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Cougar response to a gradient of human development

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Abstract. Human populations continue to increase and transform Earth's ecosystems. For large carnivores, human development reduces habitat abundance, alters predator–prey dynamics, and increases the risk of mortality, which may threaten the viability of many populations. To investigate how the cougar (*Puma concolor*) responds to a gradient of human development in four areas in Washington, USA, we used utilization distributions, county tax parcel data, Weibull modeling analysis, and multiple comparison techniques. Cougars used wildland areas the majority of the time (79% ± 2%, n = 112 cougars), with use decreasing as housing densities increased. When present in human-developed areas in eastern Washington, 99% of the habitat that cougars used had housing densities ≤76.5 residences/km^2, which was <846.0 residences/km^2 observed in western Washington ($P < 0.01$). Cougars used areas in western Washington with greater housing density likely because of the clustered nature of housing developments, the connectivity with greenbelts and forested corridors, and security cover of dense maritime vegetation. Our findings suggest a consistent, albeit nuanced response by cougars to human development that may be used by wildlife managers, landscape planners, and environmental educators to guide and enhance their efforts to minimize the impacts of human development on cougars and reduce the potential for conflicts with people. Our model may also provide guidance for thresholds of human development for other adaptable large carnivores.

Key words: cougar; human development; *Puma concolor;* residential density space use; utilization distribution; Washington.

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INTRODUCTION

The human population is projected to continue increasing from 6.5 billion to approximately 10 billion people through the mid- to late century (Lutz et al. 2001, Bongaarts 2009). As the human population continues to expand, so too will human development for industry and housing (McKee et al. 2015). Human development alters assemblages and dynamics of natural environments through direct and indirect pathways creating ecosystems that differ significantly from historic norms (Hobbs 2006, McKinney 2006). The broad reach of human development in North

America (Theobald 2005, Wade and Theobald 2010) and its ability to transform ecosystems necessitates a greater understanding of how wildlife responds to these changes and the identification of development characteristics that encourage species persistence in human-altered landscapes.

For large carnivores, development reduces habitat, changes prey species and availability, can increase mortality rates, and can influence behavioral adaptations that allow them to persist in a changed environment (Markovchick-Nicholls et al. 2008, Burdett et al. 2010, Wilmers et al. 2013, Smith et al. 2015, Moss et al. 2016). Consequently, conservation strategies have focused primarily on limiting human impacts through the establishment and maintenance of large, protected preserves and interconnected networks of wildland habitat (Quigley and Crawshaw 1992, Goodrich et al. 2010, Smith et al. 2015). While reserves and corridors will be essential for maintaining the long-term viability of many populations, these approaches may be impractical or impossible for carnivore populations already residing in landscapes with an established or expanding human presence. Ensuring large carnivore persistence within these landscapes will require specific information on how species respond to different levels and patterns of human development. Quantifying residential density thresholds that exclude large carnivores from ecosystems may be of particular importance because these values remain unknown for most species and represent a key component of habitat suitability in developed portions of wildland–urban environments.

The cougar (*Puma concolor*) is a wide-ranging, solitary carnivore that inhabits a diversity of habitats in North and South America (Sunquist and Sunquist 2002). Cougar wildland–urban ecology has received considerable attention in large part because of concerns over human impacts on population viability and the potential risks cougars present to public safety and private property (Cougar Management Guidelines Working Group 2005). Cougar distribution is governed in large part by the availability of ungulate prey and stalking cover (Koehler and Hornocker 1991, Williams et al. 1995, Dickson et al. 2005, Murphy and Ruth 2009), but behavioral and dietary flexibility, as well as the influence of human development on wild ungulate distribution (Polfus and Krausman 2012), allows cougars to exploit resources in landscapes with varying levels of human presence (Beier et al. 2010, Kertson et al. 2011*a*, *b*, 2013, Knopff et al. 2014, Jennings et al. 2016, Moss et al. 2016, Smith et al. 2016). Areas with human development may also represent an ecological trap because resources near and among people come with a significantly greater risk of mortality for cougars (Moss et al. 2016).

Investigations of cougar response to human development have primarily defined housing densities by categories (i.e., undeveloped or developed, wildland, rural, exurban, suburban, or urban for analysis; e.g., Burdett et al. 2010) and not quantified along a continuous measure of development. Examining cougar response along a continuous measure of housing density provides the ability to identify levels of development that exclude cougars and specific threshold values that may be useful to guide landscape planning and public outreach. Human development can influence species persistence by reducing habitat and changing species interactions (McDonnell and Hahs 2008); therefore, it is important to assess cougar response to a multitude and continuum of environmental influences.

To better understand how an adaptable, large carnivore responds to human development, we used utilization distributions (UDs), county and district tax parcel records, a two-parameter Weibull equation, and multiple comparison techniques to determine housing density thresholds that would preclude cougar use for four populations in Washington, USA. We used the Weibull analysis because it provided a rigorous means to quantify the level of residential development along a gradient from undeveloped wildland to areas with housing densities sufficient to be avoided by cougars. By modeling cougar responses across a continuous range of residential densities and broad environmental conditions, we tested whether we could identify human development thresholds that influenced cougar-use patterns and whether these patterns were a function of geographic location, climatic condition, or vegetation density. We discuss how our model can be applied in landscapes with a matrix of human development and cougar habitat to reduce the potential for cougar–human interactions.

Study Areas

We examined cougar responses to human development in four independent study areas in Washington between 2001 and 2009. Study areas were geographically and socially diverse and largely representative of Washington's cougar range (Fig. 1).

Westside

The Westside study area comprised 3486 km^2 of wildland and human-developed areas in King and Snohomish Counties (Universal Transverse Mercator [UTM] 590000 E, 5260000 N; Fig. 1). Land ownership was a composite of state, federal, municipal, and private holdings managed for a variety of commercial and recreational interests. The landscape was characterized by dense, coniferous forest with Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) forest associates dominant below 750 m and Pacific silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) forest associations dominant above 750 m (Franklin and Dyrness 1973, Lasmanis 1991, Koehler and Pierce 2003). Elevations ranged from 10 to 2005 m and mean annual temperatures ranged from 2°C in January to 22°C in July. Annual precipitation averaged 197 cm/yr (standard error [SE] = 30), which fell primarily as rain between 1 October and 1 July (Western Region Climate Center 2009). King County is Washington's most populous county with an estimated human density of 363 people/km^2 distributed across 5506 km^2 in 2009 (United States

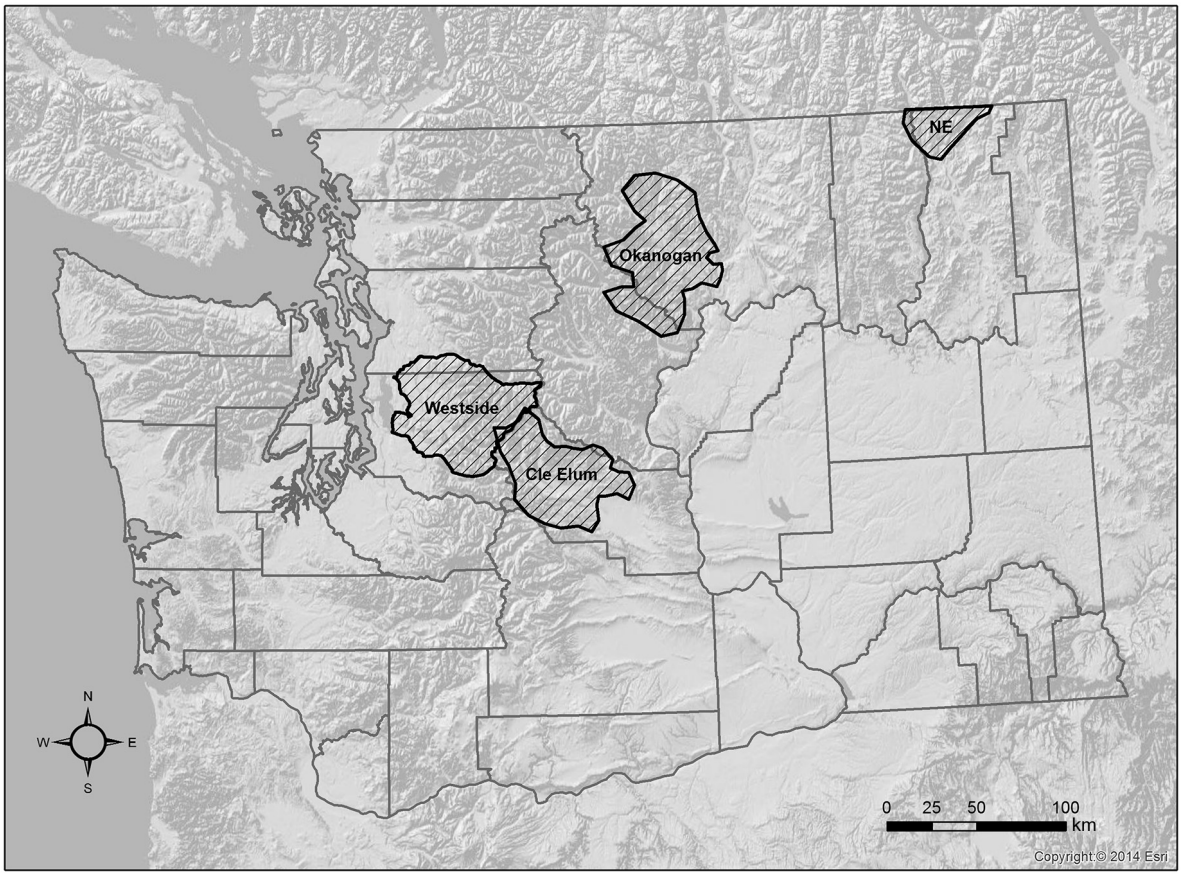

Fig. 1. Locations of Westside, Cle Elum, Okanogan, and Northeast cougar study areas relative to Washington's counties, 2001–2014. The Westside study area resides in a maritime climate and has concentrated housing density near the urban interface. The remaining study areas are located in eastern Washington where the climate is continental and housing density is more diffuse.

Census Bureau 2010). Residential development was predominantly clustered at urban and suburban densities (≥25 residences/km^2) in large communities of 10,000–200,000 people (Table 1) with little development along the east and an increasing gradient to the west with patches and corridors of forest habitat distributed throughout the development (Kertson et al. 2011*a*, *b*, 2013). The average residential development density in the Westside study area was 28.2 ± 86.5 residences/km^2 with a range from 0 to 943 residences/km^2.

Cle Elum

The Cle Elum study area encompassed 1652 km^2 of upper Kittitas County along the east-slope foothills of the Cascade Mountains (UTM 655000 E, 5230000 N; Fig. 1). The area was a mosaic of U.S. Forest Service land, commercial timber lands, agricultural lands, and private residential properties. Development occurred primarily in wide valley bottoms with limited development interspersed on the lower slopes surrounding the valleys. Elevations ranged from 462 to 2279 m with sagebrush (*Artemisia tridentata*) steppe foothills below 550 m. Forests of ponderosa pine (*Pinus ponderosa*) and Douglas-fir comprised the majority of the landscape from 550 to 1550 m, while subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), Pacific silver fir, and western hemlock dominated elevations >1550 m. Mean annual temperature ranged from −7°C in January to 27°C in July. Precipitation increased with elevation gains, averaging 56.3 cm/yr (SE = 22), which fell mostly as snow during winter (Western Region Climate Center 2013). Kittitas County was home to an estimated human density of 6.6 humans/km^2 distributed across 5950 km^2 in 2009 (United States Census Bureau 2010). Residential development mostly occurred as small communities (<5000 people) concentrated in valley bottoms at urban and suburban densities. Remaining residential development was diffuse, primarily in surrounding foothills at exurban densities (<25 houses/km^2; Table 1). The average residential development density in the Cle Elum study area was 2.3 ± 12.5 residences/km^2 with a range from 0 to 333 residences/km^2.

Okanogan

The Okanogan study area comprised 1819 km^2 of Okanogan County centered in the Methow Valley in north-central Washington (UTM 713000 E, 5360000 N; Fig. 1). Land ownership was a combination of federal, state, and private holdings with the majority of lands managed by the U.S. Forest Service and Washington Department of Fish and Wildlife. Development in the Okanogan study area occurred primarily in wide valley bottoms with development interspersed on the lower slopes surrounding the valleys. The landscape was characterized by forests of ponderosa pine and Douglas-fir below 1550 m and large tracts of lodgepole pine (*Pinus contorta*) with intermittent Engelmann spruce and subalpine fir throughout areas above 1550. Elevations ranged from 260 to 2515 m and local topography varied considerably between drainages. Mean annual temperatures ranged from −14°C in January to 32°C in July. Precipitation fell primarily as snow between November and April at an average of 36.2 cm/yr (SE = 7; Western Region Climate Center 2013). Okanogan is Washington's largest county at 13,766 km^2 and had a density of 2.9 humans/km^2 in 2009 (United States Census Bureau 2010). Okanogan is Washington's

Table 1. Proportional breakdown of human development in square kilometers for the Westside, Cle Elum, Okanogan, and Northeast study areas in Washington from 2001 to 2014.

Study area	Size (km^2)	Human development density class, km^2 (%)			
		Undeveloped	Exurban	Suburban	Urban
Westside	3486	70.48	12.73	8.41	8.38
Cle Elum	1652	84.78	13.41	1.48	0.33
Okanogan	1819	81.68	17.43	0.63	0.26
Northeast	2587	81.31	16.83	1.00	0.86
Mean		79.56	15.10	2.88	2.46
SD		6.25	2.37	3.70	3.96

Notes: SD, standard deviation. We classified human development into landcover rasters consisting of four classes: undeveloped (0 structures/km^2), exurban (>0–25 structures/km^2), suburban (25–100 structures/km^2), and urban (>100 structures/km^2).

largest county at 13,766 km^2 and had a density of 2.9 humans/km^2 in 2009 (United States Census Bureau 2010). Residential development patterns in the Okanogan study area were similar to those described for Cle Elum (Table 1). The average residential development density in the Okanogan study area was 1.0 ± 5.74 residences/km^2 with a range from 0 to 187 residences/km^2.

Northeast

The Northeast study area included 2587 km^2 of northern Stevens County, Washington, extending north into southern British Columbia, Canada (UTM 423000 E, 5410000 N; Fig. 1). Land ownership was a composite of federal, state, and privately owned lands bounded by the Columbia River to the east, Kettle River to the west, and Highway 3 in British Columbia, Canada, to the north. Development in the Northeast study area was widely distributed across valley bottoms, slopes, and ridges. The area occupied the transition between the east-slope Cascades and Northern Rocky Mountain physiographic provinces (Bailey et al. 1994). Elevations ranged from 400 to 2130 m with mixed conifer forests of Douglas-fir, western hemlock, ponderosa pine, western red cedar (*Thuja plicata*), and subalpine fir predominant throughout the landscape. Mean annual temperatures ranged from −6°C in January to 21°C in July and precipitation averaged 49 cm/yr (SE = 1) falling mostly as snow from mid-November to April (Western Region Climate Center 2013). Stevens County had an estimated human density of 6.5 humans/km^2 occupying 6419 km^2 in 2009 (United States Census Bureau 2010). Residential development within the Northeast study was widespread, but diffuse with residences scattered across both valley bottoms and surrounding foothills at exurban densities (Table 1). The average residential development density in the Northeast study area was 0.7 ± 3.4 residences/km^2 with a range from 0 to 106 residences/km^2.

Methods

Cougar capture

We captured cougars >1 yr of age, primarily December through March each year using trained dogs or cage traps with methodologies that have been described in detail elsewhere (Cooley et al. 2009, Kertson et al. 2011*a*, *b*). We recorded sex and determined aged via tooth condition and gum line recession (Laundre et al. 2000), and marked with a global positioning system (GPS) radio collar (Model GPS Plus-2; Vectronics Aerospace, Berlin, Germany [Westside and Okanogan]; Models Telus and Simplex; Televilt, Lindesberg, Sweden [Westside and Cle Elum]; or Model 4400; Lotek Wireless, New Market, Ontario, Canada [Cle Elum and Northeast]). We programmed GPS collars to attempt a satellite location fix for 180 s every four hours and retrieved GPS data via ultra high frequency (UHF) or very high frequency (VHF) remote communication during telemetry sessions, via satellite transmission, or from recovered collars. Cougars were monitored throughout the year and we attempted to change out collars when batteries died or collars malfunctioned. All cougar captures and handling were performed in accordance with the University of Washington's Institutional Animal Care and Use Committee (IACUC; Protocol No. 2185-36), Washington State University's IACUC (Protocol No. 3133), Animal Welfare Assurance Committee (Protocol No. A3485-01), and Sikes et al. (2011).

Utilization distribution estimation

We calculated an annual UD (Van Winkle 1975, Worton 1989, Kernohan et al. 2001) for each cougar monitored ≥3 months/yr using the fixed kernel density estimator available in the Hawth's Tools extension (Beyer 2004) of ArcMap 9.3 (Environmental Systems Research Institute, Redlands, California, USA). The number of locations per cougar per year exceeded the suggested minimum of >30 GPS locations per UD (Seaman et al. 1999). We smoothed kernels using the bivariate plug-in bandwidth selection method (Wand and Jones 1995) estimated with the (hpi) function in the KernSmooth package in program R (Wand 2006, R Development Core Team) and the (kde) function in Geospatial Modelling Environment (Beyer 2012). We generated kernels on a 30 × 30 m grid and defined use for cougars as the 99% volume contour for each cell within this area and assigned a probability value based on the volume (height) of the UD (Kertson and Marzluff 2010).

Human development

We used county and district tax parcel spatial and attribute data to generate a point layer of development (houses, buildings, and structures) and their distribution on the landscape (i.e., pattern; Alberti et al. 2003, Theobald 2005). We used the "Generate Centroid Points" tool in Hawth's Tools (Beyer 2004) to create the point layers, and the "Point Density" function in ArcMap 9.3 Spatial Analyst to create human development density grids in square kilometers (Kertson et al. 2013). We used the density grid as our measure of residential development for the Weibull analysis.

To compare human development patterns among the study areas, we reclassified each density grid into a human development landcover raster consisting of four development classes commonly used in the urban ecology discipline (Alberti et al. 2001, Marzluff 2001, Hansen et al. 2005) and previously applied to cougars in Washington (Kertson et al. 2013). Accordingly, we characterized the landscape as undeveloped (0 structures/km^2), exurban (>0–25 structures/km^2), suburban (26–100 structures/km^2), and urban (>100 structures/km^2) for each study area (number of cells in class *X*/total number of cells in study area).

Determining use thresholds for human development

We used a two-parameter Weibull equation (Broseth et al. 2005, Metsaranta 2008) to approximate the cumulative distribution functions of the UD values for each cougar over human development per square kilometer. The Weibull is a flexible probability distribution function that can assume a number of forms, from modal to negative monotonic, and it has been used in myriad applications in the life sciences to describe processes that attenuate (Rinne 2008). The two-parameter Weibull cumulative distribution function was fitted with the following formula:

$$(y) = 1 - \exp\left(\frac{x}{a}\right)^{b}$$

where a is the scale parameter (human development levels) and b is the shape parameter (cougar response to human development) as a function of x, the housing density. We used a nonlinear least-squares convergence to determine the parameters of the Weibull equation, and then averaged the parameters for each cougar if there were multiple years of data. We then constructed a cumulative distribution function of the UD for each cougar using a summation function for each consecutive housing density value from 1 house/km^2 to the maximum observed within each cougar's UD. Finally, we used Weibull-derived parameter values to test cougar responses to development and to identify housing densities that inhibit cougar movements through the landscape.

We tested for differences ($\alpha = 0.05$) by study area and sex using an ANOVA fixed-effects model (Zar 1999). We compared study areas with a family-wise multiple comparison controlling for type I error using Tukey's honestly significant difference (Oehlert 2000). For cougars with multiple years of data, we analyzed annual UDs and associated Weibull parameters (shape, scale, and *y*-intercept) separately, but averaged these values for a single input into the ANOVA so each cougar represented a single sampling unit.

Results

Cougar captures and monitoring

We captured and collared 112 cougars (61 males and 51 females) >1 yr of age within the four study areas between December 2001 and December 2014. The number of cougars monitored in each study area ranged between 17 and 53 individuals with an average of 1116 locations per year per individual (standard deviation [SD] = 418, n = 112, Table 2).

Human development

The study areas were largely comprised of undeveloped habitat (79.56%, SD = 6.25) with 15.10%, SD = 2.37 of the human development occurring primarily at exurban densities. The remaining land within each study area was comprised of 2.88%, SD = 3.70 suburban and 2.46%, SD = 3.96 urban development. Cle Elum, Okanogan, and Northeast study areas had similar levels of undeveloped area, while the Westside had more suburban and urban development at the square kilometer scale (Table 1).

Determining use thresholds for human development

We found no difference (scale: $F_{1,\ 107} = 0.882$, $P = 0.35$; shape: $F_{1,\ 107} = 1.453$, $P = 0.23$) between

Table 2. Summary of number of cougars by sex utilized in the analysis that were monitored for more than 3 months/yr and the associated GPS telemetry sampling (relocations per animal per year) for the Westside, Cle Elum, Okanogan, and Northeast study areas in Washington from 2001 to 2014.

Study area	Duration of each study	Total cougars sampled (*n*)			Mean telemetry locations per animal per year (*n*)	
		Male	Female	Total	Mean	SD
Westside	2004–2008	14	6	20	715	757
Cle Elum	2001–2009	13	9	22	1697	1622
Okanogan	2006–2014	28	25	53	960	452
Northeast	2004–2007	6	11	17	1093	831
Statewide		61	51	112		

Note: GPS, global positioning system; SD, standard deviation.

male and females when comparing the scale and shape parameters of the Weibull function so they were combined for each study area for the remainder of the analysis. The family-wise comparison of the average Weibull-scale parameter from the Westside study area was greater than ($F_{3,\ 107} = 4.056$, $P < 0.01$) the Northeast ($P = 0.01$), Cle Elum ($P = 0.02$), and the Okanogan ($P = 0.06$; Table 3), which may relate to the increase in use by cougars of areas adjacent to suburban and urban housing densities in the Westside study area. Ninety-nine percentage of the cougar probability of use in eastern Washington (Northeast, Okanogan, and Cle Elum) occurred in areas with a development density of ≤76.5 structures/km^2, whereas 99% of the cougar probability of use in the Westside study area was in areas with ≤846.0 structures/km^2 (Table 3). However, we found no difference in the average shape parameter of the Weibull function between areas ($F_{3,\ 107} = 1.994$, $P = 0.11$), revealing a consistent response to human development across study areas. As development increases, cougar use decreases within all study areas. The average *y*-intercept (i.e., nugget) of the cumulative density function (79%) occurred where densities of human structures were <1/km^2, revealing the majority of cougar use of habitats were in areas with no human development (Table 3, Fig. 2).

Discussion

Using a gradient approach, we were able to determine the thresholds of human development at which cougars were no longer functionally present within a variety of wildland–urban ecosystems in Washington. Understanding how carnivores respond to anthropogenic landscape alteration is increasingly critical for conservation and management (Inskip and Zimmermann 2009, Gerht et al. 2010, Bateman et al. 2012, Northup et al. 2012, Warren et al. 2016), and coexistence

Table 3. Mean and standard error for Weibull equation parameter estimates from the cumulative distribution functions derived from cougar UDs for the Westside, Cle Elum, Okanogan, and Northeast study areas in Washington from 2001 to 2014.

Study area	*n*	Weibull parameters			Number of structures/km^2†		
		Scale	Shape	Nugget‡	50% CDF	95% CDF	99% CDF
Cle Elum	22	0.44 (0.12)	0.27 (0.02)	0.77 (0.03)	0.11	24.20	117.70
Northeast	17	0.09 (0.03)	0.31 (0.03)	0.92 (0.01)	0.03	2.88	11.40
Okanogan	53	1.21 (0.34)	0.37 (0.04)	0.77 (0.03)	0.45	23.40	74.70
Westside	20	3.33 (1.43)	0.28 (0.02)	0.73 (0.04)	0.89	177.60	846.00
Eastern Washington	92	0.82 (0.20)	0.34 (0.02)	0.80 (0.02)	0.28	21.30	76.50
Statewide	112	1.27 (0.31)	0.33 (0.02)	0.79 (0.02)	0.41	36.75	137.50

Notes: UD, utilization distribution. Weibull equation for the density of structures was exp.

† Number of structures per km^2 of the average cougar cumulative distribution function (CDF) derived from the UD of each cougar (i.e., the residential threshold).

‡ The nugget represents the proportion of use that occurs in undeveloped areas.

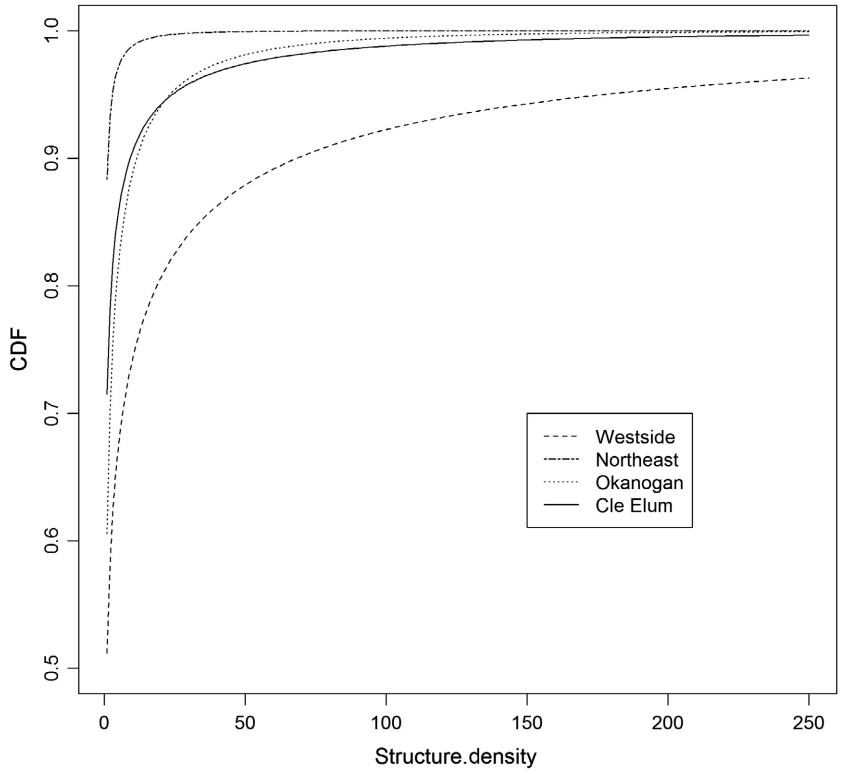

Fig. 2. Weibull function outputs (cumulative distribution functions [CDF]) for cougars in Washington from 2001 to 2014, demonstrating consistent response of decreasing use as human development increases (shape), but different tolerances across study areas (scale).

between cougars and humans requires an interdisciplinary approach involving both wildlife agencies and landscape planners. Identifying these thresholds provides new information on cougar responses to human development that can be used to guide landscape planning and cougar management decisions that may be advantageous to both cougars and people.

Cougars demonstrated varying levels of use of human development in each study area, but a consistent response of decreasing use as housing densities increased. Cougar use of developed areas occurred primarily at the wildland–urban interface and within the matrix of low-density human development (<36 houses/km^2) and undeveloped parcels connected to wildland habitats, similar to results presented by Beier et al. (2010), Jansen (2011), and Kertson et al. (2013). Ungulates and other prey are commonplace within these habitats (Happe 1982, McCullough et al. 1997, Bender et al. 2004, Prange et al. 2004, Polfus and Krausman 2012), and cougars are known to kill a variety of prey close to residences (Kertson et al. 2011*a*, *b*, White et al. 2011). Cougars used human-developed areas more often during the night (Kertson et al. 2011*a*, *b*, 2013), which is consistent with space-use patterns reported for cougars in Alberta (Knopff et al. 2014), California (Sweanor et al. 2008, Smith et al. 2015), Colorado (Lewis et al. 2015), and South Dakota (Jansen 2011) and may represent a range-wide behavioral adaptation by cougars (Burdett et al. 2010, Moss et al. 2016). While prey density, cover, and connectivity with wildlands likely contribute to cougars using developed areas (Burdett et al. 2010, Kertson et al. 2011*a*, *b*, 2013), our results reinforce other findings that increasing human development results in decreased use by cougars. Beier (1993) found that development beyond exurban levels often impedes access for cougars to suitable habitat in wildland–urban landscapes (Fig. 3). Our findings support those of

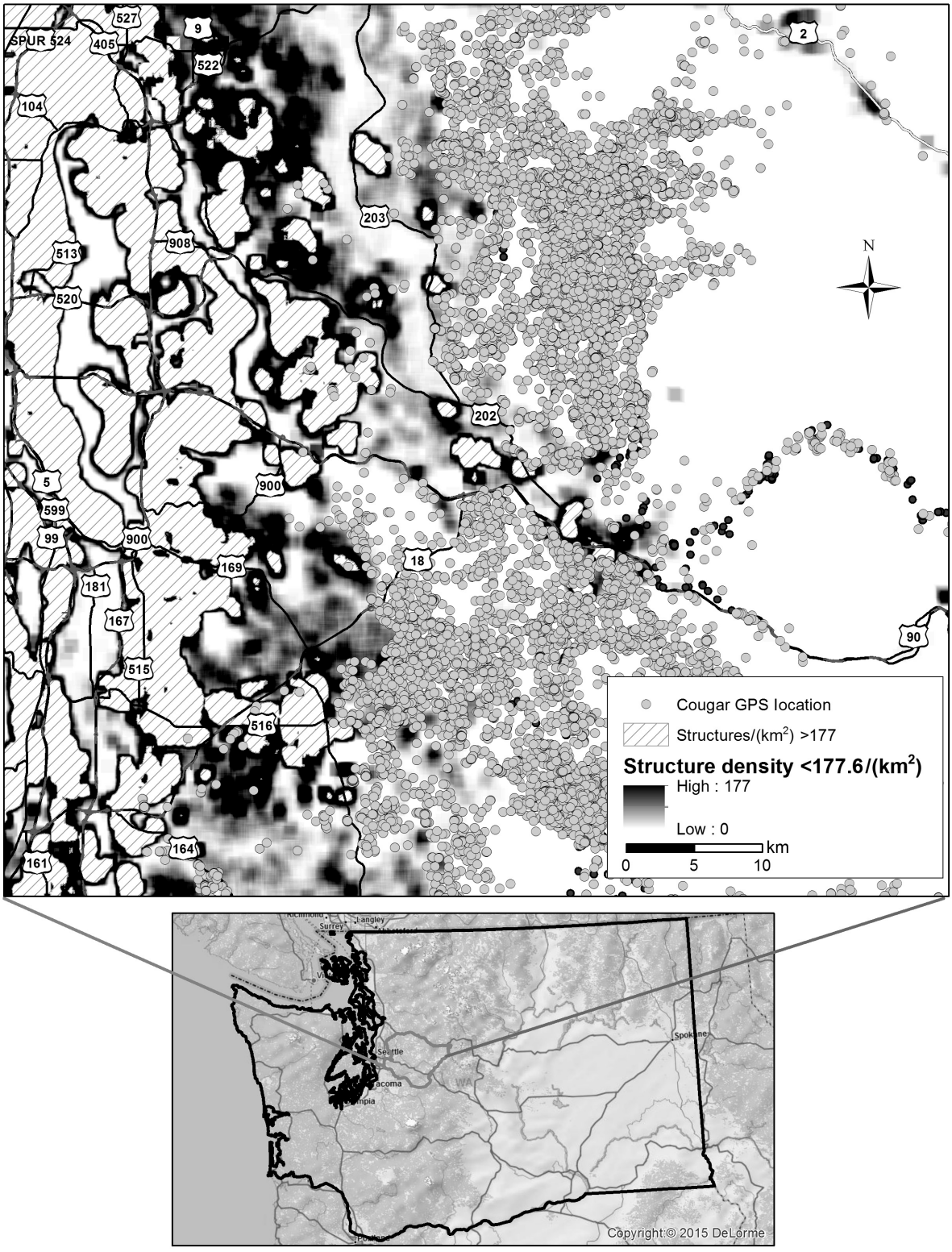

Fig. 3. An example of how cougars used habitat within the matrix of human development with housing

(*Fig. 3. Continued*)
densities <177.6 structures/km^2 in western Washington from 2001 to 2014. The gray circles represent single global positioning system (GPS) relocations of collared cougars, and the hashed light gray depicts areas with housing densities >177.6 structures/km^2, where <5% of cougar use occurred.

Beier (1993) but compliment the results by clarifying what the actual residential density that impedes use by cougars.

We found significant differences between thresholds of use by cougars in Washington's western and eastern ecoregions that may be explained by differences in vegetative densities and design and patterns of human development. Specifically, the greater threshold seen in the Westside study area may stem from the dense vegetation ensuing from a wet, maritime climate (Franklin and Dyrness 1973, Western Region Climate Center 2013) and residential development patterns that preserved landscape connectivity in residential environments by clustering homes at suburban and urban densities (Robinson et al. 2005, Reed et al. 2014). The dense vegetation provides security and stalking cover for cougars, which may allow them to move undetected in closer proximity to human development. Conversely, the eastern Washington study areas had a drier, continental climate with open conifer forests comprising less understory vegetation that precluded adequate stalking and security cover for cougars. Limited understory vegetation coupled with low-density residential development created the potential for frequent interactions with humans and may explain a lower residential threshold for cougars in the eastside study areas. Cougar density estimates for the study areas provided by Cooley et al. (2009) and Beausoleil et al. (2013) were not appreciably different and likely not a significant driver of cougar response to residential development.

The shared use of wildland–urban landscapes by people and carnivores requires strategies that simultaneously minimize risks to public safety and carnivore population viability (Gerht et al. 2010). Successful implementation of these strategies requires information on how large carnivores respond to different levels and patterns of human development as well as where to focus education on coexistence and ways to prevent potential conflict. Consequently, the ability to quantify housing density thresholds for large carnivores may be of particular interest for wildlife managers and landscape planners looking to develop comprehensive strategies for maintaining ecosystem functionality, addressing carnivore–human coexistence, and reducing cougar–human conflict.

Minimizing cougar–human interaction is a management priority for many state and provincial wildlife agencies (Cougar Management Guidelines Working Group 2005, Beausoleil et al. 2008). Strategies to reduce conflict often focus on population reductions or removal of the offending cougar and fail to account for landscape characteristics that may be attractive to cougars (Kertson et al. 2011*a*, *b*, Knopff et al. 2014). Using the Weibull equation with the coefficients estimated from empirically derived use data (i.e., the UD) allows managers to model the probability of use by cougars to identify areas where interactions are most likely to occur. This would permit management agencies to focus education and outreach on locales with greater potential for conflict.

Our analysis identifies housing densities that encompass a gradient of cougar use and the model can be used for the purpose of developing landscape management and planning strategies designed to discourage cougar use of developed areas and decrease the potential for interactions with people. Clustering human development locally at densities >178 houses/km^2 in areas with a maritime climate environment such as western Washington or >22 houses/km^2 in dry forest regions similar to eastern Washington creates a sharp contrast between wildland and developed portions of the landscape, thus decreasing permeability (Marzluff and Ewing 2001, Odell et al. 2003, Gagne and Fahrig 2010). This approach could also provide benefits for other wildlife species by reducing the spatial extent of the human footprint in wildland–urban landscapes and helping to create an interconnected network of undeveloped land (Lenth et al. 2006, Reed et al. 2014).

Conservation planning for cougars as well as other large carnivores where the portions of their

range are increasingly becoming urbanized has largely focused on minimizing habitat loss and preserving or improving landscape connectivity (McRae et al. 2008, Beier 2009, Burdett et al. 2010). The core areas of cougar home ranges (79% ± 2% of use) were situated in settings with <1 residence/km^2 throughout Washington regardless of habitat and development characteristics, further demonstrating that wildland preservation remains critical for the long-term viability of cougar populations (Cougar Management Guidelines Working Group 2005). Our approach builds upon this cornerstone and the planning recommendations of both Lenth et al. (2006) and Reed et al. (2014) by providing specific guidance that allows wildlife agencies, planners, and zoning boards to work collaboratively and incorporate quantifiable data of the impacts of human development on cougars into the land-use policy process. Improved landscape and conservation planning for large carnivores requires a more complete understanding of how a diversity of species responds to human development patterns. We suggest that analyzing animal-use patterns along a continuum of environmental parameters, as we have demonstrated, can better identify and address conservation strategies for the coexistence of animal species and humans.

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