THESIS

MAMMALIAN HABITAT USE ALONG A RESIDENTIAL DEVELOPMENT GRADIENT IN NORTHERN COLORADO

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ABSTRACT

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"Exurban" development occupies nearly five times more land in the United States than urban and suburban development combined. Understanding the effects of exurban development on biodiversity thus has important and wide-ranging implications for the planning, construction and stewardship of sustainable communities and surrounding rural lands. To assess the impact of exurban development on mammalian habitat use, wildlife cameras were placed along a unique development gradient designed to capture landscape permeability in a rapidly growing rural region of Colorado. Multiple-season species occupancy and relative activity (frequency of detections) were measured in summer and winter seasons and these data were analyzed in conjunction with a novel, acoustic-based approach to assessing human activity. Impacts of exurban housing varied by mammal species, with some species, such as bobcats, elk, and coyotes, showing decreased activity and occupancy levels at higher housing densities, whereas others, including red foxes and Abert's squirrels, occurred more frequently in these areas. Human-sourced activities associated with development and non-natural sound levels emerged as top models for most species. Relative activity rates corroborated occupancy results, indicating that some species not only use habitat in high density areas, they use it more frequently. In addition, some species, including black bears, preferentially used embedded greenbelts in high-density exurban subdivisions, suggesting that greenbelts may be important for structural and functional connectivity. This study demonstrates that the impacts of exurban development are species–dependent. However, incorporating well-designed and naturally vegetated open spaces into development projects and minimizing human disturbance may be critical to mitigating development impacts to most wildlife in regions undergoing continued exurban expansion.

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LIST OF KEY WORDS

anthropogenic noise; development gradient; exurban development; landscape permeability; multiple-season occupancy; relative activity; rural residential development; wildlife cameras

INTRODUCTION

Exurban development, or development outside of cities and towns, has widespread ecological impacts, the extent of which is poorly known (Hansen et al. 2005). Development in rural areas is often driven by the desire to live in proximity to natural amenities such as large contiguous open space, pristine lakes, rivers and coastlines. Most residential development occurs on private lands, which comprise over 60% of the land in the country and are among the most biologically productive lands in the U.S. (Scott et al. 2001). Thus, exurban development generally results in disproportionately large impacts to species and communities of conservation concern (Mitchell et al. 2002, Hansen et al. 2005). The process of urbanization, either singly or in association with other causes, has led to the decline of over half the species listed as threatened or endangered under the US Endangered Species Act (Czech et al. 2000).

Exurban development and associated infrastructure such as roads lead to habitat fragmentation, increased human access, the spread of invasive species from non-native landscaping, and increased human-wildlife conflict. Construction, landscaping and ongoing human activities alter the environment by homogenizing biota and introducing changes to disturbance regimes such as fire suppression, herbivory, and predator-prey dynamics (McKinney 2006). Habitat fragmentation from dispersed housing development can alter animal movement patterns and behavior, cause “pileup” or overlap of home ranges, and reduce fitness by intensifying inter- and intra-specific interactions (Riley 2006). Fragmentation caused by development also compromises structural and functional connectivity and can constrain the ability of some species to disperse and persist in these landscapes (Saunders et al. 1991; Crooks and Sanjayan 2006). Exurban areas with trails and elevated human activity may also impact activity patterns of mammals (George and Crooks 2006). Exurban development leads to more interactions between domestic and wild animals, which can potentially alter disease dynamics and change behavior patterns due to disturbance from domestic pets (Riley et al. 2004). Increasingly, conservationists argue that the cumulative impacts of exurban development on biodiversity and ecological processes exceed that of forestry or ranching (Marzluff and Ewing 2001, Hansen et al. 2005).

Proximity to natural amenities and open space, the advent of telecommuting, and the shift of business centers to city edges drive the recent trend of increasing exurban development in the United States (Platt 2006). By 2000, exurban development occupied nearly 15 times the area of higher density urbanized development and fully 25% of all private land in the conterminous United States (Brown et al. 2005), and currently occupies five times more land than all suburban and urban development combined (Theobald 2004). Eighty percent of housing development in the 1990s was in rural areas, and over half of these homes were on lots greater than four hectares (Heimlich and Anderson 2001). Thus, exurban development has a high per-capita footprint relative to other forms of development.

Exurban development may disproportionately impact protected lands, as many rural developments are adjacent to public- and private protected areas (Knight et al. 1995, Leinwand et al. 2010). Between 1940 and 2000, 28 million housing units were built in the US within 50 km of protected areas, and the subsequent increased edge effects are predicted to decrease the effective area and conservation value of the protected areas (Radeloff et al. 2010). If residential development continues at projected rates, the private lands that buffer zones around protected areas will be reduced by 12% nationwide by 2030 (Wade and Theobald 2010).

Since the 1990s the American West has been one of the fastest growing regions in the United States, and exurban development has become one of the predominant uses of private land.

(Rudzitis 1999; Mitchell et al. 2002). Former ranch and farm lands are typically subdivided for ranchette-style residential development within a matrix dominated by native vegetation (Knight 1999; Brown et al. 2005). From 1990 to 1998, populations in rural areas in the Rocky Mountain states grew faster than in urban areas in over 60% of counties (Theobald 2001). Considering that Western U.S. populations are predicted to continue along this trajectory, ecological research focused on the consequences of exurban development in this region has important implications for national and regional public policy, conservation practice, and land use planning. Although many studies have focused on urban sprawl (Theobald 2005), few studies until recently have addressed the conservation implications of the widespread and rapid conversion of rural natural and agricultural lands to exurban development (Hilty and Merenlender 2003).

Here, we assess mammalian habitat use in and around rural housing developments of different housing densities in northern Larimer County, Colorado. We used remotely-triggered wildlife cameras to detect medium- and large-bodied mammal species and assess their habitat use and relative activity along a development gradient that is based on housing density and landscape permeability (Theobald et al. 2012). We examined habitat use of each species via a multiple-season occupancy model framework (MacKenzie et al. 2003) based on detection/non-detection data. We also compared the relative activity of various species along the development gradient to further assess how mammals respond to the cumulative influence of housing in rural areas (George and Crooks 2006). Other studies have investigated mammalian presence at various types of land use and development (Lenth et al. 2006, Maestas et al. 2003). However, none to our knowledge have quantified the habitat use of rural residential development and surrounding areas for large mammals outside of modeling exercises (Freeman and Bell 2011, Zielinski et al. 2010), nor have they assessed landscape permeability along a gradient using empirical species occurrence data (Theobald et al. 2012). Our study poses the following specific questions about the relationship between exurban development and wildlife in exurban areas: does higher development influence affect mammalian habitat use by species? Are there thresholds of development at which mammals alter their habitat use? Does development affect the relative activity of mammals, and are activity levels higher in greenbelts embedded within higher development areas?

The use of gradients to analyze urbanizing landscapes is well-documented (Ter Braak and Prentice 1988; McDonnell and Pickett 1990; Marzluff and Ewing 2001; McDonnell and Hahs 2008), and gradients are considered important ecological tools for examining anthropogenic effects on the environment. A development gradient is a broad measure of urbanization that captures complex conditions (McDonnell et al. 2008) and can be used as a proxy for land use intensity in a rural landscape (Hansen et al. 2005). Considering habitat use and landscape permeability along a continuous gradient is useful and captures more landscape complexity in areas where patch classification and delineation is difficult such as human-altered environments (Manley et al. 2009, Theobald et al. 2012). Several studies have evaluated the impacts of development along the urban to rural gradient on the abundance and diversity of small mammals (Riem et al. 2012), birds (Blair 2004; Suarez-Rubio et al. 2011), and butterflies (Blair 2001; Bergerot et al. 2011). In general, these studies found that species richness may be greatest at intermediate levels of development along the urban-rural gradient. Thus, focusing on the intermediate or exurban portion of this gradient may further elucidate the patterns and processes that drive the relationship between development and wildlife.

Because some housing developments are spatially designed to contain green spaces to promote wildlife use, we chose to assess animal habitat use throughout the developed region of the study area to determine the importance of these greenbelts. This portion of the study has implications for an emerging approach to mitigating the negative impacts of exurban sprawl. “Conservation Development” has been suggested as an alternative to exurban sprawl, where houses are clustered to reduce their ecological footprints (Lenth et al. 2006, Pejchar et al. 2007, Milder 2007). Clustering, for example, minimizes the “halo” effect which alters animal and songbird densities around homes (Odell and Knight 2001). One criticism of clustered housing projects is that unless properly designed, the isolated fragments of open space that remain may be small and of little value to wildlife (Milder 2007). There is very little information, however, on whether development density restricts the movement of animals through mosaics of open space and exurban development, and to what degree the cumulative influence of housing effects are species-dependent. Understanding how medium- and large-sized mammals use habitat within and among developments of varying densities has the potential to help shape the design and stewardship of future development projects.

METHODS

Study Area

Our study took place in the North Fork of the Cache la Poudre River watershed in Larimer County, Colorado (lat. 40°50’N, long. 105°15’W), which is approximately 40 km northwest of Fort Collins (Maestas et al. 2003). The North Fork of the Cache la Poudre River is fed by Dale, Rabbit, Lone Pine, Bull, and Stonewall creeks, and is a tributary of the main stem of the Cache la Poudre River (Evans and Evans 1991). Land use patterns in the North Fork watershed are diverse, consisting of active ranches, protected areas and exurban residential development. Large tracts of public land consist mainly of Roosevelt National Forest (USFS) and Colorado Parks and Wildlife state land. The Nature Conservancy and Legacy Land Trust also own property and hold conservation easements in the study area.

The population of unincorporated Larimer County has grown rapidly, from 26,000 in 1970 to 71,164 in 2010 (US Census Bureau 2010). Larimer County, along with several other counties in Colorado, is at the forefront of providing incentives for rural development that is designed to enhance the protection of natural resources (Hannum et al. 2012). Residential subdivisions within the study area include Glacier View Meadows, Phantom Canyon Ranches, Cherokee Meadows, Deer Meadows, Weaver Ranch, Mill Creek, and Bonner Peak. Glacier View Meadows, the subdivision with the densest development design, consists of 970 lots, in which 650 houses are built. Lot size averages 1.5 acres (0.6 hectares). Cherokee Meadows has 57 lots, which are 35-40 acres (14.2-16.2 hectares). Bonner Peak has 82 parcels and also consists of 35-40 acre lots. There are also houses scattered through the study area that are not associated with a specific subdivision. Overall, nearly 1400 houses are in the study area and buffer zones.

The study area is bounded to the south by the Cache la Poudre River and to the north by the Wyoming border (Figure 1a). The east and west boundaries are determined by elevation. Sampling was restricted to elevations ranging between 1700m and 2400m, to control for vegetation communities and soil types. Within this elevation band, the vegetation community is defined by Rocky Mountain Ponderosa Pine Woodland and Rocky Mountain Lower Montane-Foothill Shrubland (NLCD 2009). Dominant grasses include blue gramma (*Boutela gracilis*), needle-and-thread (*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), and cheat grass (*Bromus tectorum*). Common shrubs include mountain mahogany (*Cerocarpus montanus*), bitterbrush (*Purshia tridentata*), and wax currant (*Ribes cereum*). The soils in this area are similar mixtures of Rocky Loam, Stony Loam, and Loamy Foothill Range sites (Moreland 1980).

Sampling design

To select study sites, residential houses (excluding outbuildings) were digitized using geospatial software ArcGIS 10.0 (ESRI 2011) and NAIP (National Agricultural Imagery Program 2009) satellite imagery, using a resolution of 1:4,000 to locate houses and place points (Figure 1a).

A development gradient that captures landscape permeability was created by first using a fixed kernel density estimator in ArcGIS (similar to the methods of Theobald et al. 2012). In our study, the kernel density bandwidth was scaled to each species' average home range sizes, with a buffer area along the boundary of the study area equal to the radius of each species' home range size. To produce the final gradient used for sampling (Figure 1b), the kernel density layer scaled to each species' average home range was used as a resistance layer in a least cost distance map (average home range sizes were obtained from Nowak 1991 and Crooks 2002). Least cost distance maps were created for each species where four surfaces with starting locations along the cardinal boundaries of the study area were averaged for the final gradient map.

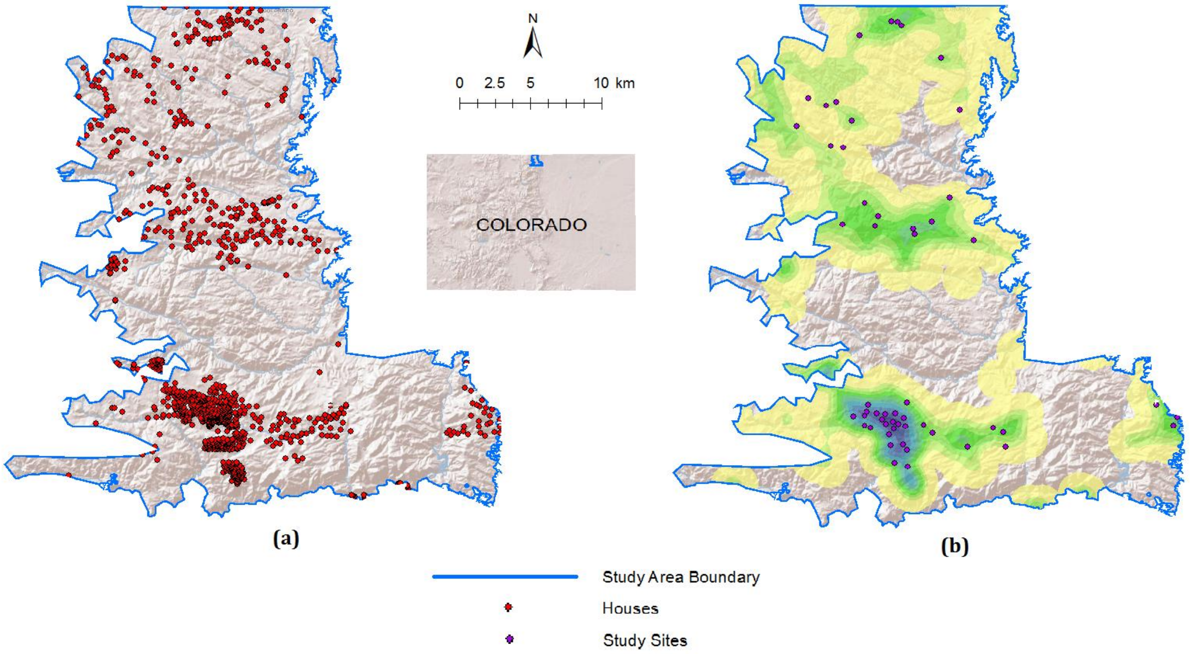

FIG. 1. (a) Study area in Northern Colorado. The southern boundary is the Cache la Poudre River; the northern boundary is the state border with Wyoming. Eastern and western boundaries represent elevation boundaries at 1700m and 2400m, respectively. Red dots show the distribution of individual housing units. (b) Study area with development gradient scaled to the coyote home range size (blue to yellow shading reflects high to low housing density) and study sites (purple dots) where wildlife cameras were located.

Least cost distance surfaces, which are based on percolation theory, reflect effective distance based on landscape resistance rather than simple Euclidean distance, which allows for greater landscape complexity to be incorporated in the model and a visualization of landscape permeability (Berry 1993). Least cost distance provides a visual representation of the relative cost an animal might accrue while traversing an exurban landscape, based on the multiplication of the resistance layer and Euclidean distance. Thus, this metric provides an ecologically relevant surface that captures the important difference between areas close to a single house, and areas that are embedded within high density subdivisions, a distinction that may influence habitat use (Theobald 2006). In essence, our development gradient reflects the cumulative influence of housing at any given location for each species in our study.

In addition, species-specific least cost distance maps were scaled at a range appropriate for each species, since landscape permeability in the same area may be perceived differently between species. The least cost distance maps were normalized using slice analysis to show the gradient at a scale of 1-100. The development gradients are quantitatively relative to this study area, yet the same process can be applied to any landscape, for any species.

The development gradient layer scaled to the coyote (*Canis latrans*) average home range size was used for sampling, since it approximates the median home range size of the suite of mammal species expected within the study area. Because the objectives of our study were to investigate habitat use of multiple species across a specific landscape, using a median species area requirement such as the coyote home range to set a sampling scheme on a relative gradient across a suite of species is appropriate. In addition, mammalian carnivores are useful focal organisms to evaluate the degree of landscape-level functional connectivity (Noss et al. 1996); and coyotes serve as excellent indicators of functional connectivity in highly fragmented areas (Crooks 2002). In our study area, the distribution of housing development across the landscape is highly skewed, so the final refinement to the gradient for sampling purposes was to exclude all cells with a value of 1, which were overrepresented in the original raster distribution and obscured variation among higher development gradient values. Within the final gradient, random points were placed via a stratified random sampling of normalized gradient values across the study area to capture the development gradient as a continuous variable. Fifty-four final points were selected based on the number of successful requests for permission to access private properties and an effort to cover the range of gradient values as evenly as possible (Figure 1b).

Although many of the sites are clustered near the subdivisions, every sampling site was placed at least 500m apart (range to nearest point: 500m-3819m).

Field methods

Data collection occurred during the summer (May-August 2012) and winter (December 2012-March 2013). At each study site, a remotely-triggered camera was placed within 150m of the original randomly established point in an area most likely to detect species, such as wildlife trails, drainages, passes, and ridgelines. The camera stations were unbaited to reduce bias and to ensure accurate estimates of habitat use since no behavioral response is required with this non-invasive technique (Kays and Slauson 2008).

Twenty-seven remotely-triggered cameras (Cuddeback Capture, Primos TruthCam 35, or Wildgame Innovations Micro Red 4) outfitted with bear boxes were placed at half of the study sites and remained in their locations for six weeks (42 trap nights), and were visited every 1-2 weeks for routine maintenance (e.g. to replace memory cards and batteries). The cameras were then moved to a new set of 27 locations for another six weeks (42 trap nights), for a total of 54 points over the sampling period. In the winter season, the cameras were placed in the same locations as the summer to allow for statistical comparison with the summer season, and operated for the same amount of time. This design provides the spatial and temporal variation necessary to capture mammalian habitat use along the development gradient while maintaining the assumption of closure of seasonal occupancy status within the multiple-season occupancy modeling framework (MacKenzie et al. 2003). One site was excluded from final analysis because it burned in the High Park Fire during the summer of 2012. Total percent canopy cover was obtained by ocular estimation in a 25m radius from the camera site.

Human presence and potential influence on wildlife habitat use beyond the presence of housing was documented using sound disturbance sampling during the two seasons. A handheld PDA attended audibility device, programmed by the National Park Service's Sounds and Night Skies division, was used to collect sound information. At each study site, three sound surveys were completed on days when the cameras were visited. Each survey lasted for 15 minutes, during which the presence and duration of natural and anthropogenic sounds were continuously noted. The average percent time anthropogenic noise was audible for each site was considered as a proxy for human activity and included as a covariate in analysis. Hereafter, this covariate will be referred to as "human activity."

Statistical analysis

Species detections (and non-detections) at each site were documented for summer and winter seasons and incorporated into a multiple-season occupancy modeling framework where each season is a primary sampling period, and each week is a secondary sampling occasion (MacKenzie et al. 2003, MacKenzie et al. 2006). Occupancy modeling is appropriate for our study because the framework combines species occurrence information with imperfect detection, which can be significant for non-invasive survey methods such as camera trapping (MacKenzie and Royle 2005). Occupancy models link the probability that an animal occupies an area with the probability that it is detected (Reed 2011), and is an effective way to account for lower detection probabilities given the species is present. The multiple-season occupancy framework is similar to Pollack's (1982) robust design used in capture-recapture studies, which requires multiple samples per primary sampling period, and can also estimate colonization and extinction rates (MacKenzie et al. 2003). The assumptions of the multiple-season occupancy models include maintaining closure within a primary sampling period, independence of sites and detections, and the correct identification of species (MacKenzie et al. 2003).

The perceived relative risks and benefits of activity in an area are species-specific and depend on landscape and habitat structure (Fahrig 2007). Thus, the response of mammals to exurban development and occupancy at various sites may also be influenced by habitat characteristics in close proximity to the camera locations, such as vegetation structure (Riem et al. 2011), and we included habitat covariates in our analysis which may capture this influence (Table 1). Along with the development gradient and human activity, we also considered road density around camera locations to test the effects of human-sourced disturbance (m/m^2). The proportion of privately-owned land in a fixed radius scaled to each species' home range size around the camera locations was included as a covariate, to test how it would compare to the development gradient scaled at the same radius for each species. To incorporate the potential effects of the High Park Fire, the proportion of area burned within a buffer, created with the fixed radius of each species' home range size, was calculated around each camera site. To test for habitat type at a species-specific scale, we calculated the proportion of the area around the camera site in a fixed radius scaled to each species' average home range size that was classified as Forest and Woodland, as well as Shrub and Grassland by the USGS National Gap Analysis (US Geological Survey 2011). At a local scale, the ocular estimate of percent canopy cover in a 25 m radius around each camera site was collected in the field and also tested. Although the presence of water may be a limiting factor for wildlife in xeric habitats, accurate data including the spatial and temporal distribution of water in stock tanks, ephemeral streams, and other natural and non-natural sources in our study area were not available. All analysis was completed at a cell size of 30m, since this was the highest resolution available for most spatial data in the study area.

TABLE 1. Description of variables considered during analysis to test the impact of exurban development on mammalian habitat use.

Covariate	**Abbreviation**	**Description**
Development gradient	gr	Cumulative influence of housing development based on housing density and landscape permeability. Scaled to each species' average home range size, sliced to a value on scale of 1-100.
Human activity	pas, paw	Average percent time anthropogenic noise is audible, calculated from three sound surveys at each camera location for each season.
Road density	road	Density (m/m^2) of all roads around camera location, sourced from US Census Bureau Tiger Roads 2012 data set
Private ownership	own	Proportion of area under private ownership within a fixed buffer with a radius scaled to each species' average home range size
High Park Fire impact	fire	Proportion of area burned in the High Park Fire in the summer of 2012 within a fixed buffer with a radius scaled to each species' average home range size.
Local percent canopy cover	pcs, pcw	Ocular estimate of canopy cover within a 25m radius of camera location, collected in the field.
Forest and woodlands cover	forest	Proportion of area with NVC land cover class Forest and Woodland within a fixed buffer with a radius scaled to each species' average home range size, obtained from USGS National GAP Analysis
Shrub and grasslands cover	shrub	Proportion of area with NVC land cover class Shrub and Grassland within a fixed buffer with a radius scaled to each species' average home range size, obtained from USGS National GAP Analysis
Elevation	elev	Elevation of camera location, in meters, collected in the field

Although other factors may affect species habitat use, *a priori* model sets were chosen based on parsimony and a limited sample size, and we consider all models to be biologically plausible explanations for differences in species occurrence in this landscape. Correlations between predictor variables were informally assessed prior to analysis in the context of parsimony using Spearman's correlation coefficient to develop the candidate model set (See Appendix 2 for correlation matrix for covariates scaled to the coyote). Covariates that had a correlation coefficient value greater than 0.7 were considered collinear (Whittington et al. 2005), and one of the collinear covariates was eliminated in model sets to avoid model over-fitting (Burnham and Anderson 2002). Collinearity was also examined using variance inflation factors (VIF) for all model sets for each species and factors that exhibited a VIF of greater than 10 (Kutner et al. 2004) were aggregated and the model reconsidered. In this analysis, road density and the development gradient were highly correlated ($r=0.769$ for coyote, Appendix 2). Since our questions pertain mainly to the development gradient, we retained this covariate in analysis.

Program PRESENCE (Hines 2006) was used to model site occupancy across multiple seasons. Maximum likelihood estimation and model averaging were used to estimate occupancy probabilities and the potential effects of habitat and anthropogenic covariates for each species (MacKenzie et al. 2006). An ad-hoc hierarchical model building procedure was used (Doherty et al. 2012), where detection probability (p) was compared by season, held constant, or varied by covariates while all other parameters were held constant. The best detection structure was then used to assess whether vital rates (γ and ε) varied by elevation, were constant, or were fixed to zero. The resulting best structure was then used to assess occupancy probabilities (ψ) based on site-specific covariates. Models were run separately for each species which were detected at least once, although some species could only support simple models due to limited detections.

Models were then ranked, compared and evaluated using Akaike's Information Criterion (AIC) with adjustments for overdispersion and small sample size, $QAIC_c$ (Burnham and Anderson 2002). Model fit was assessed by comparing the observed Pearson χ^2 statistic for the most general model for each species with χ^2 statistics obtained from 10,000 simulated bootstrap datasets to obtain a modified overdispersion parameter suitable for occupancy models (MacKenzie and Bailey 2004). The number of camera sites served as the effective size of each model set. Regression coefficients (β estimates) for covariates on ψ retained in the top models were examined for the direction of each species' relationship to housing influence and other habitat covariates, and model-averaged estimates of ψ_1 for individual sites were used for graphing the relationship between habitat use and the housing gradient.

An index of relative activity (RA) was also calculated for each camera station by dividing the number of images of a species detected in a photograph by the number of nights the camera operated at that station for all sample sessions (George and Crooks 2006). RA can be used as an indicator of frequency of habitat use along the development gradient and of potential mammalian spatial displacement from human activities. Because individuals were not identified in the photographs, absolute density was not measured at each sampling point, but the relative activity index can provide a useful measure of relative habitat use by a species. If multiple individuals were captured within a single photograph, each individual (image) was counted separately. The RA index was regressed on development gradient values to determine the effect of exurban housing on species relative activity. Relative activity was calculated for each site for each species, as well as across sites for all species.

Mean RA levels for each species detected at least twice in a greenbelt and non-greenbelt sites within the high-density subdivision in the study area were compared using a one-way

ANOVA with the Wilcoxon Signed Rank test, to determine if species preferentially use habitat in greenbelts in high density subdivisions. The non-parametric test was used because the distribution of RA values did not conform to assumptions of normality. All sites within the Glacier View Meadows area were included (n=24, 12 greenbelt and 12 non-greenbelt sites).

RESULTS

Habitat use

Our remotely-triggered camera stations detected mule deer (*Odocoileus hemionus),* elk (*Cervus canadensis),* moose (*Alces alces),* coyotes (*Canis latrans),* red foxes (*Vulpes vulpes),* black bears (*Ursus americanus*), mountain lions (*Puma concolor),* bobcats (*Lynx rufus),* striped skunks (*Mephitis mephitis)*, Abert's squirrels (*Sciurus aberti*), pine squirrels (*Tamiasciurus hudsonicus),* cottontails (*Sylvilagus nuttallii),* yellow-bellied marmots (*Marmota flaviventris*), domestic dogs (*Canis familiaris*), domestic cats (*Felis catus),* cows (*Bos primigenius),* horses (*Equus ferus caballus*) and people over the summer and winter seasons (Figure 2). There were 2147 total detections in the summer season (2138 trap nights) and 1034 detections in the winter season (2209 trap nights) and the number of detections varied greatly by species (Table 2).

Mountain lions, pine squirrels, marmots, domestic cats, horses, and cows were not detected often enough or at enough sites to allow valid occupancy analysis using Program PRESENCE. Mountain lions were included in relative activity metrics. Coyote, bobcat, Abert's squirrel, moose, elk, and striped skunk data best supported model sets that assumed vital rates (colonization and extinction) were fixed to 0, which extends the closure assumption of occupancy to the entire sample year. However, it is unlikely that these species experienced significant changes in vital rates within one year and they were therefore retained in the analyses.

FIG. 2. Selected photographs from the remotely-triggered wildlife cameras. Clockwise from top left, the species shown are mountain lion (*Puma concolor)*, bobcat (*Lynx rufus)*, American black bear (*Ursus americanus*), coyote (*Canis latrans*), mule deer (*Odocoileus hemionus)*,and moose and calf (*Alces alces)*.

TABLE 2. Species captured by the wildlife cameras, the percent of sites (n = 53) at which each species was observed, and the weighted mean relative activity rates averaged over both seasons.

Species	Percent of Observed Sites	Number of images	Weighted Mean Relative Activity (SE)
Mule Deer	100.0	2059	0.474 (0.011)
Domestic Dogs	45.3	89	0.020 (0.001)
Coyotes	45.3	24	0.006 (0.008)
Humans	41.5	351	0.080 (0.005)
Cottontails	30.2	110	0.025 (0.002)
Red Foxes	22.6	55	0.013 (0.081)
Black Bears	15.1	24	0.011 (0.0005)
Bobcats	15.1	11	0.003 (0.016)
Elk	13.2	14	0.003 (0.00004)
Abert's Squirrels	11.3	40	0.009 (0.008)
Striped Skunks	11.3	13	0.003 (0.0002)
Mountain Lions	11.3	8	0.002 (0.0001)
Horses	9.4	137	0.031 (0.003)
Moose	5.7	31	0.007 (0.0009)

Mammalian habitat use in our study area was almost universally affected by exurban housing. The development gradient covariate on ψ was retained in top model sets (ΔQAIC < 2) for all species included in occupancy analysis except for mule deer, domestic dogs and humans (Table 3, Appendix 1). Model results for all species indicated some level of uncertainty, where no model received >90% of the $QAIC_c$ weight.

Some species, such as red foxes, exhibited strong positive responses to development. ($\beta_{Fox} = 3.17$, Figure 3). Striped skunks ($\beta_{Skunk} = 1.51$), black bears ($\beta_{Bear} = 1.75$), Abert’s squirrels ($\beta_{Squirrel} = 1.96$), cottontails ($\beta_{Cottontail} = 2.16$), also had higher probabilities of habitat use at higher development levels, although some uncertainty surrounded the estimates and strength of the effect of the development gradient on habitat use due to standard error. Interestingly, coyotes and red foxes displayed opposite responses to exurban housing ($\beta_{Coyotes} = -2.51$, Figure 3). Coyotes showed a potential threshold of habitat use at higher housing influences at a relative gradient value of 20, whereas the red fox habitat use probabilities increased starting at a relative gradient value of 30. Bobcats responded negatively to high exurban housing influence ($\beta_{Bobcats}$ = -0.73), along with elk (β_{Elk} = -4.11) and moose (β_{Moose} = -0.66).

TABLE 3. Selected set of top model (ΔQAIC<2) statistics for a subset of mammal species detected in study area. Untransformed coefficients of covariate estimates (β) provided for covariates on ψ. Vital rates and detection removed in subsequent models if the structure is unchanged from top model. See Appendix 1 for model selection tables for all species.

Model	ΔQAICc	w	K	-2l	β1 (se)	β2 (se)
Abert's squirrels						
ψ(elev),p(t.)	0	0.2715	4	109.17	1.99 (1.12)	
ψ(elev+gr),p(t.)	1.88	0.106	5	108.53	1.81 (1.16)	1.96 (2.39)
ψ(elev+shrub),p(t.)	1.9	0.105	5	108.55	2.63 (1.44)	1.50 (1.90)
Bobcats						
ψ(.),p(pa)	0	0.1385	4	92.25		
ψ(forest),p(pa)	0.34	0.1169	5	90.06	-4.80 (4.04)	
ψ(forest),p(t.)	0.61	0.1021	4	92.88	-5.33 (3.62)	
ψ(gr),p(pa)	0.97	0.0853	5	90.72	-0.73 (0.69)	
ψ(.),p(t.)	1.94	0.0525	3	96.69		
ψ(shrub),p(pa)	1.99	0.0512	5	91.78	1.45 (2.21)	
Coyotes						
ψ(gr),p(pa)	0	0.2662	5	166.86	-2.51 (1.37)	
ψ(elev),p(.)	0.75	0.183	3	172.4	-2.36 (1.43)	
ψ(elev),p(pa)	1.33	0.1369	5	168.19	-2.62 (1.40)	
Red foxes						
ψ(gr+elev),γ(elev),ε(elev),p(.)	0	0.3172	8	164.04	3.17 (1.41)	-1.50 (0.98)
ψ(gr),γ(elev),ε(elev),p(.)	0.16	0.2928	7	167.02	1.84 (0.61)	
ψ(gr+own),γ(elev),ε(elev),p(.)	1.77	0.1309	8	165.83	1.90 (0.64)	-2.04 (1.92)
Mule deer						
ψ(elev),γ(.),ε(.),p(t.)	0	0.5639	6	734.95	2.34 (0.79)	

Notes: Definitions of column heads and covariates: $\Delta QAIC_c$ = QAICc distance from top-ranked model; w = Akaike weight; K = number of estimable parameters; -2l = -2 * log likelihood; $\beta_{1 \text{ and } 2}$ = Untransformed coefficients of covariates for covariates on ψ, listed in order. gr = development gradient scaled to each species, pa = percent time anthropogenic noise is audible (human activity), elev = elevation, shrub = proportion of fixed buffer of shrub cover, forest = proportion of fixed buffer of forest cover, own =proportion of fixed buffer of private ownership.

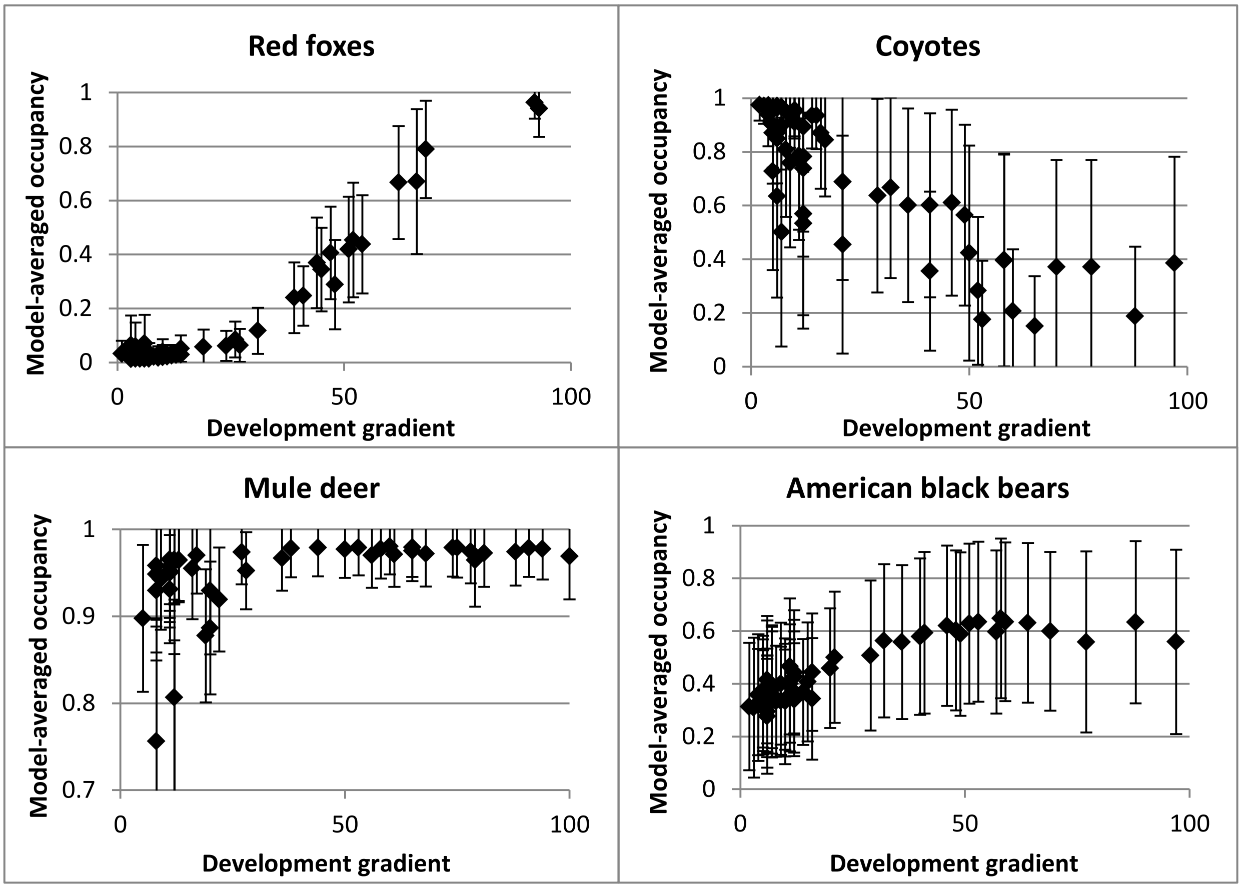

FIG. 3. Model-averaged estimates of ψ_1 for red fox, coyote, mule deer, and American black bear along the development gradient. Standard error bars are the unconditional standard error provided by model averaging.

Due to the High Park Fire during the summer of 2012, five camera sites were taken down three weeks prematurely to avoid equipment loss as the fire tracked north into the study area. Four of the five sites were utilized in the winter season and one, which completely burned, was excluded from final analysis to avoid confounding effects of the fire and possible associated changes in detection probability. Because the fire burned in the southern portion of the study area, only a few sites, depending on the species' home range radius size, were affected by the fire. Since some species had low or no detections at those points, models that included the fire covariate were only supported by three species (mule deer, coyote, and cottontail). The High

Park Fire covariate was retained in top models for the cottontail, although the relationship is not strong (Appendix 1).

Relative Activity

Mule deer were detected the most often, and had the highest mean RA across sites (Table 2). Both domestic dogs and coyotes were detected at 45.3% of sites, but only 24 images of coyotes were captured, whereas 89 images of domestic dogs were collected, leading to their strong difference in relative activity. Overall, sites higher along the development gradient are used more often, indicated by higher mean RA rates; however, species-specific RA rates varied across the gradient (Figure 4). Although the gradient is a relatively weak explanatory variable in occupancy analysis for mule deer, their RA showed that they used sites at higher densities more often than lower density sites. Red foxes also used habitat more frequently in areas with higher housing influence, which corroborates the strong relationship between occupancy probability and habitat use for this species. Notably, elk were not detected at relative development gradient values above 30 in this study; thus, their activity was focused at low influence areas and their activity levels may represent a threshold for housing influence. Bobcats also used habitat less frequently at sites higher along the development gradient.

Greenbelt sites, defined as embedded blocks of undeveloped land owned by either the US Forest Service or the Glacier View Meadows Association within the Glacier View Meadows subdivision were used preferentially by black bears. Black bears demonstrated significantly higher RA on greenbelt sites versus non-greenbelt sites (p=0.0341, Appendix 3). Cottontails and Abert’s squirrels also exhibited non-significant higher activity on greenbelts. Mule deer and red foxes displayed no difference in relative activity on greenbelt sites.

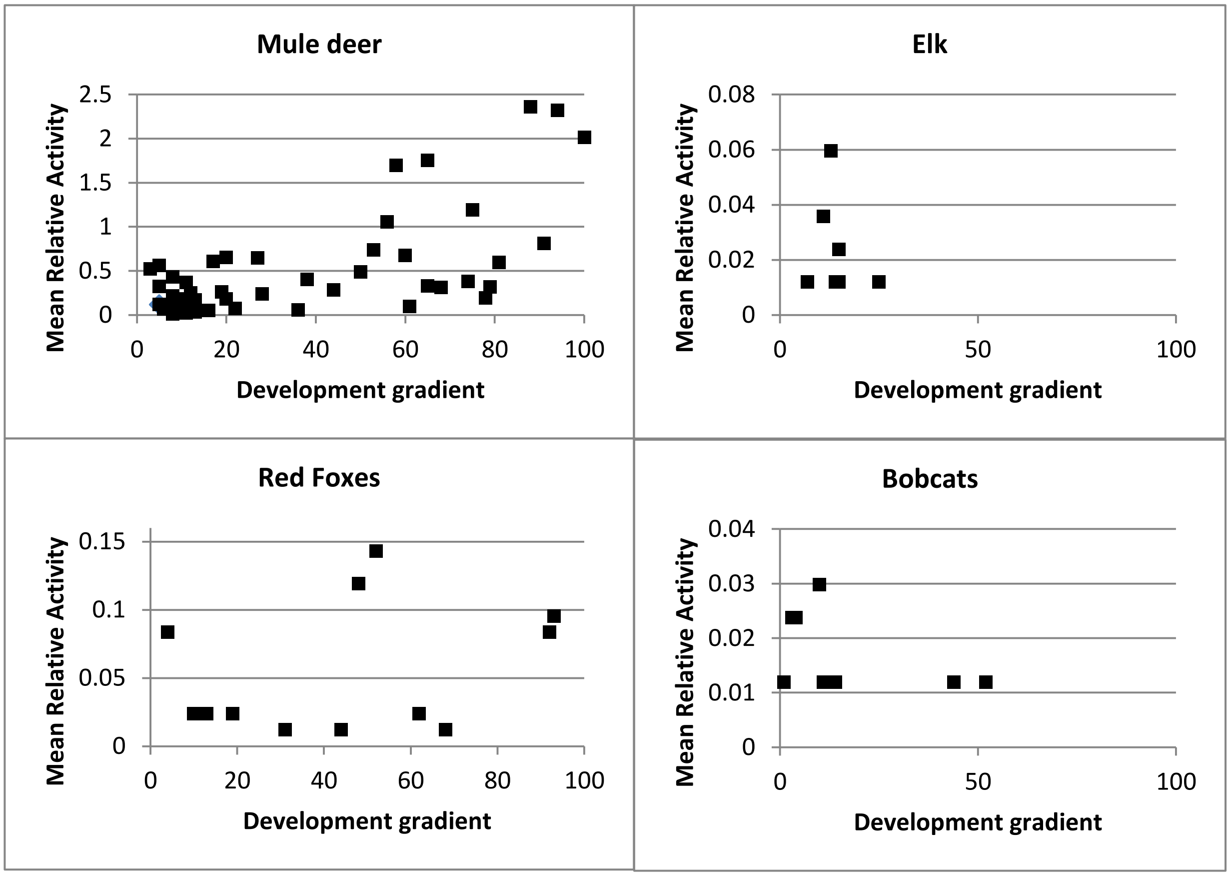

FIG. 4. Relative activity along the development gradient for selected species. Black boxes indicate sites where the species was detected at least once

DISCUSSION

The results of this study demonstrate that even in exurban areas, residential housing affects habitat use for most mammalian species. The direction of this impact varies; for example, some of the larger species in this region exhibited a negative response to higher housing influence. This corroborates previous studies which show some larger carnivores, such as mountain lions, coyotes, and bobcats, are more sensitive to human presence due to large space requirements, low population densities, and low birth rates (Noss et al. 1996; Woodroffe 2000). Consequently, they are often the first species to be locally extirpated in the face of development (McKinney 2002). Past research indicates that presence of humans and dogs affects some species negatively, such as wildlife responses to recreation (e.g. Reed and Merenlender 2011, Lenth et al. 2008). Thus, the higher "occupancy" levels of humans and dogs associated with areas subject to higher housing influence could be a factor explaining why some species such as bobcats rarely use these areas. Notably, moose, bobcats, and mountain lions were detected in higher influence areas, but did not use them frequently according to our relative activity results. For example, although we did not have enough detections of mountain lions to run habitat use models, we did have a detection in a high-influence area, so this habitat is permeable to and still occasionally used by these species, even if rarely.

Conversely, our research suggests that red foxes exhibit higher probabilities of use with high cumulative housing influence. Red foxes are attracted to trails (Lenth and Knight 2008) which may contribute to why foxes use this habitat with greater probability and with higher frequency. In addition, these patterns could be driven by the decline of some larger predators from more densely developed areas, which may result in an increase, or "mesopredator release," of the smaller predators such as red foxes and domestic cats (Crooks and Soulé 1999; Cove et al.

2012). The positive relationships between housing development and other mammal species such as black bears, Abert's squirrels, striped skunks, and mule deer may be due to the availability of human-subsidized food such as cultivated plants and lawns, as well as garbage found in developed areas (McKinney 2002, Baruch-Mordo 2011). Measuring these resources directly was beyond the scope of our study. It has also been suggested that exurban developments will create "private reserves," where deer and other species may concentrate to escape exposure to hunting and predation (Hansen et al. 2005). In our study area, the high density subdivision, Glacier View Meadows, prohibits hunting within its boundaries, so the subdivision may serve as a refuge from both human and non-human predators. In addition, our relative activity results indicate that mule deer and red foxes not only use habitat in more developed areas, they use it more frequently. The higher relative activity rates in high housing influence areas may also be a function of the fact that fewer movement options exist there as compared to undeveloped landscapes. As a result, the cameras along these few but potentially frequently used routes capture more photos of the individuals occupying the high end of the development gradient.

Several mammal species exhibited what appears to be a non-linear response to the development gradient based on graphical representation of model-averaged estimates (Figure 3); these species include red foxes, coyotes, mule deer, and elk. Although we did not test non-linear habitat use models such as quadratic functions due to limited data, the occupancy results for these species visually suggest a threshold response to the development gradient. In previous studies, the relationship between mammalian richness, abundance, and distribution and intensity of exurban development has been shown to be non-linear. For example, gray foxes in New Mexico exhibited tolerance of rural residential development up to 50-125 homes/km^2 (Harrison 1997, Hansen et al. 2005). Other studies have shown that for some bird and butterfly taxa, diversity is highest at moderate levels of development (Racey and Euler 1982; Blair 2001). A non-linear response with mule deer abundance was also detected in an urbanizing valley in Montana, with deer abundance higher in intermediate levels of development (Vogel 1989). The intermediate disturbance hypothesis may also apply to some species' responses to exurban development, considering that disturbance from exurban growth is moderate on a larger scale that includes high-density urban areas and large areas of protected open space. Exurban development may not cause enough disturbance to result in low diversity through competitive exclusion, but may result in too much disturbance to support species incapable of rapid recolonization or adaptation to fragmentation (Connell 1978). Focusing research efforts on exurban development allows for these thresholds to be more closely examined. Because thresholds have important land use and development design implications, explicitly testing the presence and strength of the thresholds that are apparent from this study is a priority for further research.

There is evidence that some species exhibit different occupancy and detection rates between seasons. For mule deer, Abert's squirrels, and cottontails, the top model included detection probabilities that were parsed out by season (p(t.), Table 3); whereas top models for bobcats, coyotes, and domestic dogs included detection that varied by the seasonally-varying covariate of human activity (p(pa.), Table 3). Bobcats and coyotes both had higher detection probabilities in the winter, when human activity levels were lower. On the other hand, mule deer, Abert's squirrels, and cottontails all had lower detection probabilities in the winter, which corroborates past research showing that the detection of some mammals is affected by seasonality (O'Connell et al. 2006), and that mule deer on the Front Range in Colorado will rest more often when snow levels are higher (Kufeld et al. 1988), making them less available for detection.

Model weights also indicated a strong influence of vegetation type on several species' habitat use probabilities, including cottontails, where the forest covariate was retained in the top model. Lagomorphs such as cottontails have been shown in past research to be obligate users of habitats with forest cover (Fuller and DeStefano 2003). The top model sets for bobcats, black bears, and moose also included the forest covariate. Elevation was retained in the top model on occupancy for mule deer, Abert's squirrels, and red fox. Elevation is likely an important driver for mule deer habitat use due to migration patterns, forage availability, and lower predation risk (Pierce et al. 2004), and Abert's squirrels are dependent on Ponderosa pine (*Pinus ponderosa),* which dominate the higher elevations of the study area (Keith 1965). However, it is noteworthy that elevation and the development gradient were relatively correlated ($r = 0.64$, Appendix 2), and all three of these species also retained the gradient in their 1st or 2nd-ranked models based on QAIC weights. Thus, the QAIC weight estimate for the development gradient may be conservative for these species.

Because the development gradient or human activity were retained in top models for all wild species except mule deer, there is evidence that housing development affects the habitat use of many species. Incorporating data on the audible stressors that may affect mammalian habitat use is important since at the process level, most mammals will respond to noise levels as well as the visual cue of structures (Schlesinger et al. 2008). Quantifying the audibility of anthropogenic sound sources can be used as a proxy for human activity, which may be perceived as a risk or an attractor by different species, and can affect habitat use (Lynch et al. 2011, Whittaker and Knight 1998, Frid and Dill 2002). Because exurban development is associated with higher presence of domestic pets, cars, trash cans, and bird feeders (Odell and Knight 2001, Maestas et al. 2003), human activity is an important variable to incorporate into an evaluation of the possible effects of rural development on wildlife. Non-natural noise can adversely affect animals by masking important information, and prolonged exposure to noise has been shown to cause wildlife to avoid certain areas, thereby effectively decreasing available habitat (Sawyer et al. 2006). The fact that these covariates appear in top models for most species implies that various species may respond differently to diverse types of disturbance, whether the disturbance is the visual stimulus of a house or the sounds that indicate higher levels of human activity.

The ‘proportion of private ownership’ covariate was retained in top model sets for only two species: black bears and red foxes. However, the QAIC weight of models including the ownership covariate was always smaller than models including the development gradient. Thus, whether a site is largely surrounded by private or public land is likely less important than the habitat characteristics around it, such as disturbance levels, for predicting wildlife habitat use.

Our relative activity analysis showed that greenbelts are valuable for black bears, which exhibit significantly higher rates of relative activity on greenbelts versus non-greenbelt sites within a high-density subdivision. Other species showed non-significant higher rates, indicating that greenbelts may serve an important function for them as well. In Glacier View Meadows, many yards are not fenced, so the boundaries between a backyard and the adjacent greenbelt are not always clear. Thus, we believe that our estimate of greenbelt importance is conservative. Greenbelts are likely to be increasingly important in developments where yards are fenced more often, since greenbelts could ‘funnel’ wildlife through appropriate habitat embedded in areas of high housing density.

Based on the results of our study, we suggest the following priorities and opportunities for future research. First, our methods can and should be replicated to produce landscape permeability gradients that are relevant to rapidly developing landscapes in other regions, and they should also be applied to other taxa of conservation concern, which may respond quite differently than mid-large mammals to housing density. Visualizing landscape permeability and testing the subsequent patterns of wildlife habitat use along exurban gradients not only allows for a greater understanding of anthropogenic land use impacts, but also provides a platform for prioritizing conservation initiatives at the regional scale (Theobald et al. 2012). Maintaining structural and functional connectivity has become an important objective of conservation scientists and practitioners (Crooks and Sanjayan 2006). The inability of species to follow historic movement paths has profound implications for species interactions, ecosystem processes and species persistence in the face of a changing climate. Managing exurban and other human-dominated landscapes for connectivity thus will become increasingly important if we are to maintain and restore local biodiversity.

Second, and importantly, we did not assess the fitness consequences of exurban development on wildlife. To understand the long-term consequences of development on population viability, it is critical to directly assess rates of survival and reproduction for all species of concern. Although these areas were used by most wildlife in our study, housing development and associated human activities could have insidious effects, resulting in difficult-to-detect ecological traps or population sinks for some species.

Third, the contrasting habitat use patterns of red foxes and coyotes in our study area support past evidence regarding the interspecific interactions between these species (Sargeant and Allen 1989). However, specifically testing the potential changes in interspecific interactions and community structure in an exurbanizing environment is a ripe area of inquiry.

Several important implications for land use planning and conservation science and practice have emerged from our study. Given that exurban developments are permeable to many species, how can we design corridors and greenbelts that allow species to safely move through high-density areas? Maintaining structural and functional connectivity for species through exurban subdivisions is important, especially since many exurban developments are embedded within open space at a larger scale. Understanding the specific characteristics of greenbelts and other corridors that can promote connectivity and wildlife habitat use more effectively will guide future restoration and development projects (Beier and Noss 1998).

Our study also showed that housing in exurban areas can impact habitat use of mammalian species. Thus, the efficacy of development designs which incentivize clustered housing and sets aside open space, such as Conservation Development and Rural Land Use Plans, should be considered more closely. These development schemes are intended to be beneficial for wildlife, but these claims have yet to be thoroughly tested (Milder 2007). Mitigating the impacts of human development and disturbance will be critical in the future to ensuring the functioning of wildlife communities (Pejchar et al. 2007). In addition, in light of the High Park Fire, development design has important implications for regional planning beyond maintaining wildlife habitat, such as response to large-scale disturbance. From our study, it is clear that maintaining a matrix of native vegetation such as in areas around Glacier View Meadows, decreasing human activity levels and housing design and configuration are important components to mitigating development impact to wildlife habitat use and movement in exurban areas. Ultimately, facilitating wildlife habitat use and species diversity in exurbanizing regions will take careful planning at multiple scales and being cognizant that different species exhibit unique responses to residential development (Marzluff 2005).

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APPENDICES

APPENDIX 1: QAIC results for all species ($\Delta QAIC_c < 2$)

Model	ΔQAICc	w	K	-2l	β1 (se)	β2 (se)
Abert's squirrels						
ψ(elev),p(t.)	0	0.2715	4	109.17	1.99 (1.12)	
ψ(elev+gr),p(t.)	1.88	0.106	5	108.53	1.81 (1.16)	1.96 (2.39)
ψ(elev+shrub),p(t.)	1.9	0.105	5	108.55	2.63 (1.44)	1.50 (1.90)
American black bears						
ψ(.),p(.)	0	0.1027	2	111.26		
ψ(shrub),p(.)	0.1	0.0977	3	109.11	-2.53 (1.89)	
ψ(gr),p(.)	0.38	0.0849	3	109.39	1.75 (1.96)	
ψ(own),p(.)	0.68	0.0731	3	109.69	-1.75 (1.47)	
ψ(.),p(forest)	0.82	0.0682	3	109.83		
ψ(gr),p(pa)	0.96	0.0636	4	107.63	2.19 (1.45)	
ψ(.),p(shrub)	1.38	0.0515	3	110.39		
ψ(forest),p(.)	1.54	0.0476	3	110.55	-1.86 (2.31)	
ψ(elev),p(.)	1.54	0.0476	3	110.55	0.38 (0.46)	
ψ(pa),p(pa)	1.91	0.0395	4	108.58	2.25 (1.55)	
Bobcats						
ψ(.),p(pa)	0	0.1385	4	92.25		
ψ(forest),p(pa)	0.34	0.1169	5	90.06	-4.80 (4.04)	
ψ(forest),p(t.)	0.61	0.1021	4	92.88	-5.33 (3.62)	
ψ(gr),p(pa)	0.97	0.0853	5	90.72	-0.73 (0.69)	
ψ(.),p(t.)	1.94	0.0525	3	96.69		
ψ(shrub),p(pa)	1.99	0.0512	5	91.78	1.45 (2.21)	
Cottontails						
ψ(forest)γ(elev)ε(elev)p(t.)	0	0.0893	8	239.43	-2.14 (1.28)	
ψ(forest+gr)γ(elev)ε(elev)p(t.)	0.29	0.0773	9	237.36	-2.71 (1.50)	2.16 (1.56)
ψ(forest)γ(.)ε(.)p(t.)	0.31	0.0765	6	244.63	-2.13 (1.27)	
ψ(fire)γ(elev)ε(elev)p(t.)	0.47	0.0706	8	239.99	6.82 (7.12)	
ψ(.)γ(elev)ε(elev)p(t.)	0.72	0.0623	7	242.71		
ψ(fire)γ(.)ε(.)p(t.)	0.76	0.0611	6	245.17	6.81 (7.08)	
ψ(.)γ(.)ε(.)p(..)	0.95	0.0556	4	250.22		
ψ(shrub)γ(elev)ε(elev)p(t.)	0.96	0.0553	8	240.59	1.58 (1.11)	
ψ(.)γ(.)ε(.)p(t.)	1.02	0.0536	5	247.89		
ψ(shrub)γ(.)ε(.)p(t.)	1.25	0.0478	6	245.76	1.58 (1.11)	
ψ(elev)γ(elev)ε(elev)p(t.)	1.45	0.0433	8	241.18	-0.41 (0.32)	
ψ(elev)γ(.)ε(.)p(t.)	1.74	0.0374	6	246.35	-0.41 (0.32)	
ψ(fire+gr)γ(elev)ε(elev)p(t.)	1.83	0.0358	9	239.22	6.69 (7.53)	1.24 (1.38)
ψ(gr)γ(elev)ε(elev)p(t.)	1.84	0.0356	8	241.65	1.41 (1.35)	
Coyotes						
ψ(gr),p(pa)	0	0.2662	5	166.86	-2.51 (1.37)	

ψ(elev),p(.)	0.75	0.183	3	172.4	-2.36 (1.43)	
ψ(elev),p(pa)	1.33	0.1369	5	168.19	-2.62 (1.40)	
Domestic Dogs						
ψ(.),γ(.),ε(.),p(pa)	0	0.2733	6	302.18		
ψ(shrub),γ(.),ε(.),p(pa)	1.8	0.1111	7	300.74	1.18 (1.01)	
Elk						
ψ(gr)p(..)	0	0.5185	3	82.92	-4.11 (7.25)	
Moose						
ψ(.),p(..)	0	0.1523	2	50.52		
ψ(.),p(t.)	0.11	0.1442	3	48.38		
ψ(forest),p(..)	0.47	0.1204	3	48.74	4.96 (3.93)	
ψ(forest),p(t.)	0.73	0.1057	4	46.66	4.78 (3.75)	
ψ(elev),p(..)	0.92	0.0962	3	49.19	1.03 (1.10)	
ψ(elev),p(t.)	1.11	0.0874	4	47.04	1.03 (1.09)	
ψ(gr),p(t.)	1.58	0.0691	4	47.51	-0.66 (0.78)	
Mule deer						
ψ(elev),γ(.),ε(.),p(t.)	0	0.5639	6	734.95	2.34 (0.79)	
Red foxes						
ψ(gr+elev),γ(elev),ε(elev),p(.)	0	0.3172	8	164.04	3.17 (1.41)	-1.50 (0.98)
ψ(gr),γ(elev),ε(elev),p(.)	0.16	0.2928	7	167.02	1.84 (0.61)	
ψ(gr+own),γ(elev),ε(elev),p(.)	1.77	0.1309	8	165.83	1.90 (0.64)	-2.04 (1.92)
Striped skunks						
ψ(.)p(.)	0	0.1738	2	96.56		
ψ(.)p(pa)	1	0.1054	4	92.02		
ψ(.)p(t.)	1.5	0.0821	3	95.62		
ψ(gr)p(.)	1.78	0.0714	3	95.97	1.51 (1.91)	
ψ(.)p(forest)	1.88	0.0679	3	96.1		
Humans						
ψ(pa),γ(pa),ε(.),p(pc)	0	0.3179	8	327.58	0.57 (0.33)	
ψ(gr),γ(.),ε(.),p(pc)	0.99	0.1938	7	332.01	0.54 (0.32)	
ψ(.),γ(.),ε(.),p(pc)	1.07	0.1862	6	335.22		
ψ(pa+gr),γ(pa),ε(.),p(pc)	1.81	0.1286	9	326.29	0.37 (0.36)	0.39 (0.35)

Notes: Definitions of column heads and covariates: $\Delta QAIC_c$ = $QAIC_c$ distance from top-ranked model; w = Akaike weight; K = number of estimable parameters; -2l = -2 * log likelihood; $\beta_{1 \text{ and } 2}$ = Untransformed coefficients of covariates for covariates on ψ, listed in order. gr = development gradient scaled to each species, pa = percent time anthropogenic noise is audible (human activity), elev = elevation, shrub = proportion of fixed buffer of shrub cover, forest = proportion of fixed buffer of forest cover, own = proportion of fixed buffer of private ownership, pc = percent canopy cover within a 25m radius around camera site.

APPENDIX 2: Spearman correlation matrix for habitat covariates considered in occupancy analysis scaled to the home range size of a coyote. Within each covariate, top number = r, bottom number = p-value with α=0.05. Own=proportion of fixed buffer under private ownership; fire=proportion of fixed buffer burned in the High Park Fire; pas=% time anthropogenic noise is audible in the summer; paw=% time anthropogenic noise is audible in the winter; pcs=% canopy cover in 25m radius in the summer; pcw=% canopy cover in 25m radius in the winter; elev=elevation of camera location; gr=development gradient value scaled to coyote home range at camera site; forest=proportion of fixed buffer of forest cover; shrub=proportion of fixed buffer of shrub cover; road=road density at camera site.

	own	**fire**	**pas**	**paw**	**pcs**	**pcw**	**elev**	**gr**	**forest**	**shrub**	**road**
own	1	-0.1848	-0.2378	0.05979	-0.2023	-0.2622	-0.2379	-0.2987	0.53249	0.61168	-0.412
		0.1853	0.0865	0.6706	0.1463	0.0579	0.0863	0.0298	<.0001	<.0001	0.0022
fire	-0.1848	1	0.14475	0.03633	0.05106	-0.0742	-0.1688	0.10338	-0.1992	0.03297	0.23621
	0.1853		0.3011	0.7962	0.7165	0.5975	0.2268	0.4613	0.1527	0.8147	0.0886
pas	-0.2378	0.14475	1	0.63241	-0.0804	-0.0568	0.15281	0.36128	-0.354	-0.1622	0.61729
	0.0865	0.3011		<.0001	0.567	0.686	0.2747	0.0079	0.0093	0.2458	<.0001
paw	0.05979	0.03633	0.63241	1	-0.1017	-0.1743	-0.1849	0.10355	-0.2194	0.17086	0.31713
	0.6706	0.7962	<.0001		0.4686	0.2119	0.185	0.4606	0.1145	0.2212	0.0207
pcs	-0.2023	0.05106	-0.0804	-0.1017	1	0.63881	0.1765	0.0918	-0.1133	-0.2387	0.03348
	0.1463	0.7165	0.567	0.4686		<.0001	0.2062	0.5132	0.4192	0.0852	0.8119
pcw	-0.2622	-0.0742	-0.0568	-0.1743	0.63881	1	0.42775	0.31704	0.14799	-0.3603	0.03827
	0.0579	0.5975	0.686	0.2119	<.0001		0.0014	0.0207	0.2903	0.0081	0.7856
elev	-0.2379	-0.1688	0.15281	-0.1849	0.1765	0.42775	1	0.64033	0.29568	-0.4373	0.37505
	0.0863	0.2268	0.2747	0.185	0.2062	0.0014		<.0001	0.0316	0.0011	0.0057
gr	-0.2987	0.10338	0.36128	0.10355	0.0918	0.31704	0.64033	1	-0.013	-0.3817	0.76897
	0.0298	0.4613	0.0079	0.4606	0.5132	0.0207	<.0001		0.9262	0.0048	<.0001
forest	0.53249	-0.1992	-0.354	-0.2194	-0.1133	0.14799	0.29568	-0.013	1	0.05773	-0.325
	<.0001	0.1527	0.0093	0.1145	0.4192	0.2903	0.0316	0.9262		0.6814	0.0176
shrub	0.61168	0.03297	-0.1622	0.17086	-0.2387	-0.3603	-0.4373	-0.3817	0.05773	1	-0.3144
	<.0001	0.8147	0.2458	0.2212	0.0852	0.0081	0.0011	0.0048	0.6814		0.0219
road	-0.412	0.23621	0.61729	0.31713	0.03348	0.03827	0.37505	0.76897	-0.325	-0.3144	1
	0.0022	0.0886	<.0001	0.0207	0.8119	0.7856	0.0057	<.0001	0.0176	0.0219	

APPENDIX 3: Results of Wilcoxon Signed Rank test for preferential greenbelt use

Species	**Mean RA Greenbelts (SD)**	**Mean RA Non-Greenbelts (SD)**	**ANOVA F Statistic**	**Wilcoxon Signed Rank (P-value)**
Mule deer	0.665 (0.671)	0.921 (0.769)	0.75	0.1901
Red foxes	0.05238 (0.046)	0.05714 (0.059)	0.02	0.891
Black bears	0.03657 (0.012)	0.08532 (0.038)	7.46	0.0325*
Abert's Squirrels	0.16071 (0.159)	0.03869 (0.026)	2.87	0.1953
Cottontails	0.21145 (0.146)	0.08955 (0.086)	3.69	0.0507

*Note: * indicates significant when α=0.05. RA = relative activity*