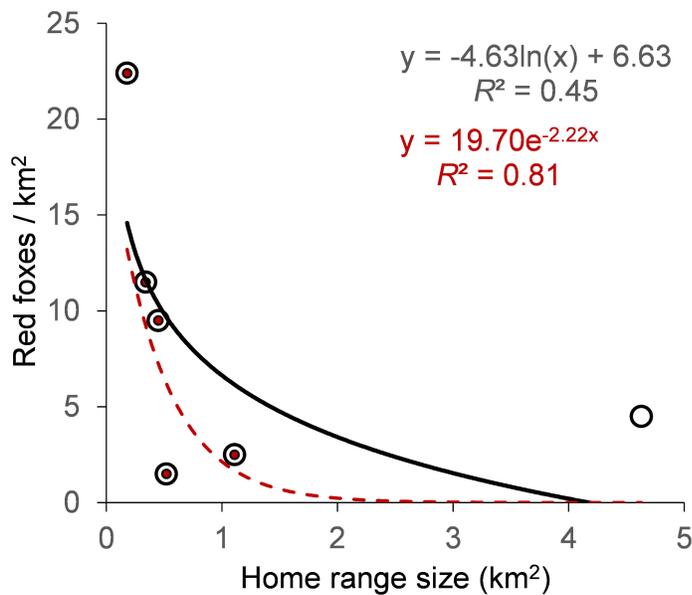
## Home range analysis

Home range size suggests greater resource availability for coyotes than for red foxes in the TCMA. Coyote home ranges were similar to or smaller than other urban studies, with other studies reporting median home ranges that were only 1.1-times larger than in the TCMA. Red fox home ranges in the TCMA, however, were 13.4-times larger than in other studies, including 12.5- and 1.4-times larger than other North American populations that are the same subspecies (*V. vulpes fulva*) as TCMA foxes (Table 7).

| Location                          | Area (km <sup>2</sup> ) |
|-----------------------------------|-------------------------|
| <b>Coyote</b>                     |                         |
| Los Angeles, CA                   | 5.0                     |
| Chicago, IL                       | 5.0                     |
| Lincoln, NB                       | 7.0                     |
| Albany, NY                        | 7.0                     |
| <i>Minneapolis-Saint Paul, MN</i> | 8.5                     |
| Lower Fraser Valley, BC           | 11.0                    |
| Tucson, AZ                        | 13.0                    |
| Tucson, AZ                        | 23.0                    |
| Cape Cod, MA                      | 36.0                    |
| <b>Red fox</b>                    |                         |
| Bristol, UK                       | 0.2                     |
| Zurich, SW                        | 0.3                     |
| Melbourne, ASTL                   | 0.5                     |
| Toronto, CA                       | 0.5                     |
| Edinburgh, UK                     | 1.1                     |
| Champaign, IL                     | 4.6                     |
| <i>Minneapolis-Saint Paul, MN</i> | 6.5                     |

**Table 7.** Annual home range sizes for coyotes and red foxes from urban studies sorted from smallest to largest for each species (adapted from Gehrt and Ridley 2010, and Soulsbury et al. 2010). The current study is italicized to facilitate comparison with other studies.

Because resource availability is often negatively correlated with home range size (abundant resources result in smaller home ranges), these contrasting inter-specific results suggest that coyotes find resources more easily (by traversing less area) than red foxes in the TCMA. Further, because of its negative correlation with population density (Figure 14; Soulsbury et al. 2010), red fox home range size suggests there was likely  $\leq 3$  foxes/km<sup>2</sup> in the TCMA (excluding an outlier population).



**Figure 14.** Negative correlation between home range size and density from urban red fox studies (data from Soulsbury et al. 2010). Data include (empty circles and solid black line) and exclude (red circles and hatched line) an apparent outlier (from Champaign, IL).

## RSFs and distribution

Examining RSF results across seasons, each of the habitat variables selected for by coyotes and red foxes within the home range suggest selection for areas of the landscape associated with low human use. Not only is this indicated by selection for low COI, low building density, and non-residential areas in coyotes, recreationists are also unlikely to spend time in areas with dangerously high slopes (e.g., in high slope areas of Mississippi Gorge Regional Park) or in the wetlands which coyotes prefer. For both species, selection for areas of the home range with high slopes could also be a function of selecting well-drained areas with suitable denning habitat (Way et al. 2001, Uruguchi & Takahashi 1998). Furthermore, coyotes selected the areas of their home ranges with low road density during the pup-rearing and non-reproductive seasons, which may be associated with avoiding areas with high vehicle traffic while caring for young.

This selection for areas with low human use appears to extend into second-order selection for coyotes, but not red foxes. While coyotes established home ranges in areas with relatively low human use (with more wetlands than average and low road density), red foxes were found in home ranges that were associated with high human use (containing residential areas and high road density). This aligns with the conclusions of another regional study of urban coyotes and red foxes, in which it was determined that they coexist in urban areas by selecting for different levels of urban development (Mueller et al. 2018). This result also aligns what would be expected in a human shield, in which a subordinate predator species uses areas of high human use as a refuge from conflict with a dominant predator (Berger et al. 2007, Gámez et al. 2021). This effect has already been shown to take place in coyotes and foxes within urban parks (Gámez et al. 2021), but our results suggest that red foxes establish home ranges in residential areas with high road density because those areas offer a refuge from conflict with coyotes. Since coyotes establish home ranges with low road density and select non-residential areas of their home

ranges, this leaves areas of the landscape for red foxes to establish home ranges which minimize the risk of encountering coyotes.

Red foxes were only associated with human-related variables on the second-order scale of selection, and within their home ranges displayed selection suggesting avoidance of where people are most active (i.e., areas with high COI) and areas with the most dwellings (i.e., areas with high building density) within those more developed landscapes. Red foxes only displayed seasonal selection for the residential areas within their home ranges while breeding, suggesting that those areas are not selected as habitat within their home ranges during most of the year even though they prefer home ranges with more residential areas.

Coyote second-order selection for higher COI in the non-reproductive season likely suggests home ranges incorporating parks with high levels of recreational activity. The areas with the highest COI values within home ranges are avoided during that season.

Non-residential areas with wetland habitat were most important for the most urban coyotes during the pup-rearing season. This result is intuitive, as coyotes would want to select the areas that were least likely to be used by people while raising pups. At least 59% of the tracked coyotes were found to use areas within wetland habitat as daytime rendezvous sites to care for pups during the pup-rearing season ( $N = 10$ ; G. Miller, pers. obs.). This result highlights the importance of the TCMA's urban wetland habitat in reducing conflict with urban coyotes during the pup-rearing season. Due to the unappealing nature of wetlands for recreational activities, these areas provide coyotes with areas in which they can remain relatively undisturbed during this high-conflict period (Breck et al. 2017).

Scale-integrated selection probability maps and predicted distribution maps suggest that the downtown areas and much of the residential areas of Minneapolis and St. Paul do not have the minimum resources necessary to support coyote home ranges (Figure 12, Figure 14A). Though coyotes are occasionally spotted in these areas, this data suggests that these individuals are not residents with stable home ranges, but rather transients or individuals in the process of dispersing. This aligns with results from Chicago, which found transients with more fluid home ranges were more likely to have home ranges including high amounts of residential and urban land (Gehrt et al. 2009, Newsome et al. 2015).

The downtown and industrial areas of Minneapolis and St. Paul also appear to lack the necessary resources to support resident red foxes, as are the areas that contain the most large, natural green spaces (i.e., NW quadrant of study area and Minnesota Valley National Wildlife Refuge; Figure 13, Figure 14B). Notably, besides the downtown areas of Minneapolis and St. Paul, the areas that have the lowest relative probability of being selected by red foxes seem to those with the highest relative probability of being selected by coyotes (Figures 12–13). This lends further support to our conclusions that avoiding areas with a high probability of encountering coyotes is one of the main driving factors in red fox distribution throughout the study area. Although our models predict that the least urbanized areas of the study area are unsuitable for red fox home ranges, these models may have little predictive power in areas beyond the metropolitan area where coyote and fox interactions with humans change (i.e., through differences in hunting and trapping practices and regulations).

Due to small sample size, we made no population-level conclusions about gray fox habitat selection patterns.

## Den sites

Variation in den sites selected by foxes and coyotes reflected other differences in behavior. Coyotes denned in non-residential areas, whereas most fox dens were in residential areas. Use of culverts shows adaptability in den site selection by coyotes and corresponds with use of industrial sites where interaction with humans was likely to be limited. In contrast, foxes often denned where human traffic was expected (e.g., near dwellings). These behaviors mirror our observations and those made by residents who reported fox pups near their homes (but not coyote pups).

## Population density

Coyote and red fox densities were lower than in many other urban settings. For coyotes, TCMA winter packs were two or three individuals, which makes 0.27 coyotes/km<sup>2</sup> (range: 0.22–0.32 coyotes/km<sup>2</sup>) the most plausible estimate we developed. This is similar to densities at one site in Los Angeles, CA (0.3–0.4 coyotes/km<sup>2</sup>) and fragmented natural areas that were urban-adjacent (0.21 coyotes/km<sup>2</sup>), but much lower than in Chicago, where densities were three- to eight-times greater (0.8–2.1 coyotes/km<sup>2</sup>; Gehrt et al. 2010).

A similar pattern emerged for red foxes. We estimated about 0.21 red foxes/km<sup>2</sup> but average densities elsewhere were 33- to 41-times larger (median 7 red foxes/km<sup>2</sup>), with a comparable estimate (0.7 red foxes/km<sup>2</sup>) only coming after a mange outbreak in Bristol, UK (Soulsbury et al. 2010). In addition to variable behavior and resource availability, widely varying field and analytical methods likely influence variation in density estimates. Regardless, our findings support the conclusion that coyote and fox densities in the TCMA are on the low end of the ranges observed in other cities.

## Management implications

Our results support the anecdotal observations made by residents and wildlife managers of a coyote population that has expanded and a fox population that has contracted. Our observations of coyote sign (tracks and scat) in nearly all large green spaces we searched suggests a population that has plateaued at a relatively low density across the TCMA. Extending this to future population size, of course, requires continued aversion by coyotes to centering their home ranges on residential areas (currently occupied by red foxes) and stable demographics (e.g., fecundity).

Our findings suggest that coyotes and foxes rarely become nuisances in the TCMA. Zero of our collared coyotes were reported as being in conflict with people and the only reported red fox conflict was due to a fox family leaving prey carcasses near a den located under a resident's shed (we collared this fox after conflict occurred). Additionally, the mate of one collared female coyote was reported as standing near its den (not departing when people arrived) at an area golf course. Of course, these results rely on incomplete reporting as it is unlikely that everyone contacted us post-conflict. However, it is likely that we would have been notified of repeated

conflicts of a collared coyote or fox (collars are visible) and that we would have been aware of any removal (euthanasia) of collared animals. Hence, it is likely that none of our collared study animals were nuisances. Conflicts have occurred in the TCMA, notably dog attacks by coyotes, but these appear to be relatively infrequent, as was the case in other studies (e.g., White and Gehrt 2009, Baker and Timm 2017).

Improving natural habitat in fragmented residential greenspaces is likely to benefit red foxes. Whereas coyotes appeared to occupy many of the large green spaces, red foxes often selected fragmented green spaces with natural vegetation in residential areas. Because of this, we expect that red foxes will benefit by management efforts that restore natural vegetation in residential greenspaces.

Wetland habitat in highly urbanized areas of the TCMA is likely a crucial element in reducing human-wildlife conflict with urban coyotes while they are raising pups. The ability to select wetlands as daytime rendezvous sites where pups are unlikely to encounter humans or pets May–Aug is likely one of the aspects of the TCMA landscape that make it amenable to territorial coyotes that successfully raise young with limited necessity for removal as a management action. Conserving these habitats should remain a primary goal in efforts to maintain urban coyote populations in the TCMA with low incidence of conflicts requiring removal.

Outreach stressing the importance of leashing pets and keeping cats inside is likely to improve the health of pets, coyotes, and foxes. Free-roaming cats and dogs come into conflict with coyotes and foxes; potentially causing injury to all animals involved. In addition to killing many small mammals, birds, and amphibians, our results show that cats diminish the health of red foxes by spreading disease (e.g., *T. gondii*). At the same time free-roaming dogs cause stress to and sometimes kill red foxes, thereby further diminishing their ability to live in the TCMA. Encouraging local residents to leash pets when they are outside will improve their health and the health of TCMA wildlife.

This study provides critical information for TCMA residents to size up the risks posed by coyotes. Many residents expressed positive attitudes about foxes in their neighborhood but attitudes were mixed with respect to coyotes. Oftentimes negative attitudes centered on fears that coyotes will attack pets and people, and perceptions of coyotes being “wolf-sized” or “at least 100 pounds”. Our results, in combination with those from many other urban studies, shows that coyotes are much smaller than many residents believed (males: 14.3 kg [31.5 lbs.]; females: 11.9 kg [26.2 lbs.]) and risk of attack is low, especially for monitored pets (negligible for people; White and Gehrt 2009, Baker and Timm 2017).

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# Appendix 1

|                  | Intercept | Buildings | Canopy | COI    | Road density | Residential | Slope  | Wetland |
|------------------|-----------|-----------|--------|--------|--------------|-------------|--------|---------|
| <u>Coyote</u>    |           |           |        |        |              |             |        |         |
| Breeding         |           |           |        |        |              |             |        |         |
| C1               | -2.63*    | 0.15*     | 0.00   | 0.16*  | 0.48*        | -0.69*      | -0.21* | —       |
| C1.1             | -2.59*    | 0.19*     | -0.09  | 0.13*  | 0.18*        | -0.53*      | -0.03  | -0.56*  |
| C2               | -2.62*    | 0.16      | 0.43*  | 0.25*  | -0.56*       | -0.04       | 0.18*  | -0.24   |
| C3               | -3.86*    | 0.02      | 0.07*  | -0.24  | -1.62*       | -0.22*      | 0.09   | 0.16*   |
| C4               | -2.50*    | -0.03     | 0.00   | -0.03  | -0.44*       | 0.19*       | 0.31*  | 0.23*   |
| C5               | -3.16*    | 0.07      | 0.23*  | -0.07  | -1.29*       | 0.23*       | -0.01  | 0.14*   |
| C5.1             | -2.66*    | 0.01      | 0.54*  | 0.10   | -0.61*       | 0.26*       | 0.00   | -0.12   |
| C6               | -3.39*    | -0.19*    | 0.16*  | -0.05  | -0.27*       | -1.61*      | 0.13*  | 0.27*   |
| C7               | -2.63*    | -0.17     | 0.00   | -0.11  | -0.16        | 0.04        | -0.16  | -1.44*  |
| C8               | -4.06*    | -0.06     | 0.42*  | 0.15   | -1.87*       | 0.28*       | 0.19*  | 0.38*   |
| C9               | -2.71     | 0.13      | 0.32   | 0.56   | 0.30         | 0.03        | 0.18   | 0.23    |
| C10              | -2.94*    | -0.49*    | 0.43*  | -0.08  | -0.87*       | 0.44*       | 0.06   | -0.14   |
| C11              | -2.43*    | -0.23*    | 0.05   | -0.18* | -0.27*       | 0.30*       | -0.34* | 0.08    |
| C12              | -9.20*    | -1.45*    | -0.07  | 0.00   | -4.99*       | 0.46*       | -0.36* | -0.14*  |
| C15              | -2.94*    | -0.27*    | 0.58*  | 0.24*  | 0.68*        | -0.28*      | -0.53* | 0.55*   |
| Pooled           | -2.69*    | 0.03      | 0.16*  | 0.07   | -0.30*       | 0.04        | 0.10   | 0.18*   |
| Pup-rearing      |           |           |        |        |              |             |        |         |
| C1.1             | -2.77*    | 0.20*     | -0.05  | 0.21*  | 0.06         | -0.64*      | 0.00   | -1.16*  |
| C2               | -2.55*    | -0.07     | 0.32*  | 0.26*  | -0.44*       | -0.08       | 0.23*  | -0.21*  |
| C3               | -3.59*    | -0.15     | -0.02  | -0.23* | -1.37*       | -0.15       | -0.08  | 0.20*   |
| C4               | -2.56*    | -0.16*    | 0.00   | 0.02   | -0.45*       | 0.33*       | 0.33*  | 0.23*   |
| C5               | -2.82*    | 0.32*     | 0.20*  | -0.08  | -1.03*       | -0.04       | 0.18*  | -0.04   |
| C6               | -2.69*    | -0.60*    | -0.03  | 0.01   | -0.42*       | —           | 0.04   | 0.33*   |
| C7               | -2.40*    | -0.07     | 0.23*  | -0.15* | -0.03        | -0.02       | -0.14  | -0.47*  |
| C8               | -3.66*    | -0.20     | 0.10   | 0.28*  | -1.57*       | 0.41*       | 0.29*  | 0.33*   |
| C9               | -3.04*    | 0.28*     | 0.46*  | 0.45*  | 0.80*        | -0.26*      | 0.20*  | -0.29*  |
| C10              | -3.02*    | -0.15     | 0.34*  | -0.02  | -1.01*       | 0.61*       | 0.21*  | -0.08   |
| C11              | -2.45*    | -0.18*    | 0.10   | -0.09  | -0.27*       | 0.12        | -0.23* | 0.25*   |
| C12              | -6.64*    | -0.74*    | -0.07  | 0.05   | -3.84*       | 0.49*       | -0.16  | -0.38*  |
| C13              | -4.57*    | -0.98*    | -0.62* | -0.20* | -2.18*       | 0.49*       | 0.20*  | -0.10   |
| Pooled           | -2.74*    | 0.06      | 0.08   | 0.09   | -0.46*       | 0.13        | 0.16*  | 0.12*   |
| Non-reproductive |           |           |        |        |              |             |        |         |
| C1.1             | -2.74*    | 0.25*     | -0.02* | 0.17*  | 0.20*        | -0.46*      | -0.14  | -1.21*  |
| C2               | -2.57*    | -0.02     | 0.21*  | 0.30*  | -0.37*       | 0.10        | 0.26*  | -0.46*  |
| C3               | -3.76*    | 0.03      | -0.01  | -0.14  | -1.47*       | -0.42*      | 0.13   | 0.26*   |
| C4               | -2.50*    | -0.03     | -0.09  | 0.07   | -0.48*       | 0.20*       | 0.29*  | 0.22*   |
| C6               | -3.85*    | -0.07     | 0.13*  | -0.18  | -0.15        | -2.25*      | 0.13*  | 0.26*   |
| C7               | -2.52*    | -0.19     | 0.32*  | -0.10  | -0.01        | -0.02       | -0.18* | -0.84*  |
| C8               | -3.57*    | -0.09     | 0.17*  | 0.23*  | -1.48*       | 0.44*       | 0.29*  | 0.39*   |
| C9               | -2.76*    | 0.33*     | 0.27*  | 0.48*  | 0.48*        | -0.29*      | 0.2*   | 0.16*   |
| C10              | -2.79*    | -0.12     | 0.36*  | -0.06  | -0.92*       | 0.35*       | 0.06   | -0.09   |
| C11              | -2.44*    | -0.16     | 0.07   | -0.08  | -0.24*       | 0.24*       | -0.57* | 0.15*   |
| C12              | -7.79*    | -0.66     | -0.22* | -0.21* | -4.43*       | 0.62*       | -0.19  | -0.26*  |
| C13              | -5.21*    | -1.55*    | -0.36* | -0.28* | -2.37*       | 0.47*       | 0.31*  | -0.05   |
| C14              | -3.43*    | -0.42*    | -0.66* | -0.05  | 0.09         | -1.49*      | -0.01  | -0.31*  |
| Pooled           | -2.76*    | 0.09      | 0.07   | 0.13*  | -0.30*       | 0.08        | 0.16*  | 0.16*   |
| <u>Red fox</u>   |           |           |        |        |              |             |        |         |
| Breeding         |           |           |        |        |              |             |        |         |
| F1               | -2.45*    | -0.15     | -0.04  | -0.05  | 0.14         | 0.43*       | 0.10   | -0.15   |
| F3               | -3.70*    | 0.03      | -0.03  | 0.15   | -1.96*       | 0.34*       | 0.28*  | 0.02    |
| F4               | -2.74*    | 0.11      | 0.39*  | -0.84* | 0.43*        | 0.08        | -0.35* | -0.30*  |
| F6               | -3.08*    | 0.15      | 0.51*  | 0.45*  | 0.78*        | -0.05*      | 0.36*  | 0.07    |
| F7               | -3.10*    | -0.21     | -0.03  | -0.60* | 0.48*        | 0.70*       | -1.06* | —       |
| F8               | -3.67*    | 0.28*     | -0.03  | 0.67*  | 1.39*        | 0.21        | 0.22*  | —       |
| F9               | -2.70*    | -0.47*    | 0.02   | 0.13   | -0.21        | 0.81*       | 0.23*  | -0.21   |
| F11              | -2.58*    | -0.17     | 0.21   | -0.13  | 0.55*        | 0.23*       | 0.10   | 0.04    |
| F12              | -2.68*    | 0.13      | -0.24  | -0.50* | 0.55*        | 0.06        | -0.48* | —       |
| F15              | -2.57*    | -0.38*    | 0.42*  | 0.12   | -0.33*       | 0.25*       | -0.44* | -0.01   |
| F16              | -3.37*    | 0.01      | 0.06   | 0.62*  | 1.21*        | 0.32*       | 0.10   | -0.06   |
| F17              | -2.56*    | -0.12     | 0.19   | 0.26*  | -0.09        | 0.34*       | -0.55* | -0.53*  |
| Pooled           | -2.78*    | 0.01      | 0.14   | 0.20*  | 0.33*        | 0.30*       | 0.06   | -0.05   |

|                         |        |        |        |        |        |       |        |        |
|-------------------------|--------|--------|--------|--------|--------|-------|--------|--------|
| <b>Pup-rearing</b>      |        |        |        |        |        |       |        |        |
| F1                      | -2.94* | -0.29* | -0.15  | -0.41* | 0.26*  | 0.48* | -0.29* | -1.51* |
| F2                      | -3.79* | 0.22*  | 0.11   | 0.40*  | 1.51*  | -0.16 | 0.25*  | -0.47  |
| F3                      | -3.19* | 0.35   | 0.02   | 0.07   | -1.56* | 0.28* | 0.23*  | -0.02  |
| F7                      | -3.22* | -0.20* | -0.19* | -0.67* | 0.91*  | 0.21* | -0.70* | -1.05* |
| F8                      | -4.06* | 0.52*  | 0.44*  | 0.98*  | 1.05*  | 0.10  | 0.33*  | -0.75  |
| F15                     | -2.63* | -0.58* | 0.49*  | 0.04   | -0.39* | -0.04 | -0.10  | -0.25* |
| F17                     | -2.80* | -0.28* | 0.26*  | 0.32*  | -0.48* | 0.41* | -0.93* | -0.88* |
| Pooled                  | -3.02* | 0.02   | 0.11   | 0.17*  | 0.30*  | 0.23* | -0.06  | -0.16  |
| <b>Non-reproductive</b> |        |        |        |        |        |       |        |        |
| F1                      | -2.68* | -0.27* | -0.21  | -0.17  | 0.42*  | 0.66* | -0.42* | —      |
| F7                      | -3.05* | -0.04  | 0.13   | -0.01  | 0.68*  | 0.42* | -1.24* | -0.26  |
| F17                     | -2.53* | -0.06  | 0.35*  | 0.10   | -0.20  | 0.33* | -0.49* | -0.45* |
| Pooled                  | -2.69* | -0.10  | 0.12   | 0.00   | 0.30*  | 0.46* | -0.59* | -0.39* |
| <b>Gray fox</b>         |        |        |        |        |        |       |        |        |
| <b>Breeding</b>         |        |        |        |        |        |       |        |        |
| F10                     | -2.61* | -0.21* | 0.12   | 0.16*  | 0.10   | 0.43* | -0.75* | -0.39* |
| F18                     | -2.54* | 0.18*  | -0.46* | -0.09  | -0.43* | 0.04  | -0.09  | -0.58* |
| Pooled                  | -2.59* | 0.04*  | -0.04  | 0.09   | -0.09  | 0.29* | -0.43* | -0.46* |
| <b>Pup-rearing</b>      |        |        |        |        |        |       |        |        |
| F10                     | -2.7*  | -0.09  | 0.03   | 0.38*  | -0.28* | 0.62* | -0.76* | -0.44* |
| <b>Non-reproductive</b> |        |        |        |        |        |       |        |        |
| F10                     | -2.59* | -0.12  | -0.02  | 0.21*  | -0.07  | 0.61* | -0.70* | —      |

\*Indicates 95% confidence interval that does not intersect 0.

**Table A1.** Second-order seasonal RSF model coefficients for individuals and pooled.

|                  | Intercept | Buildings | Canopy | COI    | Road density | Residential | Slope  | Wetland |
|------------------|-----------|-----------|--------|--------|--------------|-------------|--------|---------|
| <u>Coyote</u>    |           |           |        |        |              |             |        |         |
| Breeding         |           |           |        |        |              |             |        |         |
| C1               | -3.34*    | -0.31*    | 0.70*  | -0.70* | -0.19        | -1.83*      | 0.15   | 0.63*   |
| C1.1             | -3.04*    | -1.20*    | -0.04  | -0.51* | -0.52*       | -0.68*      | 0.42*  | 1.08*   |
| C2               | -3.36*    | -0.77*    | 0.40*  | -0.39* | -0.05        | -0.87*      | 0.04   | 0.54*   |
| C3               | -3.17*    | —         | 0.11   | -0.15  | -0.15        | -0.04       | 0.37*  | 0.34*   |
| C4               | -3.67*    | -0.84*    | 0.14   | -0.91* | -0.12        | -0.10       | 0.17*  | 0.48*   |
| C5               | -5.24*    | —         | -0.04  | -3.22* | 0.05         | -0.88*      | 0.64*  | 0.36*   |
| C5.1             | -3.49*    | -1.50*    | 0.15*  | -0.53* | -0.60*       | 0.07        | -0.05  | 0.37*   |
| C6               | -2.76*    | -0.27     | -0.01  | -0.29* | 0.37*        | —           | 0.19*  | 0.40*   |
| C7               | -2.91*    | -1.51*    | 0.52*  | -0.22  | -1.13*       | 0.01        | 0.21   | 1.20*   |
| C8               | -4.63*    | -1.80*    | -0.17* | -0.50* | -0.39        | 0.18        | 0.23*  | 0.44*   |
| C9               | -2.33*    | 0.00      | -0.12  | -0.42* | -0.48*       | -0.03       | 0.25*  | 0.12    |
| C10              | -3.18*    | -0.45*    | 0.24   | -0.55* | -0.04        | -0.55*      | 0.33*  | 0.29*   |
| C11              | -3.80*    | -1.66*    | 0.16*  | -0.18* | -0.62*       | -0.15*      | 0.37*  | 0.45*   |
| C12              | -13.50*   | —         | -0.41* | -0.74* | -5.30*       | -0.62*      | 0.46*  | 0.60*   |
| C15              | -4.22*    | -1.42*    | -0.16* | -0.77* | 1.51*        | -0.17       | -0.98* | 0.26*   |
| Pooled           | -3.07*    | -0.34*    | 0.09   | -0.41* | -0.08        | -0.24*      | 0.23*  | 0.41*   |
| Pup-rearing      |           |           |        |        |              |             |        |         |
| C1.1             | -3.50*    | -0.58*    | -0.18  | -0.45* | -0.63*       | -0.97*      | 0.72*  | 1.18*   |
| C2               | -2.94*    | -0.32*    | 0.11   | -0.29* | -0.42*       | -0.73*      | 0.08   | 0.25*   |
| C3               | -3.44*    | —         | 0.48*  | -0.37* | -0.38*       | -0.39*      | -0.01  | -0.05   |
| C4               | -3.97*    | -0.65*    | -0.02  | -0.39* | -1.38*       | -0.23       | 0.14   | 0.20*   |
| C5               | -3.43*    | -0.48*    | -0.47* | -0.51* | -0.35        | -0.11       | 0.67*  | 0.36*   |
| C6               | -3.31*    | -1.19*    | -0.07  | -0.51* | 0.16         | —           | 0.29*  | 0.24*   |
| C7               | -3.01*    | -1.55*    | 0.28*  | -0.40* | -1.27*       | -0.46*      | -0.05  | 0.42*   |
| C8               | -3.70*    | -1.65*    | -0.01  | -0.38* | -0.42*       | -0.08       | 0.14*  | -0.03   |
| C9               | -2.02*    | -0.60*    | 0.11   | -0.30* | -1.25*       | -0.57*      | 0.21*  | 0.32*   |
| C10              | -3.42*    | -0.60*    | 0.07   | -0.27* | -0.64*       | -0.36*      | 0.30*  | 0.39*   |
| C11              | -3.77*    | -1.84*    | 0.19*  | -0.41* | -0.09        | -0.45*      | 0.27*  | 0.30*   |
| C12              | -5.00*    | -0.32     | 0.02   | -0.30* | -1.29*       | -0.31*      | -0.04  | -0.07   |
| C13              | -6.20*    | —         | -0.46* | -0.64* | -1.88*       | -0.08       | 0.19*  | 0.31*   |
| Pooled           | -3.17*    | -0.60*    | 0.06   | -0.36* | -0.41*       | -0.32*      | 0.22*  | 0.23*   |
| Non-reproductive |           |           |        |        |              |             |        |         |
| C1.1             | -3.22*    | -0.56*    | -0.24* | -0.52* | -0.40*       | -1.27*      | 0.30*  | 1.14*   |
| C2               | -3.00*    | -1.00*    | -0.04  | -0.36* | -0.27*       | -0.78*      | -0.04  | 0.24*   |
| C3               | -3.60*    | —         | 0.30*  | -0.25* | -0.49*       | -0.46*      | 0.11*  | -0.01   |
| C4               | -3.49*    | -0.80*    | 0.07   | -0.63* | -0.45*       | -0.45*      | 0.08   | 0.20*   |
| C6               | -2.93*    | -0.55*    | -0.29* | -0.29* | 0.34*        | —           | 0.28*  | 0.36*   |
| C7               | -2.87*    | -1.52*    | -0.15  | -0.33* | 0.01         | -0.21       | -0.37  | 0.97*   |
| C8               | -4.18*    | -1.34*    | 0.00   | -0.23* | -0.54*       | 0.21        | 0.30*  | 0.26*   |
| C9               | -2.53*    | -0.83*    | 0.13   | -0.07  | -0.34*       | -0.30*      | 0.17*  | 0.16*   |
| C10              | -3.66*    | -0.16     | -0.07  | -0.53* | -1.04*       | -0.76*      | 0.21*  | 0.47*   |
| C11              | -3.79*    | -1.50*    | 0.21*  | -0.27* | -0.44*       | -0.37*      | 0.07   | 0.43*   |
| C12              | -7.65*    | —         | -0.54* | -0.90* | -2.18*       | -0.59*      | -0.29  | 0.34*   |
| C13              | -4.55*    | —         | -0.51* | -0.76* | -0.75*       | -0.41*      | 0.32*  | 0.17*   |
| C14              | -2.59*    | -0.81     | 0.47   | -0.86* | -0.87        | —           | 0.46*  | 0.20    |
| Pooled           | -3.19*    | -0.66*    | -0.02  | -0.31* | -0.24*       | -0.45*      | 0.19*  | 0.31*   |
| <u>Red fox</u>   |           |           |        |        |              |             |        |         |
| Breeding         |           |           |        |        |              |             |        |         |
| F1               | -2.97*    | -1.04*    | -0.09  | -0.17  | 0.45*        | 0.53*       | 0.15*  | -0.21   |
| F3               | -3.68*    | -0.61*    | 0.04   | -0.31* | -0.68*       | 0.53*       | 0.22*  | -0.20*  |
| F4               | -2.94*    | -0.47*    | 0.03   | -1.20* | -0.33        | 0.33*       | 0.23   | -0.45*  |
| F6               | -2.67*    | -0.29     | 0.07   | -0.38* | -0.34*       | 0.74*       | 0.19*  | -0.34   |
| F7               | -2.33*    | -1.31*    | 0.07   | -0.85  | -0.07        | -0.20       | 1.20*  | —       |
| F8               | -2.66*    | -0.09     | 0.08   | 0.10   | 0.06         | 0.71*       | 0.20   | 0.26    |
| F9               | -2.89*    | -0.78*    | 0.10   | -0.68  | 1.33*        | -0.11       | 0.18   | 0.72*   |
| F11              | -2.53*    | -0.55*    | -0.33* | -0.21  | -0.15        | 0.50*       | 0.36*  | 0.35*   |
| F12              | -2.95*    | -0.16     | 0.26*  | -0.92* | 0.55*        | 0.30*       | 0.63*  | 0.45*   |
| F15              | -3.82*    | -2.31*    | 0.19*  | -0.19  | -0.52*       | 0.31*       | 0.48*  | 0.15*   |
| F16              | -2.16*    | -0.76*    | 0.06   | -0.23* | -0.09        | 0.20        | 0.75*  | 0.37*   |
| F17              | -2.89*    | -0.54*    | 0.74*  | -0.70* | -0.30*       | -0.30*      | 0.61*  | -0.43   |
| Pooled           | -2.84*    | -0.45*    | 0.10   | -0.28* | 0.00         | 0.32*       | 0.32*  | 0.19    |

|                         |        |        |       |        |        |        |        |        |
|-------------------------|--------|--------|-------|--------|--------|--------|--------|--------|
| <b>Pup-rearing</b>      |        |        |       |        |        |        |        |        |
| F1                      | -3.14* | -0.61* | 0.60* | -0.51* | 0.46*  | 0.21*  | -0.17* | -0.34  |
| F2                      | -3.37* | -0.12  | 0.16  | 0.10   | 0.53*  | 0.72*  | 0.26*  | 0.33   |
| F3                      | -3.55* | -0.42* | 0.14  | -0.20* | -0.83* | 0.51*  | 0.15*  | -0.51* |
| F7                      | -2.00* | -0.25* | 0.51* | -0.46* | -0.19* | -0.23* | -0.14  | 0.96*  |
| F8                      | -2.22* | -0.06  | 0.04  | -0.17* | -0.28* | 0.44*  | 0.31*  | -0.17  |
| F15                     | -3.56* | -0.34  | 0.47  | -0.60* | -0.44* | 0.05   | 0.36   | 0.20   |
| F17                     | -2.90* | -0.60* | 0.63* | -1.03* | 0.56   | -1.11* | -0.04  | 0.00   |
| Pooled                  | -2.83* | -0.29* | 0.44* | -0.26* | -0.03  | 0.04   | 0.15*  | 0.02   |
| <b>Non-reproductive</b> |        |        |       |        |        |        |        |        |
| F1                      | -2.82* | -0.73* | 0.64* | -0.41* | 0.92*  | -0.04  | 0.01   | 0.86*  |
| F7                      | -2.14* | -0.19  | 0.32* | -0.23  | 0.12   | 0.23   | 1.06*  | 0.96*  |
| F17                     | -2.68* | -0.67* | 0.32* | -0.52* | -0.20  | -0.36* | 0.34*  | -0.77* |
| Pooled                  | -2.58* | -0.46* | 0.44* | -0.40* | 0.30   | -0.08  | 0.31*  | 0.49   |
| <b>Gray fox</b>         |        |        |       |        |        |        |        |        |
| <b>Breeding</b>         |        |        |       |        |        |        |        |        |
| F10                     | -2.77* | -0.19* | 0.21* | -0.76* | 0.35*  | 0.21   | 0.23   | 0.98*  |
| F18                     | -2.66* | -0.50* | 0.53* | -0.56* | -0.41  | -0.03  | 0.45   | 1.31*  |
| Pooled                  | -2.77* | -0.28* | 0.28* | -0.72* | 0.18   | 0.13   | 0.28   | 1.04*  |
| <b>Pup-rearing</b>      |        |        |       |        |        |        |        |        |
| F10                     | -2.72* | -0.59* | 0.87* | 0.11   | 0.57   | 0.07   | 0.16   | 0.76*  |
| <b>Non-reproductive</b> |        |        |       |        |        |        |        |        |
| F10                     | -2.51* | -0.79* | 0.80* | -0.20* | -0.11* | -0.16  | -0.14  | 1.28*  |

\*Indicates 95% confidence interval that does not intersect 0.

**Table A2.** Third-order seasonal RSF model coefficients for individuals and pooled.

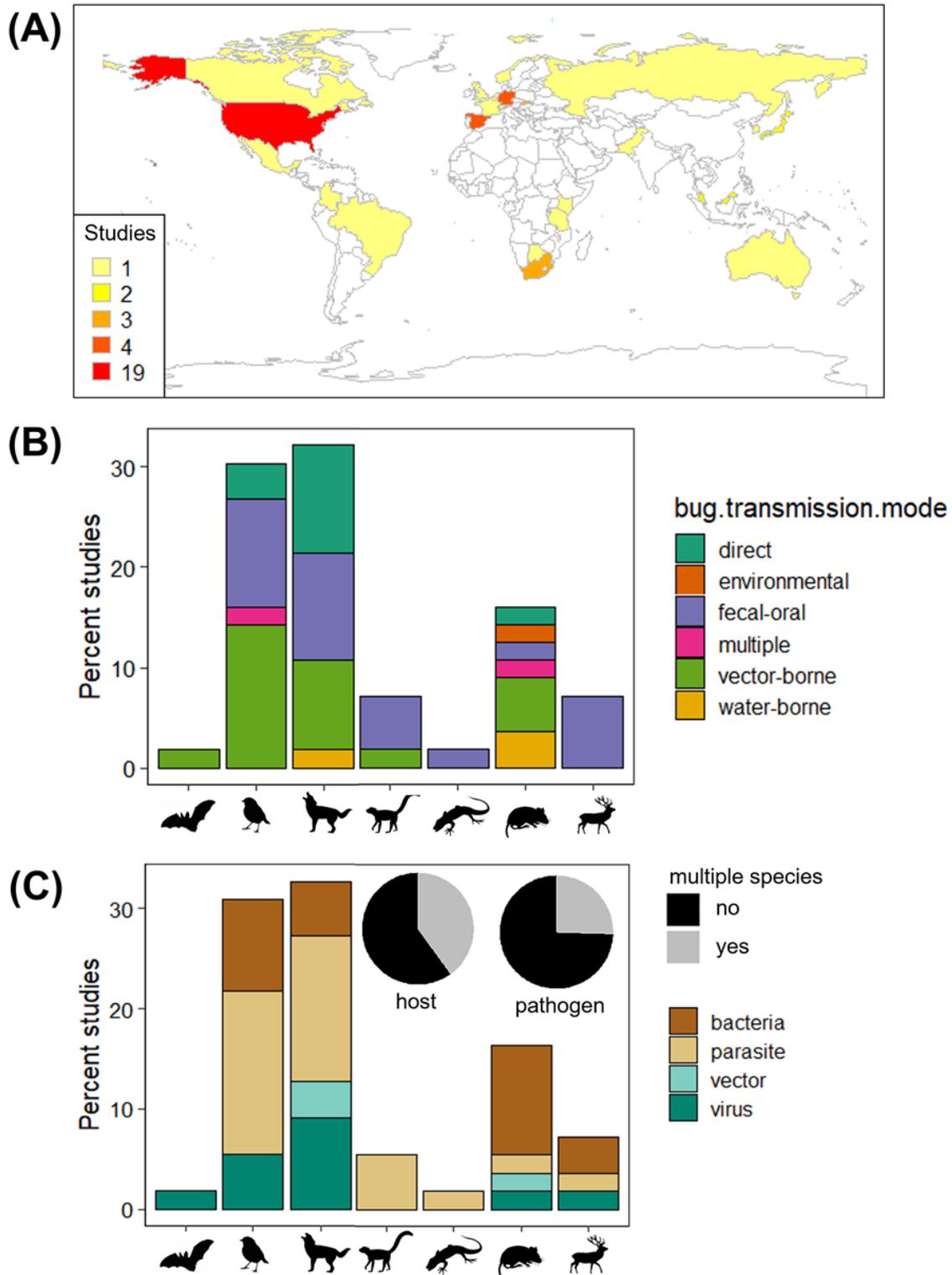
## Appendix 2

In order to evaluate the results of this study in the context of the broader literature, we are in the process of conducting a literature review on urbanization and wildlife disease. This literature review is led by a graduate student supported by this LCCMR funding. Thus far we have partnered with a Health Sciences Librarian at the University of Minnesota (Andre Nault) to perform a comprehensive search for peer-reviewed scientific articles published between 1980 and 2020 that include the three search terms urban, infectious disease/agent, and wildlife. Over 6,200 published articles were initially identified in the search, and after reading all titles and abstracts, 687 articles remained in our search. All 687 articles were read in full to exclude other articles that did not include appropriate topics or relevant statistics, leaving us with 237 articles.

Of the 237 articles, the vast majority of them were located in the United States, followed by a few in Europe and South Africa (Figure A1, panel A). The most frequently studies host taxa were birds and carnivores while the most common transmission mode of infectious agents were fecal-oral and vector-borne, with the most studies of vector-borne infectious agents in birds (Figure A1, panel B). Most studies focused on single host-single pathogen systems and most pathogens were parasites (Figure A1, panel C). These preliminary results indicate that there are not many studies considering wildlife health in the context of urban environments, and those that do are primarily based in the United States and are of vector-borne parasites in birds. We are in the process of updating data analyses to include articles published up until May 2022.

The urban metrics and approaches used to describe these studies are highly variable, making comparison across multiple systems challenging. For example, some studies measured degree of 'urbanness' by describing the density of humans, while others described the density of carnivores, while others just measured if a study site was inside or outside of a city boundary.

The next steps in this study will be to describe the directionality of the urbanization and wildlife disease association and then propose future research directions (e.g., the need to use multiple urban metrics, choosing the right spatial scale for the host – pathogen system at hand, and reducing the gap between anthropogenic landscape change and host-pathogen response to such change). We aim to submit this manuscript to the high-profile journal *Biological Reviews* before the end of 2022.



**Figure A1.** Distribution of studies by (A) geographic location; (B) host taxa and pathogen transmission mode; (C) host and pathogen taxa. See Table S1 for number of publications per host and pathogen species. From Worsley-Tonks, K.E.L. *In preparation*.