The effects of urbanization on population density, occupancy, and detection probability of wild felids

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Abstract. Urbanization is a primary driver of landscape conversion, with far-reaching effects on landscape pattern and process, particularly related to the population characteristics of animals. Urbanization can alter animal movement and habitat quality, both of which can influence population abundance and persistence. We evaluated three important population characteristics (population density, site occupancy, and species detection probability) of a medium-sized and a large carnivore across varying levels of urbanization. Specifically, we studied bobcat and puma populations across wildland, exurban development, and wildland–urban interface (WUI) sampling grids to test hypotheses evaluating how urbanization affects wild felid populations and their prey. Exurban development appeared to have a greater impact on felid populations than did habitat adjacent to a major urban area (i.e., WUI); estimates of population density for both bobcats and pumas were lower in areas of exurban development compared to wildland areas, whereas population density was similar between WUI and wildland habitat. Bobcats and pumas were less likely to be detected in habitat as the amount of human disturbance associated with residential development increased at a site, which was potentially related to reduced habitat quality resulting from urbanization. However, occupancy of both felids was similar between grids in both study areas, indicating that this population metric was less sensitive than density. At the scale of the sampling grid, detection probability for bobcats in urbanized habitat was greater than in wildland areas, potentially due to restrictive movement corridors and funneling of animal movements in landscapes influenced by urbanization. Occupancy of important felid prey (cottontail rabbits and mule deer) was similar across levels of urbanization, although elk occupancy was lower in urbanized areas. Our study indicates that the conservation of medium- and large-sized felids associated with urbanization likely will be most successful if large areas of wildland habitat are maintained, even in close proximity to urban areas, and wildland habitat is not converted to low-density residential development.

Key words: *bobcat; detection probability; exurban landscape;* Lynx rufus; *mark–resight; mountain lion; occupancy; population density;* Puma concolor; *urbanization; wildland–urban interface.*

INTRODUCTION

Urbanization, ranging from low- to high-density residential development, is a leading agent of broadscale landscape change that can substantially alter ecological patterns, processes, and communities (Chace and Walsh 2006, Shochat et al. 2006, McKinney 2008), and it is projected to be a primary cause of landscape fragmentation and biodiversity loss over the next century (Sala et al. 2000, Seto et al. 2012). By influencing habitat selection, space use, and fitness of animals, urbanization can impact wildlife populations in contrasting ways (McKinney 2002, Hansen et al. 2005, Crooks et al. 2010,

Riley et al. 2010). Urbanization can increase population density by restricting animal movement, increasing available forage, or decreasing competition by reducing the population size of competitors (e.g., Crooks and Soulé 1999, Prange et al. 2003, Riley et al. 2006). In contrast, urbanization can decrease population density by reducing habitat quality and quantity, increasing human disturbance, or increasing the population density of competitors (e.g., Bolger et al. 1997, Germaine and Wakeling 2001, Merenlender et al. 2009). Thus, although urbanization can homogenize landscape pattern (McKinney 2006) and cause population declines and reduced diversity of many native species, the juxtaposition and integration of human development with natural areas can also increase landscape heterogeneity and food resources (Murcia 1995, Irwin and Bockstael 2007) and produce greater biodiversity and abundance of some species (McKinney 2008).

Although all types of urbanization can influence habitat suitability, animal movement, and ultimately population characteristics, different forms of urbanization affect these factors to varying degrees. For example, high-density development, characterized by urban (<0.25 acres per residence; SI conversion: 1 acre = 0.405 ha) and suburban (0.25–1.68 acres per residence) areas (Theobald 2005), can create relatively impermeable anthropogenic barriers that restrict movement, inflate density, and alter habitat. The juxtaposition of residential development with wildland habitat (i.e., primarily natural habitat without human development) creates a wildland–urban interface (WUI), which is often characterized by a linear boundary that can significantly alter ecological processes (Radeloff et al. 2005). The "fence effect" (Krebs et al. 1969) and "island syndrome" (Adler and Levins 1994) hypotheses propose that populations that are bounded on all sides spatially (e.g., populations in a fenced enclosure, on an isolated island, or in an urban habitat fragment) exhibit higher densities compared to populations not bounded due to restricted dispersal. Further, populations bounded on only one side of their spatial extent have also been reported to exhibit altered population characteristics. The "home range pile-up" hypothesis predicts that a linear anthropogenic barrier can influence space use and emigration patterns of populations leading to elevated population densities (Riley et al. 2006). Specifically, bobcats (Lynx rufus) in a highly urbanized environment were reported to reach abnormally high population densities adjacent to a major highway compared to populations away from this barrier (Riley et al. 2006).

Other forms and configurations of residential development might not create impermeable barriers to animal movement, but can still considerably influence landscape pattern and heterogeneity and thus habitat characteristics and prey resources. For instance, exurban (1.68–40 acres per residence) and rural (>40 acres per residence) development is characterized by relatively low-density urbanization that is often immersed within wildland areas (Theobald 2004, Brown et al. 2005, Theobald 2005) and can permeate landscapes over much broader spatial extents compared to linear boundaries created by wildland–urban interfaces. Such development often occurs adjacent to wildland areas and can increase landscape heterogeneity through edge effects (Murcia 1995). Thus, low-density urbanization may benefit some species by increasing habitat diversity and food resources, while being permeable to animal movement for traveling and foraging (Gehrt et al. 2010). Nonetheless, anthropogenic disturbance within exurban and rural landscapes can also reduce habitat suitability and quality, animal fitness, and ultimately population density (Hansen et al. 2005, McKinney 2008).

Carnivores are particularly sensitive to altered landscape configuration and composition resulting from human activities due to their life history characteristics, including low population densities, low birth rates, large home ranges, wide-ranging movements, and social structure (Noss et al. 1996, Gittleman et al. 2001, Cardillo et al. 2005). Mammalian carnivores, however, differ in their vulnerability to urban fragmentation (Crooks 2002). Large carnivores, such as pumas (i.e., cougar, mountain lion, panther; Puma concolor), are typically most sensitive to urban fragmentation and most likely to occur in large patches of habitat that are connected to other large natural areas (Crooks 2002, Beier et al. 2010). In comparison, medium-sized carnivores, such as bobcats, may be less sensitive to fragmentation and exhibit greater tolerance to urban development, given suitable habitat and landscape connectivity (Crooks 2002, Riley et al. 2010). Although obtaining reliable information about carnivore populations has proven challenging due to their life history characteristics and secretive nature, recent methodological developments, such as motion-activated cameras (O'Connell et al. 2010), have better enabled researchers to study their populations.

Our goal was to evaluate the effects of urbanization on the populations of two carnivores, the bobcat and puma, with varying sensitivities to human impacts. We evaluated how three key ecological parameters (population density, site occupancy, and species detection probability; collectively referred to as population characteristics), differed for wild felids among landscapes influenced by varying levels of urbanization, ranging from wildland–urban interface to exurban to wildland habitat. Specifically, we estimated population characteristics for bobcats and pumas to evaluate (1) the home range pile-up hypothesis in relation to a wildland–urban interface and (2) how felid populations responded to low-density residential development. In addition to estimating population characteristics of felids, we also estimated occupancy and detection probability of key prey species to evaluate potential differences in available food resources of carnivores among different levels of urbanization. If residential development restricts movement and inflates felid density, as predicted by the home range pile-up hypothesis (Riley et al. 2006), or if it enhances landscape heterogeneity and carnivore prey populations, as might particularly be the case in low-density residential development, we would expect higher population characteristics of felids associated with these areas. Conversely, if felids avoid residential development due to human disturbance and reduced habitat suitability, we would expect lower population characteristics in such areas. By evaluating the impacts of different forms of urbanization on populations of two different wild felids, we provide novel and important information about wildlife conservation in landscapes influenced by exurban and urban development.

Study Area

We conducted our research across two study sites in Colorado, USA that exhibited varying degrees of urbanization and human influence. Within each study
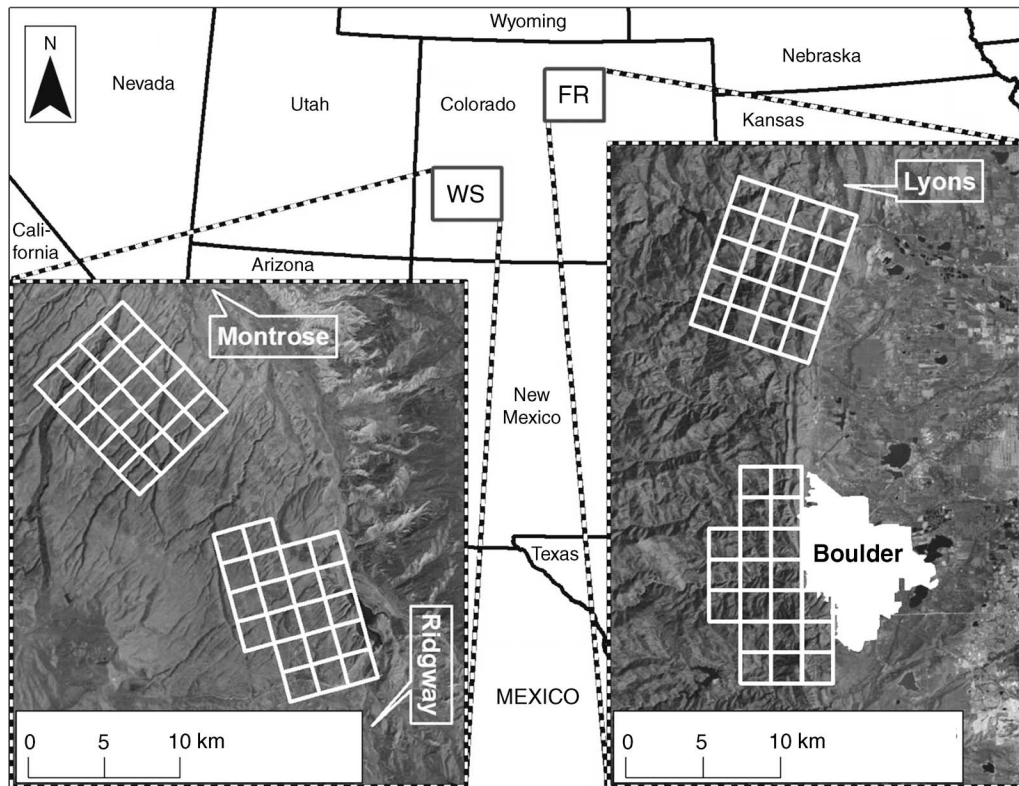
Fig. 1. Locations of two study sites in Colorado (CO), USA exhibiting varying levels of urbanization, where bobcats and pumas were fit with GPS collars and grids of motion-activated cameras were maintained. The more rural Western Slope (WS) was characterized by an exurban development south grid and a wildland north grid during 2009–2010. The more urbanized Front Range (FR) study area was characterized by a wildland–urban interface (WUI) south grid and wildland north grid during 2010–2012.

area, we evaluated felid populations that occurred on two grids that were characterized by similar elevation, vegetation types, and landscape characteristics, but differed in the degree of urbanization. Extensive areas of habitat that supported felid populations surrounded both of our study areas.

In 2009, we worked on the Western Slope (WS) of Colorado on the relatively rural Uncompahgre Plateau near the towns of Montrose and Ridgway (Fig. 1). The area was characterized by mesas, canyons, and ravines, with elevations ranging from 1800 m to 2600 m and annual precipitation of 43 cm, arriving primarily from winter snows and summer thunderstorms (NOAA National Climatic Data). Common vegetation communities included pinyon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma*), ponderosa pine (*Pinus ponderosa*), aspen (*Populus tremuloides*), Gambel oak (*Quercus gambelii*), and big sagebrush (*Artemesia tridentata*). The WS included extensive areas of undeveloped wildland habitat managed by the Bureau of Land Management (BLM), U.S. Forest Service (USFS), and private landowners. Paved and unimproved dirt roads occurred throughout the WS. We divided the WS study site into two sampling grids. The southern grid included exurban and rural residential development on Log Hill Mesa

(human population = 1041; U.S. Census Bureau 2010); housing density was low, with parcel sizes occurring at 1, 2, 5, ≥5, and ≥40 acres. Log Mill Mesa was historically used as ranchland, with the conversion to exurban residential development occurring primarily over the last 25 years. Within areas of exurban development, potential travel corridors of natural habitat and open space property, often with associated recreation trails, were present. The northern grid sampled primarily undeveloped, wildland habitat, although some small areas of low-density human residences and hunting camps occurred on or near the grid.

In 2010, we worked on the more urbanized Front Range (FR) of Colorado (Fig. 1). The area was characterized by foothills and valleys, ravines and canyons, and mountainous terrain, with elevations ranging from 1600 m to 2500 m and annual precipitation of 53 cm, arriving primarily from winter snow and summer thunderstorms (weather stations at Ridgway, Colorado for the WS and Boulder, Colorado for the FR, NOAA National Climatic Data, *available online*).[6] Common vegetation included ponderosa pine, Douglas-

[6] http://www.ncdc.noaa.gov/data-access/land-based-station-data/land-based-datasets

fir (*Pseudotsuga menziesii*), juniper, aspen, and mountain mahogany (*Cercocarpus montanus*). An extensive network of open-space properties with recreational trails were managed by Boulder City Open Space and Mountain Parks (OSMP) and Boulder County Parks and Open Space (BCPOS). The USFS and BLM also managed undeveloped land on the western portion of the FR study area. Paved and unimproved roads occurred throughout much of the FR, although several areas were only accessible by trail. Similar to the WS, we divided the FR study area into two sampling grids. The southern grid occurred adjacent to the wildland–urban interface associated with the city of Boulder (population = 97 385; U.S. Census Bureau 2010) and was characterized by OSMP and BCPOS open-space properties with some human residences on or near the grid. The WUI was characterized by a distinct boundary of urban development juxtaposed with open-space properties over the length of ~20 km, of which our grids sampled 14 km. The WUI was assumed to be a movement barrier for bobcats and pumas and this was supported by telemetry locations of felids during 2010 (J. S. Lewis, *unpublished data*). The northern grid occurred across undeveloped BCPOS and USFS properties, although a small number of human residences occurred on private property inholdings. Shortgrass prairie, agricultural fields, and associated riparian corridors occurred to the east of both sampling grids and surrounded the city of Boulder.

METHODS

Sampling grids and camera surveys

Each study area (WS and FR) contained 40 motion-activated cameras divided between two camera grid arrays spaced ~6 km apart (Fig. 1). Each grid was 80 km^2, consisting of 20 2 × 2 km grid cells (the total area sampled per study area was 160 km^2). Our study design was consistent with a retrospective observational study (Williams et al. 2002) with a treatment (exurban grid on the WS and wildland–urban interface grid on the FR) and control (wildland grids on the WS and FR).

Within each grid cell, we placed one motion-activated camera at a site that we believed maximized the opportunity to photograph bobcats and pumas. Cameras were placed along game trails, people trails, and secondary dirt roads with felid sign (primarily scats, scrapes, and marking sites) or in areas that appeared to be likely travel routes. Each camera was set up ~4 m from the travel route in a perpendicular orientation and was housed in a metal security box 0.75 m high on a tree or metal post. Our sampling was passive in that we did not use attractants (i.e., sight, sound, scent) to lure animals to the camera location. We used Cuddeback (Non Typical, Green Bay, Wisconsin, USA) capture motion-activated cameras (with a 30-s delay) with a white flash to obtain color photographs during the day and at night, except at one site along a human recreation trail on the FR, where we switched to using a Cuddeback Attack Infra-Red camera to reduce vandalism.

Cameras operated on the WS from 21 August to 13 December 2009 and on the FR from 1 October 2010 to 31 December 2010.

We considered photographs of bobcats and pumas taken at a camera site to be independent if images were obtained >1 hour apart. If two adult felids were photographed <1 hour apart and could be differentiated based on natural or artificial markings (i.e., telemetry collars and ear tags), these photographs were also counted as independent animals. Kittens and dependent offspring (individuals typically of small body size and often accompanied by their mother in photographs) were not considered independent animals and were excluded from analyses.

Animal capture

Bobcats were captured in black metal-wire cage traps (40 × 55 × 100 cm) from mid-June through March 2009–2011. All cage traps were fit with very high frequency (VHF) trap transmitters (Telonics, Mesa, Arizona, USA), which were monitored throughout the day, and indicated when trap doors closed. Captured bobcats were immobilized through hand-injection of a combination of Ketamine (10.0 mg/kg) and Xylazine (1.0 mg/km), and Yohimbine (0.125 mg/km) was used to reverse Xylazine (Kreeger et al. 2002). We fit GPS collars (210–280 g, Telemetry Solutions, Concord, California, USA) with timed drop-off mechanisms and degradable cotton spacers along the collar belting on adult-sized bobcats. GPS collars were programmed to record locations on the WS every 5–7 h and on the FR every 3–4 h. Bobcats were weighed, sex was recorded, and age was estimated based on body size, tooth development (Crowe 1975), and tooth wear and coloration (i.e., less worn, white teeth indicating younger animals and worn, yellowed teeth indicating older animals). Pumas were captured from 2005 to 2011 with the use of hounds and baited cage traps, immobilized with Telazol (5.0–9.0 mg/kg), and fit with GPS collars (Lotek, Newmarket, Ontario, Canada; Northstar, King George, Virginia, USA; Vectronics, Berlin, Germany) programmed to record a location every 5–7 h on the WS and 3–4 h on the FR. To increase the duration of time that location data were acquired for adult male pumas on the WS, some individuals were fit with VHF collars (Lotek) and aerial positional locations were obtained approximately every two weeks. Pumas were also weighed, fit with ear tags, and sex and age were recorded. If scale weights on felids were unavailable at the time of capture, body weight was estimated based on animal size and sex. Weight generally increased across categories of small females, large females, small males, and large males. Methods for animal capture were approved by the Colorado State University Animal Care and Use Committee (11-2453A).

Estimating population size and density

Using data from marked and unmarked individuals, we conducted population modeling using a two-step

approach: first we estimated the population size and then we used telemetry information of marked individuals to estimate density.

Individually marking and identifying animals.—For analyses, we created capture histories based on the resightings of individuals that were uniquely marked. Each bobcat was assigned a unique color combination between the GPS collar and ear tags; this information, along with the animal's natural pelt pattern, was used for identification of marked individuals in photographs obtained from motion-activated cameras. During captures, photographs were taken of the bobcat's head, body, legs, and tail (Heilbrun et al. 2003) to aid in identifying bobcats on motion-activated cameras prior to them being physically captured and marked. Individually marked pumas were identified by evaluating unique collar and ear tag characteristics, as well as the proximity of GPS locations to camera sites in relation to photo times. In contrast to bobcats, pumas are typically not individually identifiable by pelt patterns. Thus puma photos from motion-activated cameras obtained prior to their physical capture could not be linked to subsequent photos of individuals after they were marked; thus pumas captured partway through our camera surveys were not included in the marked sample and all of their photos were classified as unmarked. Photographs of animals that were not physically captured were classified as unmarked individuals.

Mark–resight population size estimation.—To estimate population size ($\hat{N}$), we used mark–resight techniques and the Poisson log-normal mixed-effects model (PNE; McClintock et al. 2009, Alonso 2012, McClintock and White 2012) using the R (R Development Core Team 2014) package RMark (Laake and Rexstad 2013) to construct models in Program MARK (White and Burnham 1999). Mark–resight models use encounter data (e.g., photos from motion-activated cameras) of marked and unmarked animals to estimate $\hat{N}$ (McClintock and White 2012). We used the PNE mark–resight model because, with motion-activated cameras, sampling is with replacement, and we individually identified marked animals. We satisfied the critical assumption of mark–resight models that the sighting probability of marked individuals was representative of the entire population by marking individuals via physical capture and using a different method (i.e., motion-activated cameras) to resight individuals. Three parameters were estimated in mark–resight PNE models: (1) α_j (alpha), the intercept for mean resighting rate during primary interval j; α is similar to capture probabilities in mark–recapture estimators; (2) σ_j (sigma), individual heterogeneity level of resighting during primary interval j (σ_j^2 is the additional variance due to a random individual heterogeneity effect); and (3) U_j, number of unmarked individuals in the population during primary interval j (McClintock 2012, McClintock and White 2012). If the population is not closed geographically, as was the case in our study, then mark–resight models estimate the

super population size ($\hat{N}^*$), or the number of individuals that used the sampling grids during the period of our camera surveys (McClintock and White 2012).

We considered three covariates that could affect the parameters α and σ in our mark–resight models. Weight (in kg) was included in modeling because it is positively correlated with home range size both interspecifically (Harestad and Bunnel 1979, Ottaviani et al. 2006) across mammals and intraspecifically within bobcats and pumas (Gompper and Gittleman 1991, Grigione et al. 2002); thus, we predicted animals with greater home range size would be more likely to be photographed because they would be expected to encounter more cameras on a grid. We considered Sex as a covariate due to potential differences between males and females related to photographic rates, predicting that males would move more than females and thus possibly be photographed more often. The covariates Sex and Weight were highly correlated (for WS bobcats, $r = 0.75$; for WS pumas, $r = 0.92$, for FR bobcats, $r = 0.55$, for FR puma, $r = 0.98$), where males typically weighed more than females; due to the potentially confounding interpretation of these covariates, we excluded one from our mark–resight modeling procedure. To determine which covariate was most appropriate to include in our final set of candidate models, we evaluated which hypothesis (i.e., Sex or Weight) had stronger support, based on Akaike's information criteria corrected for small sample size (AIC$_c$; Burnham and Anderson 2002), when evaluating the influence of these covariates on the parameters α and σ in mark–resight models. Based on model comparisons, Weight (α(Weight), σ(Weight)) was the more supported covariate in mark–resight models, compared to Sex (α(Sex), σ(Sex)), in three out of four evaluations (i.e., WS bobcat, WS puma, FR bobcat: ΔAIC ranged between 2.43–5.50), and each covariate demonstrated similar support in mark–resight models for the FR puma evaluation (ΔAIC = 0.39; Appendix A: Table A1). Further, Harestad and Bunnel (1979) concluded that differences in home range size related to sex were largely attributed to sex-related differences in weight. Therefore, we retained Weight in our analyses because we believed that it best reflected potential differences in space use (and thus photographic rates) across adult individuals and within gender categories; the extent of space use was predicted to increase across small females, large females, small males, and large males. Lastly, the covariate Time spent on grid for an individual (TSOG$_{indiv}$) was included because we predicted that the more time an animal spent on the sampling grid, the more likely it was to be photographed. TSOG$_{indiv}$ was estimated with telemetry data collected concurrently with the camera surveys. White and Shenk (2001) advised that telemetry data collected during times that were not concurrent with resighting surveys could also be used to estimate the time spent on the sampling grid. When this was not possible (e.g., due to collar malfunction), we used the mean value of

$TSOG_{indiv}$ across all animals ($TSOG_{pop}$) for an individual without a unique estimate of $TSOG_{indiv}$, as recommended by Cooch and White (2012: Chapter 11, Individual covariates).

Sets of candidate models were created a priori and models were compared using AIC_c. To test for individual heterogeneity (i.e., variation in resighting rates among individuals), models with no individual heterogeneity (i.e., $\sigma = 0$) were compared to models with individual heterogeneity (i.e., σ estimated). We created a candidate model set (with 20 models per set) that included all possible additive combinations of Weight, $TSOG_{indiv}$, Weight + $TSOG_{indiv}$, and constant structures (i.e., intercept-only parameterization: denoted as (.) in model names) for α and σ, and also considered models with $\sigma = 0$. We fit this model set to data from each grid, as well as both grids combined for each study area (Appendix B: Tables B1–B12). When covariates are used in mark–resight models, model convergence is sensitive to initial values for parameters; therefore, we first ran a simple model in which all parameters were constant ($\alpha(.)\sigma(.)U(.)$), and then used these parameter estimates as initial starting values in models with covariates (McClintock 2012). We report model-averaged estimates (i.e., estimates obtained by averaging values, based on AIC_c weights, across all models in a set of candidate models) of the population size (the derived parameter $\hat{N}$) to incorporate model uncertainty (Burnham and Anderson 2002). In addition, we model-averaged estimates of covariates (Lukacs et al. 2010) and calculated variable importance values for covariates across all models (Burnham and Anderson 2002, Anderson 2008).

Estimating density using $TSOG_{pop}$.—We used model-averaged estimates of population size ($\hat{N}$) from the mark–resight models and the proportion of time spent on the grid by the sampled population ($TSOG_{pop}$; referred to as $\bar{p}$ by White and Shenk 2001) to estimate population density (number of individuals per unit area, in this case 100 km^2) for our study areas (White and Shenk 2001). First, TSOG for each individual ($TSOG_{indiv}$; referred to as p_i by White and Shenk 2001) is estimated by dividing the number of telemetry locations on the grid (g_i) by the total number of locations for the individual during the time period of interest (G_i), or formally $TSOG_{indiv} = g_i/G_i$. Next, the mean of $TSOG_{indiv}$ across all telemetered individuals ($TSOG_{pop}$) and the estimate of $\hat{N}$ are used to estimate density as: $\hat{D} = (N \times TSOG_{pop})/A$, where A is the area of the sampling grid. The numerator of this expression represents the number of individuals that used the grid during the primary period multiplied by the proportion of time individuals were on the grid; thus the abundance estimate is adjusted to the area of the grid. The variance of $\hat{D}$ is estimated as (White and Shenk 2001):

$$\mathrm{Var}(\hat{D}) = \left(\hat{N}^2 \, \hat{\mathrm{Var}}(TSOG_{pop}) + TSOG_{pop}^2 \, \hat{\mathrm{Var}}(\hat{N}) \right)/A^2$$

and was used to estimate standard errors. Although photos of pumas that were physically captured (and thus marked) partway through the camera surveys were classified as unmarked animals for estimating $\hat{N}$, as described previously, their telemetry data were used to estimate $TSOG_{pop}$. In addition, if $TSOG_{indiv}$ was unavailable for a felid (e.g., due to collar malfunction) and a mean value of $TSOG_{indiv}$ was used in mark–resight models, as described previously, these values were excluded from estimation of $TSOG_{pop}$ for density.

White and Shenk (2001) cautioned that TSOG techniques can lead to estimates of $\hat{D}$ that are biased high if animals spending little time on the grid are less likely to be captured than animals that spend most of their time on the grid. In our study, we physically captured animals across the entirety of the sampling grids, including areas along the edge of the grid and areas toward the interior of the grid, as well as off of the sampling grids. In addition, due to the relatively large home ranges of bobcats and pumas, animals captured toward the interior of the grids often spent considerable time off of the grids as well. Thus, the potential for this bias was minimized. In addition, we accounted for individual variation in the resighting rate that is used to estimate abundance in mark–resight models by including the covariate $TSOG_{indiv}$.

Occupancy modeling

Occupancy models are commonly applied to evaluate the distribution of animals in relation to landscape characteristics (MacKenzie et al. 2006). Further, occupancy modeling might be appropriate to use as a surrogate for abundance because detection/non-detection data are related to population density (MacKenzie and Nichols 2004, MacKenzie et al. 2006, Noon et al. 2012). Although coarser than population density, occupancy (Ψ; the proportion of the landscape used by the species) and species detection probability (p; the probability of detecting a species given that it was present at a site) are related to the distribution of abundance across the area of interest (Royle and Nichols 2003, Royle et al. 2005). Therefore, we predicted that occupancy and detection probability would follow patterns similar to those described for population density in relation to urbanization. Animals may exhibit high estimates of occupancy across a heterogeneous landscape (indicating use of many different sites), but the relative use of sites can vary widely depending upon how animals select for habitat characteristics. This argument is the foundation for studies of resource selection in which animals may occur across broad spatial extents (i.e., occupy most of the landscape) but select for or against specific landscape characteristics depending on species–habitat relationships (e.g., Manly et al. 2002). Although many factors influence detection probability and it is often considered a nuisance parameter in occupancy models (MacKenzie et al. 2006), detection probability can be

evaluated using covariates in occupancy models to understand the relative use of sites and local population abundance (Royle and Nichols 2003, Royle et al. 2005). We evaluated the behavioral response of animals to landscape features by investigating how detection probability, which reflected the frequency of use of an area by the species, varied in relation to habitat covariates. We hypothesized that species would be more likely to frequent areas of greater habitat quality and thus exhibit higher estimates of detection probability at preferred sites, and that species would use lower quality habitat with less frequency and thus demonstrate lower estimates of detection probability at such sites.

We used single-species single-season occupancy models to estimate occupancy and detection probability (MacKenzie et al. 2006) for both bobcats and pumas in each study area across five sampling occasions, with each sampling occasion occurring over 22 days on the WS and 18 days on the FR. We used the R (R Development Core Team 2014) package RMark (Laake and Rexstad 2013) to construct occupancy models in Program MARK (White and Burnham 1999). We used a three-step approach to construct models in our occupancy analysis. First, we evaluated whether survey effort influenced detection probability at our two study areas. Although uncommon, not all cameras operated for the same number of days due to camera malfunction, expired batteries, full memory cards, vandalism, or theft of cameras. We thus calculated a covariate Effort that varied over time (i.e., five sample occasions) that reflected the amount of functional time that each camera operated for an occasion. This covariate represented the proportion of days the camera was operational during a given sampling occasion (e.g., if a camera operated 15 out of 18 days during a sampling occasion, then Effort equaled 0.83 for this occasion). Using the global model structure on the occupancy parameter (see next section), we fit a model with constant detection probability ($p(.)$) and compared it to a model in which detection probability varied with Effort (p(Effort)). If p(Effort) was more supported than $p(.)$ based on AIC_c scores, then p(Effort) was included in all subsequent models.

Second, two covariates (Grid and Human development) were used to model potential variation in occupancy and detection probability among sites (i.e., camera locations). The covariate Grid compared camera sites between either exurban and wildland areas (on the WS) or wildland–urban interface and wildland areas (on the FR). The covariate Human development characterized the amount of human influence (Lewis et al. 2011) associated with each camera location. To determine an appropriate human development value for each camera location, we created a human development layer in which each human occurrence point (HOP; residence or structure) in the study areas was digitized as a point using ArcMap10 geographic information system (GIS) software (ESRI, Redlands, California, USA) from color

orthophotos (Lewis et al. 2011). Using Arc Toolbox in ArcMap10, we fit a Gaussian kernel over each HOP, where the density, or influence, was greatest directly at the point of interest and decreased out to a specified radius of a circle; radii ranged in 100-m increments from 100–1000 m on the WS and 100–1500 m on the FR. In GIS, each camera location was intersected with the cumulative kernel density of human development across each radius. For occupancy modeling analyses, human development was standardized by subtracting the sample mean from the input variable values and dividing by the standard deviation (Schielzeth 2010). To determine which spatial scale of human development was appropriate for each species and study area, we compared univariate models in which detection probability was modeled as a function of the human development covariate across radii, and we used AIC_c model-ranking to determine the most supported scale to use (Lewis et al. 2011). Based on this approach, we used a radius of 200 m for bobcats and pumas on the WS and 1300 m for bobcats and 300 m for pumas on the FR.

Finally, we evaluated the influence of our two covariates (Grid and Human development) on both occupancy and detection probability by fitting a candidate model set consisting of all possible combinations of Grid, Human development, both, or neither (constant) structures (16 models) to data for each species and study area (Appendix B: Tables B13–B16). For each covariate and parameter, we report model-averaged estimates and variable importance values (Burnham and Anderson 2002, Lukacs et al. 2010).

Because the availability of prey is an important factor influencing felid density (Logan and Sweanor 2001, Ferguson et al. 2009, Ruth and Murphy 2010) across study areas, we estimated the occupancy and detection probabilities using camera data for the primary prey species of bobcats (cottontail rabbits *Sylvilagus* spp.; J. S. Lewis, R. N. Larson, and K. R. Crooks, *unpublished data* on scat analysis) and pumas (mule deer *Odocoileus hemionus* and elk *Cervus elaphus*) (Sunquist and Sunquist 2002) for each grid, using methods explained previously for felids evaluating Ψ(Grid), p(Grid) models.

RESULTS

Photos from motion-activated cameras

All motion-activated cameras on the WS and FR obtained at least one photograph of a felid during our surveys. On the WS, we obtained 185 photographs of bobcats across 38 sites and 80 photographs of pumas across 23 sites during 113 days (Table 1). On the FR, we obtained 150 photographs of bobcats across 32 sites and 96 photographs of pumas across 36 sites during 92 days (Table 1).

Animal capture and telemetry data

We physically captured and marked 20 bobcats and 9 pumas on the WS and 16 bobcats and 10 pumas on the

TABLE 1. Summary of marked individuals, photos, population size, TSOG (time spent on grid), and density for bobcats and pumas in relation to exurban (Exurb) and wildland (Wildl) grids on the Western Slope (WS) in 2009 and wildland–urban interface (WUI) and wildland grids on the Front Range (FR) in 2010, Colorado, USA.

	WS study area species and grids						FR study area species and grids					
	Bobcat			Puma			Bobcat			Puma		
Variable	Exurb	Wildl	Both	Exurb	Wildl	Both	WUI	Wildl	Both	WUI	Wildl	Both
No. marked animals												
Detected	9	8	17	3	6	8	5	8	13	4	5	9
Present	11	10	20	4	6	9	8	9	16	4	5	9
No. marked photos	42	24	66	17	33	50	25	20	45	28	29	57
No. photos/marked individual												
Mean	3.82	2.40	3.30	4.25	5.50	5.56	3.13	2.22	2.81	7.00	6.00	6.00
Median	3.00	1.50	2.50	5.00	3.00	4.00	2.50	1.00	2.50	7.00	6.00	6.00
Range	0–15	0–7	0–15	0–7	2–19	0–26	0–13	0–6	0–13	1–13	2–10	1–13
α (SE)†,‡	2.62 (0.57)	2.25 (0.56)	2.61 (0.45)	4.25 (1.03)	3.91 (1.25)	3.52 (0.77)	1.71 (0.99)	2.19 (0.51)	2.05 (0.56)	7.00 (1.32)	5.80 (1.08)	6.24 (0.92)
No. unmarked photos	56	49	105	22	8	30	56	49	105	22	17	39
N (SE)‡	25.55 (3.00)	30.32 (5.61)	52.62 (6.25)	9.06 (1.63)	7.35 (0.77)	14.37 (1.62)	23.07 (8.20)	30.84 (5.91)	55.07 (11.41)	7.07 (0.88)	7.58 (0.76)	14.74 (1.27)
TSOG (SE)	0.50 (0.12)	0.63 (0.10)	0.59 (0.08)	0.12 (0.02)	0.30 (0.13)	0.25 (0.09)	0.53 (0.13)	0.52 (0.11)	0.56 (0.08)	0.33 (0.13)	0.36 (0.13)	0.34 (0.09)
Area (km^2)	80	80	160	80	80	160	80	80	160	80	80	160
Density (SE) (no. individuals/100 km^2)	15.96 (2.01)	23.99 (2.87)	19.37 (3.33)	1.34 (0.30)	2.76 (1.04)	2.23 (0.76)	15.26 (3.14)	19.84 (2.71)	19.23 (4.69)	2.94 (1.21)	3.40 (1.26)	3.17 (0.89)

† Alpha is the mean resighting rate estimated from mark–resight models (see *Methods*).

‡ Model-averaged estimates and unconditional standard errors (SE).

FR (Table 1). $TSOG_{indiv}$ ranged from 0.08–1.0 for bobcats and 0.08–0.73 for pumas on the WS and 0.06–0.99 for bobcats and 0.03–0.80 for pumas on the FR. Estimates of $TSOG_{pop}$ were similar for felids between grid areas on the FR and were lower for bobcats and pumas on the exurban grid compared to the wildland grid on the WS (Table 1). Bobcats spent more time on the WS wildland grid compared to FR wildland grid, which is consistent with smaller bobcat home ranges on the WS compared to the FR (J. S. Lewis, *unpublished data*).

Density and mark–resight models

Consistent with predictions of reduced habitat suitability in low-density development, on the WS, population density appeared to be lower for wild felids in exurban development compared to wildland habitat (Fig. 2a). For bobcats, 95% confidence intervals for exurban and wildland grids overlapped by 18% (percentage overlap between margin of errors equaled 35%). For pumas, the WS wildland estimate exhibited higher variability, where the lower bound of the 95% confidence interval completely overlapped the margin of error for the exurban estimate, however, the exurban estimate exhibited a tighter 95% confidence interval, with the upper margin of error equaling 2.11. Counter to predictions regarding home range pile-up, population density was not greater for bobcats and pumas along the wildland–urban interface compared to wildland habitat on the FR (Table 1, Fig. 2b). The 95% CIs for exurban and wildland grids overlapped by 61% for bobcats and

91% for pumas, and margin of errors between grids overlapped completely for each felid. For some mark–resight model sets, larger individuals that spent more time on the sampling grid were photographed more often (i.e., exhibited the highest resighting rate; Table 2; Appendix B: Tables B1–B12). These relationships were strongest for felids on the WS when both grids were evaluated collectively; both $TSOG_{indiv}$ and Weight exhibited positive relationships with the mean resighting rate (α) (95% confidence intervals did not overlap 0; Table 2; Appendix B: Tables B1–B12). $TSOG_{indiv}$ was generally a more important covariate than Weight (based on VIVs), although both covariates helped explain mean resighting rates in models (Table 2). Models where the individual heterogeneity level of resighting (σ) was fixed to 0 were generally the most supported (Appendix B: Tables B1–B12).

Occupancy and detection probability

Occupancy estimates were similar between the grids on the WS and FR for both felids (Table 1, Fig. 2a) and the top model of occupancy for felids never included either of our two covariates (Table 3; Appendix B: Tables B13–B16). Although covariates were generally unsupported when estimating occupancy, they were supported when estimating detection probability (Table 3; Appendix B: Tables B13–B16). Detection probability of bobcats varied by grid in both the WS and FR, where the covariate Grid occurred in top models, exhibited high VIVs, and demonstrated 95% CIs that did not overlap 0 in top models (Appendix B: Tables B13 and
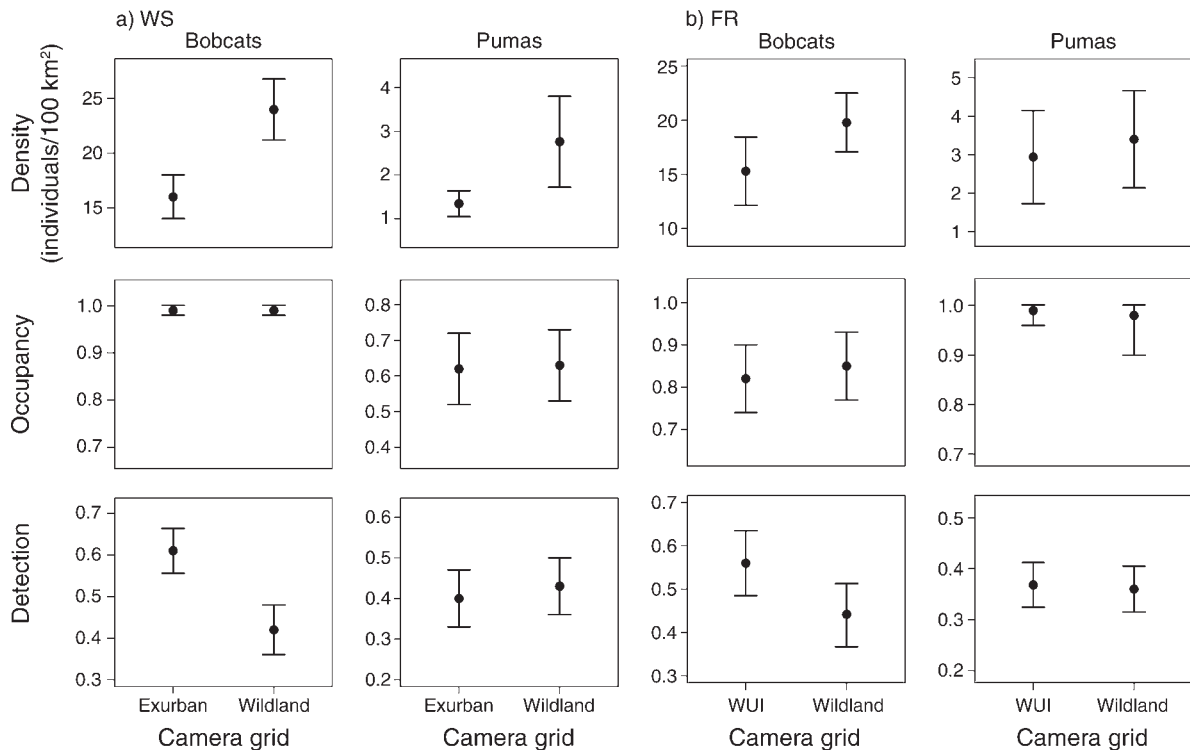
FIG. 2. Estimates ± SE for population density, site occupancy, and species detection probability of bobcats and pumas in relation to exurban and wildland grids on (a) the Western Slope (WS) in 2009 and (b) wildland–urban interface (WUI) and wildland grids on the Front Range (FR) in 2010. Each study area consisted of 40 motion-activated cameras divided between two camera grids. Density estimates were calculated from unmarked and marked felids (i.e., 20 bobcats and 9 pumas on the WS and 16 bobcats and 10 pumas on the FR) using the two sampling grids in each study area. Note that estimates occur on different scales along the y-axis.

B15; Table 3). Estimates of detection probability for bobcats appeared higher on exurban and WUI grids compared to wildland grids (Fig. 2), with a stronger relationship on the WS (95% CIs overlapping by 17% and 33% overlap between margin of errors) than on the FR (95% CIs overlapping by 61% and complete overlap of margin of errors). For pumas, detection probability was less influenced by Grid, where this covariate failed to occur in top models and exhibited lower VIVs (Appendix B: Tables B14 and B16; Table 3), and the estimates of detection probability were similar between grids on the WS and FR (Fig. 2). For both bobcats and pumas on the WS and FR, detection probability and human development were negatively related, where this covariate consistently occurred in top models for both felids in each study area and exhibited 95% confidence intervals that did not overlap 0 for WS bobcats and pumas and FR bobcats; felids were less likely to be detected as the influence of human development increased at a site (Table 3; Appendix B: Tables B13–B16). Parameter estimates for human development evaluating detection probability for pumas demonstrated a stronger relationship in top models on the WS ($\beta = -0.82$, SE = 0.45, model weight = 0.24) and FR ($\beta = -0.34$, SE = 0.21, model weight = 0.20) compared to the

model-averaged parameter estimates (Table 3; Appendix B: Tables B14 and B16). For bobcats on the WS and FR, parameter estimates in top models were generally consistent with model-averaged parameter estimates (Table 3; Appendix B: Tables B13 and B15). Lastly, for detection probability, the covariate Effort was not supported on the WS (bobcats: Ψ(Grid) p(.) $AIC_c =$ 280.96, Ψ(Grid) p(Effort) $AIC_c = 282.58$; pumas: Ψ(Grid) p(.) $AIC_c = 217.90$, Ψ(Grid) p(Effort) $AIC_c =$ 220.24) (Appendix B: Tables B15 and B16). On the FR, however, Effort was supported in occupancy models for both felids (bobcats: Ψ(Grid) p(Effort) $AIC_c = 263.33$, Ψ(Grid) p(.) $AIC_c = 264.03$; pumas: Ψ(Grid) p(Effort) $AIC_c = 265.94$, Ψ(Grid) p(.) $AIC_c = 266.74$); there was a positive relationship between Effort and detection probability for both bobcats and pumas, which indicated that the probability of detecting felids increased with the number of days that a camera operated during a sampling occasion (Table 3; Appendix B: Tables B15 and B16).

Occupancy models for prey species

On the WS, occupancy and detection probability of cottontail rabbits and mule deer were similar between the exurban and wildland grids (Table 4). On the FR,

TABLE 2. Summary of covariate estimates from mark–resight models for bobcats and pumas in relation to exurban and wildland grids on the Western Slope (WS) in 2009 and wildland–urban interface (WUI) and wildland grids on the Front Range (FR) in 2010, Colorado.

Study area, species, and grid	Mean resighting rate, α				Individual heterogeneity level, σ			
	TSOG		Body weight		TSOG		Body weight	
	β (SE)	VIV	β (SE)	VIV	β (SE)	VIV	β (SE)	VIV
WS								
Bobcat								
Exurban	2.45 (0.52)	1.00	0.14 (0.07)	0.63	na	0.00	na	0.00
Wildland	0.32 (0.41)	0.27	0.01 (0.07)	0.10	na	0.02	na	0.02
Both grids	1.60 (0.48)	0.90	0.10 (0.07)	0.54	0.50 (1.71)	0.15	0.08 (0.34)	0.12
Puma								
Exurban	0.00 (0.00)	0.00	0.00 (0.00)	0.00	na	0.00	na	0.00
Wildland	0.19 (0.35)	0.07	0.03 (0.01)	0.54	0.00 (0.00)	0.00	0.00 (0.00)	0.00
Both grids	2.07 (0.58)	0.83	0.05 (0.01)	0.85	0.05 (0.28)	0.02	0.00 (0.01)	0.06
FR								
Bobcat								
WUI	0.19 (0.47)	0.08	−0.01 (0.08)	0.03	0.01 (0.13)	0.02	0.00 (0.04)	0.02
Wildland	0.05 (0.25)	0.11	0.00 (0.04)	0.09	0.00 (0.22)	0.01	0.00 (0.05)	0.01
Both grids	0.24 (0.44)	0.23	0.00 (0.05)	0.13	0.00 (11.46)	0.13	−0.04 (11.45)	0.21
Puma								
WUI	0.00 (0.00)	0.00	0.00 (0.00)	0.00	0.00 (0.00)	0.00	0.00 (0.00)	0.00
Wildland	0.01 (0.10)	0.01	0.00 (0.00)	0.01	0.00 (0.00)	0.00	0.00 (0.00)	0.00
Both grids	0.18 (0.30)	0.21	0.00 (0.00)	0.08	−0.11 (0.39)	0.03	0.00 (0.01)	0.01

Notes: Terms are TSOG, time spent on grid for individual animal based on telemetry locations; body weight (kg) of animal; β, model-averaged (based on AIC_c weights) parameter estimate with associated SE; VIV, variable importance value based on sum of AIC_c weights; na, not applicable. See *Methods* for further description of parameters in mark–resight models. See Appendix B: Tables B1–B12 for complete results of individual models and covariate estimates for mark–resight models.

occupancy and detection probability of cottontail rabbits was similar between grids and mule deer occupancy was slightly lower on the wildland–urban interface grid compared to the wildland grid (Table 4). On both the WS and FR, elk exhibited lower occupancy on the exurban and wildland–urban interface grids compared to the wildland grids, and detection probability was similar among all grid areas (Table 4).

DISCUSSION

Low-density residential development appeared to influence wild felid populations more than habitat adjacent to a major wildland–urban interface in our study areas. Estimates of population density were lower for bobcats and pumas in exurban development compared to wildland habitat, suggesting reduced habitat quality, whereas population density for both felids appeared more similar between wildland–urban

TABLE 3. Summary of covariate estimates from occupancy models for bobcats and pumas on the Western Slope (WS) in 2009 and the Front Range (FR) in 2010, Colorado.

Study area and species	Occupancy, Ψ				Detection probability, p					
	Grid		HumDev		Effort		Grid		HumDev	
	β (SE)	VIV	β (SE)	VIV	β (SE)	VIV	β (SE)	VIV	β (SE)	VIV
WS										
Bobcat	na	0.30	na	0.21	na	na	−0.75 (0.29)	0.90	−0.29 (0.15)	0.79
Puma	0.02 (0.35)	0.22	−0.20 (0.48)	0.36	na	na	0.14 (0.24)	0.32	−0.44 (0.38)	0.57
FR										
Bobcat	0.27 (0.64)	0.27	−0.01 (0.24)	0.20	1.81 (1.04)	0.97	−0.48 (0.30)	0.63	−0.43 (0.19)	0.82
Puma	na	0.36	na	0.34	1.70 (1.07)	0.92	−0.04 (0.14)	0.22	−0.17 (0.15)	0.51

Notes: Occupancy is the proportion of the landscape used by the species; detection probability is the probability of detecting a species, given that it was present at a site; grid is a covariate comparing urban (=0) and wildland (=1) grids; HumDev is the kernel density human development covariate; Effort is a time-varying survey effort covariate; β is the model-averaged (based on AIC_c weights) parameter estimate with associated standard error; VIV is variable importance value based on sum of AIC_c weights; na, not applicable. See *Methods* for further description of parameters in occupancy models. See Appendix B: Tables B13–B16 for complete results of individual models and covariate estimates for occupancy models.

TABLE 4. Estimates of occupancy and detection probability for prey species of bobcat (cottontail rabbit) and pumas (mule deer and elk) on exurban and wildland grids on the Western Slope (WS) in 2009 and wildland–urban interface (WUI) and wildland grids on the Front Range (FR) in 2010, Colorado.

Probabilities, by prey species	WS study area and grids				FR study area and grids			
	Exurban		Wildland		WUI		Wildland	
	Est. (SE)	95% CI	Est. (SE)	95% CI	Est. (SE)	95% CI	Est. (SE)	95% CI
Occupancy, Ψ								
Cottontail	1.00 (0.00)	1.00–1.00	0.85 (0.08)	0.62–0.95	0.66 (0.11)	0.43–0.83	0.60 (0.11)	0.38–0.80
Mule deer	0.95 (0.05)	0.70–0.99	0.92 (0.07)	0.65–0.99	0.71 (0.10)	0.47–0.86	1.00 (0.00)	1.00–1.00
Elk	0.39 (0.13)	0.19–0.65	0.75 (0.14)	0.42–0.92	0.28 (0.11)	0.12–0.54	0.61 (0.13)	0.35–0.81
Mule deer and elk	0.95 (0.05)	0.71–1.00	0.96 (0.05)	0.69–1.00	0.75 (0.10)	0.52–0.89	1.00 (0.00)	1.00–1.00
Detection, p								
Cottontail	0.89 (0.03)	0.81–0.94	0.85 (0.04)	0.75–0.91	0.58 (0.06)	0.45–0.69	0.65 (0.06)	0.52–0.76
Mule deer	0.67 (0.05)	0.57–0.76	0.54 (0.06)	0.44–0.65	0.61 (0.06)	0.49–0.72	0.73 (0.04)	0.63–0.81
Elk	0.36 (0.09)	0.20–0.55	0.33 (0.07)	0.21–0.48	0.36 (0.11)	0.18–0.59	0.38 (0.08)	0.25–0.53
Mule deer and elk	0.71 (0.05)	0.61–0.80	0.64 (0.05)	0.53–0.73	0.66 (0.06)	0.55–0.76	0.78 (0.04)	0.69–0.85

Note: Occupancy is the proportion of the landscape occupied by the species; detection probability is the probability of detecting a species given that it was present at a site.

interface (WUI) and wildland habitat, in contrast to predictions of home-range pile-up and density inflation along impermeable boundaries (Riley et al. 2006). In addition, the occupancy of important felid prey (cottontail rabbit and mule deer) were generally similar between sampling grids, suggesting that felid population densities were not substantially altered by availability of these prey within study sites.

Many mechanisms associated with urbanization can influence population characteristics of animals (Shochat et al. 2006), including altered movement patterns. Populations completely surrounded by movement barriers may reach higher densities compared to unbounded populations (Krebs et al. 1969, Adler and Levins 1994). Further, the home-range pile-up hypothesis predicts that populations where animal movement is only partially restricted will also reach higher densities in habitat adjacent to an anthropogenic barrier (Riley et al. 2006). Research testing these predictions, especially for wild felids in urban systems, is limited. Home-range pile-up was reported for a bobcat population adjacent to a major highway in southern California (Riley et al. 2006), but other urban bobcat studies have not found evidence consistent with this hypothesis and report that population densities of bobcats often are not higher in urban fragments and are lower when compared to more unbounded populations in wildland areas (Lembeck and Gould 1979, Ruell et al. 2009, Riley et al. 2010). Further, although movement patterns, habitat selection, and mortality factors of pumas have been evaluated in relation to urbanization (Beier et al. 2010, Burdett et al. 2010, Wilmers et al. 2013, Riley et al. 2014), few studies have estimated the density of pumas across different levels of urbanization (Beier et al. 2010).

Although our study did not find support for the home-range pile-up hypothesis for either bobcat or puma populations associated with a major urban barrier, we provide several considerations when interpreting our results. First, the related fence-effect

hypothesis states that population density will initially increase due to restricted movement, but that density will eventually decrease due to limited resources (Krebs et al. 1969). The wildland–urban interface of Boulder, CO has existed for more than a century. It is possible that population density has already reached an equilibrium resulting from this landscape barrier. Second, the wildland–urban interface of Boulder occurs over the length of ~20 km, of which our grids sampled 14 km. Although the WUI appeared to be a barrier to movement for most felids fit the GPS collars (J. S. Lewis, *unpublished data*), perhaps a longer and more significant barrier is necessary to impact population characteristics of felids. Third, negative ecological impacts related to edge effects along the urban interface (Murcia 1995), such as mortality from people, vehicles, and disease, could suppress population densities. We did not have detailed information about animal mortality, but other studies have reported greater mortality and reduced fitness of wild felids from anthropogenic factors near urban areas and human development (Beier et al. 2010, Burdett et al. 2010). Fourth, increased densities may only be observed for specific age and sex classes (e.g., adult females; Riley et al. 2006) or during certain times of the year (e.g., winter). Our approach for estimating felid densities was not able to differentiate among different age and sex classes in the unmarked population and we thus evaluated all adult-sized individuals collectively during a single season. Lastly, populations that are bounded on only one side of their spatial extent, such as those along an urban interface in our study area, might not experience elevated population density because dispersing animals have the option to leave the population. Thus, a single linear barrier might not produce a sufficient barrier to dispersal to alter population density; abnormally high population densities might only occur in landscapes that are completely isolated, as predicted by the fence-effect or island syndrome hypotheses, where animal dispersal is

impossible or substantially diminished (Krebs et al. 1969, Adler and Levins 1994). Thus, greater levels of habitat fragmentation from urbanization (e.g., in habitat that is more constricted by development) might be necessary to cause home-range pile-up in felids.

Another mechanism that can influence populations of animals is disturbance from human activities associated with residential development, which can reduce habitat quality. Our study indicated that exurban and rural residential development decreased population density of both bobcats and pumas compared to wildland habitat. Thus, although low-density development may increase landscape heterogeneity and potentially carnivore food along ecotones and edges (Murcia 1995, Irwin and Bockstael 2007), anthropogenic disturbance (e.g., from human activities, structures, noise, lighting, roads, etc.) associated with such development across broad spatial extents appears to degrade habitat suitability and reduce wild felid density. Both bobcats and pumas spent less time on the exurban sampling grids compared to wildland areas (based on GPS collar data), and behaviorally both species were less likely to visit sites as the influence of residential development increased (based on detection probability in relation to human residences). Thus, felids used habitat associated with human development less frequently, which was likely related to disturbance and reduced habitat quality in such areas. However, both felids used natural areas intermixed within exurban development, and the exurban grid was adjacent to expansive wildland areas that supported felid populations, both of which likely mitigated the impacts of exurban development on felid populations in these areas. Consistent with our findings, pumas in urbanized California used areas of exurban development less than expected (Burdett et al. 2010). Further, pumas that use habitat near humans and development have a higher risk or mortality (Burdett et al. 2010, Wilmers et al. 2013), which could reduce the density of populations in such areas. Given that exurban residential development is one of the fastest growing forms of urbanization (Brown et al. 2005, Nelson and Sanchez 2005), it is important to consider the ecological impacts associated with this type of anthropogenic disturbance and evaluate how varying exurban development configurations affect population characteristics.

Although estimates for population density of felids were lower in the area of exurban development, estimates of occupancy for both bobcats and pumas were more similar between wildland areas and habitat associated with both exurban and WUI development, which was inconsistent with our predictions. Studies of presence–absence (Gaston et al. 2000) and occupancy (MacKenzie and Nichols 2004, MacKenzie et al. 2006, Temple and Gutiérrez 2013) of animals have reported a positive relationship between abundance and occurrence. Although this relationship is intuitive, it likely is valid only up to a certain threshold of density and therefore nonlinear (Freckleton et al. 2005, Noon et al.

2012). For example, occupancy estimates will increase only if additional sites are used as population densities increases. Alternatively, if the population size grows within sites already occupied, density will increase, but occupancy probabilities will remain unchanged; in such cases, occupancy probabilities may asymptote at 1.0 at moderate to high population densities. Unless individuals are territorial or a site can be defined to limit the number of individuals that are likely to occupy it (MacKenzie and Nichols 2004), the ability of occupancy to track total abundance within an area is limited. Further, even for large changes in population size, intensive sampling is necessary to observe changes in occupancy (Ellis et al. 2014). Thus, it has been argued that detection–non-detection data can have little power to detect changes in abundance in many systems (Strayer 1999, Pollock 2006). This appeared to be the case in our study and likely occurred because both species will use habitat components that are less preferred (and thus occupy a site), but frequent these areas less than habitat of higher suitability (see discussion on detection probability). Species that occur at low densities but range over broad areas will likely exhibit high estimates of occupancy over longer sampling occasions because of the species' ability to visit much of the landscape (MacKenzie and Royle 2005). Thus, occupancy appears to be a relatively poor metric to evaluate differences in population densities in our system.

Detection probability is another metric used to evaluate the behavior or density of animals relative to landscape characteristics. It is assumed that abundance is related to species detection probability (Royle and Nichols 2003, Royle et al. 2005); species detection probability should correspond to local abundance because more animals are available to be detected. In addition, animals would be expected to demonstrate higher detection probabilities in habitat of higher suitability because they will likely frequent these areas more often. In our study, detection probability of bobcats and pumas appeared to be a more sensitive metric than occupancy, but sometimes produced unexpected results. For example, across study areas, both felids were less likely to be detected as the amount of human influence from residential development increased; thus, although felids would use these sites, they visited developed areas less often compared to undeveloped sites. However, despite this, bobcats unexpectedly exhibited higher overall detection probabilities in both exurban and wildland–urban interface grids compared to wildland grids. This likely occurred because animals in urbanized landscapes had fewer options for places to travel due to anthropogenic barriers to movement (e.g., human residences and roads) and were thus funneled along more restrictive movement corridors. Our sampling technique of placing motion-activated cameras within these key movement corridors likely increased our detection of animals. In wildland habitat, more movement options were likely available to animals

throughout the landscape. In contrast to bobcats, detection probability for pumas was similar between urbanized grids (exurban and WUI) and wildland areas. Thus, based on detection probability across grids, bobcats and pumas might exhibit different movement behaviors when using urbanized landscapes. For carnivores, it is recommended that sampling occur along high probability travel routes to obtain sufficient data of animals (Karanth et al. 2010). It is important to consider, however, that sampling schemes that aim to increase detection of animals by directed placement of sampling devices can potentially lead to unexpected results that initially might appear counterintuitive and should be interpreted carefully.

Densities of urban-adapted species often are greater in urban systems compared to wildland habitat due to multiple ecological factors (Gehrt et al. 2010). For example, increased forage near and within urban areas can increase population densities for species such as raccoons (*Procyon lotor*) (Hadidian et al. 2010) and red fox (*Vulpes vulpes*) (Soulsbury et al. 2010). In our study, however, occupancy of important felid prey (i.e., cottontail rabbits and mule deer) was high and generally similar among exurban, wildland–urban interface, and wildland areas, suggesting availability of these prey did not contribute to differing population characteristics of felids among sampling areas. In contrast, the occupancy of elk was substantially lower in exurban and wildland–urban interface habitat compared to wildland areas, suggesting reduced availability of elk near residential development. As demonstrated for felids in our study, occupancy might not always be a sensitive index for abundance, so occupancy of prey might not reflect their relative density. In some cases, detection probability of prey varied between grids for a species (e.g., mule deer exhibited greater detection probability in exurban habitat compared to wildland areas), indicating potential differences in abundance or use. In addition, both bobcats and pumas exhibit a varied diet (Sunquist and Sunquist 2002) and it is unclear how densities across the prey community, which we were unable to measure, were impacted by urbanization and how this might have affected felid populations. Other factors that could influence the population density of felids that we did not evaluate in our study include the effect of individuals of varying competitive abilities (i.e., ideal despotic distribution; Fretwell 1972) and body size (i.e., competitive units; Milinski 1988). Our analyses also did not consider how urbanization influenced intra- or interspecific competition in felid populations, although competition can substantially influence population density of animals and community structure (Crooks and Soulé 1999).

The exploitation of animals by sport hunting and trapping can affect population characteristics (Reynolds et al. 2001), particularly for bobcats and pumas (Woolf and Hubert 1998, Stoner et al. 2006, Cooley et al. 2009, Robinson et al. 2014). Felid populations in our study were exposed to relatively low levels of annual hunting and/or trapping (Colorado Parks and Wildlife, *personal communication*), except WS pumas were not hunted for five years leading up to our camera surveys. No marked animals were killed from exploitation during our camera surveys; however, bobcats and pumas were taken for sport after our surveys during the winter. There appeared to be greater hunting and trapping pressure in wildland habitat for both the WS and FR, although animals associated with exurban and WUI habitat were also legally taken near or within these grids (J. S. Lewis, *unpublished data*; Colorado Parks and Wildlife, *personal communication*).

Likely due to varying habitat quality, bobcats exhibited smaller home ranges on the WS compared to the FR (J. S. Lewis, *unpublished data*), which is consistent with higher population densities in wildland habitat on the WS compared to the FR. Thus, due to potential differences in habitat quality between WS and FR study areas, we were limited in making direct comparisons of felid population characteristics between exurban and WUI habitat. Future work could evaluate how population characteristics of felids vary along the entire urban gradient (e.g., wildland, rural, exurban, suburban, and urban) within a single study area to control for the effect of habitat quality (Germaine and Wakeling 2001, Crooks et al. 2004, McDonnell and Hahs 2008).

Our research evaluating medium- and large-sized carnivores associated with varying levels of urbanization provides important information about the conservation of wildlife populations associated with urban and exurban residential development. Wildland habitat adjacent to urban areas can effectively support bobcat and puma populations and thus management strategies that conserve habitat associated with urbanized landscapes can potentially play important roles in the persistence of carnivore populations. For example, our estimate of puma population density in wildland–urban interface habitat are consistent with, and indeed on the higher end of, the range of reported estimates of puma population densities in other systems (Quigley and Hornocker 2009). In addition, our results indicate that the conversion of wildland habitat to low-density (exurban and rural) residential development will likely reduce population density for some native species, such as bobcat and puma, even though these forms of development are permeable to animal movement and support populations of prey species. Because animals will use habitat that is associated with human residences, there is greater potential in these areas for human–wildlife conflict, disease transmission among wildlife, humans, and domestic animals, and reduced fitness compared to felids living in wildland habitat (Hansen et al. 2005, Bradley and Altizer 2007, McDonald et al. 2008). Thus, our study indicates that the conservation of medium- and large-sized felids in landscapes associated with urbanization will likely be most successful if large areas of wildland habitat are maintained, even in close

proximity to residential and urban areas, and wildland habitat is not converted to low-density residential development.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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