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Article *in* Journal of Wildlife Management · October 2022

DOI: 10.1002/jwmg.22323

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Received: 7 February 2022 | Revised: 22 June 2022 | Accepted: 8 September 2022
DOI: 10.1002/jwmg.22323

RESEARCH ARTICLE

THE JOURNAL OF WILDLIFE MANAGEMENT
THE WILDLIFE SOCIETY

Urban coyotes select cryptic den sites near human development where conflict rates increase

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Funding information
Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: RGPIN-2017-05915; University of Alberta Faculty of Science Research Fellowship; University of Alberta Walter H. Johns Graduate Fellowship

Abstract

The establishment of coyote (*Canis latrans*) populations in urban areas across North America has been accompanied by increased rates of human–coyote conflict. One factor thought to promote physical conflict between coyotes and people or pets is the presence of coyote pups near natal dens; however, this idea has not been tested, and no multivariate study of den selection within cities has occurred. Our objectives were to conduct a multivariate analysis of third- (i.e., home range) and fourth-order (i.e., den sites) habitat selection at dens and determine whether proximity to dens is associated with reports of physical conflict with coyotes. We found 120 dens by following coyote trails using snow tracking within urban green spaces that comprise presumed high-quality habitat for coyotes in Edmonton, Alberta, Canada. We used resource selection functions to assess habitat selection for dens, testing variables related to land cover and anthropogenic features at the third order, and testing microsite habitat features via paired sites at the fourth order. We defined conflict encounters from comments in a community reporting database and used general linear models to assess their spatial proximity to the nearest den and prevalence during the pup-rearing period compared to the rest of the year. Habitat selection was strongest at the fourth order, wherein coyotes selected for abundant hiding cover, steep slopes, and eastern exposure. The prevalence of physical conflict with coyotes increased during the pup-rearing period. Conflict also increased near known dens as an overall effect and when reports occurred outside of naturalized urban areas. These results suggest that coyotes in Edmonton den in green spaces near human development in microsites that minimize detection by people via steep slopes and dense vegetation. We suggest urban wildlife managers increase public safety education about recognition of coyote denning habitat and coyote defensive behaviors, especially outside of naturalized urban areas, because of the observed increase in physical conflict near dens.

KEYWORDS

Canis latrans, coyote, dens, habitat selection, human-wildlife conflict, resource selection, urban coyote, urban ecology, urbanization, urban wildlife

Coyote (*Canis latrans*) populations in urban environments are associated with benefits and drawbacks to resident human populations (Gompper 2002, McEwan et al. 2020, Ritzel and Gallo 2020). Benefits of coyote presence to people include reductions in prey populations, removal of carrion, seed dispersal, and aesthetic enjoyment. Drawbacks can be collectively referred to as human–wildlife conflict (Soulsbury and White 2015); the most prominent form is physical conflict in which coyotes intimidate, approach, or physically attack humans or their pets (White and Gehrt 2009). In many North American cities, the rate of physical conflict with coyotes is increasing (White and Gehrt 2009, Poessel et al. 2017). Several researchers determined that human–coyote physical conflict is disproportionately high during the pup-rearing period (White and Gehrt 2009, Lukasik and Alexander 2011, Baker and Timm 2017), as is the rate of coyote attacks on domestic dogs (Frauenthal et al. 2017).

One explanation for increased physical conflict with coyotes during the pup-rearing period is increased territorial defense associated with offspring presence (Wolff and Peterson 1998). If the presence of coyote pups contributes to higher rates of physical conflict, conflict risk likely also increases near coyote dens, although this effect has not been quantified. Understanding where dens are likely to occur could therefore have implications to reduce potential conflicts, but there has been limited investigation into coyote den site selection, especially in urban environments. Relevant studies reported small sample sizes (1–17 dens), which limits the inference of multivariate statistics in rural areas (Althoff 1979, 1980; Harrison and Gilbert 1985; Kamler et al. 2005) and urban environments (Way et al. 2001, Grubbs and Krausman 2009, Way 2009, Dodge and Kashian 2013). Better ability to predict den sites in urban settings could support management to reduce physical conflict with coyotes.

Like other canines, coyotes select den sites based on several environmental factors. To keep dens sufficiently warm, coyotes may establish dens at sites with southeastern exposure (Harrison and Gilbert 1985), although 1 researcher detected selection for north and east aspects (Althoff 1980), and others failed to detect selection for aspect (Way et al. 2001). Coyotes may take advantage of certain soil types to increase the structural integrity of dens (Althoff 1980, Harrison and Gilbert 1985), and they may incorporate structural components, especially roots, into dens (Way et al. 2001). In urban environments, coyotes may use anthropogenic features for shelter and structure by denning under decks, buildings, overturned boats (Way 2009), and in dry culverts (Grubbs and Krausman 2009). Other canines select habitats that increase security of vulnerable pups. For example, Arctic fox (*Vulpes lagopus*) select den sites to avoid sympatric red fox (*V. vulpes*; Gallant et al. 2014), and wolves (*Canis lupus*) avoid patch edges (Norris et al. 2002), avoid recreational housing structures (Malcolm et al. 2020), and select rugged terrain (Capitani et al. 2006, Ahmadi et al. 2013). Coyotes select rural den sites with abundant vegetative cover (Kamler et al. 2005) and camouflaged entrances (Althoff 1979), and they select wooded den sites in urban areas (Gese et al. 2012). In urban areas, coyotes may act similarly to wolves in developed areas of Europe and the Middle

East, where they avoid proximity to linear features and buildings (Capitani et al. 2006, Ahmadi et al. 2013). In many canine species, den site selection occurs at multiple scales. In North America, den position within the home range (third order; Johnson 1980) and the microhabitat at the den site (fourth order; Johnson 1980) have been described for wolves (Trapp 2004, Trapp et al. 2008), and red fox (Zaman et al. 2020) but not coyotes.

Our objectives were to determine third- and fourth-order habitat features that urban coyotes select for denning and to determine whether proximity to coyote dens increases the prevalence of negative physical interactions between coyotes and people or pets. We hypothesized that areas free from human disturbance were a limiting factor for urban coyotes with offspring, and predicted that the strongest selection for habitat features at den sites would be related to factors that promote security, such as selection for greater distances from human infrastructure and patch edges, and locations in dense vegetation that obscure visual detection. We further hypothesized that if coyotes are defending young, reports of aggressive behavior would be more frequent closer to known dens and during the pup-rearing season. Our goal was to provide information to support mitigation for den-associated physical conflict, such as programs to discourage coyotes from denning in or near residential areas and education to help people predict where defense of dens might occur.

STUDY AREA

We conducted this study in Edmonton, Alberta, Canada, between January and August 2021. Edmonton (684.4 km^2) is centered at 53.5472°N, 113.5006°W (elevation = 645 m) and home to roughly 1 million people (City of Edmonton 2019). The city's climate was characterized by long, cold winters (Dec–Mar; Jan average temp = −10.4° C) and short, warm summers (Jun–Aug, Jul average temp = 17.7°C; Environment Canada 2022) and the study period was within historical averages. It was located at the transition between 2 major ecosystems, with prairie grasslands to the south and boreal forest to the north. The city was composed of residential, commercial, and industrial sectors, dominated by domestic housing, for-profit businesses, and industrial businesses and factories, respectively. It contained extensive urban green spaces, including a network of ravines branching off the North Saskatchewan River Valley, which bisected the city (City of Edmonton 2013). Naturalized urban areas (i.e., areas with natural vegetation and >50% forest cover) provided habitat for coyotes, white-tailed deer (*Odocoileus virginianus*), white-tailed jackrabbits (*Lepus townsendii*), snowshoe hares (*Lepus americanus*), beavers (*Castor canadensis*), and various small mammals, and were popular for human recreation (City of Edmonton 2013).

METHODS

Den identification

We detected dens by following coyote tracks in snow between 1 January and 31 March 2021. We targeted searches for coyote dens to areas accessible to the public, >250 m^2, and containing >50% tree or shrub cover. These selection criteria focused survey efforts on urban green spaces, including parks, golf courses, and quiet industrial yards (Dodge and Kashian 2013), which represent the habitat most used by urban coyotes (Riley et al. 2003, Gehrt et al. 2009, Gehrt and Riley 2010, Murray and St. Clair 2017). Within target areas, we identified coyote tracks based on track morphology and gait (Markovchick-Nicholls et al. 2008, Elbroch and MacFarland 2019), followed paths while recording them with a global positioning system (GPS), and searched visually from paths for dens. We confirmed dens as belonging to coyotes by measuring den opening(s) and comparing them to dimensions reported in the literature, and by searching for ancillary tracks or sign (Way et al. 2001). To minimize disturbance to animals, we performed these more detailed examinations in August 2021, following pup dispersal (Ahmadi et al. 2013). We also described evidence of recent use, recorded the number and dimensions of den openings, and noted the size and nature of any supporting infrastructure. Although our methods focused on dens located in sectors of the urban landscape selected extensively by coyotes, such as urban green spaces and parks (Riley et al. 2003, Atwood et al. 2004, Gehrt et al. 2009), coyotes in urban areas also den in other areas, such as on private residential property and under buildings (Way et al. 2001, Way 2009). Because we could not access private property, we did not include these dens in our analysis, although they may represent an important source of physical conflict with coyotes.

Habitat selection

We estimated third-order selection for habitat characteristics at den sites using a resource selection function (RSF) that compared remotely sensed habitat characteristics at used and available sites (Manly et al. 1993, Boyce and McDonald 1999). We selected available sites by using ArcGIS (Esri, Redlands, CA, USA) to randomly generate points along the coyote paths we followed at a ratio of 3 available sites per use site. At use and available points, we extracted covariate values from remotely sensed data available from a civic Open Data Catalogue (City of Edmonton 2021; Table 1). We determined slope (°) and aspect (°) using a 50-m resolution digital elevation model. To convert aspect to a continuous variable, we developed a south index by taking the cosine of the aspect in radians and multiplying by −1, resulting in a variable that ranged from −1 (north) to 1 (south). Similarly, we developed an east index by taking the sine of the aspect, resulting in a variable that ranged from −1 (west) to 1 (east).

To map biologically relevant patch edges, we reclassified 34 classes of land cover described in the Urban Primary and Land Vegetation Inventory (City of Edmonton 2014) into the following 5 classes: water, mowed grass (e.g., cemeteries, schoolyards, sports fields), naturalized urban area (e.g., forested ravines), anthropogenic (e.g., all impermeable surfaces), and agricultural. From the resulting matrix of patches, we built a polyline layer representing

TABLE 1 Summary statistics for third-order habitat characteristics selected by coyotes at den sites and available sites in Edmonton, Alberta, Canada, 2021.

	Use (n = 120)				Available (n = 360)				t-test results	
Variable	$\bar{x}$	SD	Min.	Max.	$\bar{x}$	SD	Min.	Max.	$\|t\|$	P
Road density (km/km^2)	1.07	4.03	0.00	23.7	6.98	15.3	0.00	114.4	6.7	≤0.001
Mowed grass (%)	3.93	15.1	0.00	100.0	12.9	28.0	0.00	100	4.5	≤0.001
Natural (%)	81.6	33.9	0.00	100.0	65.1	41.8	0.00	100	4.3	≤0.001
Water distance (km)	0.28	0.41	0.00	3.29	0.42	0.53	0.00	2.81	3.1	0.002
Anthropogenic (%)	10.6	26.4	0.00	100.0	19.2	34.3	0.00	100	2.8	0.005
Slope (°)	6.53	5.87	0.05	24.6	5.17	5.27	0.05	21.3	2.3	0.026
Edge density (km/km^2)	14.5	23.6	0.00	136.5	19.1	25.2	0.00	114.7	1.8	0.071
Road distance (m)	96.6	82.8	1.33	534	81.6	86.1	0.27	465	1.8	0.092
Agricultural (%)	1.67	12.9	0.00	100	0.61	6.90	0.00	100	0.9	0.389
East index	0.08	0.67	−1.00	1.00	0.03	0.70	−1.00	1.00	0.7	0.460
Edge distance (m)	36.5	71.0	0.03	548	31.1	63.1	0.17	674	0.7	0.464
South index	0.01	0.75	−1.00	1.00	−0.05	0.71	−1.00	1.00	0.7	0.491
Building distance (m)	85.4	68.6	7.83	450	82.0	65.9	0.00	379	0.5	0.628
Building density (buildings/km^2)	0.27	0.44	0.00	1.78	0.28	0.39	0.00	2.20	0.1	0.945

edges. We calculated Euclidean distance from points to the nearest edge, building, road, and waterbody, and we transformed these distances to decay distances using the formula decay = $e^{-\alpha/d}$, where α represents a decay term and *d* represents the Euclidean distance to the feature (Nielsen et al. 2009, Malcolm et al. 2020). To determine the most parsimonious α value for each covariate, we tested a series of univariate general linear models (GLMs) with α equal to 25 m, 50 m, 100 m, 250 m, 500 m, 1,000 m, and 1,500 m, and we proceeded with the α value that resulted in the lowest Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2001). We created raster layers representing building density (number of buildings/km^2), edge density (edge length in km/km^2), and road density (road length in km/km^2) for all of Edmonton at 4 resolutions (25 m, 50 m, 100 m, 200 m), and we determined the value of each density metric at all use and available points. We then used univariate GLMs and AIC_c weights to select the most parsimonious scale for each variable. We calculated the percent cover of each of the 4 terrestrial land cover classes within a circular polygon centered on the use or available point with a 12.5-m, 25-m, 50-m, and 100-m radius, developed univariate GLMs, and again selected the scale with the lowest AIC_c.

The North Saskatchewan River and the land adjacent to it is used by coyotes as a travel corridor (Murray et al. 2015), and it may represent a territorial boundary (Crabtree and Sheldon 1999); both circumstances would reduce the likelihood of denning. We therefore included a binary variable that categorized dens as within or outside of a 75-m buffer generated around the river's banks. We chose this width based on the use of 100 m as a riparian buffer width in a study of large mammals in northern Alberta and Saskatchewan (Dickie et al. 2020) and the assumption that this value should be somewhat reduced for a medium-sized carnivore in an urban environment.

To ensure we could pool dens for analysis regardless of recency of use, we used student *t*-tests to compare mean covariate values between dens that had been used in 2021 and those that had not. To develop candidate models, we first identified liberally significant variables ($P \leq 0.25$ using univariate GLMs; Hosmer and Lemeshow 2000). We modeled each covariate as a linear and a quadratic term and we retained quadratic terms if they produced a more predictive model (i.e., $\Delta AIC_c \geq 2$; Hosmer and Lemeshow 2000). We assessed collinearity among remaining variables by calculating Pearson's correlation values ($r > 0.6$; Dormann et al. 2013). We constructed RSFs using a binomial distribution with a use-available design and a logit link (Boyce and McDonald 1999).

Given the exploratory nature of our questions and the limitations of existing literature on coyote denning in urban areas, we generated models using all possible combinations of covariates (Eberhardt 2003, Stephens et al. 2007, Hegyi and Zsolt Garamszegi 2011, Symonds and Moussalli 2011, Tredennick et al. 2021). We used the dredge function in the MuMin package to generate all possible models, and we included a subset argument that prevented the generation of models including correlated predictors (Bartoń 2022). We considered models with $\Delta AIC_c \leq 2$ to have equivalent predictive power (Burnham and Anderson 2001). We generated an *a priori* list of biologically plausible 2-way interactions, and we added them iteratively to the top main effects models, retaining interactions only if they improved model performance (Hosmer and Lemeshow 2000). To emphasize the most explanatory variables, we averaged models within $\Delta AIC_c \leq 2$ for which all covariate coefficients were significant at $P \leq 0.100$ using model weight (Symonds and Moussalli 2011), and we used odds ratios (OR) to facilitate interpretation of model-averaged results. We reported standardized coefficients by centering (mean) and scaling (1 SD). To confirm the absence of multicollinearity, we calculated variance inflation factors for the final model. To quantify model predictive accuracy, we used stratified *k*-fold cross-validation with $k = 5$ (Tredennick et al. 2021) and receiver-operator characteristic (ROC) curves (Cumming 2000).

We determined fourth-order selection for habitat characteristics at den sites using an RSF that compared habitat characteristics measured at dens and nearby available points (Table 2). We established 1 available point per use site in the field by generating a direction (left or right) using a random number generator and by following the trail coyotes appeared to use to access the den in the selected direction for 50 paces ($n = 102$). We used this approach, as opposed to generating and following a random compass bearing, because many of Edmonton's green spaces are in linear ravines where travel perpendicular to the slope results in large changes in habitat over short distances, and the density and structure of vegetation near most dens made it impractical to travel in the absence of the trails used by coyotes to access dens.

TABLE 2 Summary statistics for quantitative fourth-order habitat characteristics selected by coyotes at den sites and paired sites in Edmonton, Alberta, Canada, 2021.

	Use (n = 102)				Available (n = 102)				t-test results	
Variable	$\bar{x}$	SD	Min.	Max.	$\bar{x}$	SD	Min.	Max.	$\|t\|$	P
Hiding cover (%)	51.5	18.8	8.88	95.8	29.7	17.8	0.25	83.3	8.5	≤0.001
Average slope (°)	7.73	5.23	0.00	20.0	4.48	4.19	0.00	18.0	4.9	≤0.001
Shrub (%)	61.2	27.0	0.00	97.5	42.9	27.2	0.00	95.0	4.8	≤0.001
East index	0.06	0.67	−1.00	1.00	−0.17	0.57	−1.00	0.98	2.6	0.010
Herbaceous (%)	29.8	30.4	0.00	100	39.3	36.0	2.50	100	2.0	0.044
Tree (%)	30.4	22.7	0.00	80.0	35.7	23.7	0.00	85.0	1.6	0.105
South index	−0.10	0.71	−1.00	1.00	−0.02	0.61	−1.00	1.00	0.9	0.368
Bare ground (%)	45.4	30.1	0.00	95.0	41.7	33.1	0.00	95.0	0.8	0.403
Canopy cover (%)	69.3	20.7	0.00	90.6	66.6	24.7	0.00	86.2	0.8	0.405
Water (%)	0.71	3.38	0.00	30.0	0.44	2.00	0.00	10.0	0.7	0.489

We conducted surveys at dens and available sites in August 2021. At each plot center, we measured slope (°; clinometer; 2 m above and 2 m below plot center) and aspect (°; compass), and we classified slope position as upper slope, mid slope, toe slope, level, or depression (Province of British Columbia 2010). We collected a soil sample and classified its texture using standard classification techniques (Province of British Columbia 2010). We measured canopy cover (%) at a height of 60 cm at 5 locations for each site (plot center, 2 m above and below plot center and 2 m from plot center parallel to slope in either direction). At the latter 4 positions, we also measured percent hiding cover as observed from plot center using a 90-cm cover pole (Trapp et al. 2008). Within a 5-m-radius circular plot, we estimated the percent cover of trees (woody plants >2 m in height), shrubs (woody plants ≤2 m in height), herbaceous plants, bare ground, and water. To increase accuracy, a single surveyor estimated cover for all plots with the assistance of templates showing various representations of percent cover in increments of 5%. Within each 5-m radius plot, we assessed the amount of garbage as absent (no garbage detected), low (1–5 pieces detected), medium (6–15 pieces), or high (>15 pieces), and we classified evidence of manipulation of garbage by coyotes (e.g., canine punctures, shredding) as absent (no manipulation detected), low (0–33% of garbage present had been manipulated), medium (34–67%), or high (68–100%).

We developed RSFs to model fourth-order selection for den sites using the same methods described for third-order selection. Sites located on flat ground had no aspect. At use and available sites with no aspect, we used the mean aspect for all use sites and available sites, respectively.

Relationship between dens and physical conflict

To assess the relationship between pup presence and physical conflict with humans or pets, we used a community reporting database administrated by the Edmonton Urban Coyote Project (EUCP 2021; J. J. Farr, University of Alberta, unpublished report). Reports collected between 2010 and 2020 (n = 7,887) were systematically coded such that each event included a GPS location, a date, and coyote behavior (J. J. Farr, unpublished report). We used only reports located within 500 m of the paths followed while searching for dens. We classified each report as occurring during the pup-rearing period (Apr–Jul) or outside of this period (Aug–Mar) based on parturition dates and patterns of den use in an urban area (Way et al. 2001), and as occurring in a naturalized urban area (i.e., area with natural vegetation and >50% forest cover) or in modified areas (i.e., all other land cover types). We removed reports for which coyote behavior was unknown, and we coded reports as 0 if coyote behavior was benign, or as 1 if coyote behavior represented physical conflict (i.e., approaching, following, or contacting people or pets). We converted the Euclidean distance between the report location and the nearest den to a decay distance term as described previously using $\alpha = 500$.

We constructed a GLM that predicted likelihood of conflict as a function of the interaction between season (i.e., during or outside of the pup-rearing period) and decay distance to the nearest den. Although coyotes are not known to use natal dens outside of the pup-rearing period, we included reports that occurred at other times to support comparison between reports in the 2 time periods and because coyote dens are located centrally within year-round coyote territories (Moorcroft et al. 2006) that tend to be stable over time (Kitchen et al. 2000). Because land cover can influence the severity and likelihood of physical conflict with coyotes (Lukasik and Alexander 2011, Poessel et al. 2013), we repeated the analysis using the subset of reports that occurred in naturalized urban areas and modified habitat. Lastly, we constructed a GLM that predicted the conflict encounters as a function of the interaction between land cover and decay distance to the nearest den. We assumed that dens detected in 2021 were relevant between 2010 and 2020 when reports were submitted because coyotes reuse den sites perennially (Lemm 1973, Camenzind 1978, Till 1992), potentially over decades (Crabtree and Sheldon 1999). To test this assumption, we repeated the analysis using the subset of reports that occurred during 2020. We used RStudio version 4.04 (RStudio, Boston, MA, USA) to conduct statistical analyses and ArcGIS version 10.7.1 to conduct spatial analyses.

RESULTS

Den identification

Between 1 January and 31 March 2021, we detected 154 prospective coyote dens. During follow up visits in 2021 August, we confirmed that 120 of these sites were coyote dens. Of these dens, 76 appeared to have been used during the preceding natal period, we did not detect definitive signs of recent use by coyotes at 22 dens, and we classified recency of use at 22 sites as unknown because of access limitations ($n = 18$) or contradictory field sign ($n = 4$). Of the 102 dens for which we could confidently count the number of openings, 73 (72%) had a single entrance, 22 dens had 2 entrances, 4 dens had 3 entrances, and we found a single den with each of 4, 6, and 7 entrances. Non-primary den openings were located an average of 3.36 ± 1.9 m (SD; $n = 73$) from the nearest den opening. Dimensions of den openings (including non-primary openings) were an average of 27.9 ± 6.7 cm high by 35.8 ± 11 cm wide ($n = 141$). Most of these dens ($n = 85$, 83.3%) featured structural support integrated into the top or sides of den walls. The most common form was tree roots ($n = 68$, 80% of supported dens), but other forms included logs ($n = 4$) or rocks ($n = 1$), and 12 dens showed incorporation of anthropogenic materials into den structure (Figure 1). Two dens were constructed in association with dry culverts, 2 dens were located under shipping containers, and 8 dens featured the integration of anthropogenic debris, which included a shopping cart, landscaping mesh, a bale of rusted wire, concrete blocks, scrap metal, tires, a discarded door, and an abandoned vehicle. There was evidence of recent porcupine (*Erethizon dorsatum*) use (i.e., fresh droppings) at 33 (32%) of the 102 dens we investigated.

Habitat selection

We used all 120 dens to develop RSFs explaining third-order habitat selection. The average values for only 3 (7.7%) of 39 covariates measured at the third order differed significantly ($P < 0.05$) between those with evidence of recent

FIGURE 1 Examples of coyote dens in Edmonton, Alberta, Canada, 2021. Most dens had dense hiding cover despite locations near well-used trails and urban centers (A). Dens were sometimes within 50 m of human dwellings, such as the houses on the other side of this fence (B). Coyotes frequently integrated anthropogenic debris or materials into den structure, such as wood and a discarded metal door (C) and concrete blocks (D).

use in 2021 and those lacking evidence of apparent recent use via independent *t*-tests, so we pooled all dens for further analysis. The decay (α) term that resulted in the most predictive model was 25 m for distance to road and edge, 1,000 m for distance to water, and 1,500 m for distance to building. Building, road, and edge density were most predictive at 200-m, 50-m, and 25-m scales, respectively. To facilitate interpretation, we selected a single scale for all 4 terrestrial land cover classes; the most predictive scale for most covariates was 25 m. On average and compared to available sites (Table 1), dens were 140 m closer to water ($P = 0.002$), and in areas with 85% lower road density ($P \leq 0.001$) and 70% less cover by mowed grass ($P \leq 0.001$). Dens sites were more frequently located outside of the 75-m riverbank buffer ($P = 0.001$), and they exhibited 45% less cover by anthropogenic habitat ($P = 0.005$), and 25% more cover by naturalized urban areas. Slopes at den sites were 26% steeper than available sites ($P = 0.026$). Used and available sites had similar values for building density and proximity to buildings. Three dens (2.5%) were located <10 m from a building, 19 dens (15.8%) were located <25 m from a building, and 83 dens (69%) were located within 100 m of a building.

The list of variables retained for our multivariate model included the linear values for slope, decay distance to water, nearest road, and nearest edge, edge density, road density, all 4 land cover covariates, and the binary term reflecting proximity to riverbanks. Our all-subsets approach generated 11 models within $\Delta AIC_c \leq 2$, but only 2 models met our criterion of all covariates having $P \leq 0.100$ (Figure 2). Adding biologically plausible interaction terms did not improve model performance. Odds ratios for model-averaged results suggested that dens were 85% less likely to be located within 75 m of the river (OR = 0.15), and for every unit increase in mowed grass (%), the likelihood of a den decreased by 2% (OR = 0.98; Table 3). Every unit increase in road density (km/km^2) decreased den likelihood by 7% (OR = 0.93). Coyotes selected for proximity to water (OR = 0.08), and they avoided proximity

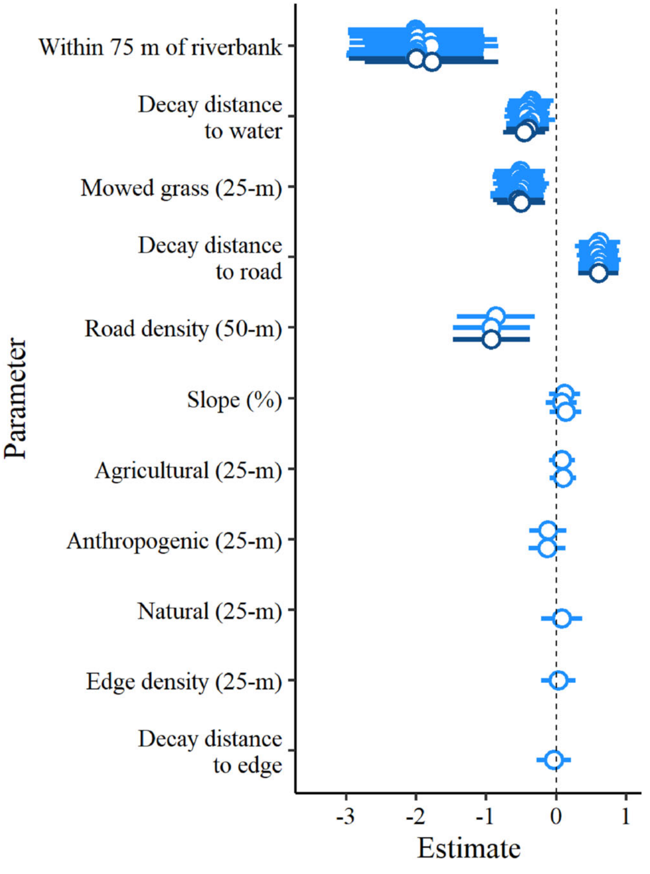

FIGURE 2 Standardized third-order parameter estimates and 95% confidence intervals for all models within 2 Akaike's Information Criterion adjusted for small sample sizes at coyote den sites in Edmonton, Alberta, Canada, 2021. Parameters are ordered by frequency of occurrence in all models from top to bottom. Dark blue coloration indicates parameters for models that met our criterion of all covariates being associated with $P \le 0.100$. Road density and edge density were measured in km/km^2 and were calculated at a resolution of 50 m and 25 m, respectively. Percent land cover was calculated for a 25-m radius circular buffer around each den.

to roads (OR = 9.40). Variance inflation factors indicated low multicollinearity among variables for both final models (all <1.1). Stratified *k*-fold cross validation resulted in an accuracy of 0.750 and 0.740 and a kappa value (κ) of 0.11 and 0, for the first and second model, respectively, indicating limited to no agreement among model folds ($k = 5$). The area under the ROC curve was 0.740 and 0.734 for the first and second models. These results suggest that this model was relatively weak at distinguishing between use and available sites.

We used 102 dens to develop RSFs representing fourth-order selection. We excluded 18 dens because of access limitations ($n = 11$), den locations under shipping containers, which prohibited accurate measurements ($n = 2$), and natural (e.g., windthrown tree; $n = 2$) or anthropogenic (e.g., infilling of den; $n = 3$) modification to microhabitat between the denning period and our summer site visits. There were no significant differences between fourth-order covariates at dens that had and had not been used recently, so we pooled dens regardless of recency of use. We summarized quantitative (Table 2) and qualitative (Table 4) covariate values for used and available sites. Compared to available sites, dens exhibited 73% greater hiding cover ($P \le 0.001$), 73% steeper slopes ($P \le 0.001$), 43% higher shrub cover ($P \le 0.001$), and 24% lower herbaceous cover ($P = 0.044$). On average, dens had greater eastern and southern exposure (circular mean aspect = 169° ± 2.1) than available sites (circular mean aspect = 205° ± 2.0;

TABLE 3 Summary metrics for the averaged results of the top 2 models explaining selection of third-order habitat characteristics at coyote den sites in Edmonton, Alberta, Canada, 2021. The 2 constituent models were within 2 Akaike's Information Criterion adjusted for small sample sizes, and all covariate values were associated with $P \leq 0.100$. We report conditional averaging results, corrected by weight. We standardized coefficients by mean-centering and scaling by 1 standard deviation.

Variable	β coefficient	*P*	95% CI (β)	Odds ratio	95% CI (Odds ratio)
Road decay distance	0.60	≤0.001	0.31, 0.89	9.40	3.21, 27.51
Within 75 m of river	−1.90	≤0.001	−2.89, −0.91	0.15	0.06, 0.40
Road density (km/km^2)	−0.93	≤0.001	−1.48, −0.38	0.93	0.90, 0.097
Mowed grass cover	−0.53	0.004	−0.88, −0.17	0.98	0.97, 0.99
Water decay distance	−0.43	0.007	−0.74, −0.12	0.08	0.01, 0.50

TABLE 4 Summary statistics for qualitative fourth-order habitat characteristics selected by coyotes at den sites and paired sites in Edmonton, Alberta, Canada, 2021.

	Use (*n* = 102)	Available (*n* = 102)	Test results	
Variable	Mode	Mode	χ^2	*P*
Mesoslope position	Mid slope	Level	19.6	0.003
Soil type	Fine sandy loam	Silty clay loam	17.9	0.118
Garbage abundance	Low	Low	2.6	0.449
Garbage manipulation	Absent	Absent	19.0	≤0.001

$t_{169} = 114.4$, $P \leq 0.001$). Dens were often on mid slopes ($n = 31$, 30%) and upper slopes ($n = 23$, 23%; Table 4). While the amount of garbage was similar at dens and available sites ($P = 0.449$), garbage manipulation was 3.4 times more likely to be classified as high at dens compared to available sites. Dens occurred in a variety of soil textures, with no difference between used and available sites.

Our final covariate list included slope, east index, hiding cover, tree cover, shrub cover, herbaceous cover, and slope position. Our modeling approach generated 3 models that were similarly predictive ($\Delta AIC_c \leq 2$), 2 of which met our criterion of $P \leq 0.010$ for all parameters (Figure 3). Interaction terms did not improve model performance, so we used the 2 final main effects models as top models. Odds ratios for model-averaged results revealed that, for every unit increase in hiding cover (%), the likelihood of a den increased by 7% (OR = 1.07; Table 5). For every unit increase in slope (°), den likelihood increased by 16% (OR = 1.16). Coyotes also selected for shrub cover (OR = 1.02) and eastern exposure (OR = 2.13), and against herbaceous cover (OR = 0.98). Variance inflation factors for both final models indicated low multicollinearity among variables (all <1.2). Stratified *k*-fold cross validation resulted in an accuracy of 0.775 and 0.725 and a kappa (κ) value of 0.55 and 0.45, for the first and second model, respectively ($k = 5$). The area under the ROC curve was 0.868 for the first model and 0.864 for the second model. These metrics suggested that these models effectively distinguished between use and available sites.

Relationship between dens and physical conflict

A GLM predicting physical conflict using all reports within 500 m of known dens ($n = 2{,}123$) indicated that conflict increased during the pup-rearing period ($\beta = 0.91$, $P < 0.001$, 95% CI = 0.69, 1.13) and near dens ($\beta = -0.21$,

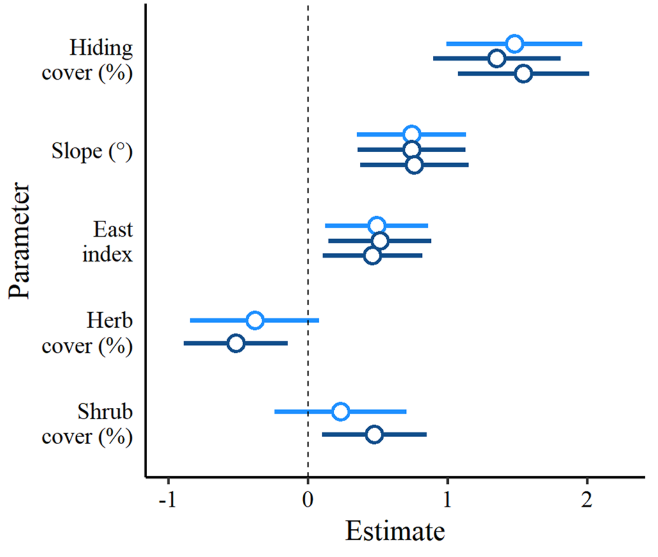

FIGURE 3 Standardized fourth-order parameter estimates and 95% confidence intervals for all models within 2 Akaike's Information Criterion adjusted for small sample sizes at coyote dens in Edmonton, Alberta, Canada, 2021. Dark blue coloration indicates parameters for models that met our criterion of all covariates being associated with $P \leq 0.100$.

TABLE 5 Summary metrics for the averaged results of the top 2 models explaining selection of fourth-order habitat characteristics at coyote den sites in Edmonton, Alberta, Canada, 2021. The 2 constituent models were within 2 Akaike's Information Criterion adjusted for small sample sizes, and all covariate values were associated with $P \leq 0.100$. We report conditional averaging results, corrected by weight. We standardized coefficients by mean-centering and scaling by 1 standard deviation.

Variable	β coefficient	*P*	95% CI (β)	Odds ratio	95% CI (Odds ratio)
Hiding cover (%)	1.49	≤0.001	0.99, 1.99	1.07	1.05, 1.10
Slope (°)	0.75	≤0.001	0.36, 1.15	1.16	1.08, 1.26
Herbaceous cover (%)	−0.52	0.007	−0.89, −0.14	0.98	0.97, 1.00
East index	0.48	0.011	0.11, 0.84	2.13	1.19, 3.79
Shrub cover (%)	0.47	0.014	0.10, 0.85	1.02	1.00, 1.03

$P = 0.002$, 95% CI = −0.34, −0.07), but the interaction term between these covariates was not significant (β = 0.12, $P = 0.280$, 95% CI = −0.10, 0.34; Figure 4A). When we considered only reports occurring within naturalized urban areas ($n = 530$), the only predictor of increased physical conflict was the pup-rearing season (β = 0.98, $P < 0.001$, 95% CI = 0.54, 1.42; Figure 4B). When we considered only reports occurring outside of naturalized urban areas ($n = 1{,}593$), physical conflict was higher during the pup-rearing season (β = 0.80, $P < 0.001$, 95% CI = 0.53, 1.08) and near dens (β = −0.27, $P = 0.001$, 95% CI = −0.43, −0.11; Figure 4C). When we modeled likelihood of conflict as a function of land cover and proximity to a den, modified land cover reduced the likelihood of conflict (β = −0.71, $P < 0.001$, 95% CI = −0.95, −0.47). A significant interaction term (β = −0.28, $P = 0.018$, 95% CI = −0.51, −0.05) indicated that likelihood of conflict decreased with increasing distance from dens in modified areas but not in naturalized urban areas (Figure 4D). Because dens were detected in 2021, whereas physical conflict reports were submitted between 2010 and 2020, we repeated this analysis for the subset of reports occurring in 2020, and we

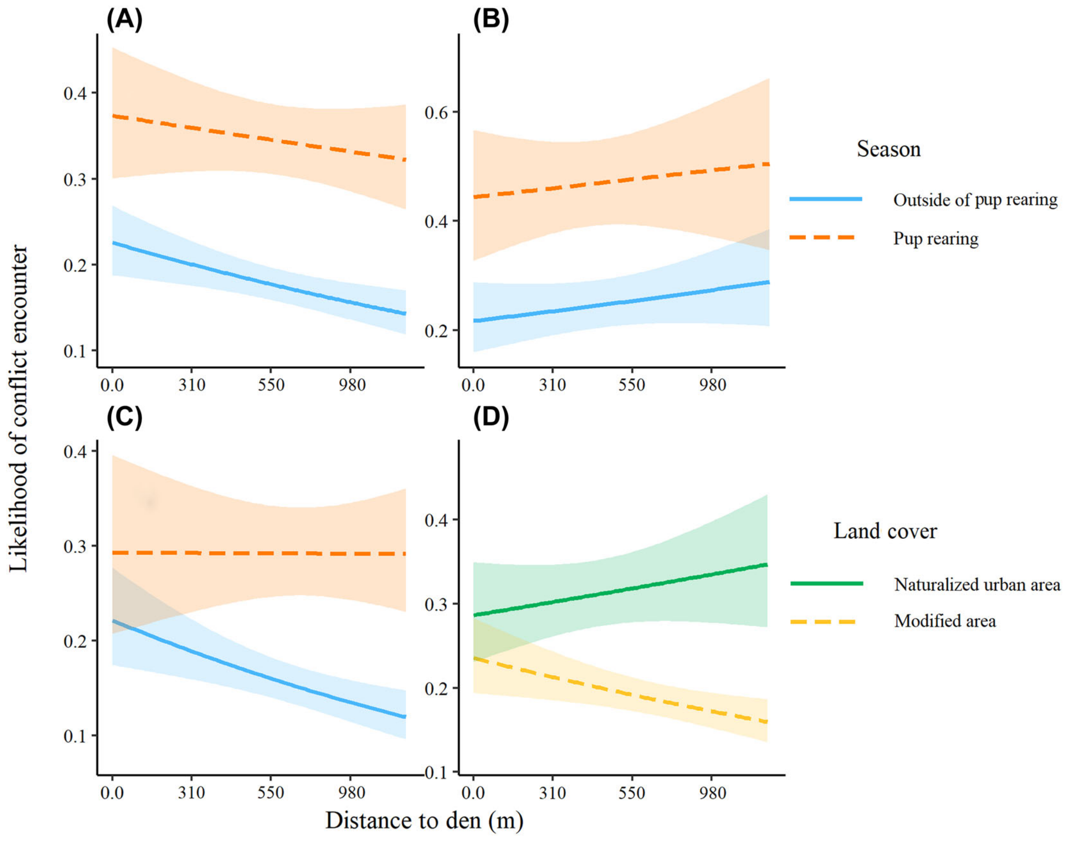

FIGURE 4 Interaction plots showing the likelihood of encounters between coyotes and humans or pets characterized by physical conflict as a function of increasing distance from known den sites in Edmonton, Alberta, Canada, 2010–2020. Among all reports (n = 2,123), physical conflict increased near dens and during the pup-rearing season (A). Among reports within naturalized urban areas (n = 530), physical conflict was highest during the pup-rearing season. Among reports outside of naturalized urban areas (n = 1,593), physical conflict increased near dens and during the pup-rearing season. Among all reports (n = 2,123), physical conflict increased near dens when reports occurred outside of naturalized urban areas, but within these areas, physical conflict was higher farther from dens. Shaded areas represent 95% confidence intervals.

achieved results that were categorically the same, but with higher P-values and lesser statistical power given smaller sample sizes.

DISCUSSION

Despite the prevalence of urban coyotes in cities across North America, little is known about their denning habits or how denning behavior relates to physical conflict with humans. In this study, we determined den site selection by coyotes at 2 spatial scales in an urban environment, and we tested whether physical conflict between coyotes and humans or pets increased near coyote dens. Consistent with our hypotheses, selection for habitat characteristics was stronger at the finer, fourth order of habitat selection compared to the third, and most of the selected habitat characteristics appeared to be associated with security from people and dogs. Unlike our prediction, coyotes exhibited tolerance of human infrastructure and artifacts near den sites, and did not avoid most metrics of human presence, both results reflecting the adaptability that enables coyotes to thrive in urban centers. Proximity to dens was a strong predictor of conflict behaviors, especially during the pup-rearing period and outside of naturalized urban areas. Our results suggest that coyote dens in Edmonton were located predictably based on habitat features, which may support future mitigation of physical conflict with coyotes.

We tested 2 spatial scales of habitat selection for den sites by coyotes and coyotes exhibited weak selection for habitat characteristics at the third order (home range) with the covariates we used. They exhibited much stronger selection at the fourth order (patch) where they preferred dense cover and steep slopes. This pair of results suggests that coyotes den in a broad range of third-order contexts, ensuring security by selecting more specific habitat characteristics at the fourth order. Others similarly reported weak habitat selection for den selection at the third order with stronger selection at the finer fourth order for several North American canids. Red fox exhibited hierarchical selection at den sites (Zaman et al. 2020), and wolves exhibited the strongest selection within 15 m of the den opening (Trapp et al. 2008). Coyotes in our study followed the same pattern wherein fourth-order habitat characteristics were the most important predictors of natal den sites. We may have detected stronger selection at the third order if we had searched for dens in a greater diversity of landscapes, such as under residential buildings, and on private residential and industrial property. We emphasized green spaces in Edmonton because urban coyotes predominantly use these areas within cities (Riley et al. 2003, Gehrt et al. 2009, Gehrt and Riley 2010, Murray and St. Clair 2017).

While third-order results should be interpreted with caution given that the models were poor at distinguishing between used and available sites, the top parameters likely still represent the most important third-order habitat characteristics that coyotes select at den sites, at least among the variables we measured, and emphasized water. A strong predictor was avoidance of the 75-m buffer adjacent to the North Saskatchewan River. Coyotes may avoid denning within 75 m of the river because it represents a travel corridor (Dickie et al. 2020), or a territorial boundary (Crabtree and Sheldon 1999), both of which could expose vulnerable offspring to potentially dangerous conspecifics (Camenzind 1978). In Edmonton, coyotes may have avoided the river because of periodic flooding events, a high prevalence of adjacent recreational trails, and unstable banks that erode over time. By contrast, we observed selection for den sites with proximity to water (other than the North Saskatchewan River), similar to a study of coyotes in the East (Way et al. 2001) and several studies of wolf dens (Norris et al. 2002, Trapp et al. 2008, Kaartinen et al. 2010, Ahmadi et al. 2013), presumably to support the increased hydration needs of lactating females.

At the third order of habitat selection, coyotes also avoided certain land covers and anthropogenic features. Their avoidance of areas with large amounts of mowed grass is consistent with literature indicating that coyotes select for habitat with abundant cover at dens (Althoff 1980, Hallett et al. 1985, Kamler et al. 2005, Gese et al. 2012). Coyotes avoided denning near roads and in areas with high road density, a phenomenon that has been observed in wolves in populated areas of Eurasia (Capitani et al. 2006, Ahmadi et al. 2013). That coyotes avoided roads but failed to respond to other metrics of human presence (e.g., anthropogenic land cover, proximity to building, building density) could suggest that coyotes avoid the mortality risk associated with vehicles (Grinder and Krausman 2001, Murray and St. Clair 2015), rather than anthropogenic presence more broadly.

Coyotes showed strong selection for habitat characteristics at the fourth order, favoring areas with abundant shrub cover, high values of vertical hiding cover, steep slopes, eastern exposure, and low herbaceous cover. Dense vegetative cover and steep slopes likely increased security from people and dogs. Fourth-order selection for security cover was observed in several studies of coyotes in rural areas (Althoff 1980, Hallett et al. 1985, Kamler et al. 2005), similar to wolves (Trapp et al. 2008) and red fox (Zaman et al. 2020). Early published accounts of coyote dens described them as difficult to detect visually (Lemm 1973) with obscured entrances (Althoff 1979). Dense hiding cover likely protects young from predators by limiting den access (Elbroch et al. 2015), but it may also provide protection against inclement weather (Bleich et al. 1996). Selection for steep slopes at den sites was previously documented at rural coyote dens (Althoff 1980, Way et al. 2001), probably because slopes reduce access by intruders (Capitani et al. 2006, Ahmadi et al. 2013), promote drainage and prevent pooling of water

(Trapp et al. 2008, Kaartinen et al. 2010), facilitate incorporation of tree roots in den roofs, and increase solar insolation. Fourth-order selection for eastern exposure could also promote warmth via increased solar radiation, and avoidance of windward exposure (Althoff 1980), given the strongest winds during the pup-rearing period in Edmonton are from the west or northwest (Environment Canada 2022). Low herbaceous cover near den sites was likely a consequence of trampling by coyotes given high use, as described at wolf dens (Trapp et al. 2008).

Coyotes exhibited tolerance for human presence near dens, including failure to avoid most metrics of human presence, proximity of dens to occupied buildings, integration of anthropogenic materials into den structure, and evidence of interaction with anthropogenic garbage at den sites. These behaviors exemplify the plasticity and adaptability characteristics of urban-exploiting species (McKinney 2002, Ritzel and Gallo 2020), including coyotes (Murray et al. 2015). Coyotes have demonstrated plasticity with respect to denning behaviors in other contexts; for example, following the reintroduction of wolves in the Yellowstone Ecosystem in the United States, and the excavation of coyote dens by wolves, coyotes began locating dens under large boulders (Crabtree and Sheldon 1999). Coyotes may have similarly adapted denning habits to urban environments through specific selection of fourth-order characteristics that promote security from humans and domestic dogs. The failure to avoid anthropogenic features and to incorporate anthropogenic infrastructure into dens is consistent with other observations of small canids denning near human centers; for example, red foxes do not avoid areas with human activity when denning (Zaman et al. 2020), and den under buildings (Dekker 1983), and Indian foxes (*Vulpes bengalensis*) frequently use anthropogenic items or debris as infrastructure to support their dens (Punjabi et al. 2013). Coyotes in urban environments dig dens in anthropogenic topographical features (Way et al. 2001, Grubbs and Krausman 2009), and den near occupied buildings (Way 2009). By contrast, wolf dens in a human-dominated area in Iran were located away from settlements (Ahmadi et al. 2013), and wolves avoid recreational housing structures during the denning period (Malcolm et al. 2020). Unlike wolves, but like other small canids, coyotes exhibited behavior that suggests exploitation of the urban landscape. The abundance of manipulated anthropogenic garbage at dens is consistent with observations of chewed garbage at wolf dens (Trapp 2004), presumably provided by parents for pups. Access to inedible anthropogenic items may promote some form of conditioning to human presence (McNay 2002). Given the tendency for boldness and habituation in coyote pups to be influenced by the environment and habituation of parents to human presence (Schell et al. 2018), prolonged exposure of coyotes to human objects at or near den sites could ultimately have long-term impacts on coyote behavior, habituation, and interactions with humans.

Reported physical conflict with coyotes increased near dens, especially during the pup-rearing season, which is consistent with reports of greater conflict in that season described by other studies (White and Gehrt 2009, Lukasik and Alexander 2011; J. J. Farr, unpublished report). These studies all support the idea that physical human–wildlife conflict for mammal species culminates from increased territorial defense associated with offspring presence (Wolff and Peterson 1998). For example, wolves exhibited aggressive behaviors to defend dens (McNay 2002), and the presence of offspring increases likelihood of grizzly bear (*Ursus arctos*) attacks on people (Smith and Herrero 2018). In coyotes, the association between physical conflict and proximity to dens has previously been inferred rather than measured directly. Our data indicated increased physical conflict near dens as an overall effect and when reports occurred outside of naturalized urban areas, but proximity to den was not an important predictor of conflict when reports occurred within naturalized urban areas. This pattern may have occurred because naturalized urban areas contain hiding cover that reduces territorial defense. The possibility that animals behave more aggressively to threats in open areas because they lack options to hide or flee has been used to explain the aggressive tendencies of grizzly bears (Herrero 1972) and sloth bears (*Melursus ursinus*; Stirling and Derocher 1990). Like coyotes, these species evolved predominantly in open environments that lacked the cover and escape opportunities associated with treed landscapes.

Our study had some characteristics that potentially limit the generality of these findings. For our assessment of third-order habitat selection, we may have failed to capture the most important covariates, such as access to food sources, although we used most of the variables described in the literature. We did not have a measure of variation in human use within urban green spaces, which may affect coyote distribution at these broader scales. Our assessment of fourth-order habitat selection reinforces several other studies, providing good evidence that coyotes generally select den sites at finer spatial scales (Althoff 1979, 1980; Harrison and Gilbert 1985). Our assessment of proximity to human use did not consider transient recreational activities, but proximity to buildings included distance to residential dwellings that might signal opportunities for human–coyote conflict. The all-subsets modeling approach we used potentially increases our detection of spurious relationships (Burnham and Anderson 2001), but this approach is common in exploratory analyses like ours (Maglianesi et al. 2014, Gibb et al. 2020, Lenoir et al. 2020, St. Clair et al. 2020), and all variables identified by our top models were biologically plausible and well supported by the literature. The correlation we found between den proximity and reports of aggressive coyotes may have been altered by reports collected outside the pup-rearing period when dens would be most likely to generate human–coyote conflict. In addition, the public reporting database exhibited large variation in the types and frequency of reports among neighborhoods, which may have altered the patterns of physical conflict we detected.

MANAGEMENT IMPLICATIONS

Our results suggest that coyotes in Edmonton are successfully integrating one of the most biologically sensitive periods of their life history—denning and pup rearing—into urban areas that are used extensively by humans, rather than avoiding humans and their infrastructure. Our study provides new information that proximity to dens increases risk of physical conflict, especially outside of naturalized urban areas, so managers should prioritize education and attractant management to reduce physical conflict on the periphery of or outside naturalized urban areas and attempt to prevent denning by coyotes within residential neighborhoods. Residential areas with den-associated conflict could thin dense vegetation to discourage denning by coyotes, and residents whose properties are adjacent to natural areas could erect fences that are tall enough to exclude coyotes (>1.68 m; Thompson 1979). Managers should work proactively to prevent the occurrence of coyote dens outside of naturalized urban areas, particularly where vulnerable individuals are likely to occur in homes, schools, and playgrounds. Equally important is to secure food sources that attract coyotes to residential neighborhoods, such as garbage, compost, small pets, pet food, bird seed, and fruit trees because these attractants may encourage denning in or immediately adjacent to residential areas and promote conflict.

ACKNOWLEDGMENTS

The authors thank J. J. Farr for leading the classification of public reports from the Edmonton Urban Coyote Project and sharing these data, and S. A. Sugden for reviewing sections of statistical code. This work was supported by a Canada Graduate Scholarship awarded to S. Raymond by the Natural Sciences and Engineering Research Council of Canada (NSERC), a Walter H. Johns Graduate Fellowship awarded to S. Raymond by the University of Alberta, and by an NSERC Discovery Grant (RGPIN-2017-05915) and a University of Alberta Faculty of Science Research Fellowship awarded to C. C. St. Clair.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

We conducted this project under Province of Alberta Research Permit 21-027, which supported access to den sites in seasons when coyotes were not expected to be using dens. We consulted with the Animal Care and Use Committee of the University of Alberta to determine we did not require their review and approval of our study because we were not manipulating animals or acting in ways that were expected to alter animal behavior.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available because of privacy or ethical restrictions. The R scripts and workspace required to reproduce all analyses and figures are available in the GitHub repository https://github.com/sageraymond/CoyoteDenSelection.

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Associate Editor: Kerry Nicholson.

How to cite this article: Raymond, S., and C. C. St. Clair. 2023. Urban coyotes select cryptic den sites near human development where conflict rates increase. Journal of Wildlife Management 87:e22323. https://doi.org/10.1002/jwmg.22323