# Using wildlife occurrence data to test permeability estimates and ecological indices used in urban planning

by

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# ABSTRACT

Increasing urban development degrades ecosystems partly by diminishing natural area connectivity and quality, ultimately reducing and homogenizing urban biodiversity. To support biodiversity, ecological planners in Edmonton, Alberta (hereafter the City) have implemented tools to incorporate wildlife habitat into land use planning. These tools include circuit-based simulation models that used permeability estimates based on coyote (*Canis latrans*) movement to approximate connectivity for urban mammals. Two other indices, biodiversity potential and ecological connectivity, estimate the ecological value of natural areas based on patch characteristics.

To evaluate the predictive capacity of these tools, this thesis compared the predicted permeability and habitat values with animal occurrence data from GPS collars, camera traps, and small mammal track tube arrays. In Chapter 2, I explored how habitat selection by 19 urban coyotes fitted with GPS collars was affected by health status (via infection with sarcoptic mange; *Sarcoptes scabiei*) and season (summer *vs.* winter) using two modelling approaches. I used two seasonal compositional analyses to explore the selection of broad categories to obtain selection estimates as log-ratios of proportionate use to compare with feature-specific permeability ratings. I then built a RSF model to assess fine-scale habitat selection and derived a habitat suitability index (HSI) to compare with cumulative landscape permeability values used in circuit-based models in linear regressions.

From compositional analyses, whether coyotes used or avoided habitat was consistent between seasons, but used natural forests, natural shrubland, modified grass/shrubland and residential areas more in winter. The RSF model showed that coyotes largely avoided developed areas, but selected steeper slopes and areas closer to natural areas, modified forests and grass/shrubland, and residential areas. Coyotes with mange were more likely to use human-dominated areas, especially in winter. The feature-specific permeability ratings used in circuit-based models undervalued residential and developed areas in both seasons and maintained grass in summer, while overvaluing most natural vegetation types and the North Saskatchewan River in winter. The landscape permeability estimates were predictive of the RSF-derived HSI, but less so in winter and when coyotes had mange, and the model fit was poor.

In Chapter 3, I used data from 89 camera traps and 47 track tube arrays placed throughout Edmonton, Alberta to measure the occurrence and relative abundance of three groups of terrestrial mammals (small, medium, and large) and 13 species. I used these as response variables to evaluate the predictive capacity of two ecological indices used by the City in zero-inflated Poisson and linear mixed models. I also modelled detections of the three groups and five species using various remotely-sensed and site-based variables. The indices of biodiversity potential and ecological connectivity used by the City correlated variably and generally with the occurrence or relative abundance of groups and species. As biodiversity potential increased, large mammals occurred more often, and white-tailed deer (*Odocoileus virginianus*) were more abundant, but the abundance of small mammals declined. By contrast, higher ecological connectivity predicted more abundant small mammals, but less abundant snowshoe hare (*Lepus americanus*) and white-tailed deer. I found high variability in the predictiveness of remotely-sensed and field-measured variables among and within species groups, with patch-level covariates predicting only small mammal abundance from track tubes. I found generally adverse effects of human disturbances, such as urban density, human activity, and off-leash areas, but with some positive associations with detections of domestic dogs.

In combination, my results suggest that expert-derived estimates of landscape permeability used to model connectivity by the City reflect habitat selection by urban coyotes. However, the accuracy of such models could be improved by using empirical data, such as those provided by GPS collars. Doing so could identify the effects of individual variation and season, and the high capability of using developed areas by urban-adapted species like coyotes. My results from the tests of ecological indices suggest that a larger buffer width may be necessary to represent connective habitat for larger species, and a lower weight for wetland habitat may better reflect habitat quality for mammal species in Edmonton. The accuracy of ecological indices used by urban planners could be increased by considering surrounding vegetation density and type, and human infrastructure and activity. Further development of such indices will assist Edmonton and other cities retain biodiversity and the many ecological benefits provided by wildlife.

## PREFACE

This thesis is an original work by Cassondra J. Stevenson. The GPS location data for coyotes used in Chapter 2 were collected by Maureen Murray. The camera trap and/or track tube data used in Chapter 3 resulted from a collaboration between the University of Alberta, the City of Edmonton, and the Urban Wildlife Information Network (UWIN). The field data were collected between May 2018 and September 2021 by Cassondra Stevenson, Kelsey Gourlie, Catherine Shier, Colleen St. Clair, Julia Shonfield, Nicole Boucher, Deanna Steckler, Garret Tierney, Robin Glover, and numerous volunteers (listed below) who provided support in both field data collection and data processing.

The data collected from camera traps and small mammal track tubes received animal ethics approval from the University of Alberta Animal Care and Use Committee ("Edmonton Urban Coyote Project"; No. AUP00002336, 2018). The City of Edmonton permitted data collection. The GPS collar data was supported by Animal Damage Control (particularly B. Abercrombie) and the City of Edmonton Animal Control & Control Centre. All animal handling was following the guidelines of the University of Alberta Animal Care and Use Committee and the Canadian Council on Animal Care.

Data chapters 2 and 3 were formatted using the pronoun "we" to recognize the collaborative work of several authors and because both were prepared for submission to a peer-reviewed journal following the thesis defense. Formatting to support publications also caused some redundancy of information between the two chapters. Citations included in the "Literature Cited" were formatted for submission to "Ecosphere" and thus to coincide with a modified Chicago Manual of Style author-date style. Chapter 2 will include Catherine Shier, Maureen Murray, and Colleen St. Clair as co-authors, and Chapter 3 will include Catherine Shier, Kelsey Gourlie, and Colleen St. Clair as co-authors.

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## GLOSSARY

**Biodiversity:** "The number and variability of organisms found within a specified geographic region; this includes diversity within species, between species and of ecosystems" (City of Edmonton 2010a).

**Biodiversity potential:** The capacity of a natural area to support biodiversity (City of Edmonton 2014a).

**Connectivity:** The degree to which a landscape facilitates or impedes movement among resource patches. It may be provided by stepping stones, corridors and/or compatible land uses (City of Edmonton 2007).

**Corridor:** "Natural or semi-natural linear vegetated patches that enhance movement among other habitat patches such as core areas or natural stepping stones" (City of Edmonton 2007). Where **core areas** "habitat patches of suitable size and quality so as to provide environmental conditions that support entire populations of animals and plants and associated ecological functions" (City of Edmonton 2007).

**Developed:** Defined as "high impact development" which is "any land use which, because of its type, scale, location or intensity, may generate negative off-site, cross-border impacts including, but not limited to, obstruction or intrusion, servicing demands, hazards to persons or property or other environmental impacts" (City of Edmonton 2010a).

**Ecological connectivity:** "The connectivity required to enable plants, wildlife, and ecological processes to persist on a landscape scale by facilitating ecological processes (e.g., nutrient flow, genetic exchange, and movement)" (City of Edmonton 2007) evaluated as the potential for use by wildlife (City of Edmonton 2014a).

**Ecological network:** "A coherent system of natural and/or semi-natural landscape elements. The basic structure of an ecological network has three main landscape elements: core areas, linkages (stepping stones and/or corridors) and a matrix" (City of Edmonton 2007); where linkages are "arrangements of natural or semi-natural vegetation that enhance either structural and/or functional connectivity (for species, communities or ecological processes) between core areas" (City of Edmonton 2007, 2010a).

**Ecological network approach:** "Configuring and managing an ecological network with the objective of maintaining or restoring ecological functions as a means to conserve biodiversity" (City of Edmonton 2007).

**Habitat:** Areas required by wildlife species (singular or multiple) to fulfill their resource requirements.

**Habitat diversity:** defined as "Site types," which are "the fundamental land unit classification nested within the land cover that includes additional categories to the Provincial PLVI that provide more information relevant to urban settings" (City of Edmonton 2014b).

**Habitat fragmentation:** "A process during which a habitat is transformed into a number of smaller patches of smaller total area and isolated from each other by a matrix of habitats unlike the original" (Fahrig et al. 2003).

**Habitat selection:** The disproportionate use of resources or conditions by living things; differs from use or association (implies choice); is commonly measured as use relative to availability or as use versus non-use (Boyce 2006; Mayor et al. 2015).

**Industrial area:** "Areas with established industrial businesses where new industrial development, associated businesses, and supporting services may locate" (City of Edmonton 2010a).

**Modified areas / modified vegetation:** Defined as "semi-natural landscape elements" which are areas that are "at least partially manicured green spaces (such as active recreation parks, schoolyards, cemeteries, conventional stormwater management facilities and some rights-of-way)" (City of Edmonton 2007).

**Natural Area:** "An area of land or water that is dominated by native vegetation in naturally occurring patterns. Such areas could include grasslands, forests, wetlands, peatlands or riparian areas. Areas such as groomed parks, sports fields and schoolyards are not natural areas" (City of Edmonton 2007, 2010a).

**Natural features:** Defined as "natural landscape elements" which are areas "that are are dominated by native vegetation in naturally occurring patterns (such as natural areas and naturalized stormwater management facilities or parks)" (City of Edmonton 2007).

**Neighbourhood:** "A residential area with an appropriate mix of housing types with convenience-type commercial facilities and where appropriate, schools or park facilities" (City of Edmonton 2010a).

**North Saskatchewan River Valley and Ravine System:** "The North Saskatchewan River Valley, its banks and the banks of its tributary system in the city of Edmonton" (City of Edmonton 2010a).

**Open space:** "Areas of land and water that are semi-natural in composition. Such spaces could include active recreation parks, schoolyards, conventional stormwater management facilities and some boulevards" (City of Edmonton 2010a).

**Parkland:** "Any property, developed or not, that is owned, controlled or maintained by the City and that is intended to be used by members of the public for recreation as a natural area, preserved as a natural area, used as a cemetery, zoned AP (public parks), A (metropolitan recreation), AN (River Valley activity node) or US (urban services), contained in the North Saskatchewan River Valley and Ravine System Protection Overlay as, described in the City bylaw governing land use, designated as municipal reserve, environmental reserve or a public utility lot pursuant to the Municipal Government Act, [or] that portion of any boulevard contiguous with, partially within, or fully within any property described above" (City of Edmonton 2010a).

**Peri-urban:** On the fringe of an urban area.

**Protected area:** Using the definition of "Enivronmental reserve" — "Land that is required to be dedicated at the time of subdivision that qualifies as environmental reserve under the Municipal Government Act, R.S.A. 2000, c. M-26, which may include ravines, land adjacent to a body of water or land subject to flooding" (City of Edmonton 2010a).

**Restoration:** "The re-establishment of habitat in order to improve ecological processes or connectivity" (City of Edmonton 2007, 2010a).

**River valley:** "The North Saskatchewan River Valley and associated system of tributary ravines" (City of Edmonton 2007).

**Semi-natural:** Defined as areas with "semi-native vegetation," which is "a plant community that includes at least some plant species native to the region" (City of Edmonton 2010a).

**Stepping-stone:** "Natural or semi-natural non-linear vegetated patches that provide many resources for species but may not be of sufficient size or quality to provide for all habitat requirements or ecological functions. They are usually separated by a less hospitable matrix or linked by corridors" (City of Edmonton 2007).

**Sustainability:** "A way of living which meets the needs of the present and does not compromise the ability of future generations to meet their own needs. Urban planning takes an integrated, holistic view of urban environments and defines sustainability in the context of interrelated ecosystems encompassing economic, social, environmental and cultural sustainability. The principle of sustainability also includes financial sustainability, ensuring urban planning recognizes and addresses resource constraints and capacities" (City of Edmonton 2010a).

**Tablelands:** "The upland areas above the North Saskatchewan River Valley and Ravine System" (City of Edmonton 2007, 2010a).

**Wetland:** "Land having water at, near, or above the its surface, or which is saturated with water long enough to promote wetland or aquatic processes, as indicated by poorly drained (hydric) soils, hydrophytic vegetation, and various kinds of biological activity that are adapted to the wet environment" (City of Edmonton 2010a).

## **CHAPTER 1 -** General Introduction

Urbanization reduces, fragments, and degrades natural areas (Grimm et al. 2008; Bongaarts 2019), which results in habitat loss, diminished natural connectivity, and ultimately biodiversity loss and homogenization of species within cities (McKinney 2006; Beninde, Veith, and Hochkirch 2015; Newbold et al. 2018). Although conservation research historically mostly ignored urban settings (Miller and Hobbs 2002), urban planners increasingly recognize the importance of proactive planning to retain biodiversity (Apfelbeck et al. 2019). However, urban areas are expanding faster than any other land use type (Bongaarts 2019), and even seemingly remote regions have become heavily urbanized (~74% of Canada’s population; Statistics Canada 2018). Such rapid growth and sprawl of urban areas increase the challenge of conserving adequate habitat for wildlife in urban areas (Angel et al. 2011; Pickett et al. 2011).

Edmonton, Alberta, Canada, is one such city where rapid population growth (Statistics Canada 2021b) and extensive urban sprawl (City of Edmonton 2017a) increase pressure to develop existing wildlife habitat located in areas of high apparent connectivity (City of Edmonton 2020b). This growing urban metropolis contains 95% of the region’s population (City of Edmonton 2017a) and Canada's largest urban park (City of Edmonton 2020b, 2022). The City of Edmonton (hereafter the City) aims to maintain the City’s “ribbon of green” and its remnant natural areas as a connected ecological network to conserve biodiversity and develop sustainably (City of Edmonton 2020b). To achieve this, urban planners need efficient tools to assess environmental sensitivities (Kay et al. 2021), such as the ecological connectivity and habitat value of natural areas, to prioritize protection, conservation, and restoration (City of Edmonton 2017b).

In Edmonton, AB, urban ecological planners have implemented tools to incorporate the needs of urban wildlife into land use planning to enhance sustainability and support biodiversity. One of these tools is a circuit-based simulation model of coyote (*Canis latrans*) movement intended to estimate connectivity for other terrestrial mammal species, created using expert-derived permeability estimates and remotely-sensed data (City of Edmonton 2017b). Two other indices, biodiversity potential and ecological connectivity, are used to estimate the ecological value of natural areas based on patch characteristics (City of Edmonton 2014a). Ideally, these tools would be verified with independent information about habitat use by representative or target species (Zeller, McGarigal, and Whiteley 2012), and such data are increasingly available for urban areas, including Edmonton.

Additional analyses could support tests of the indices used by planners because many other factors that affect habitat quality and permeability for wildlife are necessarily omitted from these estimators. For example, the permeability estimates used in cost-based connectivity analyses were based on expert-opinion using coyotes as a target species, but without considering the health status of animals. Previous work in my lab and others has shown that sarcoptic mange (*Sarcoptes scabiei*) alters habitat selection and movement by coyotes (Murray et al. 2015b; Murray and St. Clair 2017). Understanding how wildlife diseases impact spatial patterns of habitat use by animals may be especially important in urban areas, where reduced connectivity and congregation may facilitate the spread of wildlife diseases (Dougherty et al. 2018), including coyote-borne zoonoses such as *Echinococcus multilocularis* that are present in Edmonton (Luong et al. 2018; Sugden et al. 2020).

Two additional contributors to animal use of urban spaces include the conversion of natural to semi-natural spaces and the concomitant use of both of these areas by people. The two indices used by the City were designed to estimate the ecological value of areas with natural habitat types, but they were not intended to apply to parks with modified vegetation types. However, many semi-natural parks have qualities of natural areas, such as shrubs and trees, that may support species which rely on high vegetation structure, such as rodents (Glennon and Porter 2007) or snowshoe hare (Murray 2003; Holbrook et al. 2017). Semi-natural areas may also support movement (Lynch 2018). Conversely, urban green spaces may be too small or isolated (Beninde, Veith, and Hochkirch 2015), or contain vegetation that is homogenized or too simplified in structure (Bigsby, McHale, and Hess 2013) to support persistence over time. Human use also affects habitat use; however, variably among species (Nickel et al. 2020).

One more limitation of the ecological indices used by urban planners is the high variability among species in how they respond to urbanization (McIntyre 2014; Newbold et al. 2018; Fidino et al. 2021). Urban landscapes may support an increase in the abundance of species that can adapt or exploit urban areas, while others decline (McKinney 2002; Ducatez et al. 2018; Newbold et al. 2018), which often corresponds to characteristics of urban avoiders *vs.* adapters and exploiters (*sensu* Blair, 1996; McKinney, 2002). Species' behavioural traits and adaptability greatly influence habitat use (Ducatez et al. 2018), and adapted species may use low-quality habitat. However, adaptability varies among species, even among flexible species, like carnivores (Nickel et al. 2020). Differences in functional traits of species will influence habitat use and thus habitat quality, such as the ability to disperse, where smaller species are likely to persist in more disturbed and isolated areas (Aronson et al. 2016; delBarco-Trillo and O'Donnell 2020). As a result, species able to disperse more easily tend to be more abundant where habitat is fragmented (Parker and Nilon 2012), whereas smaller species decline (Barko et al. 2003; Munshi-South 2012). Habitat use by small mammals may be influenced by the avoidance of predation by domestic dogs (Lenth, Knight, and Brennan 2008), or they might prefer areas near humans to avoid natural predators (Suraci et al. 2019). Urban disturbances may also shift carnivores into more natural spaces (Parsons et al. 2019), which may indirectly alter predator-prey dynamics. Maintaining biodiversity requires protecting habitat that accommodates the needs of rare as well as abundant species in urban areas. Better planning could occur by understanding the responses of species groups and individual species that vary in size, habitat associations, natural history, and urban adaptation to various urban features and disturbances. Such information may help urban planners understand the processes by which urban biodiversity is homogenized to weigh the impacts of land use decisions for retaining species of particular interest and ultimately promote biodiversity over time.

This thesis aims to 1) advance information about the predictors of habitat selection of urban coyotes and of the occurrence and relative abundance of three groups of terrestrial mammals and individual species, and 2) to support the use of connectivity models and ecological indices used in urban planning in Edmonton, Alberta, Canada by testing their fit to measures of habitat use, animal occurrence, and relative abundance derived from empirical data. In each of the two data chapters, I combined these two goals by using empirical data from animal detections to test the predictions of models or indices used by the City of Edmonton as planning tools to protect biodiversity.

In Chapter 2, I had two objectives. First, I used pre-existing data from GPS collars fitted on urban coyotes to understand how variation in habitat selection, including that caused by infection with sarcoptic mange and season, could be predicted from remotely-sensed variables. Second, I assessed the similarity between these detection-based measures of habitat suitability and presumed permeability with expert-derived estimates of permeability used in circuit-based connectivity models by the City of Edmonton (2017b). To achieve these objectives, I used pre-existing GPS collar data for 19 urban coyotes from Edmonton to obtain feature-specific selection estimates (suitability) of 10 land cover types across two seasons (winter and summer) based on log-ratios of proportionate use. I also constructed a resource selection function (RSF) for 14 healthy coyotes and five animals with visible evidence of sarcoptic mange to understand seasonal and health-based differences in habitat selection. I assessed the selection of 13 land cover features by coyotes and obtained a habitat suitability index (HSI) specific to disease status and season. Finally, I compared the feature-specific suitability estimates from log-ratio analyses with the feature-specific permeability ratings used in circuit-based models, and the RSF-derived HSI values with the cumulative landscape permeability estimates, along with health status and season in linear regressions.

In Chapter 3, again, I had two objectives. First, I used data from camera traps and small mammal track tube arrays to a) test the predicted habitat value of two indices used by the City (City of Edmonton 2014a). Second, I assessed the predictive value of a variety of remotely-sensed and site-based variables for the occurrence and relative abundance of terrestrial mammals detected between 2018 and 2021. To achieve these objectives, I acquired measures of occurrence and relative abundance of urban terrestrial mammals from 89 camera traps and 47 small mammal track tube arrays placed in both natural and semi-natural areas. I used camera data to calculate relative abundance as detection rate (O'Brien, Kinnaird, and Wibisono 2003; Palmer et al. 2018; Kays et al. 2020) as the frequency of independent detections per month for (a) the three mammal groups and (b) 13 individual species. I also modelled the occurrence and relative abundance of the three species groups and five species, expressing a range of sizes and habitat associations using a combination of remotely-sensed and site-based variables.

By addressing the objectives of my two data chapters, I sought to increase an understanding of the best ecological predictors of habitat use by coyotes, and of the occurrence and relative abundance of other mammal species across an urban gradient, and test and advance models of urban ecological connectivity and habitat value. I hope this work can tangibly contribute to proactive ecological planning in the City of Edmonton and other cities to mitigate the adverse effects of urban development on biodiversity.

## **CHAPTER 2 -** Methods used to model connectivity predict habitat suitability for GPS-collared urban coyotes (*Canis latrans*)

### 2.1 INTRODUCTION

Urbanization reduces, fragments, and degrades natural areas (Grimm et al. 2008), resulting in habitat loss, diminished natural connectivity, and, ultimately, biodiversity loss within cities (Beninde, Veith, and Hochkirch 2015). This occurs when land use change adversely affects individual behaviour and movement patterns (Apfelbeck et al. 2019), which alters population dynamics and species distributions (Shochat et al. 2006; Aronson et al. 2016). As a result, urbanization causes a reduction in the number of species and changes in species composition in the remaining natural areas of urban landscapes (McKinney 2006; Beninde, Veith, and Hochkirch 2015). Cities strive to limit this loss in part because biodiversity is essential to the many ecological processes (Bongaarts 2019) that support human well-being (Fuller et al. 2007). The connectivity that supports population persistence over time is challenging to maintain in cities due to habitat loss and fragmentation caused by the high interspersion of built environments that generally inhibit animal movement (Cadenasso, Pickett, and Schwarz 2007; Forman 2016).

Although conservation research historically mostly ignored urban settings (Miller and Hobbs 2002), urban planners increasingly recognize the importance of proactive planning to retain biodiversity (Apfelbeck et al. 2019). Ideally, urban planners could use the recently expanding body of urban research to incorporate wildlife considerations in planning decisions. However, different environmental conditions between cities often lead to highly variable responses of wildlife species (Magle et al. 2019). In Edmonton, Alberta, Canada, there is an opportunity to investigate the varying effects of urbanization on wildlife because it combines rapid growth (Statistics Canada 2021b) and sprawling infrastructure (City of Edmonton 2017a) with considerable wildlife habitat located in areas of high apparent connectivity in an extensive system of protected areas concentrated in a river valley and ravine system (City of Edmonton 2020b). The City of Edmonton (hereafter the City) aims to maintain Edmonton's natural areas as a connected ecological network, even amid increasing development (City of Edmonton 2007). Realizing this goal necessitates information on environmental sensitivities, such as ecological connectivity, to prioritize protection, conservation, and restoration (City of Edmonton 2017b).

Edmonton city planners have attempted to advance this information partly by commissioning an estimate of ecological connectivity via circuit-based simulation models using Circuitscape (McRae et al. 2008; City of Edmonton 2017b).

Circuitscape software uses circuit theory, a branch of network theory, to evaluate the connectivity of a landscape by estimating movement as 'current flow' as the product of conductance (i.e., permeability) and voltage (McRae et al. 2008). Permeability is estimated for features or map units as weights of "attraction" or "avoidance" that signify the probability of moving through particular features or spatial units. Landscape permeability is then approximated for an entire mapping surface as the cumulative score of many feature-specific estimates or as one value derived from a habitat suitability model (Zeller, McGarigal, and Whiteley 2012). Sources and ground nodes are placed, and voltage is applied to model movement across the landscape (McRae et al. 2008). When enough paired nodes are placed, circuit-based models reflect the various movement alternatives (rather than the "best" route; McRae et al. 2008; Koen et al. 2014; McRae et al. 2016), which supports evaluating tradeoffs between ecological sensitivity and development objectives (City of Edmonton 2017b).

The City used expert opinion on the permeability of a variety of human disturbances and natural features with a model species of urban coyotes (*Canis latrans),* a representative of medium to large-sized, urban-adapted mammals*,* to parameterize two seasonal landscape permeability layers (City of Edmonton 2017b). These layers were then used to construct two seasonal connectivity models with the specific goal of identifying areas where movement may be constricted to prioritize restoration efforts (City of Edmonton 2017b). Seasonal models accommodated the expectation that the North Saskatchewan River, which bisects the City, may be a conduit to movement in the winter but a barrier in the summer (Harrison 1992; City of Edmonton 2017b). Ideally, such estimates of landscape permeability would be verified with independent information about habitat use or movement by representative or target species (Zeller, McGarigal, and Whiteley 2012), and such data are increasingly available for urban areas. Exploring the fit between modelled and measured movement could increase the utility of tools like Circuitscape for ecological planners in other cities.

An ideal source for testing cost-based connectivity models is occurrence data, such as telemetry data acquired via GPS collars. Telemetry data are often used to estimate the probability of use (or suitability) of features by comparing the characteristics of used *vs.* available resources

(Manly et al. 2002). Habitat suitability values reflect the relative ease (or cost) of use, where highly suitable habitat is interpreted as highly permeable (Zeller, McGarigal, and Whiteley 2012). Ergo, such habitat suitability models are well-suited to validate connectivity models that use expert opinion to assign estimates of permeability, such as the model the City commissioned for urban coyotes. The suitability of features is commonly estimated as the probability of selection using either compositional analyses (Aebischer, Robertson, and Kenward 1993) or resource selection functions (RSFs; Manly et al. 2002).

Compositional analyses can be used to obtain habitat-specific suitability estimates by using log-ratio analyses that compare the proportional use and availability of each habitat relative to the use and availability of all other habitat types simultaneously (Aebischer, Robertson, and Kenward 1993). The log-ratio approach is commonly used to address the unit-sum constraint by transforming proportions into log-ratios (Aebischer, Robertson, and Kenward 1993; Manly et al. 2002). These log-ratios can also be used to evaluate differences in use between habitat types, to rank habitats types based on relative use (Aebischer, Robertson, and Kenward 1993), or to estimate the strength of selection for each habitat type either for individuals or as a population average (Conner, Smith, and Burger 2003; Gosselink et al. 2003; Mueller, Drake, and Allen 2018). Log-ratios of proportional use are sometimes used to create resistance layers to model connectivity (Kautz et al. 2006; LaPoint et al. 2013), indicating that they provide feature-specific suitability estimates that could be used to evaluate expert-based permeability ratings. However, there are some constraints when using compositional analyses, including that they are less suitable for features that lack area (e.g., lines or points), require relatively high sample sizes to compare selection between groups (Aitchison 1982; Aebischer, Robertson, and Kenward 1993), and are generally inadequate to address interactions. Interactions may be particularly important in urban areas with high heterogeneity (Cadenasso, Pickett, and Schwarz 2007; Forman 2016), which may lead to more complex patterns of selection.

Resource selection functions (RSFs) can evaluate the probability of use of features regardless of area, such as roads, incorporate distance-based metrics that mitigate error associated with GPS bias, and evaluate interactions, thus addressing constraints of compositional analyses. RSFs constructed via logistic regression can be used to estimate the suitability of particular resources (or suites of resources) by comparing landscape characteristics at used GPS locations *vs.* randomly generated available locations (Boyce et al. 2002; Manly et al. 2002;

Johnson, Seip, and Boyce 2004). Model equations from RSFs can be applied to particular locations or grid squares to predict the suitability of resources where presence/absence data has not been collected (Boyce et al. 2002; Manly et al. 2002; Johnson, Seip, and Boyce 2004), providing a form of habitat suitability index (HSI; Boyce et al. 2002; Meyer and Thuiller 2006). RSFs can be used to create similar estimates to expert-based landscape permeability values (Zeller, McGarigal, and Whiteley 2012). However, using logistic regression to evaluate habitat selection has been criticized for a variety of reasons, including issues with spatial autocorrelation (Fieberg et al. 2010), using points as the sampling unit rather than individuals (individual variation and/or sampling intensity; Aebischer, Robertson, and Kenward 1993), and the inability to demonstrate non-use (Boyce et al. 2002). Yet, mixed models can be used to simultaneously consider the behaviour of the population (average individual) while accounting for both individual variability and sampling intensity, thereby allowing population-level inference (Aarts et al. 2008). At the same time, the additional complexity in habitat selection analyses occurs due to variation in behaviour (Greenberg and Holekamp 2017; Murray and St. Clair 2017), age (Desbiez et al. 2020), sex (Saïd et al. 2011; Desbiez et al. 2020), and disease status (Cross et al. 2016; Hoverman and Searle 2016).

For coyotes, habitat selection is known to vary with individual behaviour (Murray and St. Clair 2015; Newsome et al. 2015)**,** sex (Mueller, Drake, and Allen 2018), and disease status (Murray et al. 2015b; Reddell et al. 2021). Wildlife diseases can alter wildlife movement patterns through higher energetic demand (Selakovic, de Ruiter, and Heesterbeek 2014), decreased movement (Cross et al. 2016; Süld et al. 2017), or diminished capacity to maintain high-quality territory (Pence and Windberg 1994). One of the diseases that affects coyotes is sarcoptic mange (*Sarcoptes scabiei*), a globally distributed parasitic mite that is common in wild canids (Bornstein, Mörner, and William 2001) and present in Edmonton, AB (Murray et al. 2015b). Infection with diseases such as mange can alter habitat selection by increasing energetic demand (Cross et al. 2016), resulting in larger home ranges, and can increase diurnal activity (Murray et al. 2015b), reliance on urban areas (Murray et al. 2015b; Reddell et al. 2021), and proclivity for conflict (Contesse et al. 2004; Goodrich et al. 2011; Murray et al. 2015a; Murray et al. 2015b). These multiple effects on habitat selection suggest that connectivity will differ for healthy *vs.* diseased wildlife, especially in urban areas where the prevalence of mange is likely intensified by high densities of coyotes (Bornstein, Mörner, and William 2001).

The purpose of this study was to advance information about the habitat selection of urban coyotes and use that information to test predictions of the City's planning models to improve their utility in future. More specifically, our objectives were to use data acquired from GPS collars fitted on urban coyotes to (1) understand how variation in habitat selection, including that caused by infection with sarcoptic mange and season, can be predicted from remotely-sensed variables and (2) assess the similarity between these detection-based measures of habitat suitability and presumed permeability, with expert-derived estimates of permeability used by the City to model urban connectivity in Edmonton. To achieve this, we used pre-existing GPS collar data for 19 urban coyotes from Edmonton to first perform log-ratio analyses of proportionate use of categorical habitat compositions to evaluate differences in habitat use between two seasons (winter and summer) and to obtain feature-specific habitat selection estimates. Secondly, we constructed a Resource Selection Function (RSF) for healthy ($n$ = 14) and diseased ($n$ = 5) coyotes to estimate their habitat selection in two seasons (winter and summer) and to obtain a habitat suitability index. Finally, we compared the feature-specific selection estimates obtained from log-ratio analyses for coyotes to the expert-derived permeability ratings and the RSF-based habitat suitability index for coyotes with the expert-derived landscape permeability estimates used as the input for circuit-based models.

## 2.2 MATERIALS AND METHODS

### *2.2.1 Study area*

This study took place in Edmonton, Alberta, Canada (53.5472° N, 113.5006° W) and the surrounding peri-urban area (within a 3.2 km buffer of the city boundary; Fig. 2.1). The buffered peri-urban area was included to remove bias associated with artificial edges (Koen et al. 2014). The city area is 783 km$^2$ (City of Edmonton 2019c), with a metropolitan population of over 1.4 million (Statistics Canada 2021b) and a population density of 1,370 people/km$^2$ (Statistics Canada 2017). Edmonton is 671 m above sea level, has a mean annual temperature of 3.9°C, and a mean annual precipitation of 476.9 mm (Government of Canada 2021). Edmonton has the largest urban park in Canada (City of Edmonton 2020b, 2022), comprised of an extensive river valley and ravine system of 7,400 ha in area and spanning a linear distance of 100 km with the many ravines and tributaries (City of Edmonton 2020b) preserving a high degree of connectivity for wildlife. Edmonton's natural areas consist predominantly of Aspen parkland (City of Edmonton 2020b) with interspersed urban green spaces (golf courses, urban parks, cemeteries, and remnant natural patches).

### *2.2.2 Coyote location data and resource use and availability*

We used pre-existing GPS collar data for 14 healthy and five mange-infected urban coyotes captured from October 2009 to February 2013 (as detailed by Murray et al. 2015b). This data was collected to evaluate associations between urban coyote age, sex, health, individual variation, habitat selection, and the use of anthropogenic resources (Murray et al. 2015b; Murray and St. Clair 2015; Murray et al. 2016; Murray and St. Clair 2017). We rarefied telemetry locations to a 3-hour fix rate (11,817 points) to ensure inconsistent fix-frequency between coyotes did not affect measures of selection (Johnson and Ganskopp 2008). We used telemetry locations for coyotes with a minimum of 30 locations per season (winter: Dec.1 – Mar. 31 and summer: Apr. 1 – Nov. 31) to ensure stable estimates of home range size (Seaman et al. 1999). We used these points to evaluate two orders of selection in a used-available method (below; Manly et al. 2002): (1) within seasonal individual home ranges using compositional analyses (3rd -order selection) and (2) individual locations within winter and summer population ranges using a RSF (2nd-order; Meyer and Thuiller 2006, adapted from Johnson 1980). We first performed compositional analyses by comparing the proportions of landscape features at coyote GPS locations in both winter and summer seasons (used) to the proportion of each habitat type within respective seasonal home ranges (available; Aebischer, Robertson, and Kenward 1993; Manly et al. 2002). We used the *adehabitatHR* package in R (Calenge 2006; R Core Team 2019) to estimate seasonal 95% fixed kernel home ranges for each individual using least-square cross-validation (LSCV; Seaman and Powell 1996). We considered all telemetry locations within these 95% fixed kernel home ranges (individual and season respective; $n$ = 11,473). We used individual GPS points to develop a RSF model that compared landscape features at coyote GPS locations (used) to random locations (available; Manly et al. 2002; Johnson et al. 2006). We first calculated two seasonal (winter and summer) 95% minimum convex polygons (MCPs; Lortie et al. 2020) in ArcMap (v10.7.1, Redlands, CA). We identified seasonal used locations as telemetry locations that fell within respective MCPs ($n$ = 11,748) and randomly generated available locations at a 1:2 ratio (used:available; Table 2.1). To support a more realistic estimation of habitat selection, we excluded buildings (City of Edmonton 2018a) from the available area for both winter and summer in both analyses, and additionally, water bodies for the summer season (City of Edmonton 2018d) for the RSF model.

### *2.2.3 Environmental Data*

We used a Geographic Information System (ArcMap, v10.7.1, Redlands, CA) to derive 10 proportional and 13 continuous explanatory variables (Table 2.2; Fig. 2.2) from six geographic information system layers, including slope (Nielsen, unpublished data, 2020), buildings (City of Edmonton 2018a), roads (City of Edmonton 2018c), land cover (City of Edmonton 2018d), and unique landforms (river valley/ravine [City of Edmonton unpublished data 2016c]). To derive explanatory metrics related to land cover, we collapsed land cover information from the City of Edmonton urban Primary Land and Vegetation Inventory (uPLVI) and unique landforms as 13 land cover types: natural forest, natural grass, natural shrub, modified forest, modified grass/shrub (excluding maintained grass), maintained grass, agricultural, residential, developed, transportation surface, the river valley and ravine system, natural areas, and the North Saskatchewan River (City of Edmonton 2018d). This information is adapted from provincial vegetation inventories to incorporate unique urban features (City of Edmonton 2014b).

We derived proportional variables for compositional analyses (below); they described the used and available proportions of 10 land cover types, including the North Saskatchewan River (Table 2.2; Fig. 2.2). We identified the proportions of used habitat as the proportion of GPS points from each individual located in each habitat type in both winter and summer, except for the North Saskatchewan River, for which we used points that were at least 15 m from the river's edge to account for GPS collar error (Rettie and McLoughlin 1999). We then quantified available proportions as the proportion of each habitat type within individual 95% fixed kernel HRs for both seasons. We used continuous variables to develop a resource selection model; they described slope and proximity to 12 landscape features, including land cover types, buildings, and roads (Table 2.2; Fig. 2.2). Because the importance of a feature is expected to decline with distance to it, we applied an exponential decay function ($e^{-\alpha d}$ where d was the distance in meters, and $\alpha$ was set at 0.001) that negated the influence of features farther than 1000 m away (Nielsen, Cranston, and Stenhouse 2009).

### *2.2.4 Habitat selection*

To obtain habitat-specific selection estimates to compare with expert-derived permeability ratings, we conducted two seasonal compositional analyses (Aitchison 1982; Aebischer, Robertson, and Kenward 1993) at the home range scale to investigate the selection of 10 land cover types (Table 2.2; Fig 2.2). We did not assess the selection of all the features used in the circuit-based models due to sample size limitations and because some land cover types were unavailable to most individuals (Aebischer, Robertson, and Kenward 1993). Instead, we grouped select land cover types that were given similar permeability ratings and lumped otherwise excluded categories into "other" (Table 2.2), which was necessary to obtain selection estimates relative to the use and availability of other features.

We used these proportions (Appendix 2.1 - Table 1) first to create matrices of the pairwise differences of the natural log-ratios ("pwd") of the use to available proportions of habitat for each individual, where a positive pwd suggests that a habitat type is selected for, zero indicates random use, and a negative pwd suggests avoidance (Aebischer, Robertson, and Kenward 1993). Since a zero value in either the numerator or denominator of a ratio is invalid, if a habitat type was available but not used by an individual, we replaced the zero proportion of unused habitat with a value corresponding to 10% of the least available habitat proportion (Aebischer, Robertson, and Kenward 1993). When zeros persisted in the residual log-ratios, we replaced the missing values with the weighted mean lambda (described in Aebischer, Robertson, and Kenward 1993). We used the *adehabitatHS* package in R (Calenge 2006, 2011; R Core Team 2019) to determine if habitat selection was non-random (Wilk's Lambda; $p < 0.05$). We then used weighted one-way ANOVAs (square root of the number of GPS locations per individual; Aebischer, Robertson, and Kenward 1993) for each habitat type to determine if use differed by season and excluded log-ratios when both used and available proportions were missing (habitat type not available to the individual). Lastly, we averaged the pwd values for each habitat type across individuals for each season as the weighted mean pwd.

We then built a RSF model to compare the effects of season and health status on habitat selection by coyotes and to support the comparison of habitat selection with circuit-based connectivity models. We evaluated urban coyote selection of slope and proximity to each of buildings, roads, the river valley and ravine system, natural areas and eight other land cover types as described above (Table 2.2; Fig. 2.2). We used distance-based variables to eliminate the need for an arbitrary reference category, to avoid issues of scale and GPS error (Conner, Smith, and Burger 2003; Benson and O'Hara 2013), and to more meaningfully evaluate interactions that may occur if the selection of one feature is dependent on the nearness of another. Therefore, we inferred a higher probability of use when used locations were closer to features than available (random) locations.

We built resource selection functions using three steps. First, we investigated all main effects and interactions using univariate statistics and retained those that were liberally significant ($p < 0.25$; Hosmer and Lemeshow, 1989). Second, if two or more variables were correlated (Pearson's correlation coefficient exceeding an absolute value of 0.6), we applied principal components analysis (PCA) to combinations of correlated variables to obtain composite metrics using the axis scores from the principal components explaining ~70% of the variance. Because we were interested in the most predictive model, we subsequently tested each PCA metric against its components and retained the one with the lowest AIC score (Akaike 1978; Burnham and Anderson 2002). We assessed two-way and three-way interactions between both health status and season, and each of the variables associated with human development (buildings, roads, residential areas, developed areas, maintained grass, and/or PCA terms), or natural land cover and contiguous habitat (the river valley and ravine system, natural areas, natural forest, natural grass/shrub, and/or PCA terms), or modified grassland/agricultural areas, and/or PCA term; Table 2.2). We deemed interactions with season and health status relevant to our objectives, including differentiating potential effects of season (winter vs summer) and health status (healthy vs mange-infected) on habitat selection. We additionally assessed two-way interactions between variables associated with human development and natural land cover. We deemed interactions with human development and variables related to modified and natural land covers relevant because of the potential for vegetated features to alter anthropogenic effects. We included interactions between natural land cover due to our goal of identifying the most predictive model. We rescaled continuous variables between 0 and 1 to support the comparison of coefficients and to assess the relative magnitude of effect sizes.

After identifying our list of liberally significant variables and their interactions, we built a combined model using the R package *lme4* (Bates et al. 2015) with a binary (0 = available, 1 = used) response variable. Because we were primarily interested in prediction, not hypothesis testing, we used an all-subsets approach to model habitat selection by coyotes. We identified the most parsimonious top model among competing generalized linear mixed-effect models (GLMMs) with a logit link for our used-available response variable and retained models within 2 ΔBIC (Schwarz 1978). We used a random effect for individual coyotes to account for unequal sampling effort and partition variance appropriately. We penalized models for more terms with the Bayesian Information Criterion (BIC; Schwarz 1978) because it more heavily penalizes complex models (Boyce et al. 2002; Hastie, Tibshirani, and Friedman 2008) to favour parsimony. We assessed the model fit to the whole dataset using $k$-fold cross-validation ($k = 10$; reps = 3; Boyce et al. 2002; Pearce and Boyce 2006). We determined the explanatory value of the random effect by comparing the deviance of the top model with and without it using a likelihood-ratio Chi$^2$ test, and used an approximated $p$-value to account for the random effect (Pr > ChiSq / 2; Bolker et al. 2009). We then used the RSF model equation to obtain a habitat suitability index (HSI) for each used GPS location.

### *2.2.5 Circuitscape models*

The City commissioned two seasonal Circuitscape (McRae et al. 2008) models, prepared by Solstice Canada Corp., to evaluate seasonal landscape connectivity using estimated permeability for coyotes, a representative of medium to large-sized urban-adapted mammals, for both winter (Dec.1 – Mar. 31) and summer (Apr. 1 – Nov. 31 [City of Edmonton 2017b]). Seasonal models accommodated the hypothesis that the North Saskatchewan River, which bisects the City, may be a conduit for movement in the winter but a barrier in the summer (Harrison 1992; City of Edmonton 2017b). The model authors modelled movement based on patterns during evening and dusk (when coyotes are most active) using locally relevant literature on urban coyote movement (City of Edmonton 2017b).

The model authors created two seasonal permeability layers to serve as the input for Circuitscape by first creating feature-specific layers and scoring each 10x10 m cell based on the expected influence of that feature on connectivity (permeable, a barrier, or modifiers [City of Edmonton 2017b]). The assigned values ranged from -10 (least permeable) to 10 (suitable). They included categories of habitat type (e.g., natural forest), human use (e.g., parks trails), open space (e.g., maintained turf), physical barriers (e.g., buildings), railways, roads, and whether the cell was in the North Saskatchewan River floodway (Table 2.2 [City of Edmonton 2017b]). The model authors created 'modifying layers' to adjust ratings for spatially coincident features that were expected to further influence connectivity, which included slope, culverts, human use (e.g., parks), and land use (e.g., residential areas; Table 2.2 [City of Edmonton 2017b]). The various layers were combined by adding weights for overlapping cells to create two seasonal permeability layers to model connectivity (City of Edmonton 2016b, 2017b). We used these layers to extract the expert-derived landscape permeability estimates for each used point respective of the season that each GPS fix occurred.

### *2.2.6 Testing permeability estimates with habitat suitability indices*

To compare the predictive accuracy of the expert-derived permeability ratings with feature-specific estimates of use by coyotes, we scaled the weighted mean pwds for each habitat type from both seasons (obtained above) relative to the most or least selected feature from either season (most positive or negative value; 10 or -10). We did so to allow the comparison between pwds, expert-based ratings, and between seasons on the same relative scale (between -10 and 10; Table 2.2 [City of Edmonton 2017b]). We compared these values by assessing whether the expected permeability ratings for each feature were within the 95% confidence interval of the weighted average pwd values.

To assess the predictive accuracy of the expert-derived landscape permeability estimates (used as the input layer to construct circuit-based models), we then used generalized linear models (GLMs) in an all-subsets approach to compare the landscape permeability values with RSF-derived HSI values from used locations, as well as two-way and three-way interactions between both health status and season. We included interactions between health status and season to explore the influence of mange infection and season on the predictive ability of the expert-derived cumulative permeability layer. We identified the most parsimonious top model among competing GLMs with different transformations on landscape permeability values and our HSI response variable (logarithmic, square root, cubic) and retained models within 2 ΔAIC (Akaike 1978; Burnham and Anderson 2002). We performed all analyses in R 3.6.1 (R Core Team 2019).

## 2.3 RESULTS

### *2.3.1 Habitat selection*

We conducted two seasonal compositional analyses to evaluate differences in selection by season using weighted ANOVAs and to obtain habitat-specific selection estimates as weighted pwd. The seasonal compositional analyses produced weighted mean pwd values between -68.7 and 48.83 in winter and between -45.86 and 26.1 in summer (Table 2.3). Habitat use differed from random predictions in both the winter ($\Lambda = 0.017$; $p = 0.006$) and summer ($\Lambda = 0.008$; $p = 0.001$). In weighted ANOVAs, habitat use was higher in winter for natural forests, natural shrubland, modified grass/shrubland and residential areas, but there were no significant differences in seasonal use of natural grassland, maintained grass, developed areas, transportation surfaces, and the North Saskatchewan River (Table 2.4; Fig. 2.3).

For the RSF analysis using composite metrics, only one PCA metric was more explanatory than its components; it approximated natural areas and included proximity to natural forests and the river valley and ravine system (PC1 = 87.5%). The final list of uncorrelated variables evaluated in the RSF model of coyote habitat selection included slope, proximity to each of natural areas (PCA metric; with positive values indicating closer proximity to natural areas), modified forests, modified grass/shrubland, residential areas, developed areas, and all 25 tested interactions. The most parsimonious top model (rank 1) for predicting the probability of resource use by coyotes included all six main effects, as well as 25 interactions (18 significant; Table 2.5; Fig. 2.4). There were no competing top models (Appendix 2.1 - Table 3). The probability of use increased with increasing slope, and closer to each of natural areas, modified forests, modified grass/shrubland, and residential areas, whereas the probability of use decreased closer to developed areas (Table 2.5; Fig. 2.4). Based on odds ratios (Table 2.5), the likelihood of coyotes selecting natural areas was higher than in modified forests (~1.5 times), modified grass/shrubland (~2.4 times), residential (~1.7 times) and developed areas (~5.9 times). The probability of use of modified forests was ~1.1 times greater than residential and ~3.8 times greater than developed areas. Modified grass/shrubland was ~2.4 times more likely to be used than developed areas (Table 2.5; Fig. 2.4).

Among 15 significant two-way interactions involving season, disease status, and land cover (Table 2.5; Fig. 2.4), three positive interactions revealed that the probability of use of modified forest was ~1.1 times higher in winter, and use of residential and developed areas increased if animals had mange (~1.6 and ~1.3 times higher, respectively). Two other positive interactions indicated that when natural areas were closer, coyotes were ~1.2 times more likely to use modified grass/shrub and ~1.1 times more likely to use developed areas. Three more positive interactions revealed that the probability of use of residential areas also increased when modified forests (~1.3 times higher) or modified grass/shrubland (~1.2 times higher) were closer, and use of modified grass/shrub increased when developed areas were closer (~1.1 times higher). Four significant negative two-way interactions showed that in winter, the probability of using either modified grass/shrubland and residential areas was ~1.4 times lower, and use declined for natural areas and modified forests when animals had mange (~2.2 and ~1.25 times lower, respectively). Three more negative interactions revealed that the probability of use of residential areas was 1.5 times lower when either natural areas or developed areas were closer, and the use of modified forests was ~1.5 times lower when developed areas were closer. Three significant three-way interactions demonstrated the complex nature of habitat selection when combined with health status and season. When animals had mange, positive associations for the probability of use of modified forests was ~1.3 times higher in winter. However, mange reduced the dampening effects of winter on the likelihood of using residential areas (~1.3 times higher). One more three-way interaction showed that the probability of use of natural areas decreased in winter when animals had mange (~1.3 times lower). Six other interactions contributed to the best fit of our top model but were not significant (Table 2.5; Fig. 2.4). The predictive accuracy of the most parsimonious top model (rank 1) using *k*-fold cross-validation was 0.760 (±0.070 SD), suggesting a moderately high fit. Including a random effect for individuals significantly improved the model ($p < 0.001$).

### *2.3.2 Comparing habitat suitability index with expert-derived permeability values*

To discuss the differences between habitat use of each habitat type measured from locations of coyotes and expert-based ratings on the same relative scale (between -10 and 10 [City of Edmonton 2017b]), we scaled weighted mean pwd values from both seasons relative to the North Saskatchewan River in winter (given a value of -10; Table 2.3). The seasonal compositional analyses produced scaled mean pwd values between -10 and 7.11 in winter and between -6.68 and 3.8 in summer (Table 2.3; Fig. 2.3). When we determined whether expert-derived ratings fell within 95% confidence intervals of measured scaled weighted mean pwd, the expert-derived ratings were higher than the scaled weighted mean pwd in both winter and summer for natural forests, natural grass, modified forests, and for the North Saskatchewan River in winter, and additionally, in summer for natural shrubs and modified grass/shrub (Table 2.3; Fig. 2.3). The expert-derived ratings were slightly above the scaled weighted mean pwd values for natural shrubs in winter but within the confidence interval range for transportation surfaces in both seasons and for modified grass/shrub and maintained grass in winter (Table 2.3; Fig. 2.3). The expert-derived ratings were lower than the scaled weighted mean pwd for residential and developed areas in both seasons and additionally for maintained grass and the North Saskatchewan River in the summer (Table 2.3; Fig. 2.3).

We used GLMs to compare the accuracy of cumulative permeability estimates in predicting RSF-derived HSI values (Table 2.6) while including season, mange, two-way, and three-way interactions. The most parsimonious top model included square-root transformed cumulative permeability estimates, season, mange, and all four interactions, all of which were significant, with RSF-derived logarithmic HSI values as the response variable (Table 2.7; Fig. 2.5). There were no competing top models (Appendix 2.1 - Table 4). The HSI values were higher when expert-derived landscape permeability estimates increased and in winter, but lower when coyotes had mange (Table 2.7; Fig. 2.5). Four significant 2-way and 3-way interactions revealed that HSI values were higher for mangy coyotes in winter and that the expert-derived landscape permeability values were less related to HSI values when coyotes had mange, in winter, and especially when coyotes had mange in winter (Table 2.7; Fig. 2.5). Additionally, even when using the best fit model (lowest AIC) of multiple tested models with different transformation types, the model fit was poor ($R^2 = 0.072$; Table 2.7; Appendix 2.1 - Table 4).

## 2.4 DISCUSSION

Ecological connectivity is believed to be an essential contributor to the retention of biodiversity in urban areas, but there are few tools with which it can be measured to support emphasis by urban planners. We tested the predicted permeability estimates used in the City of Edmonton's planning models of coyote movement commissioned by the City of Edmonton with GPS collar data. We evaluated habitat selection of healthy and mange-infected urban coyotes across winter and summer in compositional analyses and a RSF. We then compared the feature-specific suitability estimates from compositional analyses to expert-derived ratings and the RSF model HSI to landscape permeability values. We used compositional analyses to assess broad-scale habitat associations and a RSF model to develop a HSI at a finer scale that could be compared to landscape permeability values. We found that coyotes used natural forests, natural shrubs, modified grass/shrubland, and residential areas more in the winter. The RSF model showed that urban coyotes avoided developed areas, but were attracted to areas with steeper slopes and closer to each of natural areas, modified forests, and residential areas, with various interactions that suggest habitat preference differed by season and health. When evaluating the accuracy of expert-based ratings using feature-specific selection estimates, the expert-based ratings were accurate for some features, but consistently underestimated the use of residential and developed areas and overestimated the value of natural grass, modified forests, and the North Saskatchewan River. When we compared HSI values derived from a RSF to corresponding landscape permeability estimates, the expert-derived values predicted the HSI for urban coyotes, but were less accurate in winter and when coyotes had mange, and the model fit was poor.

The strongest predictors of habitat selection in the RSF model were an attraction to natural areas composite metric and avoidance of developed areas. The natural areas variable in our final model was a composite PCA metric of natural forests and the river valley and ravine system. The inclusion of the river valley and ravine system within the most explanatory PCA metric for natural areas suggests the importance of contiguous habitat for coyotes. Based on odds ratios, coyotes selected natural areas ~1.5 times more than modified forests, ~2.4 times more than modified grass/shrubland, ~1.7 times more than residential areas, and ~5.9 times more than developed areas. Urban coyotes seem to prefer natural land use types over modified or developed types (Poessel, Breck, and Gese 2016; Franckowiak, Perdicas, and Smith 2019), especially in densely vegetated areas, such as forests (Atwood, Weeks, and Gehring 2004; Greenspan, Nielsen, and Cassel 2018). This preference presumably stems from high prey availability (Richer et al. 2016) and vegetation that provides hiding cover (Gosselink et al. 2003), facilitating habitat use and movement. When natural areas were closer, coyotes were ~1.2 times more likely to use modified grass/shrubland and ~1.1 times more likely to use developed areas, suggesting that natural areas may buffer anthropogenic effects (Reddell et al. 2021), allowing coyotes to withstand the negative impacts of developed areas by remaining close to natural cover and high-quality habitat. However, modified grass/shrublands had very similar buffering effects.

Coyotes were attracted to modified grass/shrubland and residential areas, perhaps due to congregated anthropogenic food subsidies, such as garbage, fruit trees, or bird feeders (Murray and St. Clair 2017). Anthropogenic food subsidies are widespread in urban areas, influence resource use for various urban species, and frequently contribute to overabundant wildlife populations (DeStefano and DeGraaf 2003), especially urban-adapting species. Accordingly, coyotes appear to thrive in cities partially due to their ability to find, access, and consume food subsidies provided by anthropogenic waste (Murray et al. 2016; Murray and St. Clair 2017). Attractants were the most significant predictor of space use for dingoes (*Canis lupus dingo*; Newsome et al. 2015). Residential gardens are also valuable habitats for mammals (Van Helden, Close, and Steven 2020) and may promote the abundance of small rodent prey species. Coyotes used both modified grass/shrubland and residential areas ~1.4 times less in winter, coinciding with when fewer attractants are present. Some sources of anthropogenic food also cause disease in wildlife or increase infection rates (Murray et al. 2015b), contribute to high densities of species (Wright and Gompper 2005), and alter space use when diseased individuals seek out such attractants (Murray et al. 2016).

Urban coyotes also relied on modified habitat types more than developed types areas, some of which may increase the tolerance of coyotes to human disturbances. Coyotes used modified forests ~1.1 times more than residential areas and ~3.8 times more than developed areas and used modified grass/shrubland ~2.4 times more than developed areas. These areas likely provide cover, host a variety of small rodent prey (Morey, Gese, and Ghert 2007; Ofori et al. 2018), and separate coyotes from adjacent human activity (Gallo et al. 2017; Wurth, Ellington, and Gehrt 2020), and may serve as stepping-stones (Lynch 2018) through highly fragmented landscapes. Coyotes were also ~1.1 times more likely to use modified grass/shrublands when developed areas were nearby, suggesting that even modified vegetation types increase the tolerance of coyotes to the disturbances that occur in urban areas. However, this effect was slight and given that coyotes are known urban-adapters (McIntyre 2014; Perry et al. 2020) which generally appear to be less reliant on the most natural areas than other species, species-specific analyses are likely warranted before concluding that modified vegetation types act as conservation features for other species.

Coyotes infected with mange preferred human-dominated areas and more so in winter months. Mange-infected coyotes were ~1.6 times more likely to select areas closer to residential areas, ~1.3 times more likely to select developed areas, and two times less likely to select natural areas. A few of these preferences increased in winter months; coyotes infected with mange were ~1.5 times more attracted to residential areas and made even less use of natural areas (~0.8 times), despite that the overall study population used residential areas less and natural areas more in winter months. Since infection with mange can reduce internal fat stores (Bornstein, Mörner, and William 2001), their greater use of human-associated areas may have resulted from increased energetic demand and diminished capacity to maintain high-quality territory (Pence and Windberg 1994). The areas they selected are also more likely to have anthropogenic food subsidies (Murray et al. 2016; Murray and St. Clair 2017), which may encourage dispersal from natural areas and increase coyote tolerance of coyotes to human disturbances, especially in the winter when harsh weather reduces food availability. Using the same GPS collar data, another research team in our group found that coyotes with mange were more likely to use more developed areas (Murray et al. 2015b). Others have reported that winter can result in larger home ranges of coyotes (Gosselink et al. 2003; Ellington, Muntz, and Gehrt 2020) that are also less responsive to disturbances when foraging (Ellington, Muntz, and Gehrt 2020). Moreover, this period coincides with increased sightings (and conflict) of coyotes and in less natural spaces (Poessel et al. 2012). Our results reveal the complex nature of habitat selection when combined with health status and season and emphasize the importance of considering wildlife disease in habitat selection analyses, which may be especially relevant in urban areas where wildlife diseases are prevalent (Bradley and Altizer 2007; Reddell et al. 2021).

A core purpose of our work was to compare the expert-derived permeability ratings assigned to specific features to feature-specific habitat selection estimates obtained from log-ratio analyses of compositions. The expert-based ratings were fairly accurate for transportation surfaces in both seasons, for natural shrubs, modified grass/shrub and maintained grass in winter and the North Saskatchewan River in summer. However, our results suggest that the expert-based ratings may have overestimated the permeability of natural forests, natural grass, modified forests, and the North Saskatchewan River in winter, and additionally of natural shrubs and modified grass/shrub in summer. We included the North Saskatchewan River to acknowledge the hypothesis that it may be a conduit for movement in the winter; we believed that the probable bias from GPS error (Conner, Smith, and Burger 2003; Ganskopp and Johnson 2007) would be similar across seasons, but we expected that the relative difference between seasonal estimates might approximate the extent of differential use. Despite the 15 m buffer used to reduce GPS error, locations occurred in the river in both seasons. Increased "use" in summer is likely partially related to accessing the adjacent and highly valuable floodplains, wetlands, and riparian areas (Pringle 2017). We did not detect a difference in use between seasons, suggesting that the river does not act as more of a conduit for movement in winter as expected (Harrison 1992; City of Edmonton 2017b). However, estimates of use from compositional analyses have been scrutinized because classification is prone to error (Conner, Smith, and Burger 2003; Ganskopp and Johnson 2007). Our sample size was also fairly small. Our results also suggest that the expert-based ratings may have underestimated the permeability value of residential and developed areas in both seasons and for maintained grass in the summer. The lack of association for these features supports the hypothesis that residential areas are more permeable than the expert-derived ratings suggested, especially for highly adaptable coyotes (McIntyre 2014; Perry et al. 2020); others have shown readily use areas associated with human development (Poessel, Breck, and Gese 2016; Reddell et al. 2021). Our results also suggest that seasonal models may better match habitat use by coyotes.

A final purpose of our study was to determine whether permeability estimates based on expert-derived assessments of landscape permeability generated similar predictions to a RSF model of habitat suitability based on GPS data. We found a significant positive relationship between expert-derived permeability estimates and HSI values, but the model that best explained this relationship included season, health, and several interactions. Even with these additional variables, however, the model fit was poor. Expert-derived estimates were even less accurate for coyotes with mange, in winter, and especially for mangy coyotes in winter. Mange-infected coyotes used areas with significantly lower quality habitat, and our RSF model results also suggest they relied more on human-dominated areas. Without considering health-based effects, it seems that expert-derived ratings underestimated the permeability of modified and developed areas to diseased coyotes, especially in winter when cold temperatures further these effects. Higher accuracy in summer may have resulted from greater use of natural areas to avoid humans while denning (Gehrt, Anchor, and White 2009; Wurth, Ellington, and Gehrt 2020), or when natural food is more abundant, as suggested by larger dietary niche breadth (Sugden et al. 2021). Coyotes were likely to use areas with higher HSI values in summer, such as natural areas, for which the permeability value may have been easier to predict. These results indicate insensitivity of the expert-derived estimates to both the higher perceived permeability of disturbed areas to diseased coyotes and fluctuating habitat requirements across seasons. A further limitation of the expert-based permeability values was that they estimated permeability for all land uses associated with human development, such as residential areas, to be consistently low (ranging from 0 to -7), thereby producing very low landscape permeability estimates in these areas. Yet, coyotes used areas that were expected to impede movement, which produced zero-inflated permeability values when derived for GPS locations. Even when using the exhaustive approach of testing multiple models with different variable transformations, the zero-inflated nature of the permeability values likely contributed to the very poor fits. The results suggest that consideration of both season and health influence the accuracy of expert-derived permeability estimates and imply that connectivity will also differ for healthy *vs.* diseased coyotes and by season.

There are some limitations to our study that affect its interpretations. First, resource use may have been influenced by several factors we did not measure in this study, as indicated by the significant random effect for individuals. This suggests variation in resource use within the sampled population, which may have stemmed from age, breeding status, and relative population density. Others have found that coyotes vary in their use of anthropogenic resources (Newsome et al. 2015), avoidance of roads (Benson, Mahoney, and Patterson 2015; Murray and St. Clair 2015), and that females generally have smaller home ranges (Mueller, Drake, and Allen 2018). A second limitation of our study as a test of the importance of expert-derived permeability estimates is the choice of coyotes as a model species. A carnivore may not represent the needs of other species targeted by biodiversity planning and may be an especially poor umbrella species for sensitive species (Beier, Majka, and Newell 2009; Cushman and Landguth 2012). Coyotes have large home ranges (Šálek, Drahníková, and Tkadlec 2014) and are notoriously able to adapt to urban areas (McIntyre 2014; Perry et al. 2020). Other species may have lower dispersal ability in urban areas (Cushman, Landguth, and Flather 2013). A better approach might be identifying a few focal species to represent the varying tolerance to fragmentation, life history, and dispersal ability (Beier, Majka, and Spencer 2008; Cushman and Landguth 2012). A third limitation is the small and unbalanced sample size of 14 healthy and five mange-infected coyotes. Since we considered individuals as the sampling unit in compositional analysis, we could not evaluate differences in habitat selection based on health (Aebischer, Robertson, and Kenward 1993). This may be the reason we did not detect differences in the use of most land cover types between seasons in the compositional analysis, despite apparent differences in the RSF model. However, others have also noted differences in results between these methods, and suggest that the RSF model is more accurate (Long et al. 2009).

Despite these limitations, our study offers some insights into promoting urban biodiversity. Model coefficients from the RSF model could help urban planners weigh the relative cost or benefit of maintaining certain vegetated land classes, create predictive maps or movement models to identify pinch points, or adjust the expected permeability of features to increase the accuracy of their circuit-based models. The model coefficients could also be used to assist wildlife managers and urban planners mitigate human-wildlife conflict, and reduce the significant ecological and health problems associated with wildlife diseases (Herrera and Nunn 2019). Movement analyses using occurrence data may also offer valuable insights into the consequences of altered spatial patterns, such as reduced connectivity, for the spread of wildlife diseases (Dougherty et al. 2018). Such tools may be especially applicable in Edmonton, where coyotes have an unusually high prevalence of the zoonotic tapeworm, *Echinococcus multilocularis* (Luong et al. 2018). Perhaps the most important result of our work is to demonstrate the extensive use coyotes make of residential and developed areas relative to the predictions of the Circuitscape model.

In summary, resource use by coyotes was driven by natural land use type and human development, with natural and developed areas being the most influential over natural grass/shrubland, modified forests, modified grass/shrubland, maintained grass, residential areas, roads, and buildings. The results from the RSF model strongly suggest that resource use is influenced by health and season, where mange-infected coyotes were more reliant on residential and developed areas, and less reliant on natural areas, especially in winter for some effects. Our results also suggest that tolerance to human infrastructure increases with proximity to natural areas, and certain modified habitat types may buffer the adverse effects of urban development. We suggested how these results could help urban planners in a variety of ways. We concluded that the circuit-based models based on expert opinion might be a cost-effective tool for modelling urban connectivity, but with less precision than movement data from animals can provide and without the capacity to identify individual differences that might often stem from animal condition and other circumstances.

## 2.5 TABLES

**Table 2.1** Summary of the number of coyotes, used and available points, and available area used to model habitat selection of 14 healthy and five mange-infected coyotes in winter and summer in Edmonton, Alberta, via compositional analyses and a resource selection function (RSF).

| Analysis | Season† | Health | Number of coyotes | Number of radiotelemetry (used) points‡ | Number of available points§ | Available area ($km^2$)¶ |
|---|---|---|---|---|---|---|
| Compositional analysis | Winter | - | 14 | 4259 | - | 27.4 |
| | Summer | - | 15 | 7145 | - | 29.7 |
| Resource selection function (RSF) | Winter | Healthy | 19 | 3243 | 6486 | 232.2 |
| | | Mangy | | 1208 | 2416 | |
| | Summer | Healthy | | 4265 | 8530 | 282.7 |
| | | Mangey | | 3032 | 6064 | |

† Seasons were defined as winter: Dec.1 – Mar. 31 and summer: Apr. 1 – Nov. 31.

‡ The number of used points as radiotelemetry (GPS) locations by season; for compositional analyses: those within individual 95% fixed kernel home ranges; for the RSF: those within 95% minimum convex polygons (MCPs) around seasonal population ranges.

§ Randomly generated within each seasonal MCP at a 1:2 ratio (used:available).

¶ For compositional analyses: average area within seasonal/individual 95% fixed kernel home ranges; for RSF: area within 95% MCPs around seasonal population ranges.

**Table 2.2** The variables used to parameterize permeability layers for circuit-based connectivity models by the City of Edmonton (2016b, 2017b), with asset category, feature name, and ratings (left side of the table), and comparable variables (some were grouped for variable reduction), data ranges, and PCA terms used in seasonal compositional analyses and a resource selection function (RSF; right side of the table) for 19 urban coyotes in Edmonton, Alberta.

| Circuitscape Asset | Circuitscape feature | Permeability rating | Compositional analysis variable name | Compositional data range (Continuous; proportional) | RSF variable name | RSF data range (Continuous; proximity) | RSF PCA terms† |
|---|---|---|---|---|---|---|---|
| | ‡ | ‡ | ‡ | ‡ | River valley and ravine system | 0.01 - 1 | Natural area (PC1)§ |
| | ‡ | ‡ | ‡ | ‡ | Natural areas | 0.14 - 1 | |
| **Permeable** - Habitat | Natural forest; decid./conif. | 10 | Natural forest | 0.03 - 0.81 | Natural forest | 0.14 - 1 | |
| | Natural shrubby; mod. to high density¶ | 9 | Natural shrub | 0 - 0.31 | Natural grass/shrub | 0.03 - 1 | |
| | Natural grassland/ pasture¶ | 6 | Natural grass | 0 - 0.04 | Agricultural | 0 - 1 | OR Modified grass/shrub (PC1; pasture) |
| | Ornamental tree; low density | 6 | Modified forest | 0 - 0.05 | Modified forest | 0.07 - 1 | ‡ |
| | Ornamental shrub; low density¶ | 6 | Modified grass/shrub | 0.01 - 0.93 | Modified grass/shrub | 0.15 - 1 | Modified grass/shrub (PC1) |
| | Crop | 4 | | | Agricultural# | # | |
| | Grassland, turf | 6 | Maintained grass | 0 - 0.2 | Maintained grass | 0.05 - 1 | ‡ |
| | Wetland | 7 | ‡ | ‡ | ‡ | ‡ | ‡ |
| **Permeable** - River (winter) | North Sask. river floodway | 3 | North Sask. (winter) | 0 - 0.26 | ‡ | ‖ | ‡ |
| **Barrier-** River (summer) | | -5 | North Sask. (summer) | 0 - 0.24 | ‡ | ‖ | ‡ |
| **Barrier -** Human use / physical (parks) | Bridge | -5 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | Stairs | -5 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | Trail | -1 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | Cleared pad area | -6 | ‡ | ‡ | ‡ | ‡ | ‡ |
| **Barrier -** Open space | Maintained turf | -4 | Maintained grass# | # | Maintained grass# | # | ‡ |
| **Barrier -** Physical | Rail fence | -5 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | Chain link fence | -8 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | Retaining wall | -4 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | Buildings | -10 | Developed | 0 - 0.66 | Buildings | 0.1 - 1 | Urban (PC1) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Barrier -** Rail | Railway + 10 m buff. | -4 | Transp. Surface | 0 - 0.08 | ‡ | ‡ | ‡ |
| **Barrier -** Road | Highway/Arterial | -5 | | | Roads | 0.44 - 1 | Urban (PC1) |
| | Secondary | -4 | | | | | |
| | Residential | -3 | | | | | |
| | Alley | -1 | | | | | |
| **Modifier -** Slope | Level (0-4.9%) | 0 | ‡ | ‡ | Slope (degrees) | 0 - 42.86 | ‡ |
| | Moderate (5-15%) | -2 | | | | | |
| | Strong (14.9-30%) | -5 | | | | | |
| | Very strong/steep (>30%) | -10 | | | | | |
| **Modifier -** Culvert | Small terrestrial (0.3-1 m diam) | 6 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | Medium mammal & amphibian (1-2.3 m diam) | 7 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | Large mammal (>2.4 m diam) | 9 | ‡ | ‡ | ‡ | ‡ | ‡ |
| **Modifier -** Human use (parks) | Greenway | 0 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | Natural area | 0 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | City Park | -2 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | Other land use (cemetery) | -2 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | School & Community Park | -4 | ‡ | ‡ | ‡ | ‡ | ‡ |
| **Modifier -** Land use | Vacant/ Undeveloped | 0 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | Recreation/Open space | 0 | ‡ | ‡ | ‡ | ‡ | ‡ |
| | Transportation†† | 0 | Transp. Surface# | # | ‡ | ‡ | ‡ |
| | Agricultural | -2 | Modified grass/shrub# | # | Agricultural# | # | Modified grass/shrub (PC1) |
| | Acreage | -4 | | ‡ | | ‡ | ‡ |
| | Telecommunication/ utility | -2 | Developed# | # | Developed | 0.45 - 1 | Urban (PC1) |
| | Institutional | -5 | | | | | |
| | Commercial | -5 | | | | | |
| | Industrial | -5 | | | | | |
| | Residential | -7 | Residential | 0 - 0.53 | Residential | 0.01 - 1 | |

† Used in RSF model only.

‡ Not included/not applicable.

§ In the final list of uncorrelated variables for evaluation in the RSF model.

¶ Used as separate variables in compositional analyses but combined in the RSF model.

# Similar coverage in another variable or covered above.

|| Covered in study design by including/excluding The North Saskatchewan River in seasonal available domains.

†† "Transportation" in Circuitscape permeability ratings includes railways.

‡‡ All road types were considered as one variable.

**Table 2.3** The weighted mean pairwise log-ratio differences ("pwd;" Aebischer, 1993) calculated using log-ratio analyses of compositions of 10 land cover types in two seasons for 19 urban coyotes in Edmonton, Alberta, with scaled pwd values, and the permeability ratings used to create circuit-based connectivity models by the City of Edmonton (2016b, 2017b).

| Season† | Land cover | Weighted mean pwd‡ | Weighted mean pwd 95% LCL | Weighted mean pwd 95% UCL | Scaled pwd§ | Scaled pwd 95% LCL | Scaled pwd 95% UCL | Circuitscape permeability rating¶ |
|---|---|---|---|---|---|---|---|---|
| Winter | Natural forest | 48.83 | 40.16 | 57.49 | 7.11 | 5.85 | 8.37 | 10 |
| Summer | | 23.54 | 19.72 | 27.36 | 3.43 | 2.87 | 3.98 | |
| Winter | Natural shrub | 47.33 | 32.92 | 61.73 | 6.89 | 4.79 | 8.99 | 9 |
| Summer | | 26.10 | 21.04 | 31.15 | 3.80 | 3.06 | 4.53 | |
| Winter | Natural grass | -22.26 | -59.08 | 14.56 | -3.24 | -8.60 | 2.12 | 6 |
| Summer | | -1.60 | -14.13 | 10.92 | -0.23 | -2.06 | 1.59 | |
| Winter | Modified forest | -35.19 | -75.19 | 4.81 | -5.12 | -10.94 | 0.70 | 6 |
| Summer | | -4.19 | -14.57 | 6.18 | -0.61 | -2.12 | 0.90 | |
| Winter | Modified grass/shrub | 37.30 | 25.83 | 48.77 | 5.43 | 3.76 | 7.10 | 6 |
| Summer | | 13.62 | 8.70 | 18.55 | 1.98 | 1.27 | 2.70 | |
| Winter | Maintained grass | -21.18 | -54.45 | 12.09 | -3.08 | -7.92 | 1.76 | -4 |
| Summer | | 0.37 | -3.58 | 4.33 | 0.05 | -0.52 | 0.63 | |
| Winter | Residential | 12.59 | -2.81 | 27.98 | 1.83 | -0.41 | 4.07 | -7 |
| Summer | | -12.88 | -22.00 | -3.77 | -1.88 | -3.20 | -0.55 | |
| Winter | Developed | 19.15 | -3.56 | 41.87 | 2.79 | -0.52 | 6.09 | -5 |
| Summer | | -5.01 | -15.51 | 5.48 | -0.73 | -2.26 | 0.80 | |
| Winter | Transp. surface | -37.31 | -71.95 | -2.67 | -5.43 | -10.47 | -0.39 | -5 to -1 |
| Summer | | -11.31 | -19.98 | -2.63 | -1.65 | -2.91 | -0.38 | |
| Winter | North Sask. River | -68.70 | -108.86 | -28.55 | -10.00 | -15.85 | -4.15 | 3 |
| Summer | | -45.86 | -57.09 | -34.64 | -6.68 | -8.31 | -5.04 | -5 |
| Winter | Other | 10.86 | -16.35 | 38.06 | 1.58 | -2.38 | 5.54 | ‡ |
| Summer | | 8.23 | -2.59 | 19.05 | 1.20 | -0.38 | 2.77 | |

† Seasons were defined as winter: Dec.1 – Mar. 31 and summer: Apr. 1 – Nov. 31. Number of coyotes used: winter = 14; summer = 15.

‡ Weighted by the square root of the number of points used for each individual.

§ Scaled relative to the North Sask. River in winter (assigned -10) to correspond with relative permeability ratings.

¶ Feature-specific permeability ratings that were used to create the cumulative permeability layers used in circuit-based models by the City of Edmonton (2016b, 2017b).

**Table 2.4** One-way weighted ANOVA tests evaluating differences between seasons in pairwise log-ratio values (relative use) obtained from compositional analyses for 10 land cover types by 19 urban coyotes in Edmonton, Alberta.

| Landcover | | Sum of squares | Mean square | df | *F*-value | *p*-value |
|---|---|---|---|---|---|---|
| Natural forest | Season (Winter)† | 84,579 | 84,579 | 1 | 28.24 | <0.001 |
| | Residuals | 80,874 | 2,995 | 27 | | |
| Natural shrub | Season (Winter) | 59,642 | 59,642 | 1 | 7.817 | 0.009 |
| | Residuals | 205,999 | 7,630 | 27 | | |
| Natural grass | Season (Winter) | 52,156 | 52,156 | 1 | 1.156 | 0.293 |
| | Residuals | 1,128,350 | 45,134 | 25 | | |
| Modified forest | Season (Winter) | 127,115 | 127,115 | 1 | 2.318 | 0.14 |
| | Residuals | 1,480,813 | 54,845 | 27 | | |
| Modified grass/shrub | Season (Winter) | 74,149 | 74,149 | 1 | 14.29 | <0.001 |
| | Residuals | 140,153 | 5,191 | 27 | | |
| Maintained grass | Season (Winter) | 58,831 | 58,831 | 1 | 1.738 | 0.199 |
| | Residuals | 846,318 | 33,853 | 25 | | |
| Residential | Season (Winter) | 82,151 | 82,151 | 1 | 7.71 | 0.010 |
| | Residuals | 266,383 | 10,655 | 25 | | |
| Developed | Season (Winter) | 77,263 | 77,263 | 1 | 3.677 | 0.066 |
| | Residuals | 567,334 | 21,012 | 27 | | |
| Transp. surface | Season (Winter) | 89,475 | 89,475 | 1 | 2.188 | 0.151 |
| | Residuals | 1,104,164 | 40,895 | 27 | | |
| North Sask. River | Season (Winter) | 57,731 | 57,731 | 1 | 1.056 | 0.316 |
| | Residuals | 1,147,806 | 54,657 | 21 | | |
| Other | Season (Winter) | 912 | 912 | 1 | 0.032 | 0.859 |
| | Residuals | 765,217 | 28,341 | 27 | | |

† Seasons were defined as winter: Dec.1 – Mar. 31; summer: Apr. 1 – Nov. 31. Number of coyotes used: winter = 14; summer = 15.

**Table 2.5** Estimated coefficients (β), lower and upper 95% confidence limits (LCL and UCL, respectively) for the most parsimonious top model of the logistic mixed regression models (resource selection) for habitat selection by 19 urban coyotes in Edmonton, Alberta, including odds ratio (OR).

| Parameter | β | 95% LCL | 95% UCL | Odds ratio (OR) | OR 95% LCL | OR 95% UCL | *p*-value |
|---|---|---|---|---|---|---|---|
| Intercept*** | **-1.072** | -1.264 | -0.881 | 0.34 | 0.28 | 0.41 | <0.001 |
| Slope*** | **0.473** | 0.440 | 0.505 | 1.60 | 1.55 | 1.66 | <0.001 |
| Natural areas*** | **0.995** | 0.943 | 1.046 | 2.70 | 2.57 | 2.85 | <0.001 |
| Modified forest*** | **0.565** | 0.506 | 0.623 | 1.76 | 1.66 | 1.87 | <0.001 |
| Modified grass/shrub** | **0.112** | 0.041 | 0.183 | 1.12 | 1.04 | 1.20 | 0.002 |
| Residential*** | **0.437** | 0.370 | 0.503 | 1.55 | 1.45 | 1.65 | <0.001 |
| Developed*** | **-0.774** | -0.843 | -0.705 | 0.46 | 0.43 | 0.49 | <0.001 |
| Natural area x Modified forest | 0.027 | -0.002 | 0.055 | 1.03 | 1.00 | 1.06 | 0.066 |
| Natural area x Modified grass/shrub*** | **0.205** | 0.177 | 0.234 | 1.23 | 1.19 | 1.26 | <0.001 |
| Natural area x Residential* | **-0.040** | -0.079 | -0.002 | 0.96 | 0.92 | 1.00 | 0.040 |
| Natural area x Developed* | **0.051** | 0.011 | 0.091 | 1.05 | 1.01 | 1.10 | 0.012 |
| Modified forest x Modified grass/shrub | 0.011 | -0.022 | 0.045 | 1.01 | 0.98 | 1.05 | 0.507 |
| Modified forest x Residential*** | **0.253** | 0.211 | 0.295 | 1.29 | 1.24 | 1.34 | <0.001 |
| Modified forest x Developed*** | **-0.422** | -0.466 | -0.378 | 0.66 | 0.63 | 0.69 | <0.001 |
| Modified grass/shrub x Residential*** | **0.178** | 0.125 | 0.232 | 1.20 | 1.13 | 1.26 | <0.001 |
| Modified grass/shrub x Developed* | **0.068** | 0.013 | 0.123 | 1.07 | 1.01 | 1.13 | 0.015 |
| Residential x Developed*** | **-0.425** | -0.466 | -0.384 | 0.65 | 0.63 | 0.68 | <0.001 |
| Season‡ x Natural area | 0.066 | -0.724 | -0.595 | 1.07 | 0.49 | 0.55 | 0.069 |
| Season x Modified forest** | **0.131** | -0.360 | -0.195 | 1.14 | 0.70 | 0.82 | 0.002 |
| Season x Modified grass/shrub*** | **-0.345** | -0.014 | 0.174 | 0.71 | 0.99 | 1.19 | <0.001 |
| Season x Residential*** | **-0.311** | 0.377 | 0.581 | 0.73 | 1.46 | 1.79 | <0.001 |
| Season x Developed | 0.039 | 0.194 | 0.386 | 1.04 | 1.21 | 1.47 | 0.363 |
| Mange† x Natural area*** | **-0.660** | -0.005 | 0.137 | 0.52 | 1.00 | 1.15 | <0.001 |
| Mange x Modified forest*** | **-0.277** | 0.048 | 0.214 | 0.76 | 1.05 | 1.24 | <0.001 |
| Mange x Modified grass/shrub | 0.080 | -0.443 | -0.247 | 1.08 | 0.64 | 0.78 | 0.095 |
| Mange x Residential*** | **0.479** | -0.404 | -0.219 | 1.61 | 0.67 | 0.80 | <0.001 |
| Mange x Developed*** | **0.290** | -0.046 | 0.124 | 1.34 | 0.96 | 1.13 | <0.001 |
| Season x Mange x Natural area*** | **-0.283** | -0.387 | -0.179 | 0.75 | 0.68 | 0.84 | <0.001 |
| Season x Mange x Modified forest*** | **0.271** | 0.137 | 0.405 | 1.31 | 1.15 | 1.50 | <0.001 |
| Season x Mange x Modified grass/shrub | -0.002 | -0.147 | 0.143 | 1.00 | 0.86 | 1.15 | 0.980 |
| Season x Mange x Residential*** | **0.379** | 0.212 | 0.547 | 1.46 | 1.24 | 1.73 | <0.001 |
| Season x Mange x Developed | 0.015 | -0.157 | 0.186 | 1.01 | 0.86 | 1.20 | 0.866 |

*Notes:* The level of significance ($p < 0.05$) is indicated with asterisks for parameters and bolded coefficients (β).

† Using 14 healthy coyotes and five mange-infected urban coyotes.

‡ Seasonal effect of winter; seasons were defined as winter: Dec.1 – Mar. 31 and summer: Apr. 1 – Nov. 31.

**Table 2.6** Summary statistics for habitat suitability index (HSI) derived from a resource selection function (RSF) equation and expert-derived permeability values (used in circuit-based models) obtained for used GPS locations of 19 urban coyotes in Edmonton, Alberta.

| Habitat value type | Mean (± SE) | Median (± SD) | Data range | Skew[X] |
|---|---|---|---|---|
| Habitat suitability† | 0.39 (± 0.01) | 0.49 (± 1.28) | -4.09 - 4.66 | -0.439 |
| Permeability‡ | 31.31 (± 0.21) | 28 (± 23.08) | 0 - 159 | 0.496 |

*Notes:* Shown are means, standard errors (SE), medians, standard deviations (SD), data ranges, and skewness (Skew[X]). Both habitat suitability index (HSI) and permeability were obtained from 11,748 radiotelemetry locations.

† Habitat suitability index (HSI) from a resource selection function (RSF) model equation modelled using 19 urban coyotes (14 healthy and five mange-infected).

‡ Estimated permeability was obtained from the expert-derived seasonal permeability layers (cumulative) by the City of Edmonton (2016b, 2017b).

**Table 2.7** Estimated coefficients (β) and lower and upper 95% confidence limits (LCL and UCL, respectively) for GLMs comparing habitat suitability index (HSI) with expert-derived permeability values (used in circuit-based models) values, season, and health-status for used GPS locations for 19 urban coyotes in Edmonton, Alberta.

| Parameter | β | 95% LCL | 95% UCL | *p*-value |
|---|---|---|---|---|
| Intercept*** | **1.025** | 1.024 | 1.027 | <0.001 |
| Permeability est.*** | **0.012** | 0.010 | 0.013 | <0.001 |
| Season*** | **0.008** | 0.006 | 0.011 | <0.001 |
| Season x Permeability est.** | **-0.004** | -0.006 | -0.001 | 0.003 |
| Mange*** | **-0.023** | -0.025 | -0.020 | <0.001 |
| Mange x Permeability est.*** | **-0.006** | -0.009 | -0.004 | <0.001 |
| Mange x Season* | **0.005** | 0.001 | 0.010 | 0.024 |
| Mange x Season x Permeability est.* | **0.005** | 0.000 | 0.009 | 0.036 |
| | | | AIC | -35127.6 |
| | | | df | 11740 |
| | | | $R^2$ | 0.072 |
| | | | *Pseudo* $R^2$ | -0.004 |

*Notes:* Shown are degrees of freedom (df), log-likelihood (LL), Akaike Information Criterion (AIC), R-squared ($R^2$), and Nagelkerke Pseudo $R^2$ (Nagelkerke, 1991). The habitat suitability index (HSI) tested was derived from a resource selection function (RSF) model equation modelled using 19 urban coyotes ($n$ = 11,748 "used" radiotelemetry locations) and logarithmically transformed. The level of significance ($p < 0.05$) is indicated with asterisks and bold for estimated coefficients (β).

† Estimated permeability obtained from expert-derived permeability layers (cumulative) used to create circuit-based models by the City of Edmonton (2016b, 2017b) and square-root transformed.

‡ Seasons were defined as winter: Dec.1 – Mar. 31 and summer: Apr. 1 – Nov. 31.

§ Using 14 healthy coyotes and five mange-infected coyotes.

## 2.6 FIGURES

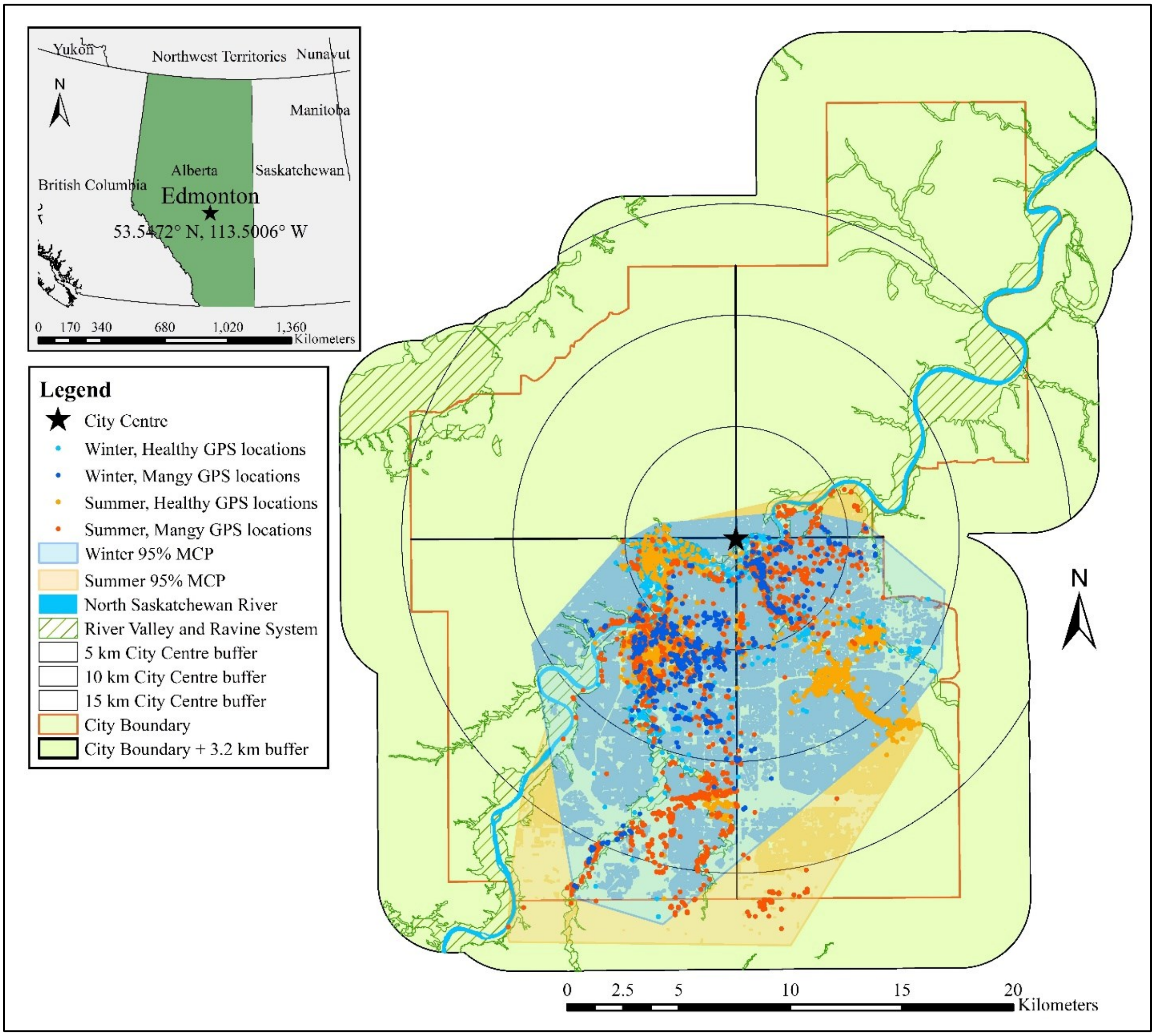

**Fig. 2.1** Edmonton study area in Alberta and coyote GPS collar fix locations for 14 healthy and five mange-infected, subadult and adult coyotes captured between October 2009 to February 2013, with the available domain defined as 95% minimum convex polygons by season (MCPs; buildings excluded; water bodies excluded for summer). The inset map shows the study area location in Alberta, Canada.

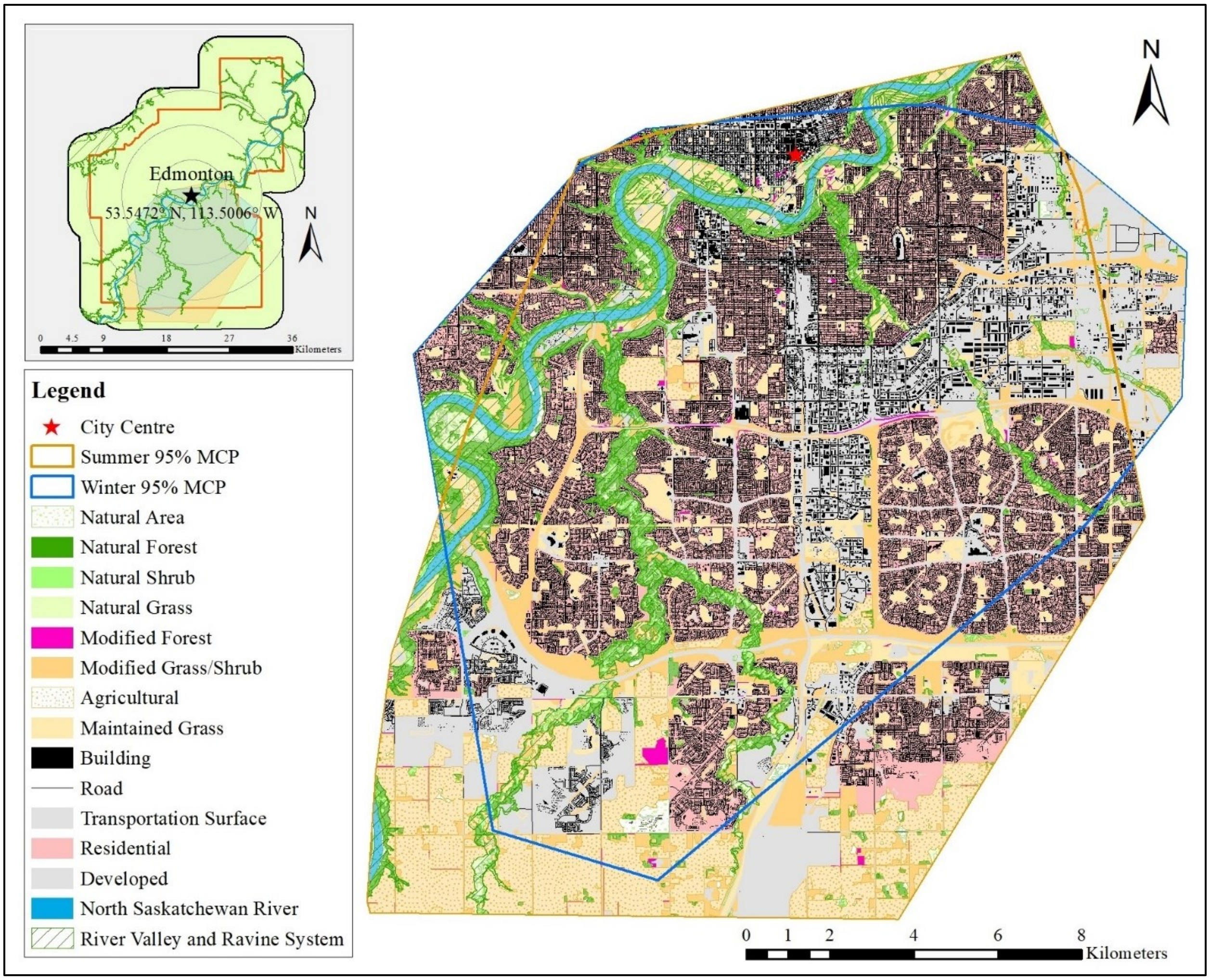

**Fig. 2.2** Variables related to land use, contiguous habitat, and human development considered for habitat selection analyses of healthy and mange-infected urban coyotes in Edmonton, Alberta.

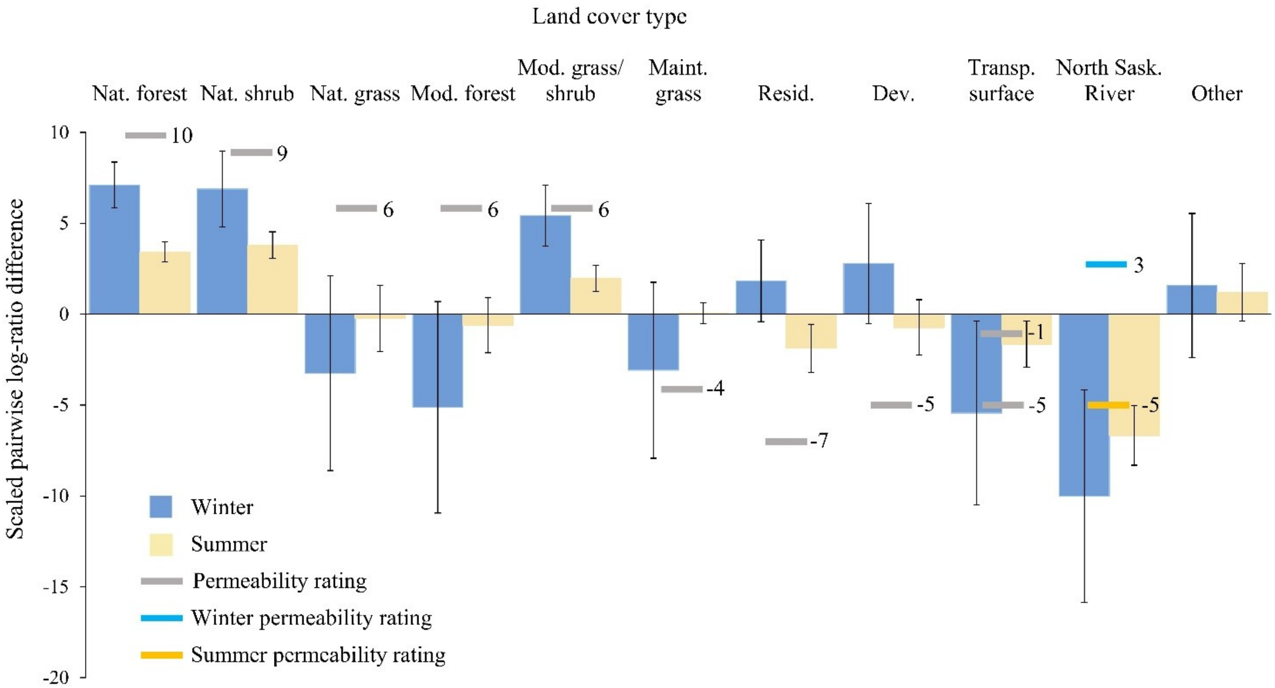

**Fig. 2.3** Average scaled pairwise log-ratio difference ("pwd") for each habitat type (scaled relative to the North Saskatchewan River in winter) from two seasonal compositional analyses (winter: Dec.1 – Mar. 31; summer: Apr. 1 – Nov. 31) evaluating habitat selection of 19 urban coyotes in Edmonton, Alberta, including 95% CI values and the expert-derived permeability ratings used to parameterize permeability circuit-based models by the City of Edmonton (2016b, 2017b).

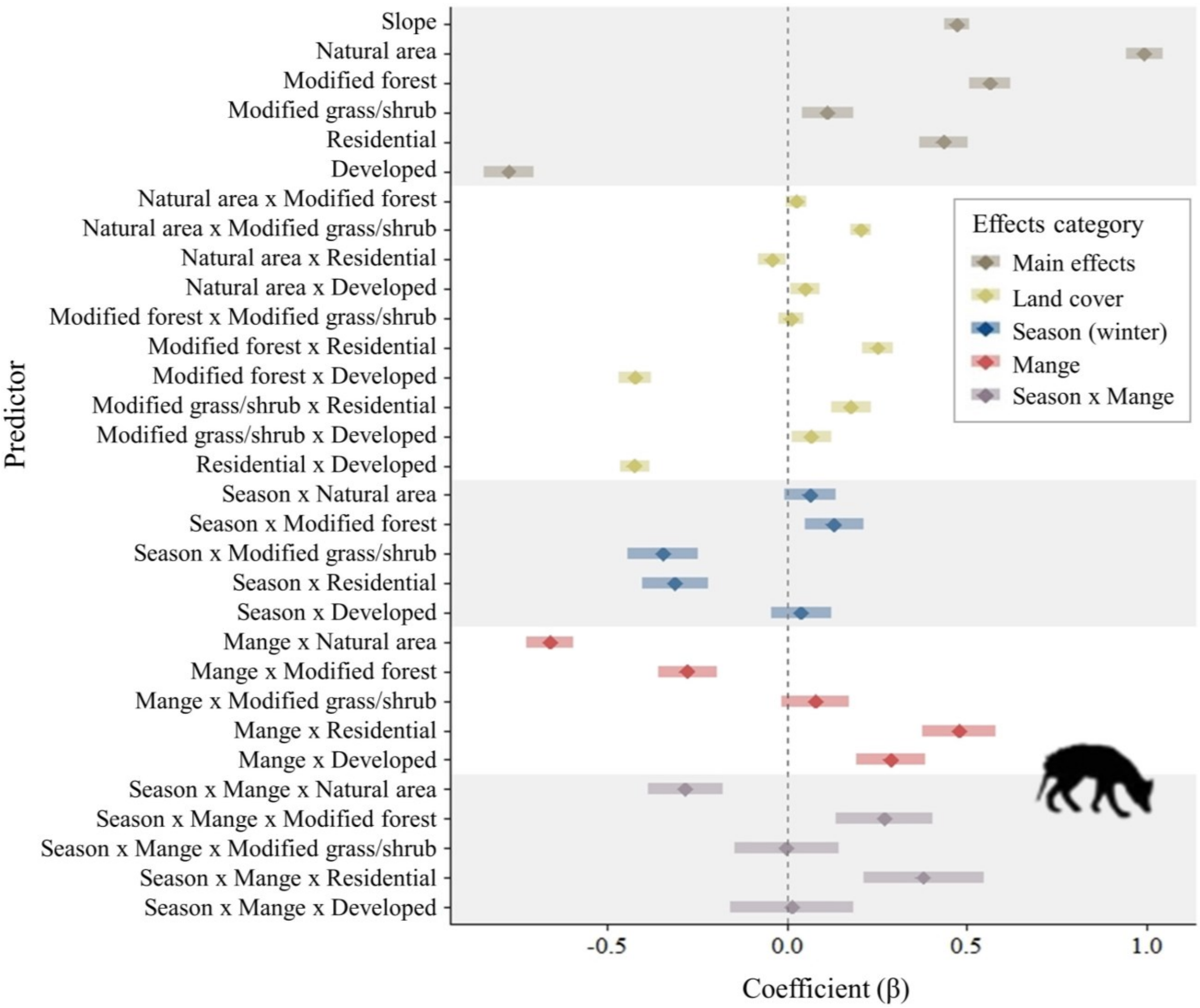

**Fig. 2.4** Model coefficients for a generalized linear mixed model evaluating habitat selection in a resource selection function (RSF) for 14 healthy and five mange-infected urban coyotes in Edmonton, Alberta, including season (winter: Dec.1 – Mar. 31 and summer: Apr. 1 – Nov. 31) and health, with top model predictor variables, corresponding coefficients, and 95% confidence intervals. Clip-art from Murray et al. (2016).

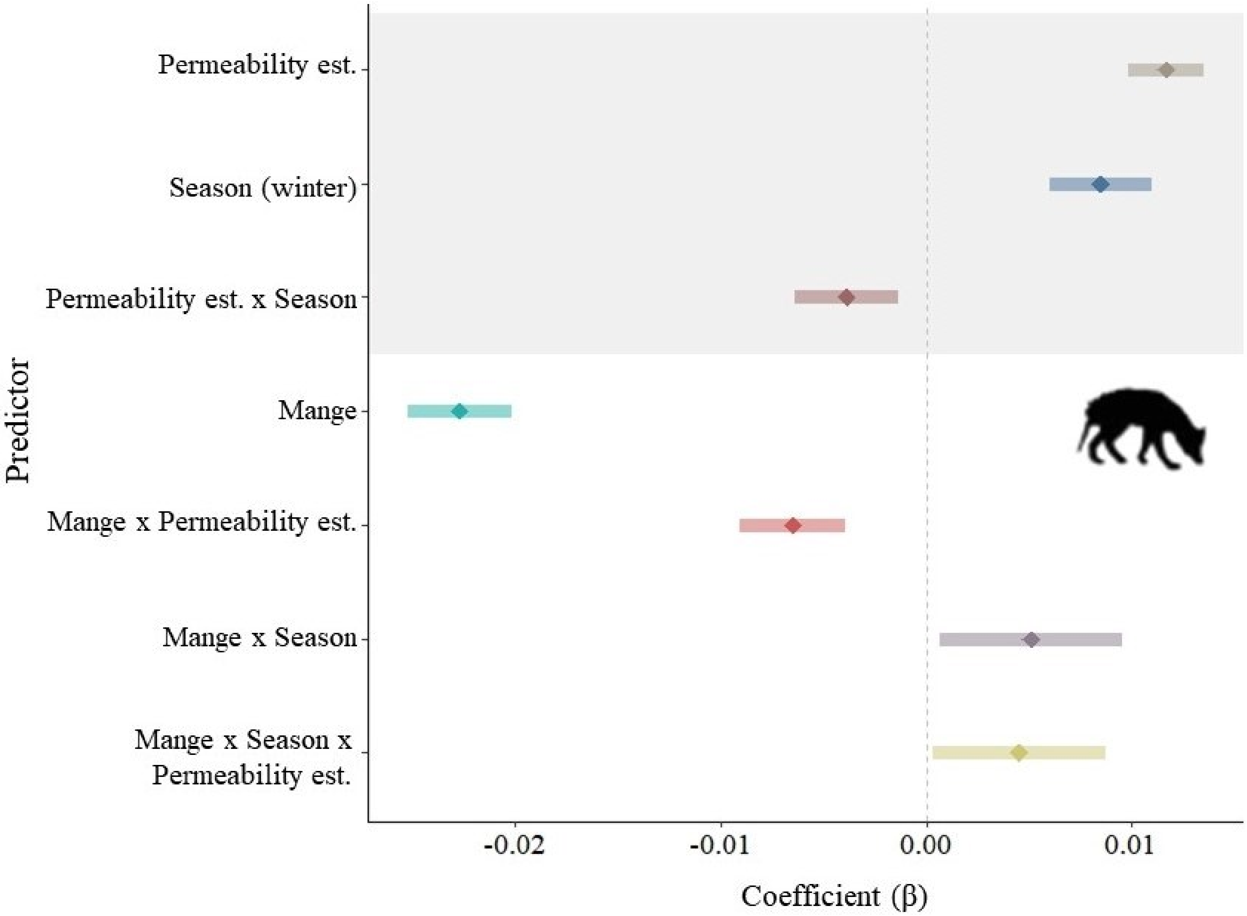

**Fig. 2.5** Model coefficients for a generalized linear mixed model comparing a habitat suitability index (HSI) derived from resource selection function (RSF) model for 14 healthy and five mange-infected urban coyotes in Edmonton, Alberta, with expert-derived cumulative permeability estimates used in circuit-based models by the City of Edmonton (2016b, 2017b), including season (winter: Dec.1 – Mar. 31 and summer: Apr. 1 – Nov. 31) and health, with top model predictor variables, corresponding coefficients, and 95% confidence intervals. Clip-art from Murray et al. (2016).

## **CHAPTER 3 -** Urban mammal occurrence and relative abundance at camera traps correlate weakly with estimators of habitat ecological value used in urban planning

### 3.1 INTRODUCTION

Urbanization causes both a reduction in the number of species and changes the composition of species in the remaining natural areas of urban landscapes (Beninde, Veith, and Hochkirch 2015). These detrimental effects occur in part because development reduces, fragments, and degrades areas that previously supported wildlife (Grimm et al. 2008). Impervious urban infrastructure diminishes habitat quality and connectivity (Cadenasso, Pickett, and Schwarz 2007; Forman 2016) and typically increases with human population density (Newbold et al. 2018). Urban landscapes tend to support an increasing abundance of species that can adapt to or exploit urban areas, while other species decline (McKinney 2002; McIntyre 2014; Beninde, Veith, and Hochkirch 2015). Cities strive to limit this loss because greater biodiversity supports many ecological processes (Bongaarts 2019) and human well-being (Fuller et al. 2007). Retaining urban biodiversity requires the protection of the natural areas that accommodate the needs of rare, as well as abundant, species in urban areas.

As cities expand to accommodate human population growth, surrounding natural areas are being lost throughout the world (Bongaarts 2019), including relatively remote parts of North America, where urban sprawl is encouraged by the lower cost of rural land (Carruthers and Ulfarsson 2002). Edmonton, Alberta, Canada, is one such city, where rapid population growth (Statistics Canada 2021b) and urban sprawl (City of Edmonton 2017a) increase the challenge of conserving adequate habitat for wildlife. Edmonton has the largest urban park in Canada, which comprises an extensive river valley and ravine system (City of Edmonton 2020b; 2022) and preserves a high degree of connectivity for wildlife. The City of Edmonton (hereafter the City) aims to maintain this system along with upland natural areas (tablelands) as a connected ecological network even amid increasing development (City of Edmonton 2007).

The urban planners that developed Edmonton's ecological network approach emphasized the configuration of natural areas as movement pathways for wildlife and their composition or ecological integrity as wildlife habitat (City of Edmonton 2007). To support subsequent land use decisions to retain biodiversity, ecological planners developed two related indices termed biodiversity potential and ecological connectivity (City of Edmonton 2014a). Both indices are calculated as relative scores based on patch characteristics using remotely sensed data (City of Edmonton 2014a). Biodiversity potential is intended to estimate the integrity and function (habitat quality), and it is scored based on the size, shape, and habitat diversity of a natural area (City of Edmonton 2014a). Conversely, ecological connectivity is intended to estimate the movement and dispersal potential of animals, and it is scored based on the area of upland and wetland habitats within a 100 m buffer of a natural area (City of Edmonton 2014a). The City described these indices in the Phase II Ecological Network Report (ENRII [City of Edmonton 2014a]) as a consistent and scientifically-based means to evaluate trade-offs in future land use decisions (City of Edmonton 2014a). Although these indices were based on information in the ecological peer-reviewed literature (City of Edmonton 2014a), they have not been compared to wildlife occurrence data, such as that obtained from camera traps and similar census techniques. Tests of the indices used by planners could be supported by additional analyses because many other factors that affect habitat quality for wildlife are necessarily omitted. Two additional contributors to animal use of urban spaces include the conversion of natural to semi-natural spaces and the concomitant use of both of these areas by people. The two indices used by the City were designed to estimate the ecological value of areas with natural habitat types, but they were not intended to apply to parks with modified vegetation types. However, many semi-natural parks have qualities of natural areas, such as shrubs and trees, that may support species which rely on high vegetation structure, such as rodents (Glennon and Porter 2007) or snowshoe hare (Murray 2003; Holbrook et al. 2017). Semi-natural areas can serve as stepping-stones for movement between natural habitats if the density is high enough (Lynch 2018). Even somewhat disturbed urban green spaces with simplified vegetation, such as cemeteries and golf courses, can have similar species diversity to natural areas (Gallo et al. 2017). Conversely, semi-natural areas may be low-quality habitat for many species, such as if they are too small or isolated (Beninde, Veith, and Hochkirch 2015), or if they contain homogenous or simplified vegetation (Bigsby, McHale, and Hess 2013). Human use also affects habitat use; however, the effects on wildlife habitat use vary among species (Nickel et al. 2020).

One more limitation of the ecological indices used by urban planners is the high variability among species in how they respond to urbanization (McIntyre 2014; Newbold et al. 2018; Fidino et al. 2021). Urban landscapes tend to support an increase in the abundance of species that can adapt or exploit urban areas, while others decline (McKinney 2002; Ducatez et al. 2018;

Newbold et al. 2018). This homogenization often corresponds to characteristics of urban avoiders *vs.* adapters and exploiters (*sensu* Blair, 1996; McKinney, 2002). Species adaptability greatly influences habitat use (Ducatez et al. 2018). For example, some species adjust diel activity patterns to reduce overlap with humans by becoming more active at night (Gaynor et al. 2018; Gallo et al. 2022), which may increase use of land cover types that are predicted to be poor quality. However, adaptability also varies among species, even among flexible species, like carnivores (Nickel et al. 2020). Differences in functional traits will influence habitat use and thus habitat quality for wildlife species, such as dispersal ability, where smaller species are less likely to occur or persist in more disturbed and isolated areas. As a result, species able to disperse more easily tend to be more abundant where natural areas are fragmented (Parker and Nilon 2012), whereas smaller species decline (Barko et al. 2003; Munshi-South 2012). Selection pressures also influence habitat use. For example, prey species such as rodents or hares may be sensitive to domestic dogs that mimic predators (Lenth, Knight, and Brennan 2008), but may also prefer to use areas closer to human activity to shield natural predators (Suraci et al. 2019). Urban disturbances can result in increased use of natural spaces by carnivores and thus increasing species interactions, which may indirectly alter habitat use by other species (Parsons et al. 2019). Maintaining biodiversity requires protecting habitat that accommodates the needs of rare as well as abundant species in urban areas. Better planning could occur by understanding the responses to various urban features and disturbances of species groups that vary in size and of individual species habitat associations, natural history, and urban adaptation.

Camera traps are an increasingly common tool for measuring wildlife occurrence, distribution, abundance, habitat use, and behaviour (O'Connell, Nichols, and Karanth 2011; Burton et al. 2015). Camera traps offer high accuracy rates with less cost and invasiveness than other forms of census (Burton et al. 2015; Kucera and Barrett 2011; O'Connell, Nichols, and Karanth 2011; O’Brien 2011; Steenweg et al. 2017), and they may also help to engage citizens in wildlife monitoring and protection (Wearn & Glover-Kapfer 2017). However, camera traps are less effective at monitoring small species, such as rodents (O’Brien, Kinnaird, and Wibisono 2011), for which track tubes containing boards treated with ink or carbon can passively sample footprints (Glennon, Porter, and Demers 2002; Duffie et al. 2019). Track tubes effectively estimate the relative abundance of small mammals and they can be used to measure a range of microtine rodents (e.g., mice and voles) and larger animals, such as squirrels (Glennon, Porter, and Demers 2002).

This study used remote cameras at 89 sites (between 2018-2021) and track tubes at 47 sites (in 2020 only) to census mammals in natural and semi-natural parks in Edmonton, Alberta, to test the predictive ability of two ecological indices used by the City, and then of a variety of other remotely-sensed and site-based variables. We did so by comparing the index values with the presence (hereafter occurrence) and detection rate (hereafter relative abundance) of similarly sized groups of terrestrial mammals, including small (e.g., red squirrel [*Tamiasciurus hudsonicus*]), medium (e.g., hare/rabbit [*Lepus* spp.] to coyote), and large mammals (e.g., mule deer [*Odocoileus hemionus*]) that were designated as ecological design groups (hereafter species groups) by the City of Edmonton (City of Edmonton 2010b; 2014a) and several mammal species individually. We then compared detections of the three species groups and five species chosen as representatives of each species group to (a) several covariates associated with land cover that were measured remotely and (b) site-based variables that were measured in the field. In addition to the objectives described for this study, our camera data contributed to the Urban Wildlife Information Network (UWIN, 2021), a collaborative group of over 40 cities that uses a standardized protocol to set and report information from camera traps. Our purpose was to support ecological planning in the City of Edmonton while contributing to broader studies of urban biodiversity.

## 3.2 MATERIAL AND METHODS

### *3.2.1 Study area and site selection*

This study took place in Edmonton, Alberta, Canada (53.5472° N, 113.5006° W) and the surrounding peri-urban area (within a 3.2 km buffer of the city boundary; Fig 3.1), which allowed us to capture a gradient of urban density. The city area is 783 km² (City of Edmonton 2019c), with a metropolitan population of over 1.4 million (Statistics Canada 2021a) and an average population density of 1,370 people/km² (Statistics Canada 2017). Edmonton is 671 m above sea level, has a mean annual temperature of 3.9°C, and a mean annual precipitation of 476.9 mm (Government of Canada 2021). The river valley and ravine system is 7,400 ha in area and spans a linear distance of 100 km, with the many ravines and tributaries (City of Edmonton

2020b). Edmonton's 9% natural areas (City of Edmonton 2007) consist predominantly of Aspen parkland (City of Edmonton 2020b) with interspersed semi-natural urban green spaces (golf courses, urban parks, cemeteries, and remnant natural patches).

To survey terrestrial mammals, we deployed 89 camera traps between May 2018 and September 2021 and 47 small mammal track tube arrays in July and August 2020 throughout Edmonton and the city periphery. Of these, we placed 69 camera traps and 37 track tube arrays in natural areas (including Edmonton's river valley and ravine system) and 20 camera traps and 9 track tube arrays in semi-natural urban locations (Fig. 3.1). We selected these locations following a standardized protocol (Magle et al. 2019; UWIN n.d.) across a gradient of urban density across four transects emanating from Edmonton's urban centre in the NE, NW, SE, and SW directions. Two transects ran parallel to the river valley corridor (NE and SW), with some duplication of the SW transect in the Whitemud Creek Ravine owing to its extensive natural habitat and interest to the City. These transects were assumed to include highly connective forested habitat that supports several mammal species (City of Edmonton 2010b). Two other transects ran approximately perpendicular to Edmonton's river valley corridor (NW and SE), encompassing both natural and semi-natural areas in which conservation theory would predict lower landscape-level connectivity due to isolated green spaces and disconnected ravines. We selected sites within ~2 km of each transect, and either separated by at least 1 km or without temporal overlap (UWIN n.d.). We expected a 1 km separation distance to reduce spatial autocorrelation as it exceeds the home range size of many urban species (Magle et al. 2019).

### *3.2.2 Detection data*

At each of the 89 camera trap locations, we placed one camera, triggered by either motion or infrared heat, on a tree or post at 1 m height facing an open area, game trail, or between two trees (Magle et al. 2019). We mainly used Reconyx Hyperfire cameras (PC800, PC900, or HF2X [Reconyx, Holmen, WI, USA]), but we also deployed a small number of Bushnell cameras (X-8 [Bushnell Corp., Overland Park, KS, USA]) early in the study. We placed a synthetic fatty acid scent lure (Pocatello Supply Depot, Pocatello, ID, US) ~2 m in front of each camera for four months of the year (January, April, July, and October) until July 2019, when the network jointly discontinued the use of lure due to limited evidence of efficacy. Due to camera thefts, vandalism, and malfunction, and periodic logistical constraints, both the temporal and spatial coverage of camera traps were variable. We deployed an average of 43 camera traps per month (min = 26; max = 61) and obtained data from 1,783 camera trap months.

After we retrieved cameras, we used AI technology (Microsoft 2020) to remove images of humans and then used Timelapse2 (Greenberg 2018) to derive monthly detection rates as an index of relative abundance of terrestrial mammal species (O'Brien, Kinnaird, and Wibisono 2003; Palmer et al. 2018; Kays et al. 2020). We expressed detection rate as the count of independent detections per month using 30 minutes as the threshold of elapsed time between consecutive images of the same species to define separate events (Burton et al. 2015; Avrin et al. 2021). We summarized detections for each species and, as counts, summed them into three ecological design groups: small, medium, and large terrestrial mammals (Table 3.1 [City of Edmonton 2010b, 2014a]). Ecological design groups (hereafter species groups) are groups of species of similar body size, life history characteristics, and mitigation requirements used by the City to assess development impacts on wildlife movement and use (City of Edmonton 2014a) and for the planning of wildlife passages (City of Edmonton 2010b).

We analyzed detection data for three mammal groups and 13 species (Table 3.1) to assess the predictive accuracy of the two ecological indices for species with diverse habitat preferences, dispersal ability, and urban sensitivity and to compare the predictiveness between species groups and individual species. For subsequent multivariate modelling, we analyzed data for three mammal groups and five individual species, chosen to represent each group to support the comparison of remotely-sensed and site-based predictors between groups and species. We selected one species to represent each of the small and large mammal groups, and three from the medium-sized mammal group to accommodate the high variability of life-history strategies of species within that group (Table 3.1). Thus, we created models of occurrence and relative abundance for three species groups, red squirrel, snowshoe hare (*Lepus americanus*), porcupine (*Erethizon dorsatum*), coyote, and mule deer. Camera traps are sometimes used to study small mammal populations (Burton et al. 2015), and those with infrared sensors are more likely to capture smaller species (Swann, Kawanishi, and Palmer 2011). However, using camera traps to survey small mammals has been criticized because the low detectability of smaller species results in unreliable detection data (O’Brien, Kinnaird, and Wibisono 2011; Anile and Devillard 2016). For this reason, we used track tubes to provide comparable estimates to live-trapping (Glennon, Porter, and Demers 2002) as a supplement to camera data.

We measured the relative abundance of small mammals at 47 track tube sites over three sampling periods (July and August of 2020). For each deployment, we placed three track tubes at each site; the first was placed ~5 m in front of the camera, and the other two were placed at 45-degree angles, resulting in a triangular arrangement with approximately ~20 m spacing between tubes (Glennon, Porter, and Demers 2002). Each track tube consisted of a track board nested inside a PVC pipe approximately 30 m long with a diameter that was either small (8 cm diam. x 25 cm length) or large (12 cm diam. x 30 cm length). We used two sizes of piping to maximize the likelihood of capturing a diversity of small mammals (Palma and Gurgel-Gonçalves 2007). Each track board consisted of an 8 cm x 22 cm board cut from corrugated plastic affixed with a 4 $cm^2$ inkpad made of felt material that was glued to the center of the board, and two 8 cm x 12 cm strips of chemically treated contact paper taped to either end of the board. We treated the contact paper with a solution of tannic acid, ethanol, and water (King and Edgar 1977). We surrounded each inkpad with a 1 cm silicone bead to control ink bleed and applied an ink solution of ferric nitrate, polyethene glycol, Anthrox BL725, and distilled water (King and Edgar 1977). When animals enter the tube, the solution transfers onto the contact paper to leave a waterproof and smudge-proof print. We baited each track tube with a dime-sized amount of peanut butter smeared in the center of the roof of each tube.

We expressed relative abundance from track tubes as the proportion of total sampled area (contact paper) covered by tracks for each deployment and per day deployed (proportion occupied/deployment/day). To quantify this, we created a 1 $cm^2$ grid on each side of the two segments of contact paper from each tube to control for variability in the size of contact paper, ink-bleeding, and damage. We counted the number of readable grid cells for each track board as those entirely on the contact paper and less than 50% obscured by ink bleed or other damage (sampled area). We counted cells containing one or more tracks (occupied cells); tracks that overlapped multiple cells we only counted once. We then separately summed the total number of occupied and readable cells from all the track tubes for each deployment. We divided the total occupied cells/readable cells and then by the number of days the track tube was deployed. Each sampling period was ~8 days on average, and we collected relative abundance data for 130 deployments (103 deployments from 38 natural sites; 27 deployments from 9 modified sites).

### *3.2.3 Environmental data*

To further explore predictors of mammal occurrence and relative abundance, we used remotely-sensed data, site-specific information from field surveys, camera traps, and track tubes to derive one categorical, three binary, and 32 continuous variables to develop independent variables and models (described below; Table 3.2; Fig. 3.1). For the remotely-sensed data, we used a Geographic Information System (ArcMap, v10.7.1, Redlands, CA) to derive eight geographic information system layers, including buildings (City of Edmonton 2018a), roads (City of Edmonton 2018c), sidewalks (City of Edmonton 2021b), neighbourhoods (City of Edmonton 2021a), land use (City of Edmonton 2021c), dog off-leash areas (City of Edmonton 2020a), urban Primary Land and Vegetation Inventory (uPLVI [City of Edmonton 2018d]), and unique landforms (river valley/ravine [City of Edmonton unpublished data 2016c]). To extract explanatory metrics related to land cover, we collapsed land cover from the City's uPLVI, unique landforms, and land use layers as five land cover types: natural forest, natural grass/shrub, modified vegetation (grass/shrub/trees; excluding maintained grass), maintained grass, the river valley and ravine system, and housing. The uPLVI was adapted from provincial vegetation inventories to incorporate unique urban features (City of Edmonton 2014b). We derived housing density as the density of dwellings and population density by combining neighbourhood data with census data (City of Edmonton 2019a, 2019b). We used the uPLVI, sidewalk, road, and building layers (listed above) to calculate the cover of impervious surfaces, which we used, along with other human disturbance-related variables, to create an urbanization index using principal component analysis (PCA; below). This approach was similarly implemented in a variety of other studies in the UWIN group (Fidino, Lehrer, and Magle 2016; Magle, Lehrer, and Fidino 2016; Fidino and Magle 2017; Gallo et al. 2017; Gallo et al. 2019) to control for the influence of highly correlated disturbance-related variables.

Remotely-sensed metrics comprised 14 explanatory variables (Table 3.2), including the density of vegetated land cover types (four), urban density, distance to the river valley and ravine system, vegetation type (natural forest; *n* = 43, natural grassland; *n* = 16, maintained grass/transplanted treed; *n* = 20), and site occurrence in natural areas (*n* = 69; vs modified; n = 20) and off-leash dog parks (*n* = 17). Of the 14 remotely-sensed metrics, we derived patch-level metrics analogous to the components used to score the ecological indices. We did so to assess the predictive capacity of similar patch-level metrics to those used in the indices when evaluated along with other predictors relevant to both natural and semi-natural areas. The variables used to represent biodiversity potential included patch area (ha), shape index, and habitat diversity within the natural area. The variable used to represent ecological connectivity for models for camera data was the amount of contiguous habitat as the combined area (ha) of upland and wetland area within a 100 m buffer. For track tube data, the variable used to represent ecological connectivity was whether sites were in contiguous habitat (*vs.* disconnected parks; natural and semi-natural). These variables differed for camera traps and track tubes to provide comparable variables on biological relevant scales (other variables largely measured at such scales using 500 m/30 m).

We derived density metrics (buildings, roads, population, and land cover; Table 3.2) within a 500 m buffer of each site for models using camera data and within a 30 m buffer for models using track tube data. Because the importance of a feature is expected to decline with distance to it, we applied an exponential decay function to proximity metrics ($e^{-\alpha d}$ [Taylor, 1967]), where d was the distance in meters, and α was set to correspond with each scale. We chose a 500 m scale for variables used to model camera data because it encompassed the home range of many of the focal species (Etter et al. 2002; Hämäläinen, Fey, and Selonen 2018), while avoiding pseudoreplication (Manly et al. 2002; Miguet et al. 2015). This scale also supported the comparison of effects between species (Miguet et al. 2015) and was used in other multi-species urban studies (Fidino, Lehrer, and Magle 2016; Fidino and Magle 2017; Gallo et al. 2017; Gallo et al. 2019). We chose a 30 m scale for variables used to model track tube data based on the home range size of rodent species (Schirmer et al. 2020) and scales used in other studies (Glennon and Porter 2007).

We conducted field surveys at 71 camera locations in the summer of 2019 to obtain 12 continuous explanatory variables. These included forest or grassland structure, land cover type, tree density, vegetative diversity, anthropogenic impact, human and game trails, and various cover measures (e.g., canopy, shrubs, coarse woody debris, etc.; Table 3.2). Surveys were guided by the City of Edmonton Temporary Sample Plot (TSP) and Permanent Sample Plot (PSP) Procedures (City of Edmonton 2016a) and Urban Ecological Field Guide (City of Edmonton 2015). We measured characteristics either as the count (i.e., game trails) or average value (e.g., forest structure class) within a 30 m buffer or the average of four cover plots placed at 30 m from each camera in all cardinal directions. We replaced missing field data with the average values from non-missing sites based on whether the site was in a natural or modified area (replaced: 14 sites; 112 sample months, four sites; 15 sample months, respectively).

Lastly, we used data from camera traps, track tubes, and temporal values from the literature (ABMI 2018, 2021) to derive eight additional continuous variables as measures of species co-occurrence, site-specific human disturbance, and those that may influence detection probability (Table 3.2). We used data from cameras to derive the number of images of humans and domestic dogs and the number of detections of predator (coyote; for small mammals [group], red squirrel, snowshoe hare, and porcupine) and prey species (small mammals; for coyote models) per month. We used track tube data to derive a secondary measure of the prevalence of small mammal prey as the average proportion of occupied cells/day and used the average values for two sites where data was missing. We included season (summer: Apr. – Oct.; winter: Nov. – Mar.) and lured as the proportion of the month that lure was effective (~3 weeks [Wildlife Control Supplies 2018]). To account for variability in the camera field of view, we used temporal values from the literature (ABMI 2018, 2021) to calculate the effective detection distance (EDD) based on species, season, and habitat type; for the species groups, we averaged the values for species within each group.

### *3.2.4 Ecological indices*

To determine whether ecological indices were good predictors of occurrence or relative abundance for our target species and guilds, we derived biodiversity potential and ecological connectivity scores for 69 camera trap locations and 38 track tube arrays in natural areas. The indices were designed to assess the value of natural areas, and they were not intended to apply to the urban parks we monitored as part of a broader set of camera traps and track tubes. We used the uPLVI (City of Edmonton 2018d) to derive scores by replicating the scoring process used by the City described in the Phase II Ecological Network Report (ENRII; Appendix 3.1 - Table 1 [City of Edmonton 2014a]). Thus, we delineated natural areas as “contiguous natural land cover” (City of Edmonton 2018b) by dissolving all adjacent polygons of the following land classifications: naturally wooded, non-wooded, wetland, and natural water bodies, excluding the North Saskatchewan River (City of Edmonton 2018d). We scored biodiversity potential (out of a total of 35) by deriving and combining scores based on the total area (0 to 15), shape (-8 to 0), and habitat diversity (1 to 4; Appendix 3.1 - Table 1 [City of Edmonton 2014a]). We scored ecological connectivity (out of a total of 20) as the combined score for the area of nearby upland (0 to 10) and wetland habitat (0 to 10) found within a 100 m buffer of each natural area (Appendix 3.1 - Table 1 [City of Edmonton 2014a]). For the 69 camera trap locations and 38 track tube arrays, we extracted values of biodiversity potential (-4 to 33; 0 – 33, respectively) and ecological connectivity (both 0 - 13) to compare with detection data.

### *3.2.5 Analytical approach - Testing ecological indices*

To evaluate the predictive accuracy of two ecological indices, we used two types of generalized linear mixed models, including one method that could address the zero-inflation we encountered in the count (Poisson) data from camera traps. Count data often contain a disproportionate number of zeros relative to the count distribution (Poisson) or are "zero-inflated" (Lambert 1992), suggesting that some zeros relate to the probability a species will occur, which results from a separate process (Martin et al. 2005). Because excess zeros can result from environmental causes, the inability to detect present individuals (i.e., imperfect detection [MacKenzie, Bailey, and Nichols 2004]), and chance (Martin et al. 2005), particular models are needed to partition variance appropriately and avoid biased parameter estimates (Harrison 2014; Blasco-Moreno et al. 2019).

Zero-inflated Poisson models (hereafter ZIP; Lambert 1992) fit two linear models simultaneously to address the sources of zero-inflation (probability of a zero value; inversely, probability of occurrence) separately from zeros that belong to the count distribution (Lambert 1992; Blasco-Moreno et al. 2019). The zero-inflation model-part is a logistic regression, and since counts are repeatedly measured over time, the binary response serves as a detection history (Dénes et al. 2015). Thus, the zero-inflation model-part can include predictors of "false" zeros (e.g., imperfect detection) and "true" zeros that relate to occurrence (Lambert 1992; Blasco-Moreno et al. 2019). Additionally, this model-part can also mitigate problematic variability from other "false" zeros (e.g., not present but generally occurs, or uses the feature, but not at that site). The second model-part is a Poisson model used to assess predictors of the counts (relative abundance given presence [Lambert 1992; Wenger and Freeman 2008]).

We used ZIP models with random effects (i.e., mixed models) to compare the indices to the occurrence and relative abundance of three groups and 13 species (Table 3.1) from camera traps and generalized linear mixed models (hereafter LMM) to compare relative abundance from track tubes. In both model sets, we used an all-subsets approach to assess the predictive capacity of biodiversity potential and ecological connectivity, along with season and the two-way interactions between the indices and season. For both model types, we first determined whether the indices were correlated (Pearson's correlation coefficient; $r > 0.6$). We then rescaled scores between 0 and 1 to support the comparison of coefficients and to assess the relative magnitude of effect sizes.

For ZIP models, we included all variables and interactions in both the zero-inflation (or inversely, occurrence; $\psi$) and conditional (relative abundance; $\lambda$) components of the two-part model. We included an offset term to account for partial months by converting each count to a rate (log of the number of active days per deployment) and a random effect for site to account for repeated measures and unequal sampling effort. We identified the most parsimonious top model among competing ZIP mixed-models with a logit link for the binary response variable (detected = 1, not detected = 0) and a log link for the count response (number of detections per month) and retained those within 2 ΔBIC (Schwarz 1978; Zuur, Ieno, and Smith 2007). We used Bayesian Information Criterion (BIC; Schwarz 1978) because it more heavily penalizes complex models to favour parsimony (Hastie, Tibshirani, and Friedman 2008) and reduces type 1 errors in the presence of overdispersion (Campbell and O'Hara 2021). Since the coefficients from the zero-inflation model-part corresponds with the probability of zeros (absence; Brooks et al. 2017), we inversely transformed these coefficients to obtain estimates that corresponded with the probability of occurrence ($\psi$). To compare the same predictors to the relative abundance from track tubes, we used a similar approach as in ZIP models, aside from a few adjustments for the different response variable. We used LMMs with a square root transformation for the response variable calculated from the proportion of occupied cells/deployment/day. No offset was necessary, but we included a random effect for site to account for repeated measures. We identified the most parsimonious top model among competing LMMs using Akaike's Information Criterion for small sample sizes (AICc; retained those within 2 ΔAICc; Akaike 1978; Burnham and Anderson 2002).

### *3.2.6 Analytical approach - Modelling wildlife occurrence and relative abundance*

To complement these assessments, we used the same model types to evaluate the predictive value of several remotely-sensed, human-use, and field measurements on the occurrence and relative abundance of groups and individual species. We built ZIP mixed models to evaluate the influence of 30 explanatory variables (Table 3.2) on the occurrence and relative abundance of red squirrel, snowshoe hare, porcupine, coyote, mule deer and three species groups (small, medium, and large mammals; Table 3.1) from camera traps. We then built LMMs to assess the effects of 27 variables on the relative abundance of small mammals from track tubes.

To build models, we first used camera data from 13 species (Table 3.1) to create an urbanization index by applying principal component analysis (PCA) to variables that proxied urban intensity, including the density of roads, buildings, population, housing, and impervious surfaces, as well as proximity to buildings and roads (Table 3.2). We applied PCA to all combinations of correlated variables ($r > 0.5$ [Burnham and Anderson 2002]) and identified principal components with single-axis scores explaining ~70% of the variance. Because we were interested in the most predictive urban index, we subsequently tested PCA metrics in both the zero-inflation (inversely occurrence; $\psi$) and conditional model parts (abundance; $\lambda$) for each species and retained the PCA metric that was most consistently within 2 ΔBIC (Schwarz 1978; Zuur, Ieno, and Smith 2007). Because we wanted a single index of urbanization (Fidino, Lehrer, and Magle 2016; Magle, Lehrer, and Fidino 2016; Fidino and Magle 2017; Gallo et al. 2017; Gallo et al. 2019), we discarded any development-related variables from subsequent modelling regardless of correlation coefficients.

For both model types, we then investigated all variables using univariate statistics and retained those that were liberally significant ($p < 0.25$ [Hosmer and Lemeshow 1989]). For ZIP models, we did so first for the zero-inflation part of the two-part model. If two or more variables (including the PCA metric) were correlated ($r > 0.5$), we retained the most explanatory using best-fit, defined as the variable with the lowest BIC score (Schwarz 1978) for ZIP models and lowest AICc (Akaike 1978) for LMMs. We rescaled continuous variables between 0 and 1 and then built combined models using an all-subsets approach because we were primarily interested in prediction, not hypothesis testing.

For ZIP mixed models, we built combined occurrence ($\psi$) models in the zero-inflation model-part, which included a log-offset term and a random effect for site. We used BIC (Schwarz 1978) to identify parsimonious top $\psi$ models among competing ZIP mixed models (Poisson GLMM) with a logit link for the binary response variable (detected = 1, not detected = 0), retaining models within 2 ΔBIC (Zuur, Ieno, and Smith 2007). Retaining the variables from top ψ models, we repeated the above steps to build combined conditional models (relative abundance; λ) to identify parsimonious top λ models among competing ZIP mixed models with a log link for the count response variable. We inversely transformed the coefficients from the zero-inflation part to correspond with the probability of occurrence (ψ). To model relative abundance data from track tubes, we followed similar steps to build combined LMMs for the square-root-transformed proportion occupied/deployment/day response variable. We included a random effect for site and used AICc (Akaike 1978) to identify parsimonious top models (retained models within 2 ΔAICc; Burnham and Anderson 2002).

For all analyses, we assessed model fit using Nakagawa's $R^2$ for mixed models (Nakagawa, Johnson, and Schielzeth 2017) using the *performance* package (Lüdecke et al. 2021). This approach to assessing fit accounts for zero-inflation via the *insight* package (Lüdecke et al. 2022). We determined the explanatory value of the random effect by comparing the deviance of the top model with and without it using a likelihood-ratio $\mathrm{Chi}^2$ test with an approximate *p*-value to account for the random effect (Pr > ChiSq / 2 [Stram and Lee 1994; Hall 2000; Bolker et al. 2009]). For ZIP models, we also used the *DHARMA* package (Hartig 2021) to derive dispersion parameters ($\hat{c}$) for the global (Burnham and Anderson 2002) and best-fit models (Liu, Ma, and Johnstone 2020; Markle et al. 2020) and to visually assess Q–Q plots based on simulated residuals. We performed all analyses in R 3.6.1 (R Core Team 2019) using the additional packages, *lme4* (Bates et al. 2015), *glmmTMB* (Brooks et al. 2017), and *MuMin* (Barton 2009).

## 3.3 RESULTS

We collected occurrence and relative abundance for terrestrial mammal species throughout Edmonton, AB, during 1,783 camera trapping months from camera traps deployed at 89 locations between May 2018 and September 2021 (Appendix 3.1 - Table 2; Fig. 3.2). We collected 1,520 of these camera months from the 69 camera traps placed in natural areas and the remaining 263 camera months from the 20 camera traps placed in modified urban parks. We collected 21,996 detections of 23 terrestrial mammal species or genera (Table 3.1; Fig. 3.2); the number of detections per species averaged 818 (SD = 1,838.46; median = 31; SE = 383.35) and ranged from 1 for cougar (*Puma concolor*) and elk (*Cervus canadensis*) to 7,662 for coyote (*Canis latrans*; Table 3.1; Fig. 3.2). We had sufficient detections of 13 species for subsequent modelling.

### *3.3.1 Testing ecological indices*

We used ZIP mixed models and LMMs to compare values for indices of biodiversity potential and ecological connectivity, developed by the City of Edmonton, with the occurrence and relative abundance from camera traps and track tubes placed in natural areas. We tested these indices for three species groups and for 13 individual species from camera traps and the relative abundance of small mammals from track tubes. The indices had some predictive value for only the small and medium groups, and snowshoe hare, coyote, and white-tailed deer from camera traps (Table 3.3), but the direction of these effects varied (Table 3.4; Fig. 3.3).

Among six significant effects of the indices and six interactions between indices or with season (Table 3.4; Fig. 3.3), as a main effect, higher biodiversity potential predicted lower relative abundance of the small mammal group, but higher occurrence of large mammals and relative abundance of white-tailed deer. Higher ecological connectivity predicted higher relative abundance of the small mammal group, and lower relative abundance of both snowshoe hare and white-tailed deer. Significant two-way interactions between the indices showed that higher ecological connectivity values increased the positive effect of biodiversity potential on the relative abundance of white-tailed deer, but reduced the negative effect of biodiversity potential on coyotes. Five significant interactions between indices and season revealed that the predictive ability of the ecological indices was sometimes dependent on season. The winter season increased the negative effect of biodiversity potential on the relative abundance of small mammals, but reduced its negative effect on coyotes. Winter reduced the positive effect of ecological connectivity on the relative abundance of small mammals and increased its negative effect on snowshoe hare and white-tailed deer (Table 3.4; Fig. 3.3).

Each of these models had a single top model, except for large mammals, which had two (Table 3.3). As an indication of model fit, the dispersion parameters ($\hat{c}$) from the global models for snowshoe hare, coyote, and the large species group models suggested overdispersion of data ($\hat{c} > 1$; ranged from 0.02 to 1.90; Table 3.3; Burnham and Anderson 2002). However, none of the test statistics from overdispersion tests were significant (global models; Table 3.3), and Q-Q plots suggested the fits were adequate. The $R^2$ values (Nakagawa, Johnson, and Schielzeth 2017) were also reported (Table 3.3). However, they should be interpreted cautiously for models with $\hat{c} > 1$ because overdispersion may inflate conditional $R^2$ values (Harrison 2014). Including a random effect for site improved models for all species groups and species ($p < 0.001$).

### *3.3.2 Modelling occurrence and relative abundance*

We used ZIP mixed models and LMMs to examine the predictive value of several environmental variables for the occurrence and relative abundance of three design groups used by the City and five species from camera traps and the relative abundance of small mammals from track tubes. One urbanization index from the PCA was the most explanatory component among models for each species. It included density of impervious surfaces and natural forests (PC1 = 75.3% for camera data; 87.5% for track tube data), where higher values indicated increasingly dense, impervious surfaces and housing (approximating urban intensity). For ZIP models for each group and species from camera traps, we first modelled the zero-inflation ($\psi$; inversely, occurrence) from the final list of uncorrelated and most explanatory variables (best-fit in $\psi$ model part; Appendix 3.1 - Table 3). We identified the variables within the most parsimonious top $\psi$ models and held them constant for the $\psi$ component of the two-part model to subsequently model relative abundance via the conditional model ($\lambda$; Table 3.5; Appendix 3.1 - Table 3).

For small-sized mammals, we ran a ZIP mixed model for red squirrel as an individual species from camera traps, but we also used LMMs to model the relative abundance of small mammals at track tubes (Table 3.6; Fig. 3.4). Red squirrel occurrence declined with increasing amounts of modified vegetation and increased in winter. Relative abundance of red squirrels declined with human detections, and increased with dog detections and the winter season. For the small mammal group, occurrence declined with increasing cover of both grasses/forbes and shrubs, and increased with the number of dog detections from cameras. Abundance of small mammals declined with modified vegetation and human detections and increased with dog detections and in winter. Relative abundance of small mammals from track tubes increased in connected habitats and with increasing cover of trees and coarse woody debris (Table 3.6; Fig. 3.4).

For medium-sized mammals, we ran individual models for snowshoe hare, porcupine, and coyote (Table 3.6; Fig. 3.5). Occurrence of snowshoe hare declined with increasing maintained grass; both occurrence and relative abundance increased in winter. Occurrence of porcupines declined with increasing urban density and winter, but there were no significant predictors of relative abundance. Both occurrence and relative abundance of coyotes increased with the relative abundance of prey (defined as detection on camera traps), presence of lure and in winter. Coyote occurrence declined with increasing urban density, and relative abundance increased with dog detections and natural *vs.* modified habitats. As a group, medium mammal occurrence and relative abundance both increased with detections of dogs, use of lure, and winter, season, whereas occurrence declined with increasing tree cover (Table 3.6; Fig. 3.5).

For large mammals, we ran a separate model only for mule deer (Table 3.6; Fig. 3.6), for which occurrence increased with modified vegetation and declined in winter, while relative abundance declined with increasing forest structure and urban density. For the large mammal group, occurrence increased with natural forests and modified vegetation and declined with human detections and in winter (Table 3.6; Fig. 3.6). The relative abundance of large mammals declined in areas designated as off-leash (Table 3.6; Fig. 3.6).

There was a single top model for every species and species group, with no competing top models (Table 3.5). Regarding model fit of ZIP mixed models, the dispersion parameters ($\hat{c}$) from global models for snowshoe hare, coyote, and the medium species group models suggested overdispersion ($\hat{c} > 1$; Table 3.5; Burnham and Anderson 2002). The simulation-based residual tests indicated that the dispersion parameters from global models ranged from 0.01 to 2.05 (Table 3.5). However, none of the test statistics from overdispersion tests were significant (global models), and the Q-Q plots suggested adequate fits (Table 3.5). The $R^2$ values (Nakagawa, Johnson, and Schielzeth 2017) were also reported (Table 3.5). Again, $R^2$ values should be interpreted cautiously for models with $\hat{c} > 1$ because overdispersion may inflate the conditional $R^2$ (Harrison 2014). The model fit of LMMs modelling relative abundance of small mammals from track tubes suggested the fit was adequate (conditional $R^2 = 0.34$ and marginal $R^2 = 0.20$; Table 3.5). Including a random effect for site improved models for all species groups and species in ZIP mixed models ($p < 0.001$), with support of improved LMMs modelling relative abundance from track tubes ($p = 0.059$).

## 3.4 DISCUSSION

Mitigating urban biodiversity loss requires conserving adequate habitat to accommodate the needs of diverse species, which urban planners sometimes attempt to predict with indices of habitat value derived from remotely-sensed information. We tested two such indices used by the City of Edmonton and explored several remote and field-based measures on the occurrence and relative abundance of mammals detected with camera traps and, for small mammals, track tubes. We found that the City's indices rarely predicted greater occurrence or relative abundance of species groups and individual species; however, biodiversity potential was more generally predictive of higher occurrence or abundance than was ecological connectivity. Among the remotely sensed variables we tested, species occurrence or relative abundance typically increased with the naturalness of vegetation density and declined with various forms of human disturbance, such as urban density, human detections from camera traps, and in designated off-leash areas, but with some positive responses to the abundance of domestic dogs. In addition to assessing predictors of species occurrence and abundance, we showed that camera traps effectively captured 13 different mammal species, several of which are rarely observed in Edmonton.

A core purpose of our work was to compare the occurrence and detection rates of urban terrestrial mammals with two ecological indices developed by the City of Edmonton that we scored for natural areas throughout the city. We found inconsistent predictive power of the indices among groups and species, but biodiversity potential performed closer to expectations than ecological connectivity. As biodiversity potential increased, we found that large mammals were more likely to occur, and that white-tailed deer were more abundant. Because the index of biodiversity potential reflects the larger size, more rotund shape, and greater habitat diversity of natural areas, it logically correlates with the presence of ungulates, which rely on large patches with less edge habitat (at a 2 km scale; Kie et al. 2002). White-tailed deer prefer diverse habitats (Miller, Muller, and Demarais 2003) and habitat edges between habitat types, but less so when edges are heterogeneous (Quinn, Williams, and Porter 2013). Biodiversity potential was weakly negatively predictive for the abundance of coyotes, but with confidence intervals that broadly overlapped zero. The negative effect of biodiversity potential on small mammals may have stemmed from the high proportion of upland-loving red squirrels in our sample of small mammals. Although red squirrels are specialists on spruce in the boreal forest near Edmonton (Wheatley, Larsen, and Boutin 2002), they appear to thrive in uplands of every sort (Yahner 2003). Red squirrels may tolerate small patches and disturbed edges more easily when considering the home range size and tolerance to urban disturbances of similar species (Fey, Hämäläinen, and Selonen 2016; Uchida et al. 2016). Since biodiversity potential is scored for the entire natural area, this scale could be too large to reflect high-quality habitat for smaller species (Fisher, Anholt, and Volpe 2011).

We found that higher ecological connectivity values were associated with a higher relative abundance of the small mammals, which increased in winter, but a lower relative abundance of snowshoe hare and white-tailed deer that was reduced in winter. Because the index of ecological connectivity was based on the presence of nearby upland and wetland areas, the positive association for small mammals could be due to the high prevalence of tree squirrels within this group. Many tree squirrels are tolerant of urban disturbances (Uchida et al. 2016) that may be more prevalent at patch edges. In contrast, snowshoe hares tend to avoid edge habitat (Lewis et al. 2011), and so do white-tailed deer when edges are heterogeneous (Quinn, Williams, and Porter 2013). Thus, wetland areas interspersed in natural areas may have low value for both snowshoe hare (Murray 2003) and white-tailed deer. White-tailed deer, in particular, appear to avoid water bodies in urban areas (Magle et al. 2014). The predicted value for ecological connectivity was not correlated with detections of beaver (nor was biodiversity potential), a wetland specialist (Baker and Hill 2003), suggesting that the score for wetland habitat may not reflect the expected benefit even for those which rely on wetlands. Ecological connectivity may have limited predictive value because of the 100 m scale used to measure connective habitat. Perhaps 100 m adequately encompasses the area necessary to support the movement of small mammals, but not for large mammals with higher dispersal ability. Higher dispersal ability is often associated with greater reliance on connective habitat (Cushman and Landguth 2012), but also very scale-dependent habitat associations (Bowyer and Kie 2006). Thus, positive correlations may have occurred if ecological connectivity scores were calculated using a larger buffer width. Ecological connectivity was weakly negatively predictive of the abundance of coyotes, but with broad confidence intervals suggestive of little effect. This outcome may stem from the tremendous breadth of habitats occupied by urban coyotes (Grubbs and Krausman 2009; Hinton, van Manen, and Chamberlain 2015; Franckowiak, Perdicas, and Smith 2019; Wurth, Ellington, and Gehrt 2020).

To complement assessments of the indices used by the City, we examined the predictive capacity of several remotely-sensed and field-based covariates, including similar patch-level metrics to those used to score the indices. We included the three design groups used by the City to assess the similarities in habitat use of species groups and similar-sized individual species, and did so separately for small, medium, and large mammals. Beginning with the small mammals and based on camera data, the occurrence of small mammals declined with increasing cover of grasses/forbes and shrubs, perhaps because this group contained mainly tree squirrels, which prefer forests (Yahner 2003). A similar squirrel species, the Eurasian red squirrel (*Sciurus* *vulgaris*), seems to prefer more densely treed urban areas (Hämäläinen, Fey, and Selonen 2018), despite the capacity to occupy a variety of habitats (Uchida et al. 2016). Many of the sites possessing high coverage of grasses occurred in semi-natural urban parks, which differ from the preferred habitat of many small mammals for natural shrubs and dense, coarse woody debris (Glennon and Porter 2007). This general preference explains why we found that red squirrels occurred less often, and small mammals were less abundant as modified vegetation increased. Such areas likely limit the movement of smaller rodents that are highly vulnerable to fragmented urban areas (Barko et al. 2003; Munshi-South 2012), and perhaps for some tree squirrel species which seem to be less impacted by disturbances such as roads (Fey, Hämäläinen, and Selonen 2016), but still have smaller home ranges (Hämäläinen, Fey, and Selonen 2018). These factors combine to isolate small mammal populations in urban green spaces (Munshi-South 2012), and our track tube results suggest that their populations are supported by a combination of tree cover, coarse woody debris, and connected habitat. Together, these results indicate that connected natural areas increase habitat quality, even for small species, to support greater rodent diversity in urban areas (Johnson and Karels 2015).

Medium mammals and coyotes responded to fairly similar features, but their predictors did not much overlap with snowshoe hare and porcupine. For example, medium mammals were negatively associated with tree cover, snowshoe hare declined with maintained grass, and only urbanization (negatively) predicted porcupines. The negative association with forest cover for the medium mammal group was probably driven by the high rates of occupancy and relative abundance of coyotes, which thrive in open areas (Hinton, van Manen, and Chamberlain 2015) because forested areas are typically preferred by snowshoe hare (Murray 2003; Lewis et al. 2011) and porcupine (Harder 1980; Roze and Ilse 2003). Snowshoe hares may have occurred less when maintained grass was dense because they rely on highly complex vegetation structure and cover for reproduction and to evade predation (Murray 2003; Holbrook et al. 2017). The negative association between medium mammals and forest cover could stem from reduced detectability (Iknayan et al. 2014; Hofmeester et al. 2019) rather than habitat avoidance. Coyotes may prefer natural areas to avoid human activity and access more available prey (Richer et al. 2016) and cover (Gosselink et al. 2003). The negative effect of urbanization on coyotes and porcupines may have stemmed partly from their high sensitivity to road networks (Roze and Ilse 2003; Franckowiak, Perdicas, and Smith 2019).

Large mammals and mule deer responded opposingly to forest density and structure but otherwise had similar habitat preferences. We found that large mammals occurred more often where forest density was high, whereas mule deer, were less abundant when forest structure increased. Many ungulates use forested habitats (Mackie et al. 2003; Miller, Muller, and Demarais 2003), especially white-tailed deer, which require higher quality forage (Miller, Muller, and Demarais 2003) and that were the most common large species in our dataset. In contrast, mule deer prefer open forests, shrubland areas, and watercourses (Mackie et al. 2003) to explain their avoidance of highly structured forests. Forest structure may have been a predictor of detectability, considering a higher structure would have made it more difficult to differentiate between the deer species, which were sometimes identified only to genus. Large mammals and mule deer both occurred more often where modified vegetation was dense, a feature that could increase hiding cover to support movement among larger patches of natural habitat if the density is high enough (Lynch 2018). These features may also increase opportunities for a combination of grazing and browsing that are favoured by deer (Miller, Muller, and Demarais 2003), and especially the preference for shrubs exhibited by mule deer (Berry et al. 2019). It was not surprising that large mammals occurred less often as human detections increased and in off-leash areas, and that mule deer were less abundant in more urban areas. Others have found that white-tailed deer are generally highly tolerant of urbanization (Miller, Muller, and Demarais 2003) and have even been referred to as "quintessential" urban species (Magle et al. 2021), compared to the historic higher sensitivity to infrastructure of mule deer (Mackie et al. 2003). Nonetheless, urbanized populations of mule deer are rapidly increasing in more rural settings (McCrory, Paquet, and Parr 2017; CBC 2020).

We found little similarity among groups of similar-sized species in the land cover types associated with either occurrence or relative abundance. For example, modified vegetation negatively affected small mammals, red squirrels, and snowshoe hare, but generally positive effects on larger animals, including mule deer. We speculate that since larger species rely on connective habitat (Cushman and Landguth 2012), semi-natural areas may be suitable as stepping-stones for ungulates, but not for smaller dispersal-limited species. Additionally, modified habitats such as mowed grass may have lacked the habitat structure needed by smaller species, such as the ground "forms" of snowshoe hare (Murray 2003), which were sensitive to maintained grass in particular. Among the individual species we examined, urbanization was predictive of negative responses only for coyotes, porcupines, and deer, suggesting that red squirrels could accommodate high rates of urban density within 500 m provided they had adequate cover for their territories of typically ~90 m diameter (Larsen and Boutin 1994). Urbanization can be detrimental to many species, but the impact on coyotes may be more consistent (Fidino et al. 2021), and porcupines may have more specific habitat requirements than other species (Harder 1980; Roze and Ilse 2003).

We were surprised to find a positive effect of domestic dogs on red squirrels, small and medium mammals, and coyotes and suspect this stems from one or more indirect effects. First, dogs may have been attracted to the scent, sight or sound of all prey in the vicinity of our cameras, especially squirrels, which are common targets for dogs in urban areas (Weston et al. 2014). Second, people may prefer to walk their dogs in the most natural areas of their local neighbourhoods (Bijker and Sijtsma 2017), which may also support relatively greater biodiversity of other species, especially if these are the only remaining natural areas for less adapted species (Parsons et al. 2019). Third, dogs may create or reinforce trails used by wildlife (e.g., 99% of domestic dogs in natural areas [Parsons et al. 2016]). A fourth reason for the positive association with dogs is that many species may use locations where domestic dogs occur (Parsons et al. 2019), but reduce temporal overlap by being more active at night (Parsons et al. 2016). Finally, the presence of dogs may frequently indicate the presence of people nearby, which could increase habitat attractiveness for other species because humans act as predator shields (Suraci et al. 2019), or because they frequently leave anthropogenic sources of food (e.g., bird feed that attracts small mammals [Jokimäki et al. 2017]).

There are some limitations to our study that affect its interpretations. The biggest of these is the variation among sites, species, and seasons in detectability. Unmeasured variation in detectability can cause large errors in estimates of both occurrence and abundance (Burton et al. 2015; Dénes et al. 2015; Kays et al. 2021). For example, obscured detection may have caused the negative effects of cover for small and medium mammals and forest structure for mule deer (Iknayan et al. 2014; Hofmeester et al. 2019) rather than avoidance (as described above). ZIP mixed models can be used to model predictors of detectability and minimize other confounding variation when species are relatively common, and sampling sites over extended periods reduces the variation in detection probability (O'Brien 2011). Others have suggested that ZIP models are still an option that can address model detection probability through the zero-inflation model-part and do not assume that detection probability is independent of abundance (Johnson 2008; Etterson, Niemi, and Danz 2009). However, since we did not assess detection probability at sites and for groups and species prior to modelling, we still could not differentiate preference from detectability (Jennelle, Runge, and MacKenzie 2002), which is a limitation of camera studies (Burton et al. 2015; Dénes et al. 2015; Kays et al. 2021). Future research could consider model types that consider a third model-part, as suggested by Wenger and Freeman (2008)

Three more limitations include an important limitation of our study was the use of camera traps to survey small mammals, which are often undetected due to their small size (O'Brien, Kinnaird, and Wibisono 2011; Anile and Devillard 2016). This is the reason we used track tubes as a secondary method to support conclusions for small mammals, but the results from models using track tube data were inconsistent with the model for small mammals using camera data. Future studies of small species using cameras could address this constraint by including body size as a parameter (O'Brien, Kinnaird, and Wibisono 2011). A third limitation is the use of groups comprising detections of many species. The preferences of the most abundant species heavily influenced these groups, which could have been avoided by weighting the detections from each species respective to their prevalence. A fourth limitation of our study is that some dispersion parameters suggested data were overdispersed, which could have biased our results toward type 1 errors (Harrison 2014; Blasco-Moreno et al. 2019). We could not address this bias using zero-inflated negative binomial (ZINB) models due to inconsistent zero-inflation within random effect levels; we felt it was more important to use a model that allowed correlated random effects (Min and Agresti 2005). These models may not be accurate if very low habitat suitability leads to a consistent absence of species (Kéry, Royle, and Schmid 2005), and they ignore overdispersion related to landscape heterogeneity that may relate to habitat suitability (Etterson, Niemi, and Danz 2009). We expect this source of bias to be minimal because we used BIC, a conservative approach to variable selection (Campbell and O'Hara 2021), and our simulation-based dispersion tests were not significant (Harrison et al. 2018).

Despite these limitations, our study offers some insights into using remotely-sensed information, including indices derived from it, to support planning for urban biodiversity. The index of biodiversity potential, which was based on natural area size, shape, and habitat diversity, predicted the presence of large mammals and more abundant white-tailed deer, suggesting some utility for the larger urban-dwelling species that may otherwise decline with habitat loss. Biodiversity potential appears to have less utility for small mammals. The negative correlation of biodiversity potential with the relative abundance of small mammals may have stemmed from the high prevalence of tree squirrel detections, but it could also be a matter of scale. Ecological connectivity, however, may have value for small mammals, but perhaps not for snowshoe hare and white-tailed deer (or the remaining 10 species). This could have occurred due to sensitivity, or lack thereof, to edge habitat. However, our results suggest that for ecological connectivity, a larger scale may be necessary to represent connective habitat for larger species, and a lower weight for wetland habitat may better represent the habitat needs of various species present in Edmonton. We also found similarly high variability in the other predictors (remotely-sensed and field-measured) of occurrence and relative abundance among and within these mammal groups, suggesting that simple, comprehensive metrics for predicting urban biodiversity may not exist. We found generally adverse effects of human disturbances, such as urban density, human detections on cameras, and areas designated as off-leash for dogs, corroborating the generally negative effects of urban development on biodiversity from many other studies (Rodewald and Gehrt 2014; Beninde, Veith, and Hochkirch 2015; Newbold et al. 2018; Murray et al. 2019). Nonetheless, the positive responses of some species to domestic dogs, which are typically accompanied by people, suggest that these effects are nuanced and context-specific. Taken together, these results suggest that future indices of habitat suitability should consider the type and density of surrounding vegetation and infrastructure, and the degree of use by people. Our study also contributes to the growing body of urban research exploring approaches to urban biodiversity conservation (Collins, Magle, and Gallo 2021) and supported concurrent multi-city analyses led by others (Magle et al. 2021; contributed data to 10 others in prep). Together, a growing literature on urban biodiversity may assist urban planners to mitigate the adverse effects of urban development in cities throughout the world.

## 3.5 TABLES

**Table 3.1** Number of independent detections per month for three ecological design groups (small, medium, and large terrestrial mammals [City of Edmonton 2010b, 2014a]) and 23 individual species (including “sp.” abbreviated identified to genus), and the number of sites where each was detected from 89 camera traps placed throughout Edmonton, Alberta from May 2018 to September 2021.

| Ecological design group | Species | Num. of detections | Num. of unique sites |
|---|---|---|---|
| Small mammals†§ | Red squirrel (*Tamiasciurus hudsonicus*)†§ | 1,763 | 59 |
| | Small mammal (spp.) | 352 | 44 |
| | Mouse/vole (spp.) | 94 | 9 |
| | Northern flying squirrel (*Glaucomys sabrinus*)† | 91 | 18 |
| | Least chipmunk (*Eutamias minimus*)† | 57 | 8 |
| | Squirrel (spp.) | 14 | 4 |
| | Weasel (*Mustela* spp.) | 6 | 4 |
| | Richardson’s ground squirrel (*Spermophilus richardsoni*) | 3 | 2 |
| | Total small | 2,380 | 69 |
| Medium mammals†§ | Coyote (*Canis latrans*)†§ | 7,662 | 85 |
| | Snowshoe hare (*Lepus americanus*)†§ | 2,964 | 53 |
| | Lepus (*Lepus* spp.) | 728 | 51 |
| | White-tailed jackrabbit (*Lepus townsendii*)† | 685 | 32 |
| | Porcupine (*Erethizon dorsatum*)†§ | 382 | 40 |
| | Canid (*Canis* spp.) | 100 | 34 |
| | Beaver (*Castor canadensis*)† | 31 | 8 |
| | Striped skunk (*Mephitis mephitis*)† | 30 | 2 |
| | Red fox (*Vulpes vulpes*)† | 21 | 8 |
| | Raccoon (*Procyon lotor*) | 9 | 10 |
| | Fisher (*Martes pennanti*) | 6 | 4 |
| | Badger (*Taxidea taxus*) | 4 | 2 |
| | Muskrat (*Ondatra zibethicus*) | 2 | 1 |
| | Lynx (*Lynx canadensis*) | 2 | 2 |
| | Cougar (*Puma concolor*) | 1 | 1 |
| | Total medium | 12,627 | 86 |
| Large mammals†§ | White-tailed deer (*Odocoileus virginianus*)† | 4,261 | 47 |
| | Deer (*Odocoileus* spp.) | 1,982 | 52 |
| | Mule deer (*Odocoileus hemionus*)†§ | 583 | 36 |
| | Moose (*Alces alces*)† | 162 | 16 |
| | Elk (*Cervus canadensis*) | 1 | 1 |
| | Total large | 6,989 | 60 |
| | **Total** | **21,996** | **88** |

† Compared with two ecological indices (zero-inflated Poisson mixed models; ZIP).

‡ Used in occurrence and relative abundance models (zero-inflated Poisson mixed models; ZIP).

**Table 3.2** Variables used to model terrestrial mammal occurrence and relative abundance at 89 camera traps and 47 track tube arrays placed throughout Edmonton, Alberta, via zero-inflated Poisson (ZIP) and linear mixed models (LMM), with data type, group, variable name, abbreviation, units, and data range.

| Data type | Data group | Variable name | Abbreviation | Units | Data range |
|---|---|---|---|---|---|
| Remotely sensed | Density (30/500 m buff.) | Natural forest | %Natural forest | Continuous (%) | 0 - 0.46 |
| | | Natural grass/shrub | %Natural grass/shrub | Continuous (%) | 0 - 0.42 |
| | | Modified veg.† | %Modified veg. | Continuous (%) | 0 - 0.7 |
| | | Maintained grass† | %Maint. grass | Continuous (%) | 0 - 0.21 |
| | | Building† | %Building | Continuous (%) | 0 - 0.25 |
| | | Housing‡ | %Housing | Continuous (%) | 0 - 0.62 |
| | | Road† | %Roads | Continuous (%) | 0 - 0.21 |
| | | Impervious surface‡ | %Impervious | Continuous (%) | 0.01 - 0.95 |
| | | Population density† | Popln. dens. | Continuous | 17.54 - 2560.4 |
| | Proximity (500 m dist. decay) | Building† | Prox. buildings | Continuous | 0.22 – 0.98 |
| | | Roads† | Prox. roads | Continuous | 0.25 - 0.98 |
| | | River valley/ravine system | Prox. Riv/rav | Continuous | 0 - 1 |
| | Patch | Patch size (ha)§ | Patch.size | Continuous (ha) | 0.47 - 8194.55 |
| | | Shape index§ | Shape index | Continuous | 0.08 - 18.48 |
| | | Connective habitat (100 m buff)¶ | Connective hab.ar | Continuous (ha) | 0 - 16.2 |
| | | Habitat diversity | Hab.diversity | Continuous | 0 - 8 |
| | Site-specific | Connected site¶ | Site.Connected | Binary | 0/1 |
| | | Natural/modified | Nat./mod. | Binary | 0/1 |
| | | Off-leash area | Off-leash area | Binary | 0/1 |
| | | Site vegetation category | Veg. type | Categorical | - |
| Field surveys | Site-specific (avg. within 30 m buff.) | Forest structure | Site.Forest structure | Continuous | 0 - 4 |
| | | Grass structure | Site.Grass structure | Continuous | 0 - 4 |
| | | Anthropogenic disturbance | Site.Anthro dist. | Continuous | 0 - 6 |
| | | Human trails | Site#Human.trail | Continuous (Count) | 0 - 4 |
| | | Game trails | Site.#Game.trail | Continuous (Count) | 0 - 7 |
| | Site-specific (avg of 4 cover plots) | Canopy cover | Site.%Canopy | Continuous (%) | 0 - 0.98 |
| | | Tree cover | Site.%Treed | Continuous (%) | 0.21 |
| | | Shrub cover | Site.%Shrub | Continuous (%) | 0 - 0.7 |
| | | Grass/forb cover | Site.%Grass/forbe | Continuous (%) | 0 - 1 |
| | | Coarse woody debris cover | Site.%CWD | Continuous (%) | 0 - 0.41 |
| | | Bare ground cover | Site.%Bare | Continuous (%) | 0 - 0.44 |
| | | Open water cover | Site.%Water | Continuous (%) | 0 - 0.54 |
| | | Vegetative diversity | Site.Veg.diversity | Continuous (Count) | 0 - 7.5 |
| Detection | Detection | Domestic dog abundance | Domestic dog | Continuous (Count) | 0 - 70 |
| | | Human abundance | Human | Continuous (Count) | 0 - 2728 |
| | | Predator relative abundance | Pred. abundance | Continuous (Count) | 0 - 41 |
| | | Prey relative abundance | Prey abundance (CT) | Continuous (Count) | 0 - 38 |
| | | | Prey abundance (TT) | Continuous (Prop.) | 0 - 0.08 |
| Known/ derived | Imperfect detection | Season (winter)# | Season | Binary | - |
| | | Lure | Lure | Continuous (Prop.) | 0 - 1 |
| | | Effective detection distance | Effective.detect.dist. | Continuous | 5.48 - 11.02 |

† Evaluated in "urban" PCA metrics.

‡ Included in "urban" PCA metric for analyses.

§ Evaluated in models using camera trap data (ZIP mixed), but not track tube data (LMMs).

¶ "Connective habitat" used for camera trap data; "connected site" as a scale-appropriate proxy for track tube data.

# Seasons were defined as winter: Nov. – Mar and summer: Apr. – Oct.

**Table 3.3** Most parsimonious top zero-inflated Poisson (ZIP) mixed regression models (within 2 ΔBIC) comparing the occurrence and relative abundance of two ecological design groups (City of Edmonton 2010b, 2014a) and three individual species from 69 camera traps placed in natural areas throughout Edmonton, Alberta, to two ecological indices used by the City of Edmonton (2014a) along with season.

| | | Most parsimonious top model(s) | | | | | | | Global model | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species/ group | Top model | BIC | LL | df | ĉ† | *p*‡ | $R^2_{Cond}$ | $R^2_{Marg}$ | ĉ | *p* | $R^2_{Cond}$ | $R^2_{Marg}$ |
| Small EDG (camera trap) | ψ§(.), λ¶(BP + EC + Season [winter]# + BP*Season + EC*Season) | 4000.7 | -1967.4 | 9 | 0.50 | 0.460 | 0.50 | 0.05 | 0.31 | 0.500 | 0.53 | 0.07 |
| Snowshoe hare | ψ(Season), λ†(BP + Season + EC*Season) | 4652.0 | -2296.7 | 9 | 1.90 | 0.112 | 0.60 | 0.09 | 1.94 | 0.116 | 0.56 | 0.09 |
| Coyote | ψ(Season), λ(BP + EC + Season + BP*EC + BP*Season | 9738.8 | -4832.8 | 10 | 1.71 | 0.080 | 0.60 | 0.09 | 1.52 | 0.168 | 0.63 | 0.08 |
| Large EDG | ψ(BP + Season), λ(.) | 7351.7 | -3653.9 | 6 | 1.04 | 0.212 | 0.70 | 0.00 | 1.21 | 0.164 | 0.67 | 0.18 |
| | ψ(Season), λ(BP) | 7352.6 | -3654.3 | 6 | 1.71 | 0.104 | 0.66 | 0.11 | | | | |
| White-tailed deer | ψ(Season), λ(BP + EC + Season + BP*EC + EC*Season) | 5568.6 | -2747.7 | 10 | 0.02 | 0.668 | 0.58 | 0.16 | 0.01 | 0.712 | 0.61 | 0.15 |

*Notes:* Shown are Bayesian Information Criterion (BIC; top as within 2 ΔBIC), log-likelihood (LL), degrees of freedom (df), dispersion parameter (ĉ) of global and best-fit models with associated p-values, and conditional ($R^2_{Cond}$) and marginal ($R^2_{Marg}$) Nakagawa's $R^2$ for mixed models. Abbreviations: BP, biodiversity potential; EC, ecological connectivity. *n* = 1,520 for all species groups and individual species.

† Dispersion parameters from comparisons of observed to simulated residuals.

‡ Test statistics from simulation-based tests for overdispersion.

§ ψ = probability of occurrence (ψ; logit link) in zero-inflation models.

¶ λ = relative abundance modelled as counts conditional on occurrence (λ; log link) in zero-inflation models.

# Seasons were defined as winter: Nov. – Mar and summer: Apr. – Oct.

**Table 3.4** Estimated coefficients (γ/β) with lower and upper (LCL and UCL) 95% confidence limits for the most parsimonious top zero-inflated Poisson (ZIP) mixed models comparing the occurrence and relative abundance of two ecological design groups (City of Edmonton 2010b, 2014a) and three individual species from 69 camera traps placed in natural areas throughout Edmonton, Alberta to two ecological indices used by the City of Edmonton (2014a) along with season.

| Species | Measure | Parameter | γ†/β‡ | 95% LCL | 95% UCL | OR/ RR | OR 95% LCL | OR 95% UCL | *p* |
|---|---|---|---|---|---|---|---|---|---|
| Small EDG (camera trap) | Occurrence (ψ) | zi(Intercept)*** | **3.073** | 3.471 | 2.675 | 0.05 | 0.03 | 0.07 | <0.001 |
| | Relative abundance (λ) | cond(Intercept)*** | **-3.364** | -3.847 | -2.880 | 0.03 | 0.02 | 0.06 | <0.001 |
| | | Biodiversity potential* | **-0.537** | -0.997 | -0.076 | 0.58 | 0.37 | 0.93 | 0.023 |
| | | Ecological connectivity* | **0.429** | 0.021 | 0.836 | 1.54 | 1.02 | 2.31 | 0.039 |
| | | Season (winter)§*** | **0.327** | 0.209 | 0.446 | 1.39 | 1.23 | 1.56 | <0.001 |
| | | Biodiversity potential x Season*** | **0.453** | 0.309 | 0.597 | 1.57 | 1.36 | 1.82 | <0.001 |
| | | Ecological connectivity x Season*** | **-0.368** | -0.511 | -0.225 | 0.69 | 0.60 | 0.80 | <0.001 |
| Snowshoe hare | Occurrence (ψ) | zi(Intercept)*** | **1.627** | 2.253 | 1.000 | 0.20 | 0.11 | 0.37 | <0.001 |
| | | Season** | **1.390** | 1.770 | 1.009 | 0.25 | 0.17 | 0.36 | <0.001 |
| | Relative abundance (λ) | cond(Intercept)*** | **-3.076** | -3.466 | -2.687 | 0.05 | 0.03 | 0.07 | <0.001 |
| | | Ecological connectivity* | **-0.457** | -0.855 | -0.060 | 0.63 | 0.43 | 0.94 | 0.024 |
| | | Season*** | **0.641** | 0.559 | 0.723 | 1.90 | 1.75 | 2.06 | <0.001 |
| | | Ecological connectivity x Season*** | **0.359** | 0.261 | 0.457 | 1.43 | 1.30 | 1.58 | <0.001 |
| Coyote | Occurrence (ψ) | zi(Intercept)*** | **4.632** | 4.238 | 5.026 | 0.01 | 0.01 | 0.01 | <0.001 |
| | | Season*** | **0.761** | 0.438 | 1.085 | 0.47 | 0.34 | 0.65 | <0.001 |
| | Relative abundance (λ) | zi(Intercept)*** | **-2.060** | -2.304 | -1.816 | 0.13 | 0.10 | 0.16 | <0.001 |
| | | Biodiversity potential | -0.112 | -0.351 | 0.127 | 0.89 | 0.70 | 1.14 | 0.358 |
| | | Ecological connectivity | 0.221 | -0.022 | 0.464 | 1.25 | 0.98 | 1.59 | 0.074 |
| | | Season*** | **0.523** | 0.472 | 0.573 | 1.69 | 1.60 | 1.77 | <0.001 |
| | | Biodiversity potential x Ecological connectivity* | **-0.290** | -0.548 | -0.032 | 0.75 | 0.58 | 0.97 | 0.027 |
| | | Biodiversity potential x Season*** | **-0.144** | -0.199 | -0.088 | 0.87 | 0.82 | 0.92 | <0.001 |
| Large EDG | Occurrence (ψ) | zi(Intercept)*** | **3.622** | 4.514 | 2.729 | 0.03 | 0.01 | 0.07 | <0.001 |
| | | Biodiversity potential** | **1.311** | 2.099 | 0.523 | 0.27 | 0.12 | 0.59 | 0.001 |
| | | Season*** | **-1.080** | -0.678 | -1.482 | 2.94 | 1.97 | 4.40 | <0.001 |
| | Relative abundance (λ) | cond(Intercept)*** | **-2.296** | -2.732 | -1.861 | 0.10 | 0.07 | 0.16 | <0.001 |

|  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|
| White-tailed deer | Occurrence (ψ) | zi(Intercept)*** | **5.633** | 8.478 | 2.788 | 0.00 | 0.00 | 0.06 | <0.001 |
|  |  | Season*** | **-1.014** | -0.789 | -1.239 | 2.76 | 2.20 | 3.45 | <0.001 |
|  | Relative abundance (λ) | cond(Intercept)*** | **-4.993** | -5.715 | -4.271 | 0.01 | 0.00 | 0.01 | <0.001 |
|  |  | Biodiversity potential*** | **1.542** | 0.820 | 2.264 | 4.68 | 2.27 | 9.62 | <0.001 |
|  |  | Ecological connectivity* | **-0.857** | -1.594 | -0.120 | 0.42 | 0.20 | 0.89 | 0.023 |
|  |  | Season*** | **0.249** | 0.170 | 0.328 | 1.28 | 1.19 | 1.39 | <0.001 |
|  |  | Biodiversity potential x Ecological connectivity* | **0.843** | 0.074 | 1.612 | 2.32 | 1.08 | 5.01 | 0.032 |
|  |  | Ecological connectivity x Season*** | **0.145** | 0.080 | 0.210 | 1.16 | 1.08 | 1.23 | <0.001 |

*Notes:* Shown are odds ratios (OR) from zero-inflation model-part / risk ratios (RR) from conditional model-part, lower and upper (LCL and UCL) 95% confidence limits. The level of significance ($p < 0.05$) is indicated with asterisks for parameters and bolded coefficients (α/β). $n$ = 1,520 for all species groups and individual species.

† γ = Inversely transformed coefficients from zero-inflation models (probability of occurrence; ψ; logit link); β = coefficients from conditional models (relative abundance; λ; log link).

§ Seasons defined as winter: Nov. – Mar and summer: Apr. – Oct.

**Table 3.5** Most parsimonious top models from zero-inflated Poisson (ZIP) mixed regression models and linear mixed models (LMMs) evaluating predictors of the occurrence and relative abundance of three ecological design groups City of Edmonton (2010, 2014a) and five individual species from 89 camera traps and 48 track tube arrays in Edmonton, Alberta.

| | | Most parsimonious top model | | | | | | | Global model | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species/ group | Top model | BIC/ AICc† | LL | df | ĉ‡ | *p*§ | $R^2_{Cond}$ | $R^2_{Marg}$ | ĉ | *p* | $R^2_{Cond}$ | $R^2_{Marg}$ |
| Small EDG (track tube)¶ | λ#(Site.Connected + Site.%Treed + Site.%CWD) | -371.6 | 192.1 | 6 | - | - | 0.34 | 0.2 | - | - | - | - |
| Small EDG (camera trap) | ψ\|\|(Site.%Grass/forbe + Site.%Shrub + Domestic dog), λ(%Modified veg. + Human + Domestic dog + Season [winter]††) | 4779.4 | -2348.5 | 11 | 0.22 | 0.536 | 0.56 | 0.09 | 0.13 | 0.636 | 0.54 | 0.24 |
| Red squirrel | ψ(Site.%Grass/forbe + Site.%Shrub + Domestic dog), λ(%Modified veg. + Human + Domestic dog + Season) | 3618.6 | -1775.6 | 9 | 0.01 | 0.624 | 0.46 | 0.04 | 0.35 | 0.460 | 0.40 | 0.31 |
| Medium EDG | ψ(Site.% Treed + Domestic dog + Season + Lure), λ(Domestic dog + Season + Lure) | 14232.5 | -7075.1 | 11 | 0.22 | 0.536 | 0.66 | 0.08 | 1.79 | 0.152 | 1 | 0.39 |
| Snowshoe hare | ψ(%Maint. grass + Season), λ(Pred. abundance + Season) | 4803.1 | -2371.6 | 8 | 0.87 | 0.260 | 0.59 | 0.03 | 2.48 | 0.144 | 0.67 | 0.54 |
| Porcupine | ψ(%Urban + Season), λ(.) | 1516.1 | -731.9 | 7 | 1.24 | 0.196 | 0.43 | 0.00 | 0.56 | 0.888 | - | 0.92 |
| Coyote | ψ(%Urban + Prey abundance (CT) + Season + Lure), λ(Nat./mod. + Prey abundance (CT) + Domestic dog + Season + Lure) | 10600.9 | -5251.8 | 13 | 2.05 | 0.064 | 0.63 | 0.11 | 1.25 | 0.432 | 0.63 | 0.24 |
| Large EDG | ψ(%Natural forest + %Modified veg. + Human + Season), λ(Off-leash area) | 7758.0 | -3845.3 | 9 | 0.22 | 0.536 | 0.75 | 0.42 | 0.88 | 0.496 | 0.19 | 0.17 |
| Mule deer | ψ(%Modified veg. + Season), λ(Site.Forest structure + %Urban) | 1542.2 | -737.4 | 9 | 1.12 | 0.280 | 0.37 | 0.21 | 0.74 | 0.624 | - | 0.88 |

*Notes:* Shown are Bayesian Information Criterion (BIC; top as within 2 ΔBIC) or Akaike's Information Criterion for small sample sizes (AICc; top as within 2 ΔAICc), log-likelihood (LL), degrees of freedom (df), dispersion parameter (ĉ) of global and best-fit models and associated *p*-values, and conditional ($R^2_{Cond}$) and marginal ($R^2_{Marg}$) Nakagawa's $R^2$ for mixed models.

† BIC was used in ZIP mixed models for camera trap data; AICc was used for LMMs for data from track tubes.

‡ Dispersion parameters from comparisons of observed to simulated residuals.

§ Test statistics from simulation-based tests for overdispersion.

¶ LMMs used for data from track tubes (*n* = 130); ZIP mixed models used elsewhere (*n* = 1,783).

# λ = relative abundance (λ) modelled from proportional relative abundance in LMMs (track tubes) or as counts conditional on occurrence in ZIP mixed models (log link; camera traps).

|| ψ = probability of occurrence (ψ; logit link) modelled as zero-inflation and inversely transformed.

†† Seasons were defined as winter: Nov. – Mar and summer: Apr. – Oct.

**Table 3.6** Estimated coefficients (γ/β) and lower and upper (LCL and UCL) 95% confidence limits from the most parsimonious top zero-inflated Poisson mixed (ZIP) and linear mixed models (LMMs) evaluating predictors of occurrence and relative abundance of three ecological design groups (City of Edmonton 2010b, 2014a) and five mammal species from 89 camera traps and 48 track tube arrays in Edmonton, Alberta.

| Species | Measure | Parameter | γ/β† | 95% LCL | 95% UCL | OR/ RR | OR 95% LCL | OR 95% UCL | *p* |
|---|---|---|---|---|---|---|---|---|---|
| Small EDG (track tubes)‡ | Relative abundance (λ)§ | (Intercept)*** | **0.127** | 0.113 | 0.141 | - | - | - | <0.001 |
| | | Connected habitat** | **0.038** | 0.013 | 0.062 | - | - | - | 0.003 |
| | | Site.%Treed* | **0.012** | 0.001 | 0.023 | - | - | - | 0.040 |
| | | Site.%CWD* | **0.014** | 0.002 | 0.026 | - | - | - | 0.026 |
| Small EDG (camera traps) | Occurrence (ψ) | zi(Intercept)*** | **3.222** | 3.525 | 2.918 | 25.07 | 1.19 | 1.40 | <0.001 |
| | | Site.%Grass/forbe* | **-0.441** | -0.105 | -0.776 | 0.64 | 1.19 | 1.45 | 0.010 |
| | | Site.%Shrub** | **-0.419** | -0.130 | -0.709 | 0.66 | 0.09 | 0.26 | 0.005 |
| | | Domestic dog | 0.381 | 0.810 | -0.048 | 1.46 | 2.00 | 4.89 | 0.082 |
| | Relative abundance (λ) | cond(Intercept)*** | **-3.622** | -4.058 | -3.185 | 0.03 | 0.31 | 0.64 | <0.001 |
| | | % Modified veg.** | **-0.531** | -0.930 | -0.131 | 0.59 | 0.02 | 0.06 | 0.009 |
| | | Human*** | **-0.402** | -0.571 | -0.233 | 0.67 | 0.60 | 0.89 | <0.001 |
| | | Domestic dog*** | **0.255** | 0.175 | 0.335 | 1.29 | 1.23 | 1.46 | <0.001 |
| | | Season (winter)#*** | **0.274** | 0.178 | 0.370 | 1.31 | 1.24 | 1.55 | <0.001 |
| Red squirrel | Occurrence (ψ) | zi(Intercept)*** | **1.865** | 2.383 | 1.348 | 6.46 | 0.03 | 0.05 | <0.001 |
| | | % Modified veg.*** | **-1.141** | -0.694 | -1.588 | 0.32 | 1.11 | 2.17 | <0.001 |
| | | Season*** | **0.817** | 1.183 | 0.451 | 2.26 | 1.14 | 2.03 | <0.001 |
| | Relative abundance (λ) | cond(Intercept)*** | **-3.393** | -3.926 | -2.860 | 0.03 | 0.44 | 1.05 | <0.001 |
| | | Human** | **-0.317** | -0.515 | -0.119 | 0.73 | 0.02 | 0.04 | 0.002 |
| | | Domestic dog*** | **0.294** | 0.206 | 0.381 | 1.34 | 0.39 | 0.88 | <0.001 |
| | | Season*** | **0.326** | 0.213 | 0.439 | 1.39 | 0.56 | 0.79 | <0.001 |
| Medium EDG | Occurrence (ψ) | cond(Intercept)*** | **5.148** | 5.633 | 4.663 | 172.10 | 0.47 | 0.88 | <0.001 |
| | | Site.% Treed* | **-0.453** | -0.080 | -0.827 | 0.64 | 0.20 | 0.61 | 0.017 |
| | | Domestic dog** | **1.280** | 2.109 | 0.450 | 3.60 | 0.42 | 0.80 | 0.002 |
| | | Season*** | **1.121** | 1.468 | 0.773 | 3.07 | 0.68 | 0.96 | <0.001 |
| | | Lure** | **0.262** | 0.447 | 0.078 | 1.30 | 0.03 | 0.07 | 0.005 |
| | Relative abundance (λ) | zi(Intercept)*** | **-1.786** | -1.967 | -1.606 | 0.17 | 1.58 | 4.63 | <0.001 |
| | | Domestic dog*** | **0.100** | 0.078 | 0.123 | 1.11 | 1.11 | 1.15 | <0.001 |
| | | Season*** | **0.534** | 0.497 | 0.571 | 1.71 | 1.05 | 1.13 | <0.001 |
| | | Lure*** | **0.125** | 0.105 | 0.145 | 1.13 | 1.57 | 1.74 | <0.001 |
| Snowshoe hare | Occurrence (ψ) | zi(Intercept)*** | **1.409** | 2.025 | 0.792 | 4.09 | 0.00 | 0.01 | <0.001 |
| | | % Maint. grass*** | **-0.988** | -0.466 | -1.510 | 0.37 | 1.08 | 2.29 | <0.001 |
| | | Season*** | **1.543** | 1.915 | 1.170 | 4.68 | 0.12 | 0.64 | <0.001 |
| | Relative abundance (λ) | cond(Intercept)*** | **-3.198** | -3.699 | -2.697 | 0.04 | 0.23 | 0.46 | <0.001 |
| | | Pred. abundance*** | **0.105** | 0.087 | 0. 4 | 1.11 | 0.64 | 0.92 | <0.001 |
| | | Season*** | **0.451** | 0.367 | 0.535 | 1.57 | 0.14 | 0.20 | <0.001 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Porcupine | Occurrence (ψ) | zi(Intercept)*** | **2.430** | 3.010 | 1.851 | 11.36 | 1.08 | 1.13 | <0.001 |
| | | % Urban*** | **-1.013** | -0.571 | -1.454 | 0.36 | 1.64 | 1.77 | <0.001 |
| | | Season*** | **-1.216** | -0.726 | -1.706 | 0.30 | 1.11 | 1.16 | <0.001 |
| | Relative abundance (λ) | cond(Intercept)*** | **-4.687** | -5.421 | -3.953 | 0.01 | 0.13 | 0.45 | <0.001 |
| Coyote | Occurrence (ψ) | zi(Intercept)*** | **4.769** | 5.126 | 4.413 | 117.81 | 1.59 | 4.53 | <0.001 |
| | | % Urban** | **-0.439** | -0.129 | -0.748 | 0.64 | 0.15 | 0.31 | 0.005 |
| | | Prey abundance*** | **1.052** | 1.616 | 0.489 | 2.86 | 0.02 | 0.07 | <0.001 |
| | | Season*** | **0.550** | 0.875 | 0.225 | 1.73 | 1.09 | 1.13 | 0.001 |
| | | Lure* | **0.216** | 0.393 | 0.038 | 1.24 | 1.44 | 1.71 | 0.017 |
| | Relative abundance (λ) | cond(Intercept)*** | **-3.190** | -3.678 | -2.702 | 0.04 | 0.05 | 0.16 | <0.001 |
| | | Natural *vs.* modified*** | **0.994** | 0.457 | 1.532 | 2.70 | 0.23 | 0.56 | <0.001 |
| | | Prey abundance*** | **0.124** | 0.106 | 0.142 | 1.13 | 2.07 | 5.51 | <0.001 |
| | | Domestic dog*** | **0.083** | 0.046 | 0.121 | 1.09 | 0.00 | 0.02 | <0.001 |
| | | Season*** | **0.503** | 0.454 | 0.552 | 1.65 | 0.01 | 0.01 | <0.001 |
| Large EDG | Occurrence (ψ) | zi(Intercept)*** | **3.574** | 4.143 | 3.004 | 35.64 | 0.09 | 0.19 | <0.001 |
| | | % Natural forest*** | **1.518** | 2.073 | 0.963 | 4.56 | 0.02 | 0.14 | <0.001 |
| | | % Modified veg.*** | **1.150** | 1.663 | 0.637 | 3.16 | 0.06 | 0.52 | <0.001 |
| | | Human** | **-1.517** | -0.596 | -2.438 | 0.22 | 0.32 | 0.98 | 0.001 |
| | | Season*** | **-0.956** | -0.579 | -1.333 | 0.38 | 1.56 | 4.17 | <0.001 |
| | Relative abundance (λ) | cond(Intercept)*** | **-2.049** | -2.425 | -1.673 | 0.13 | 0.00 | 0.03 | <0.001 |
| | | Off-leash area*** | **-2.919** | -3.862 | -1.976 | 0.05 | 0.24 | 0.66 | <0.001 |
| Mule deer | Occurrence (ψ) | zi(Intercept)** | **1.733** | 2.806 | 0.659 | 5.65 | 1.13 | 1.19 | 0.002 |
| | | % Modified veg.* | **0.572** | 1.125 | 0.019 | 1.77 | 0.02 | 0.05 | 0.043 |
| | | Season*** | **-0.935** | -0.442 | -1.428 | 0.39 | 0.13 | 0.38 | <0.001 |
| | Relative abundance (λ) | cond(Intercept)*** | **-4.511** | -5.595 | -3.427 | 0.01 | 0.19 | 0.53 | <0.001 |
| | | Site. Forest structure*** | **-0.915** | -1.414 | -0.416 | 0.40 | 1.81 | 11.44 | <0.001 |
| | | % Urban*** | **-1.112** | -1.658 | -0.566 | 0.33 | 1.78 | 3.79 | <0.001 |

*Notes:* Shown are odds ratios (OR) from zero-inflation model-part / risk ratios (RR) from conditional model-part, lower and upper (LCL and UCL) 95% confidence limits. The level of significance ($p < 0.05$) is indicated with asterisks for parameters and bolded coefficients (α/β).

† γ = Inversely transformed coefficients from zero-inflation models (probability of occurrence; logit link; ψ); β = coefficients from conditional models (relative abundance; log link; λ).

‡ LMMs used for data from track tubes ($n$ = 130); ZIP mixed models used elsewhere ($n$ = 1,783).

§ Seasons defined as winter: Nov. – Mar and summer: Apr. – Oct.

## 3.6 FIGURES

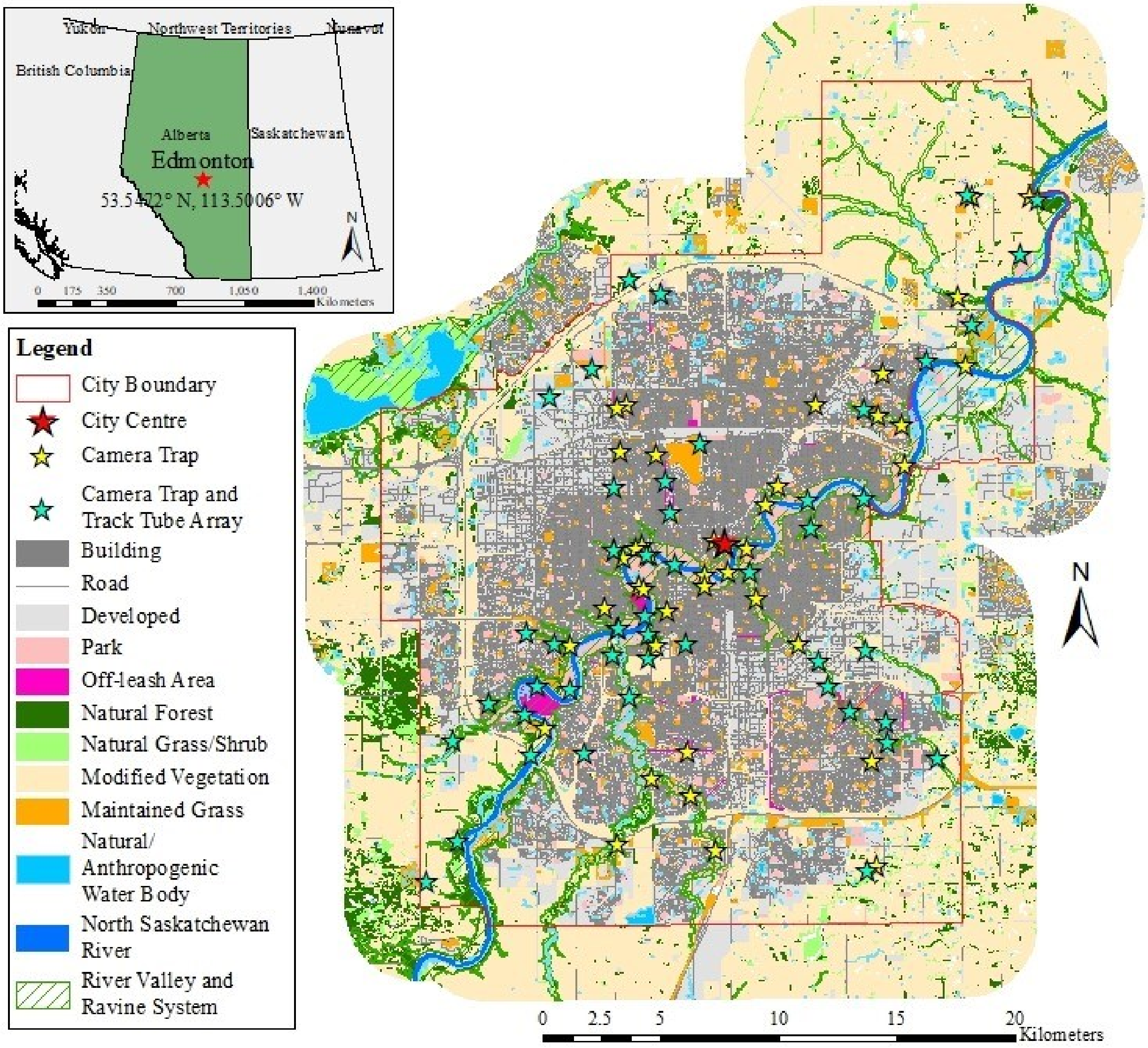

**Fig. 3.1** Study area in Edmonton, Alberta and 89 site locations (89 camera traps; 47 track tube arrays) deployed between May 2018 and September 2018. Where overlap of features occurs (e.g., parks occuring in vegetated areas), rarer features are shown as the most forward layers. The inset map shows the study area location in Alberta, Canada.

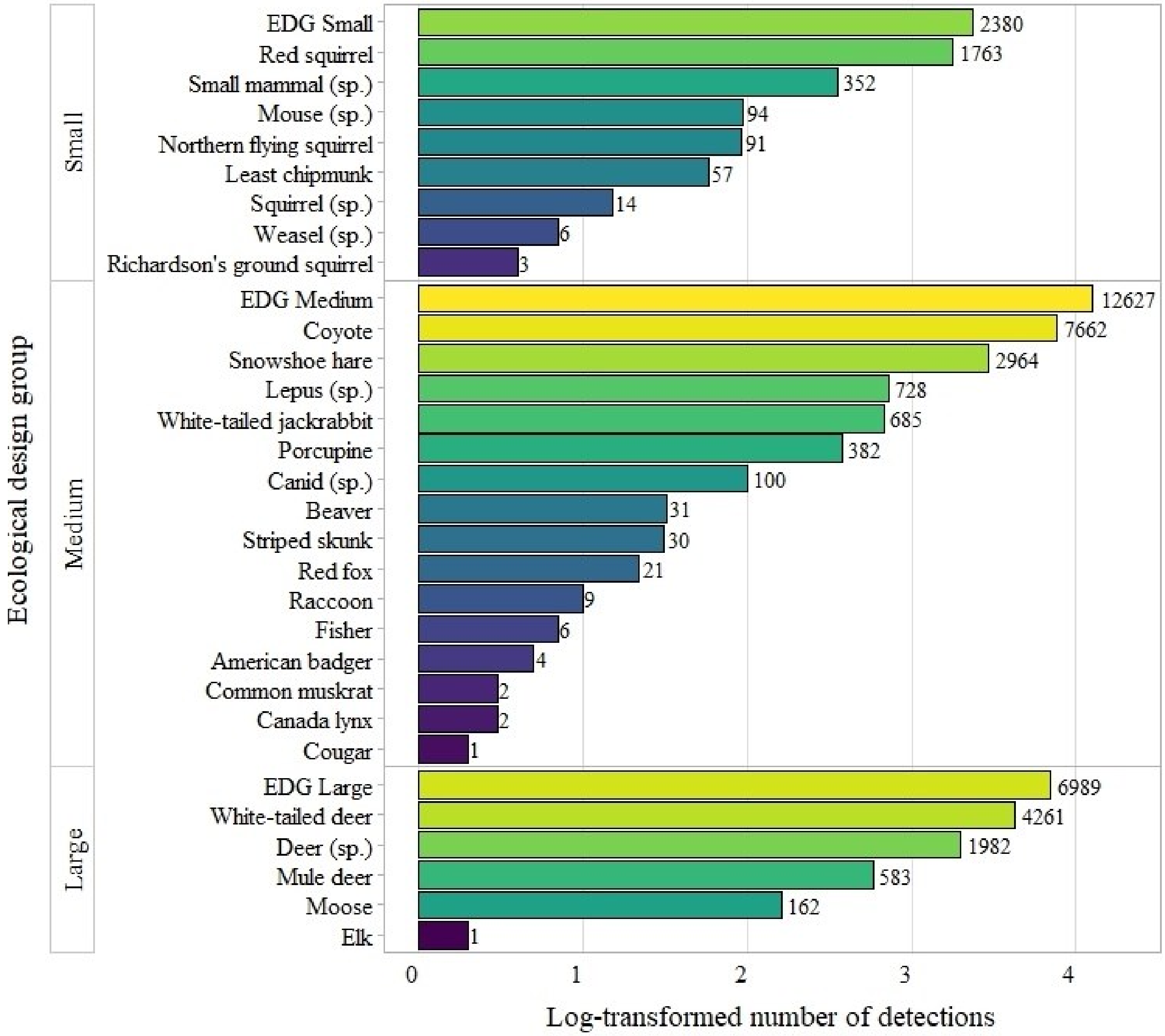

**Fig. 3.2** Log-transformed number of detections for three ecological design groups (small, medium, and large terrestrial mammals; [City of Edmonton 2010b, 2014a]) and 23 individual species (including "sp." abbreviated identified to genus) from 89 camera traps placed in natural and semi-natural parks in Edmonton, Alberta from May 2018 to September 2021. The purpose of the colouration is to highlight the variation in detections.

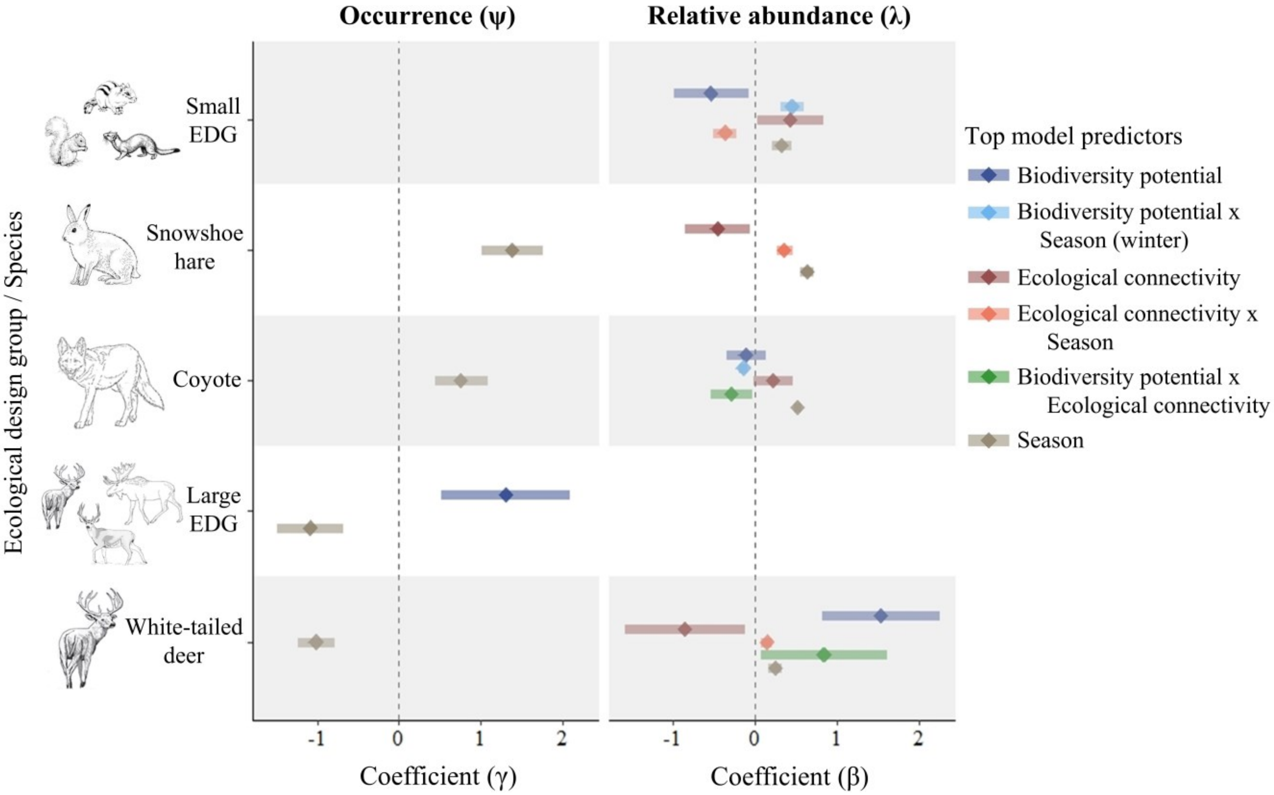

**Fig. 3.3** Model coefficients from zero-inflated Poisson (ZIP) mixed models comparing the occurrence and relative abundance of two ecological design groups (EDG [City of Edmonton 2010b, 2014a]) and three species from 69 camera traps (n = 1,520) placed in natural areas in Edmonton, Alberta to two ecological indices used by the City of Edmonton (2014a) along with season (winter: Nov. - Mar and summer: Apr. - Oct.), with top model predictor variables, corresponding coefficients, and 95% confidence intervals.

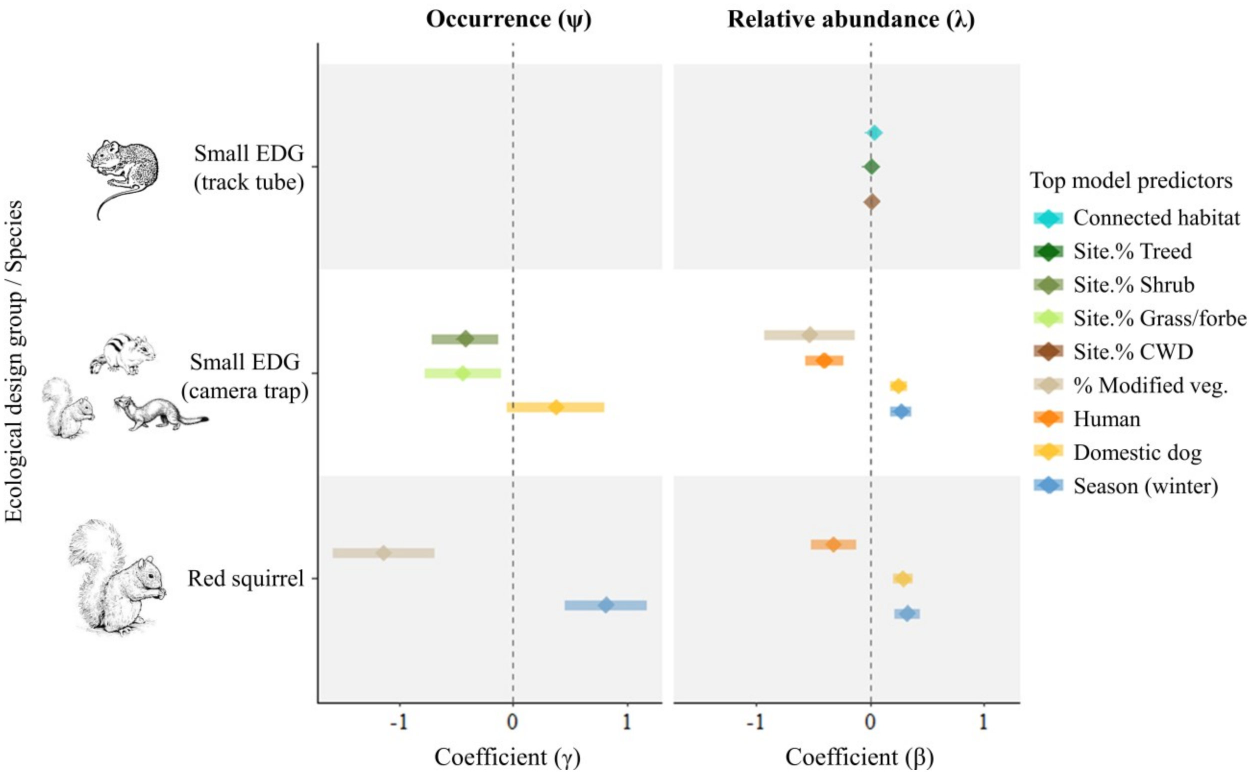

**Fig. 3.4** Model coefficients for zero-inflated Poisson (ZIP) mixed and linear mixed models (LMM) that were used to evaluate the predictors of the occurrence and relative abundance of red squirrel and the small mammal ecological design groups (EDG [City of Edmonton 2010b, 2014a]) from 89 camera traps (n = 1,783) and 48 track tube arrays (n = 130) placed in natural and semi-natural parks in Edmonton, Alberta, with top model predictor variables, corresponding coefficients, and 95% confidence intervals.

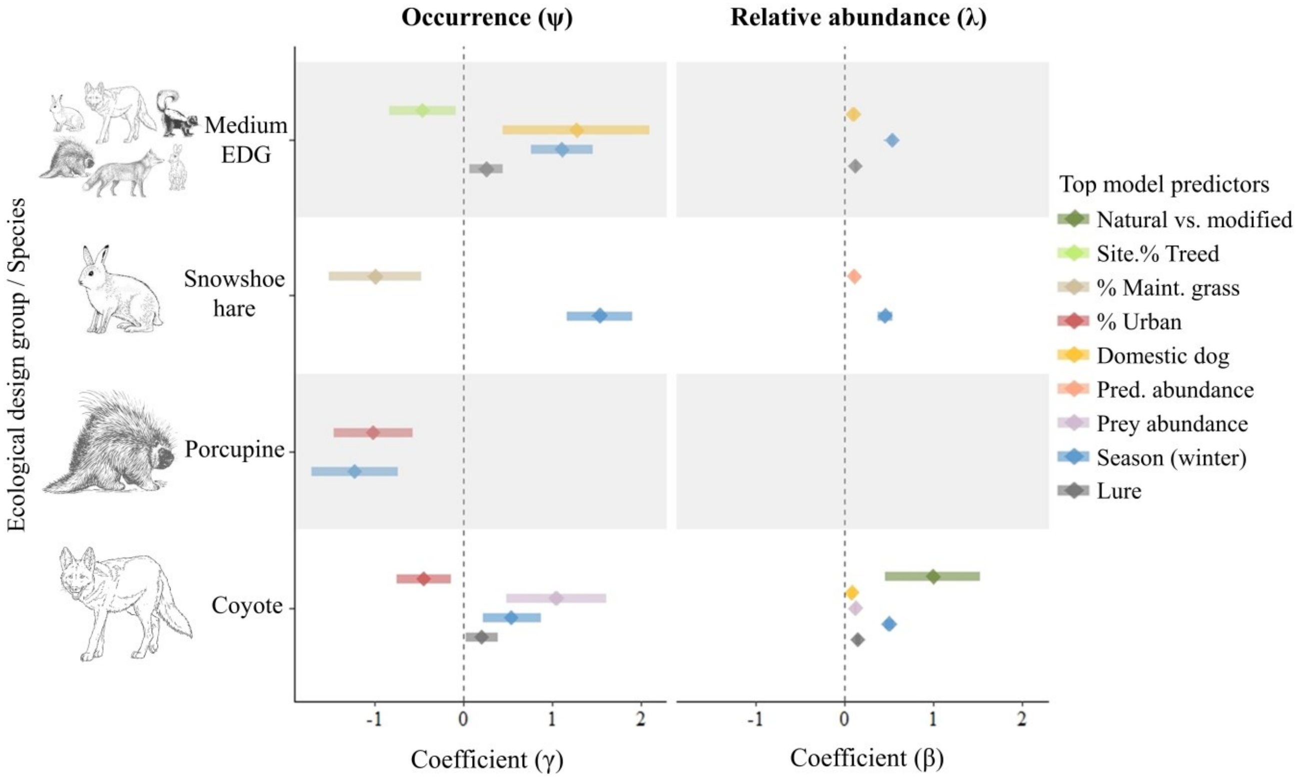

**Fig. 3.5** Model coefficients for zero-inflated Poisson (ZIP) mixed models that were used to evaluate the predictors of the occurrence and relative abundance of coyote, porcupine, snowshoe hare, and the medium mammal ecological design groups (EDG [City of Edmonton 2010b, 2014a]) from 89 camera traps (n = 1,783) placed in natural areas in Edmonton, Alberta, with top model predictor variables, corresponding coefficients, and 95% confidence intervals.

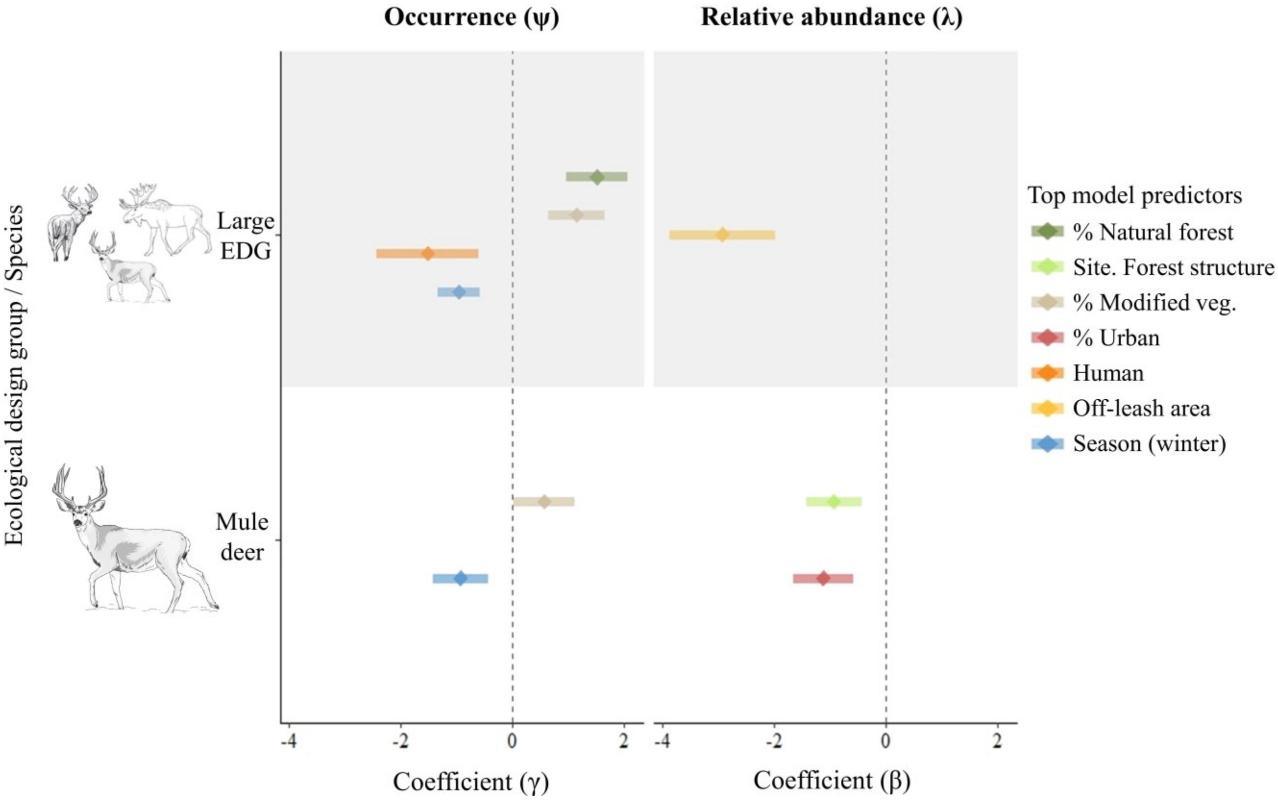

**Fig. 3.6** Model coefficients for zero-inflated Poisson (ZIP) mixed models that were used to evaluate the predictors of the occurrence and relative abundance of mule deer and the large mammal ecological design group (EDG [City of Edmonton 2010b, 2014a]) from 89 camera traps ($n$ = 1,783) placed in natural areas in Edmonton, Alberta, with top model predictor variables, corresponding coefficients, and 95% confidence intervals.

## **CHAPTER 4 -** Conclusion

Urbanization reduces, fragments, and degrades natural areas (Grimm et al. 2008), resulting in habitat loss, diminished natural connectivity, and ultimately species loss and homogenization in the remaining natural areas of cities (McKinney 2006; Beninde, Veith, and Hochkirch 2015; Newbold et al. 2018). Rapid urban growth and sprawl increase the challenge of conserving adequate connectivity and habitat quality to support biodiversity in many cities (Angel et al. 2011; Pickett et al. 2011). Mitigating the loss of urban biodiversity requires conserving adequate habitat connectivity and quality to accommodate the needs of diverse species, which urban planners sometimes predict using GIS-based estimates of habitat value.

In Edmonton, AB, urban ecological planners use two methods to consider wildlife habitat in land use planning to conserve biodiversity and mitigate adverse effects of development (City of Edmonton 2020b). The first of these tools was a commissioned estimate of connectivity created as two seasonal circuit-based simulation models using the movement of coyotes as a representative terrestrial mammal (City of Edmonton 2017b). Two other indices, biodiversity potential and ecological connectivity, were developed to predict the ecological value of natural areas based on characteristics of natural areas (City of Edmonton 2014a) and remain in use to support planning in the vicinity of natural areas.

In my thesis, I addressed two broad goals; 1) I advanced information about the predictors of habitat selection of urban coyotes and of the occurrence and relative abundance of three groups of terrestrial mammals and individual species, and 2) I supported the use of connectivity models and ecological indices used by ecological planners in Edmonton by testing their fit with measures of urban wildlife habitat use, occurrence, and relative abundance obtained from detection data in Edmonton, Alberta. In each of the two data chapters, I combined these two goals by using empirical data from animal detections to test the predictions of models or indices used by the City of Edmonton (hereafter City) as planning tools to protect biodiversity.

In Chapter 2, I used data from GPS collars fitted urban coyotes to a) understand how sarcoptic mange, season, and remotely-sensed metrics influenced habitat selection of urban coyotes, (b) generate a habitat suitability index (HSI) for areas throughout the City, and c) compare the HSI values to the predicted permeability estimates that were used to create the circuit-based models previously developed by the City (City of Edmonton 2016b, 2017b). To achieve these objectives, I obtained selection estimates for 10 broad categories of land cover as log-ratios from seasonal compositional analyses (winter and summer), and compared these feature-specific estimates to the expert-derived permeability ratings used to parameterize the permeability layers used in the circuit-based models. I also evaluated habitat selection by coyotes with predictor variables of mange, season, and 13 finer-scale land cover features by constructing a RSF model using GPS collar data, and used this model to derive HSI values, which I compared with cumulative landscape permeability values used to create the circuit-based models.

The results from the habitat selection models in Chapter 2 suggested that resource use by coyotes was driven by natural land use types and human development, with the largest responses to natural (positive association) and developed areas (negative association) relative to land covers of natural grass/shrub, modified forest or grass/shrub, maintained grass, residential, roads, and buildings. From compositional analyses, habitat use by coyotes was similar between seasons, but in winter, they were more likely to use natural forests, natural shrubs, modified grass/shrubs, and residential areas. The RSF model revealed that coyotes selected natural areas most strongly, followed by avoidance of developed areas, but they also selected steeper slopes and areas closer to modified forests, modified grass/shrubland, and residential areas. These results supported work by others showing that urban coyotes preferred areas with more natural land covers (Poessel, Breck, and Gese 2016; Franckowiak, Perdicas, and Smith 2019). Coyotes may be attracted to forests (Atwood, Weeks, and Gehring 2004; Greenspan, Nielsen, and Cassel 2018) to access prey and cover (Gosselink et al. 2003; Richer et al. 2016). Additional to the preference for modified grass/shrubland, coyotes were attracted to residential areas, perhaps because of the congregated anthropogenic food subsidies (Murray and St. Clair 2017). However, coyotes used modified forests and grass/shrubland more than developed types. Modified areas with little development may provide natural prey (Morey, Gese, and Ghert 2007; Ofori et al. 2018), a separation from humans (e.g., golf courses with relatively lower activity [Gallo et al. 2017; Wurth, Ellington, and Gehrt 2020]), and facilitate movement (Lynch 2018).

Urban coyotes used land use features differently as a function of season, infection with mange, and when certain other features were nearby. Coyotes used both modified grass/shrubland and residential areas less in winter, perhaps because fewer attractants were present then. Coyotes used modified grass/shrubs and developed areas more often when natural areas were nearby, and they used modified grass/shrublands more when developed areas were nearby, which suggested that coyotes may tolerate development provided it is close to high-quality habitat (Reddell et al. 2021). It is also possible that some modified vegetation types can buffer impacts of development, but the effect sizes were small. The results from the RSF model also showed that health and season were highly influential to resource use by coyotes. Mainly, mange-infected coyotes were more likely to use human-dominated areas (e.g., modified forests, residential, and developed), and were less reliant on natural areas, especially in winter. It seemed likely that the reduced body condition caused by mange-infection (Bornstein, Mörner, and William 2001) resulted in coyotes using residential areas to access anthropogenic food (Murray et al. 2016; Murray and St. Clair 2017). Such food sources may encourage dispersal from natural areas, especially in winter when mange infection can reduce internal fat stores (Bornstein, Mörner, and William 2001).

I addressed a second objective in Chapter 2 by comparing detection-based using the RSF model to derive a habitat suitability index (HSI) using various types of land cover in Edmonton and comparing it to the expert-derived estimates of landscape permeability used in circuit-based models. I found that the feature-specific ratings used to create the permeability layers underestimated the permeability of residential and developed areas in both seasons, and of maintained grass in summer. The permeability estimates also overestimated the value of most vegetated land cover types, albeit with some seasonal variation, and the North Saskatchewan River in winter. My results suggested that the North Saskatchewan River does not act as a conduit for movement in winter as expected (Harrison 1992; City of Edmonton 2017b), although this result could have occurred from GPS error (Conner, Smith, and Burger 2003; Ganskopp and Johnson 2007). The landscape permeability values predicted the HSI based on coyote detections, but less so in winter and when coyotes had mange. Additionally, the model fit was poor, which may be partly attributed to the low estimated permeability of residential and developed areas.

Overall, my results from Chapter 2 could help urban planners in a variety of ways. First, my models of habitat selection by coyotes supported the cumulative landscape permeability used in prior circuit-based models, suggesting that these may be a cost-effective tool for estimating urban connectivity. However, the RSF model also suggested that such expert-derived estimates are less precise than habitat suitability models based on animal occurrence data and lack the capacity to incorporate individual variation owing to health and other unmeasured variables. Using expert opinion is sometimes the best available option when the required data is unavailable or not feasible to obtain (Clevenger et al. 2002). In these cases, validation using occurrence data, as I presented in Chapter 2, is especially important to address such uncertainty (Johnson and Gillingham 2004; Pullinger and Johnson 2010). Perhaps the most important result of this comparison was to demonstrate the extensive use of residential and developed areas by coyotes relative to the predictions of the circuit-based model. There may be other uses of my results, such as using the RSF model to weigh trade-offs of retaining certain landscape features, create predictive maps for occurrence or movement, meet the City's objective of identifying pinch points using other modelling methods, or increase the accuracy of their circuit-based models.

In Chapter 3, I used data from camera traps and small mammal track tube arrays to test a) the predicted habitat value of two ecological indices used by the City, and b) various other remotely-sensed and site-based variables as explanatory variables for the occurrence and relative abundance of terrestrial mammals detected between 2018 and 2021.  I used the camera traps to derive monthly detection rates of three groups of mammals (City of Edmonton 2010b, 2014a) and 13 individual species, expressed these as binary occurrences and counts for relative abundance and compared both response variables to the indices of biodiversity potential and ecological connectivity, simultaneously using zero-inflated Poisson (ZIP) mixed models (camera trap data). I used proportion occupied/deployment/day from the track tube data and generalized linear mixed models (LMMs) to assess relative abundance using data from sites in natural areas. I subsequently modelled the occurrence and relative abundance of the three species groups and five individual species using a combination of remotely-sensed and site-based variables in a similar analytical approach, additionally using data from semi-natural parks.

The City's indices rarely predicted greater occurrence or relative abundance of the 13 species I tested, but the indices had some predictive value for the small and medium groups, and snowshoe hare, coyote, and white-tailed deer. Biodiversity potential performed better than ecological connectivity, which occurred as positive correlations only for larger mammals; as biodiversity potential increased, large mammals were more likely to occur, and white-tailed deer were more abundant. I speculated that this was due to their reliance on larger, rounder, more diverse patches owing to their body size (Kie et al. 2002), but also to the preferences of white-tailed deer (Miller, Muller, and Demarais 2003; Quinn, Williams, and Porter 2013). Biodiversity potential predicted a lower relative abundance of small mammals, likely due to the group containing mainly tree squirrels, which generally prefer forested areas (Yahner 2003). Because biodiversity potential was scored for each entire natural area, this scale may have been too large to reflect high-quality habitat for smaller species that may be detected over smaller spatial scales (Fisher, Anholt, and Volpe 2011). Although ecological connectivity was positively related to the relative abundance of small mammals, it was negatively associated with the relative abundance of snowshoe hare and white-tailed deer. This may have resulted from the sensitivity of these species to edge habitat (Lewis et al. 2011; Quinn, Williams, and Porter 2013; Uchida et al. 2016). Similarly, the lack of fit for beaver with ecological connectivity, in particular, suggested that the score for wetland habitat was weighted too highly, at least for the species in this study. It could also be that the scale used for this index is too small to reflect connective habitat for the larger species (Cushman and Landguth 2012). My results suggested that helpful adjustments might be made to the scale used to calculate both scores, specifically, by using a smaller scale to calculate biodiversity potential, a larger buffer width to calculate ecological connectivity, and reconsidering the weighting of wetland habitat.

I addressed a second objective of Chapter 3 by using data from natural and semi-natural areas to model the occurrence and relative abundance of three species groups and five individual species. Among the remotely sensed variables I tested, species occurrence or relative abundance typically increased with the naturalness of vegetated land cover, where ungulates responded positively to forested areas. Some of the habitat preferences I detected for reduced cover or structure likely stemmed from imperfect detection (Iknayan et al. 2014; Hofmeester et al. 2019) because dense habitat reduces the detection distances of remote cameras (Burton et al. 2015). I found that the response to modified vegetation types was variable, wherein larger species responded positively to those areas, but smaller species responded negatively. This variability may have been related to dispersal ability because larger species rely more on modified areas as connected habitats (Cushman and Landguth 2012). Conversely, both the negative responses of smaller species and positive responses of larger species could have resulted from the higher abundance of particular species, such as the prevalence of tree squirrels in the small mammal group, or because these features may also increase opportunities for grazing or browsing that are favoured by deer (Miller, Muller, and Demarais 2003; Berry et al. 2019). I found negative impacts of increasing urban development for porcupine, coyote, and mule deer and some seemingly nuanced negative effects of other human disturbances, such as humans and off-leash areas, for red squirrel, and small and large mammals, but some positive associations with domestic dogs. A positive correlation between wildlife and domestic dog detections may have occurred because dogs were attracted to sites with scents from wildlife (Weston et al. 2014). It may be that city parks are preferred by both wildlife and dog-walkers as the most natural spaces in residential areas (Bijker and Sijtsma 2017), or that wildlife and dogs may both use game trails (e.g., 99% of domestic dogs in natural areas [Parsons et al. 2016]). It could also be that both wildlife and dogs were attracted to anthropogenic attractants (e.g., bird feed that attracts small mammals [Jokimäki et al. 2017]). Two more reasons for the positive association with dogs is that many species may use locations where domestic dogs occur (Parsons et al. 2019), but reduce temporal overlap by being more active at night (Parsons et al. 2016). Lastly, wildlife may prefer areas closer to humans, because they provide shields from predators (Suraci et al. 2019).

By completing this work, my thesis advanced two broader goals that I expressed in Chapter 1 and above to (1) advance information about the predictors of habitat selection of urban coyotes and of the occurrence and relative abundance of three groups of terrestrial mammals and individual species, and 2) support the use of connectivity models and ecological indices used by ecological planners in Edmonton by testing their fit with measures of urban wildlife habitat use, occurrence, and relative abundance obtained from detection data in Edmonton, Alberta. I addressed the first goal in Chapter 1 by showing how infection with mange and season altered habitat use by coyotes, along with many other environmental variables. In Chapter 2, I identified and determined the best predictors of occurrence and relative abundance of mammal species, as groups of similarly sized species and five individual species varied with land cover characteristics across an urban gradient. I addressed the second goal in these two chapters by testing and suggesting refinements to planning tools used by the City to integrate wildlife into land use planning. I did so in Chapter 1 by exploring the similarity between estimators of permeability and habitat suitability for coyotes, and in Chapter 2, by comparing measures of animal occurrence and abundance to indices of predicted habitat value. Together, this information tangibly contributes to proactive ecological planning in the City of Edmonton and other cities to mitigate the adverse effects of urban development on biodiversity.

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# APPENDICES

## 4.1 APPENDIX 2.1

**Appendix 2.1 - Table 1** Average used and available proportions of 10 habitat types by season, with data ranges, used in compositional analyses to derive feature-specific selection estimates for 19 coyotes in Edmonton, Alberta, to compare with feature-specific permeability ratings used to parameterize permeability layers (used in circuit-based models) by the City of Edmonton (2016b, 2017b).

| Season† | Land cover | Mean used proportion‡ | Mean available proportion§ | Used proportion data range | Available proportion data range |
|---|---|---|---|---|---|
| Winter | Natural forest | 0.42 | 0.15 | 0.04 - 0.81 | 0.05 - 0.28 |
| Summer | | 0.41 | 0.14 | 0.12 - 0.76 | 0.03 - 0.27 |
| Winter | Natural shrub | 0.08 | 0.02 | 0 - 0.22 | 0.01 - 0.04 |
| Summer | | 0.10 | 0.02 | 0.01 - 0.31 | 0 - 0.1 |
| Winter | Natural grass | 0.01 | 0.01 | 0 - 0.03 | 0 - 0.03 |
| Summer | | 0.01 | 0.01 | 0 - 0.04 | 0 - 0.02 |
| Winter | Modified forest | 0.01 | 0.01 | 0 - 0.05 | 0 - 0.01 |
| Summer | | 0.01 | 0.01 | 0 - 0.05 | 0 - 0.02 |
| Winter | Modified grass/shrub | 0.19 | 0.15 | 0.01 - 0.93 | 0.01 - 0.66 |
| Summer | | 0.23 | 0.17 | 0.03 - 0.74 | 0.01 - 0.45 |
| Winter | Maintained grass | 0.04 | 0.10 | 0 - 0.12 | 0 - 0.18 |
| Summer | | 0.05 | 0.10 | 0 - 0.11 | 0.03 - 0.2 |
| Winter | Residential | 0.15 | 0.32 | 0 - 0.53 | 0 - 0.5 |
| Summer | | 0.08 | 0.29 | 0 - 0.27 | 0.01 - 0.42 |
| Winter | Developed | 0.08 | 0.15 | 0 - 0.36 | 0.01 - 0.52 |
| Summer | | 0.08 | 0.17 | 0 - 0.23 | 0.01 - 0.66 |
| Winter | Transp. Surface | 0.02 | 0.05 | 0 - 0.08 | 0.03 - 0.08 |
| Summer | | 0.01 | 0.06 | 0 - 0.06 | 0.01 - 0.1 |
| Winter | | 0.00 | 0.08 | 0 - 0.01 | 0 - 0.26 |
| Summer | North Sask. River | 0.00 | 0.08 | 0 - 0.01 | 0.01 - 0.24 |
| Winter | Other | 0.01 | 0.01 | 0 - 0.03 | 0 - 0.03 |
| Summer | | 0.02 | 0.02 | 0 - 0.08 | 0 - 0.04 |

† Seasons defined as winter: Dec.1 – Mar. 31 (*n* = 14) and summer: Apr. 1 – Nov. 31 (*n* = 15).

‡ Average proportion of radio locations for individual coyotes occurring in each habitat type.

§ Average percentage of each habitat type within 95% fixed kernel seasonal home ranges.

† Evaluated in "urban" PCA metrics.

‡ Included in "urban" PCA metric for analyses.

**Appendix 2.1 - Table 2** Combined simplified ranking matrix illustrating pairwise comparisons of selection between habitat types, along with ranks based on randomization tests from compositional analyses of 3rd -order selection in two seasons of 19 urban coyotes in Edmonton, Alberta.

| Season† | Land cover | Nat forest | Nat shrub | Nat grass | Mod forest | Mod. grass/ shrub | Maint grass | Resid | Develop | Transp Surf | North Sask River | Other | Rank |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Winter | Nat forest | | + | +++ | +++ | +++ | +++ | +++ | +++ | +++ | +++ | +++ | 1 |
| Summer | | | - | +++ | +++ | +++ | +++ | +++ | +++ | +++ | +++ | +++ | 2 |
| Winter | Nat shrub | | | +++ | +++ | + | +++ | +++ | + | +++ | +++ | + | 2 |
| Summer | | | | +++ | +++ | +++ | +++ | +++ | +++ | +++ | +++ | +++ | 1 |
| Winter | Nat grass | | | | + | --- | + | - | - | + | +++ | - | 7 |
| Summer | | | | | + | --- | - | + | - | + | +++ | - | 7 |
| Winter | Mod forest | | | | | --- | - | --- | - | + | + | - | 9 |
| Summer | | | | | | --- | - | + | - | + | +++ | - | 8 |
| Winter | Mod grass/ shrub | | | | | | +++ | +++ | +++ | +++ | +++ | + | 3 |
| Summer | | | | | | | +++ | +++ | +++ | +++ | +++ | + | 3 |
| Winter | Maint grass | | | | | | | - | - | + | + | - | 8 |
| Summer | | | | | | | | +++ | + | +++ | +++ | - | 5 |
| Winter | Resid | | | | | | | | - | +++ | +++ | + | 5 |
| Summer | | | | | | | | | - | - | +++ | --- | 10 |
| Winter | Develop | | | | | | | | | +++ | +++ | + | 4 |
| Summer | | | | | | | | | | + | +++ | - | 6 |
| Winter | Transport Surf | | | | | | | | | | + | --- | 10 |
| Summer | | | | | | | | | | | +++ | --- | 9 |
| Winter | North Sask River | | | | | | | | | | | --- | 11 |
| Summer | | | | | | | | | | | | --- | 11 |
| Winter | Other | | | | | | | | | | | | 6 |
| Summer | | | | | | | | | | | | | 4 |

*Notes:* Each sign replaces each mean element; a single sign represents that the habitat type in the row was used more than the habitat type in the column; a triple sign represents a significant deviation from random ($p < 0.05$). Redundant values excluded (reciprocal relationship). Abbreviations: Nat., natural; Mod., Modified; Maint., Maintained; Resid., Residential; Transp. Surf., Transportation Surface; North Sask, North Saskatchewan.

† Seasons defined as winter: Dec.1 – Mar. 31 ($n$ = 14) and summer: Apr. 1 – Nov. 31 ($n$ = 15).

**Appendix 2.1 - Table 3** The top 5 generalized linear mixed models (logistic GLMM) used as a resource selection function (RSF) for 14 healthy and five mange-infected urban coyotes in Edmonton, Alberta.

| Parameter | Coefficients | | | | |
|---|---|---|---|---|---|
| Intercept | **-1.072** | **-1.068** | **-1.071** | **-1.081** | **-1.115** |
| Slope | **0.473** | **0.458** | **0.458** | **0.457** | **0.453** |
| Natural areas | **0.995** | **1.018** | **1.017** | **1.025** | **1.019** |
| Modified forest | **0.565** | **0.520** | **0.522** | **0.523** | **0.520** |
| Modified grass/shrub | 0.112 | **0.201** | **0.203** | **0.204** | **0.240** |
| Residential | **0.437** | **0.444** | **0.445** | **0.440** | **0.515** |
| Developed | **-0.774** | **-0.700** | **-0.694** | **-0.676** | **-0.729** |
| Natural areas x Modified forest | **0.027** | **0.084** | **0.082** | **0.080** | **-** |
| Natural areas x Modified grass/shrub | **0.205** | - | - | - | - |
| Natural areas x Residential | **-0.040** | **-0.082** | **-0.078** | **-0.079** | **-0.071** |
| Natural areas x Developed | **0.051** | - | -0.010 | -0.020 | 0.088 |
| Modified forest x Modified grass/shrub | 0.011 | 0.010 | 0.010 | 0.013 | 0.016 |
| Modified forest x Residential | **0.253** | **0.256** | **0.256** | **0.253** | **0.286** |
| Modified forest x Developed | **-0.422** | **-0.421** | **-0.425** | **-0.415** | **-0.413** |
| Modified grass/shrub x Residential | **0.178** | **0.184** | **0.182** | **0.195** | - |
| Modified grass/shrub x Developed | **0.068** | - | - | -0.051 | - |
| Residential x Developed | **-0.425** | **-0.424** | **-0.424** | **-0.430** | **-0.458** |
| Season (winter)† x Natural areas | 0.066 | 0.039 | 0.041 | 0.042 | 0.042 |
| Season (winter) x Modified forest | **0.131** | **0.144** | **0.144** | **0.144** | **0.145** |
| Season (winter) x Modified grass/shrub | **-0.345** | **-0.322** | **-0.323** | **-0.321** | **-0.326** |
| Season (winter) x Residential | **-0.311** | **-0.295** | **-0.295** | **-0.294** | **-0.321** |
| Season (winter) x Developed | 0.039 | 0.047 | 0.049 | 0.046 | 0.053 |
| Mange x Natural areas | **-0.660** | **-0.656** | **-0.655** | **-0.655** | **-0.658** |
| Mange x Modified forest | **-0.277** | **-0.227** | **-0.227** | **-0.229** | **-0.243** |
| Mange x Modified grass/shrub | 0.080 | -0.069 | -0.069 | -0.058 | -0.018 |
| Mange x Residential | **0.479** | **0.452** | **0.453** | **0.455** | **0.444** |
| Mange x Developed | **0.290** | **0.279** | **0.275** | **0.281** | **0.308** |
| Season (winter) x Mange x Natural areas | **-0.283** | **-0.308** | **-0.308** | **-0.309** | **-0.307** |
| Season (winter) x Mange x Modified forest | **0.271** | **0.279** | **0.279** | **0.277** | **0.284** |
| Season (winter) x Mange x Modified grass/shrub | -0.002 | -0.077 | -0.077 | -0.076 | -0.064 |
| Season (winter) x Mange x Residential | **0.379** | **0.386** | **0.385** | **0.385** | **0.384** |
| Season (winter) x Mange x Developed | 0.015 | -0.032 | -0.030 | -0.028 | -0.029 |
| Model Rank | 1 | 2 | 3 | 4 | 5 |
| df | 33 | 30 | 31 | 32 | 29 |
| LL | -15336.73 | -15437.9 | -15437.8 | -15436.0 | -15461.6 |
| BIC | 31018.97 | 31189.95 | 31189.95 | 31207 | 31226.9 |
| ΔBIC | 0.00 | 170.98 | 181.15 | 188.07 | 207.89 |
| Wtc | 1 | 0 | 0 | 0 | 0 |
| $R^2_c$ | 0.54 | 0.54 | 0.54 | 0.54 | 0.53 |
| $R^2_m$ | 0.51 | 0.51 | 0.51 | 0.51 | 0.51 |

*Notes:* The models are shown in decreasing rank order (left to right), with the degrees of freedom (df), log-likelihood (LL), Bayesian Information Criterion (BIC), BIC difference (ΔBICc), and BIC weight (Wtc). The level of significance ($p < 0.05$) is indicated using bolded coefficients (β).

† Seasons were defined as winter: Dec.1 – Mar. 31 and summer: Apr. 1 – Nov. 31.

‡ Conditional ($R^2_{Cond}$) and marginal ($R^2_{Marg}$) $R^2$ for mixed models (Nakagawa, Johnson, and Schielzeth 2017).

**Appendix 2.1 - Table 4** The top 5 generalized linear models (GLMs) comparing habitat suitability index (HSI) derived from a resource selection function (RSF) model equation with expert-derived permeability values used in circuit-based models but the City of Edmonton (2016b, 2017b), season, and health-status for GPS locations for 19 urban coyotes in Edmonton, Alberta.

| Parameter | Coefficients (β) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Intercept | **1.025** | **1.025** | **1.025** | **1.025** | **1.025** | **1.029** | **1.021** | **1.016** | **1.021** |
| Permeability est.† | **0.012** | **0.011** | **0.010** | **0.009** | **0.008** | **0.009** | **-** | **0.010** | **0.008** |
| Season (winter)‡ | **0.008** | **0.010** | **0.010** | **0.010** | 0.010 | -0.023 | **-** | **0.013** | - |
| Mange§ | **-0.023** | **-0.021** | **-0.021** | **-0.021** | **-0.021** | **-** | - | - | - |
| Permeability est. x Season (winter) | **-0.004** | **-0.003** | **-** | -0.002 | - | - | **-** | -0.002 | - |
| Permeability est. x Mange | **-0.006** | -0.005 | -0.005 | - | - | -0.004 | - | - | - |
| Season (winter) x Mange | **0.005** | - | - | - | - | - | - | - | - |
| Permeability est. x Season (winter) x Mange | 0.005 | - | - | - | - | - | - | - | - |
| Model Rank | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| df | 11740 | 11742 | 11743 | 11743 | 11744 | 11744 | 11747 | 11744 | 11746 |
| LL | -35127.6 | -35123.2 | -35119.0 | -35100.1 | -35099.9 | -35029.8 | -34718.3 | -34700.5 | -34541 |
| AIC | 0.00 | 4.42 | 8.58 | 27.49 | 27.76 | 97.83 | 409.30 | 427.10 | 586.63 |
| ΔAIC | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Wtc | 17801.4 | 17797.15 | 17794.1 | 17785 | 17783 | 17748 | 17361 | 17583.8 | 17502 |
| $R^2$ | -0.004 | -0.004 | -0.004 | -0.004 | -0.004 | -0.004 | - | -0.002 | -0.001 |

*Notes:* The models are shown in decreasing rank order (left to right), with the degrees of freedom (df), log-likelihood (LL), Akaike Information Criterion (AIC), AIC difference (ΔAICc), AIC weight (Wtc), and Nagelkerke's Pseudo $R^2$. The habitat suitability index (HSI) tested was derived from a resource selection function (RSF) model equation modelled using 19 urban coyotes (*n* = 11,748 "used" radiotelemetry locations) and logarithmically transformed.

† Estimated permeability obtained from expert-derived permeability layers (cumulative) used to create circuit-based models by the City of Edmonton (2016b, 2017b) and square-root transformed.

‡ Seasons were defined as winter: Dec.1 – Mar. 31 and summer: Apr. 1 – Nov. 31.

§ Using 14 healthy and five mange-infected coyotes.

## 4.2 APPENDIX 3.1

**Appendix 3.1 - Table 1** Part A of the City of Edmonton's Phase II Ecological Network Report (ENRII [City of Edmonton 2014a]) natural area scoring system, with factor, variable, metric, scoring criteria, score, variable score, and factor score calculations used to derive estimates of ecological value for natural areas via two indices, biodiversity potential and ecological connectivity, for 69 camera traps and 38 small mammal track tube arrays in Edmonton, Alberta.

| Factor | Variable | Metric | Criteria | Score | Variable Score Calculation | Factor Score Calculation |
|---|---|---|---|---|---|---|
| Biodiversity Potential | Size | Area (ha) | <0.5 | 0 | Score out of 15 | Add variable scores = score out of 35 |
| | | | 0.5 – 1 | 1 | | |
| | | | >1– 3 | 2 | | |
| | | | >3 – 6 | 5 | | |
| | | | >6 – 9 | 8 | | |
| | | | >9– 12 | 11 | | |
| | | | >12 | 15 | | |
| | Shape | Shape | Simple round/square shape | 0 | Score down to -8 | |
| | | | A few linear/narrow areas | -2 | | |
| | | | Mix of linear/narrow areas and rounder/wider areas | -4 | | |
| | | | Linear/narrow throughout | -8 | | |
| | Habitat diversity | Number of different habitat types (> 0.5 ha) present within the natural area | Open water | 3 | Add all that apply = score out of 20 | |
| | | | Marsh wetland | 3 | | |
| | | | Shrub wetland | 2 | | |
| | | | Peatland (bog or fen) | 4 | | |
| | | | Deciduous upland | 2 | | |
| | | | Coniferous upland | 2 | | |
| | | | Mixedwood upland | 3 | | |
| | | | Meadow/naturalized field | 1 | | |
| Ecological connectivity | Presence of nearby upland habitat | Area (ha) of wooded, meadow, or naturalized field habitat within 100 m buffer | 0 – 0.5 | 0 | Score out of 10 | Add variable scores = score out of 20 |
| | | | >0.5 – 1 | 1 | | |
| | | | >1 – 2 | 3 | | |
| | | | >2 – 3 | 5 | | |
| | | | >3 – 5 | 7 | | |
| | | | >5 | 10 | | |
| | Presence of nearby wetland habitat | Area (ha) of wetland habitat within 100 m buffer | 0-1 | 0 | Score out of 10 | |
| | | | >1-3 | 3 | | |
| | | | >3 – 5 | 5 | | |
| | | | >5 | 10 | | |

**Appendix 3.1 - Table 2** Number of camera trap months, independent detections, species diversity of terrestrial mammal species, and percentage of total detections from three ecological design groups (City of Edmonton 2010b, 2014a) from 89 camera traps located throughout Edmonton, Alberta, from May 2018 to September 2021, with an asterisk indicating the 69 sites in natural sites used to evaluate the predictive accuracy of two ecological indices (City of Edmonton 2014a).

| Site name | Latitude | Longitude | Num. of camera months | Num. of detections | | Species richness | | % of detections† | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Total | Avg. / month | Total | Avg. / month | Small | Medium | Large |
| Abbottsfield§ | 53.5696 | -113.3776 | 4 | 46 | 11.5 | 4 | 1.5 | 7 | 93 | 0 |
| Airport¶ | 53.5783 | -113.5090 | 24 | 540 | 22.5 | 5 | 1.5 | 0 | 63 | 36 |
| Anthony Henday Bridge§ | 53.4603 | -113.6173 | 15 | 791 | 52.7 | 6 | 2.5 | 0 | 7 | 93 |
| Bannerman§ | 53.6091 | -113.3632 | 41 | 218 | 5.3 | 6 | 1.4 | 25 | 75 | 0 |
| Belgravia¶ | 53.5149 | -113.5300 | 8 | 353 | 44.1 | 9 | 3.1 | 75 | 25 | 0 |
| Belgravia Dog Park¶ | 53.5060 | -113.5420 | 16 | 82 | 5.1 | 5 | 1.9 | 41 | 59 | 0 |
| Belvedere¶ | 53.5929 | -113.4350 | 8 | 40 | 5.0 | 2 | 1.4 | 0 | 100 | 0 |
| Big Island§ | 53.4281 | -113.6650 | 40 | 703 | 17.6 | 9 | 3.5 | 4 | 61 | 34 |
| Blackmud Creek Ravine§ | 53.4448 | -113.5159 | 41 | 524 | 12.8 | 10 | 1.9 | 3 | 23 | 74 |
| Blue Quill¶ | 53.4617 | -113.5180 | 33 | 196 | 5.9 | 6 | 1.2 | 2 | 98 | 1 |
| Brookside§ | 53.4984 | -113.5650 | 40 | 524 | 13.1 | 8 | 2.3 | 8 | 88 | 3 |
| Buena Vista§ | 53.5132 | -113.5442 | 28 | 437 | 15.6 | 5 | 2.0 | 16 | 84 | 0 |
| Callingwood§ | 53.5069 | -113.6200 | 40 | 21 | 0.5 | 4 | 0.3 | 5 | 76 | 19 |
| Canon Ridge§ | 53.5849 | -113.3800 | 5 | 25 | 5.0 | 2 | 1.4 | 0 | 100 | 0 |
| Cashman§ | 53.4237 | -113.5000 | 4 | 9 | 2.3 | 2 | 0.8 | 0 | 33 | 67 |
| City Center¶ | 53.5414 | -113.5004 | 2 | 0 | 0.0 | 0 | 0.0 | - | - | - |
| Cloverdale§ | 53.5384 | -113.4790 | 5 | 56 | 11.2 | 4 | 0.8 | 5 | 57 | 38 |
| Davies Industrial West§ | 53.5019 | -113.4470 | 4 | 5 | 1.3 | 1 | 0.8 | 0 | 100 | 0 |
| Decoteau 2§ | 53.4172 | -113.3980 | 4 | 34 | 8.5 | 2 | 1.3 | 0 | 12 | 88 |
| Decoteau 3§ | 53.4157 | -113.4040 | 38 | 989 | 26.0 | 12 | 3.0 | 2 | 25 | 73 |
| Dovercourt¶ | 53.5759 | -113.5600 | 6 | 6 | 1.0 | 2 | 0.3 | 33 | 67 | 0 |
| Edgemont§ | 53.4661 | -113.6670 | 40 | 178 | 4.5 | 8 | 1.6 | 15 | 70 | 15 |
| Goodridge Corner§ | 53.6413 | -113.5530 | 38 | 1117 | 29.4 | 10 | 3.7 | 3 | 39 | 58 |
| Graydon Hill§ | 53.4263 | -113.5630 | 33 | 215 | 6.5 | 8 | 1.2 | 0 | 23 | 76 |
| Hairsine¶ | 53.6044 | -113.3910 | 2 | 3 | 1.5 | 2 | 1.0 | 0 | 100 | 0 |
| Hawrelak Park 1§ | 53.5246 | -113.5480 | 5 | 17 | 3.4 | 6 | 2.0 | 29 | 71 | 0 |
| Hawrelak Park 2§ | 53.5231 | -113.5450 | 32 | 100 | 3.1 | 8 | 1.6 | 13 | 84 | 3 |
| Horse Hill 1§ | 53.6718 | -113.3330 | 4 | 31 | 7.8 | 5 | 2.0 | 3 | 58 | 39 |
| Horse Hill 2§ | 53.6721 | -113.3360 | 34 | 195 | 5.7 | 9 | 1.8 | 1 | 55 | 45 |
| Humane Society§ | 53.5968 | -113.6046 | 40 | 196 | 4.9 | 8 | 1.4 | 12 | 85 | 3 |
| Inglewood¶ | 53.5645 | -113.5310 | 17 | 28 | 1.6 | 4 | 0.7 | 4 | 96 | 0 |
| Kennedale Ravine 1§ | 53.5888 | -113.3950 | 7 | 78 | 11.1 | 4 | 1.9 | 17 | 81 | 3 |
| Kennedale Ravine 2§ | 53.5910 | -113.4038 | 34 | 224 | 6.6 | 7 | 1.3 | 14 | 84 | 2 |
| Kiniski Gardens§ | 53.4763 | -113.4140 | 40 | 131 | 3.3 | 4 | 0.8 | 15 | 85 | 0 |
| Laurier Heights Park¶ | 53.5164 | -113.5700 | 2 | 3 | 1.5 | 3 | 1.0 | 33 | 67 | 0 |
| Leger¶ | 53.4613 | -113.5840 | 11 | 55 | 5.0 | 4 | 1.7 | 0 | 76 | 24 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| MacKinnon Ravine 1§ | 53.5399 | -113.5460 | 2 | 10 | 5.0 | 3 | 1.5 | 0 | 100 | 0 |
| MacKinnon Ravine 2§ | 53.5389 | -113.5501 | 4 | 15 | 3.8 | 3 | 0.8 | 7 | 87 | 7 |
| MacKinnon Ravine 3§ | 53.5354 | -113.5580 | 4 | 55 | 13.8 | 3 | 2.0 | 55 | 45 | 0 |
| MacKinnon Ravine 4§ | 53.5381 | -113.5640 | 7 | 1 | 0.1 | 1 | 0.1 | 100 | 0 | 0 |
| MacKinnon Ravine 5§ | 53.5380 | -113.5639 | 23 | 133 | 5.8 | 4 | 1.4 | 5 | 93 | 2 |
| Magrath Heights§ | 53.4512 | -113.5410 | 41 | 364 | 8.9 | 8 | 1.7 | 4 | 41 | 55 |
| Marquis Two§ | 53.6337 | -113.3430 | 12 | 151 | 12.6 | 6 | 2.2 | 12 | 56 | 32 |
| McCauley§ | 53.5549 | -113.4671 | 2 | 46 | 23.0 | 3 | 2.0 | 0 | 98 | 2 |
| Meadows¶ | 53.4718 | -113.3910 | 24 | 51 | 2.1 | 4 | 0.8 | 12 | 88 | 0 |
| Millwoods Golf Course§ | 53.4861 | -113.4280 | 37 | 146 | 3.9 | 6 | 1.0 | 3 | 93 | 3 |
| Muttart 2§ | 53.5294 | -113.4770 | 37 | 316 | 8.5 | 6 | 1.5 | 1 | 92 | 7 |
| Parkallen¶ | 53.5024 | -113.5180 | 6 | 7 | 1.2 | 3 | 0.5 | 71 | 29 | 0 |
| Prince Charles¶ | 53.5743 | -113.5370 | 3 | 24 | 8.0 | 4 | 1.7 | 13 | 83 | 4 |
| Pylypow Industrial§ | 53.4994 | -113.4040 | 39 | 676 | 17.3 | 9 | 2.2 | 3 | 92 | 5 |
| Quarry Ridge§ | 53.6226 | -113.3340 | 28 | 538 | 19.2 | 8 | 2.3 | 0 | 24 | 76 |
| Queen Mary Park¶ | 53.5523 | -113.5277 | 16 | 191 | 11.9 | 3 | 1.9 | 46 | 54 | 0 |
| R.V. Aspen Gardens§ | 53.4821 | -113.5548 | 41 | 873 | 21.3 | 6 | 2.3 | 1 | 32 | 68 |
| R.V. Cameron 1§ | 53.4705 | -113.6082 | 4 | 57 | 14.3 | 2 | 1.0 | 0 | 2 | 98 |
| R.V. Cameron 2§ | 53.4761 | -113.6217 | 20 | 395 | 19.8 | 8 | 2.5 | 0 | 35 | 64 |
| R.V. Highlands§ | 53.5565 | -113.4400 | 41 | 246 | 6.0 | 6 | 1.0 | 0 | 99 | 0 |
| R.V. Mayfair 1§ | 53.5362 | -113.5410 | 11 | 59 | 5.4 | 6 | 2.1 | 17 | 81 | 2 |
| R.V. Mayfair 2§ | 53.5365 | -113.5431 | 28 | 449 | 16.0 | 9 | 2.6 | 24 | 71 | 4 |
| R.V. Oleskiw§ | 53.4856 | -113.5920 | 14 | 89 | 6.4 | 3 | 1.2 | 3 | 15 | 82 |
| R.V. Rundle§ | 53.5574 | -113.4040 | 41 | 1217 | 29.7 | 9 | 2.8 | 35 | 65 | 0 |
| R.V. Terwillegar§ | 53.4865 | -113.6130 | 40 | 244 | 6.1 | 4 | 1.6 | 30 | 69 | 1 |
| R.V. Victoria§ | 53.5329 | -113.5250 | 23 | 373 | 16.2 | 10 | 2.4 | 25 | 70 | 5 |
| R.V. Walterdale§ | 53.5287 | -113.5059 | 5 | 10 | 2.0 | 3 | 1.0 | 0 | 60 | 40 |
| Rampart Industrial§ | 53.6072 | -113.5769 | 11 | 189 | 17.2 | 6 | 2.2 | 0 | 69 | 31 |
| Rapperswill§ | 53.6355 | -113.5330 | 22 | 1125 | 51.1 | 6 | 2.5 | 5 | 93 | 2 |
| Rio Terrace§ | 53.5023 | -113.5920 | 2 | 28 | 14.0 | 4 | 2.0 | 57 | 39 | 4 |
| Ritchie§ | 53.5195 | -113.4730 | 2 | 2 | 1.0 | 1 | 0.5 | 0 | 100 | 0 |
| Riverview Area 1§ | 53.4128 | -113.6851 | 41 | 500 | 12.2 | 11 | 2.1 | 1 | 13 | 86 |
| Roper Road§ | 53.4957 | -113.4340 | 39 | 284 | 7.3 | 6 | 1.3 | 27 | 65 | 8 |
| Rossdale§ | 53.5297 | -113.4911 | 5 | 139 | 27.8 | 6 | 3.2 | 88 | 12 | 0 |
| Rural Sturgeon§ | 53.6496 | -113.3024 | 19 | 335 | 17.6 | 7 | 2.5 | 1 | 18 | 81 |
| Silver Berry§ | 53.4644 | -113.3905 | 17 | 170 | 10.0 | 5 | 2.2 | 40 | 60 | 0 |
| South Campus§ | 53.5021 | -113.5374 | 2 | 6 | 3.0 | 2 | 1.5 | 0 | 83 | 17 |
| South Sturgeon 1§ | 53.6714 | -113.2960 | 3 | 27 | 9.0 | 4 | 2.3 | 0 | 74 | 26 |
| South Sturgeon 2§ | 53.6700 | -113.2910 | 35 | 900 | 25.7 | 10 | 3.1 | 2 | 12 | 86 |
| Star Blanket Park§ | 53.4573 | -113.4009 | 5 | 56 | 11.2 | 1 | 0.4 | 100 | 0 | 0 |
| Sturgeon County§ | 53.6076 | -113.3380 | 4 | 24 | 6.0 | 3 | 1.8 | 0 | 83 | 17 |
| Tamarack§ | 53.4582 | -113.3590 | 38 | 186 | 4.9 | 6 | 0.8 | 0 | 96 | 4 |
| Terrace Heights§ | 53.5458 | -113.4380 | 40 | 265 | 6.6 | 6 | 1.5 | 35 | 63 | 2 |
| University Farm§ | 53.4969 | -113.5427 | 36 | 396 | 11.0 | 6 | 1.7 | 2 | 57 | 41 |
| Virginia Park¶ | 53.5623 | -113.4590 | 8 | 14 | 1.8 | 3 | 1.0 | 7 | 93 | 0 |
| Walterdale§ | 53.5242 | -113.5060 | 7 | 28 | 4.0 | 4 | 1.4 | 11 | 39 | 50 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Wedgewood Heights¶ | 53.4803 | -113.6447 | 37 | 504 | 13.6 | 6 | 2.1 | 0 | 87 | 13 |
| Wellington 1¶ | 53.5937 | -113.5557 | 7 | 72 | 10.3 | 2 | 0.9 | 0 | 100 | 0 |
| Wellington 2¶ | 53.5925 | -113.5616 | 9 | 52 | 5.8 | 3 | 0.7 | 0 | 100 | 0 |
| Wolf Willow Ravine§ | 53.5026 | -113.6020 | 33 | 152 | 4.6 | 5 | 1.6 | 28 | 50 | 22 |
| Woodcroft¶ | 53.5622 | -113.5640 | 24 | 249 | 10.4 | 5 | 1.7 | 53 | 47 | 0 |
| Zoo 1§ | 53.5088 | -113.5622 | 5 | 170 | 34.0 | 3 | 2.0 | 1 | 99 | 0 |
| Zoo 2§ | 53.5084 | -113.5610 | 34 | 1218 | 35.8 | 6 | 2.1 | 3 | 95 | 3 |

† Percentage of the total detections from species within three ecological design groups used by the City of Edmonton (see Fig. 3.2 and Table 3.1 for species within groups [City of Edmonton 2010b, 2014b]).

‡ The total number of detections from each site; temporal coverage variable as "Num. of camera months"; study occurred from May 2018 to September 2021.

§ From 69 sites in natural areas used to test two ecological indices (City of Edmonton 2014a).

¶ From 89 sites in both natural and semi-natural parks used to model occurrence and relative abundance using remotely-sensed and site-based variables.

**Appendix 3.1 - Table 3** List of uncorrelated and most-explanatory variables for zero-inflated Poisson (ZIP) mixed models and linear mixed models (LMM) modelling predictors of occurrence and relative abundance of three ecological design groups (EDG [City of Edmonton 2010b, 2014a]) and five individual species from 89 camera traps and 48 track tube arrays placed in natural and semi-natural parks in Edmonton, Alberta.

| Species/ group | Model-part† | Variables assessed in combined models‡ |
|---|---|---|
| Small EDG (track tube)§ | Relative abundance (λ) | Natural/modified, Site.Connected, %Natural grass/shrub, Site.%Treed, Site.%Shrub, Site.%Grass/forbe, Site.%CWD, Site.#Game.trail, Urban |
| Small EDG (camera trap) | Occurrence (ψ) | Connective.hab.area, Prox.Riv/rav, Site.#Game.trail, %Modified.veg., Site.%Shrub, Site.%Water, Site.%Bare, Domestic.dog, Pred.abundance, Season, Lure |
| | Relative abundance (λ) | Veg.type, %Maint.grass, Site.#Human.trail, Human, Domestic.dog, Pred.abundance, Season, Lure |
| Red squirrel | Occurrence (ψ) | %Modified.veg., Site.%Shrub, Veg.type, Prox.Riv/rav, Patch.size, Site.%CWD, Site.#Human.trail, Site.#Game.trail, Domestic.dog, Urban, Pred.abundance, Season |
| | Relative abundance (λ) | Site.%Canopy, Vegetation.type, %Modified.veg., Site.#Human.trail, Human, Domestic.dog, Season |
| Medium EDG | Occurrence (ψ) | Connective.hab.area, Site.Forest.structure, Site.%CWD, Human, Domestic.dog, Off-leash.area, Urban, Season, Lure |
| | Relative abundance (λ) | Connective.hab.area, Site.Grass.structure, Domestic.dog, Off-leash.area, Season, Lure |
| Snowshoe hare | Occurrence (ψ) | Natural/modified, %Maint.grass, Site.%Shrub, Site.%Grass/forbe, Site.Grass.structure, Site.Anthro.dist., Site.#Human.trail, Site.#Game.trail, Human, Domestic.dog, Urban, Pred.abundance, Season |
| | Relative abundance (λ) | Natural/modified, %Natural.forest, Site.%Shrub, Site.%Grass/forbe, %Maint. grass, Site.%Water, Site.%Bare, Domestic.dog, Pred.abundance, Season |
| Porcupine | Occurrence (ψ) | Natural/modified, %Natural.forest, Site.%Shrub, Site.Grass.structure, Prox.Riv/rav, Site.#Game.trail, Site.%CWD, Site.%Water, Urban, Season, Lure |
| | Relative abundance (λ) | Natural/modified, Prox.Riv/rav, Site.%Canopy, Site.#Game.trail, Site.%CWD, Urban, Season |
| Coyote | Occurrence (ψ) | Natural/modified, Connective.hab.area, Site.Forest.structure, Site.Veg.diversity, Site.#Game.trail, Site.%CWD, Site.%Water, Human, Domestic.dog, Off-leash.area, Urban, Prey.abundance(CT), Season, Lure |
| | Relative abundance (λ) | Natural/modified, Site.%Shrub, Site.Grass.structure, Shape.index, Domestic.dog, Urban, Prey abundance(CT), Season, Lure |
| Large EDG | Occurrence (ψ) | Natural/modified, Connective.hab.area, %Natural.forest, Site.Veg.diversity, %Modified.veg., %Maint.grass, Site.%Bare, Site.Anthro.dist., Site.#Human.trail, Site.#Game.trail, Human, Domestic.dog, Off-leash.area, Urban, Season |
| | Relative abundance (λ) | Patch.size, Natural/modified, %Natural.forest, Site.%Shrub, Site.Veg. diversity, Site.#Game.trail, %Modified.veg., Site.#Human.trail, Off-leash.area, Urban, Season |
| Mule deer | Occurrence (ψ) | Natural/modified, Connective.hab.area, %Natural.forest, Site.Forest.structure, Site.%Shrub, %Modified.veg., Site.Anthro.dist., Human, Domestic.dog, Off-leash.area, Urban, Season, Lure |
| | Relative abundance (λ) | Connective.hab.area, %Natural.forest, Site.Forest.structure, Site.#Game.trail, %Modified.veg., %Maint.grass, Site.%Bare, Domestic.dog, Off-leash.area, Urban, Season, Lure |

† From camera traps in ZIP mixed models (§): zero-inflation model-part (inversely, probability of occurrence; logit link; ψ), conditional model-part (relative abundance; log link; λ); from track tubes in LMMs (‡): conditional model (relative abundance; λ).

‡ Liberally significant ($p < 0.25$ [Hosmer and Lemeshow 1989]) and the most explanatory defined as best-fit using for Bayesian Information Criterion (BIC; Schwarz 1978) for ZIP mixed models and Akaike's Information Criterion for small sample sizes (AICc; Akaike 1978) for LMMs.

§ LMMs used for data from track tubes ($n$ = 130); ZIP mixed models used elsewhere ($n$ = 1,783).