Journal of Mammalogy, 94(2):269–281, 2013

Demographic influences on cougar residential use and interactions with people in western Washington

Brian N. Kertson,* Rocky D. Spencer, and Christian E. Grue

School of Forest Resources, College of the Environment, University of Washington, Seattle, WA 98195, USA (BNK)
Washington Department of Fish and Wildlife, 1775 12th Avenue NW, Suite 201, Issaquah, WA 98027, USA (RDS; deceased)
United States Geological Survey, Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fisheries Sciences, University of Washington, Seattle, WA 98195, USA (CEG)

* *Correspondent: brian.kertson@dfw.wa.gov*

Sound management of large carnivore populations in wildland–urban environments requires accurate information regarding the ecology of these populations and factors contributing to their interactions with people. We quantified cougar (*Puma concolor*) residential use and interactions with people in western Washington from 2003 to 2008 to characterize the ecology and risks associated with an adaptable large carnivore residing in a wildland–urban environment. We fitted cougars with global positioning system and very-high-frequency radiocollars, quantified residential use, and tested for differences between demographic classes using analysis of variance fixed-effects and multiple-comparison models. We investigated interaction reports to quantify interaction rates and tested for differences among interaction levels for different cougar demographic classes. We captured 32 cougars (16 males and 16 females) and estimated 33 annual utilization distributions (UDs) for 27 individuals. Ninety-three percent of cougars ($n = 27$; 15 males and 12 females) used residential areas with an average UD overlap of 16.86% ($SD = 17.05\%$, $n = 33$). There were no differences between male and female ($F_{1,29} = 0.77$, $P = 0.49$) or resident and transient ($F_{1,29} = 0.0003$, $P = 0.99$) use of residential areas, but subadult use was significantly higher than that of adults ($F_{1,29} = 7.20$, $P = 0.01$). Twenty-nine percent of reports were confirmed ($n = 73$), with livestock depredations accounting for 67% of confirmed reports. The interaction rate for radiocollared cougars was low (1.6 interactions/1,000 radiodays) and all demographic classes were involved in similar numbers of interactions. Use of residential areas in western Washington appears to be a function of the adaptive and mobile nature of the cougar exploiting suitable habitat and resources within the matrix of residential development. Interaction appears to be a function of individual behavior. Management strategies that target problem individuals and maintain older age structures in local populations coupled with proactive landscape planning and public education in residential areas at the wildland–urban interface may provide an effective strategy for decreasing cougar–human interaction.

Key words: cougar, demographics, *Puma concolor*, residential use, Washington, wildland–urban interface, wildlife–human interaction

DOI: 10.1644/12-MAMM-A-051.1

Anthropogenic influences on ecosystems can be substantial and pervasive (Pickett et al. 2001; Vitousek et al. 1997). When humans alter ecosystems with residential development they threaten the long-term viability of many wildlife species (Ewing et al. 2005; Hansen et al. 2005). However, residential development frequently occurs across the landscape along a gradient of densities (Theobald 2005), resulting in a wildland–urban environment that may maintain, or create, features that are beneficial or attractive to some wildlife (Donnelly and Marzluff 2006; Gehrt et al. 2010). For large carnivores, increased spatial and temporal overlap with people increases conflict and the potential for persecution and extirpation of local populations (Cardillo et al. 2004; Inskip and Zimmermann 2009; Jackson and Nowell 1996; Woodroffe 2000). The elimination of large carnivores can alter ecosystem composition and function (Ray et al. 2005) and the impacts of anthropogenic landscape conversion extend beyond residential boundaries (Pickett et al. 2001). Consequently, the presence of large carnivores within wildland–urban environments presents unique challenges for wildlife managers attempting to maintain viable populations within wildlands while minimizing risks to public safety and private property within residential areas. Development of sound management and conservation strategies for large carnivores living within and adjacent to human population centers requires accurate information on the spatial ecology of these carnivores and factors contributing to their interactions with people.

The cougar (*Puma concolor*) is a highly adaptable carnivore that occupies a wide variety of habitats throughout the Western Hemisphere (Sunquist and Sunquist 2002). Once perceived as a wilderness species (Gill 2009), cougars now frequent areas with an extensive human presence and interactions with people are increasingly common (Beier et al. 2010; Torres et al. 1996). Cougar–human interactions (sightings, encounters, depredations on livestock and pets, and attacks on people) are a function of the spatial and temporal co-occurrence of cougars and humans. Increasing residential density levels decreases the intensity of cougar use of an area (Burdett et al. 2010; Kertson et al. 2011b). However, low-density residential development modifies the habitat, but maintains enough wildland characteristics to encourage moderate levels of cougar use and maximize the probability of interaction with humans (Burdett et al. 2010; Kertson et al. 2011b). The intensity and spatial extent of cougar use of the wildland–urban interface and residential portions of the landscape has not been extensively investigated, so quantifying use of these areas provides valuable information for improving our understanding of cougar wildland–urban ecology and implications for humans sharing these landscapes (Beier et al. 2010; Cougar Management Guidelines Working Group 2005; McKinney 2011).

The number and frequency of cougar–human interactions have increased in recent years, raising public safety concerns and garnering greater management emphasis (Apker et al. 2011; Beier 1991; Cougar Management Guidelines Working Group 2005; Fitzhugh et al. 2003; Mattson 2007). Although cougar–human interactions have been studied in many parts of North America (Anderson 1991; Aune 1991; Herbert and Lay 1997; Kertson et al. 2011b; Shuey 2005; Torres et al. 1996), factors contributing to observed increases are poorly understood. Explanations for increases include greater probability of encounter due to a growing number of cougars or people in cougar habitat, cougar space-use patterns, presence of individuals in the cougar population that are more aggressive than others toward people, and cougar behavioral changes such as habituation (Burdett et al. 2010; Cougar Management Guidelines Working Group 2005; Kertson et al. 2011b). However, the importance of these factors remains largely speculative. Cougars within different demographic classes also may be more likely to interact with people (Apker et al. 2011; Beier 1991; Cougar Management Guidelines Working Group 2005; Ruth 1991). Consequently, identification of cougars with a predisposition for using residential areas and interacting with people would provide an opportunity for targeted management efforts that minimize impacts to the cougar population while decreasing the potential for conflict.

Western Washington provides an ideal environment to study cougar spatial ecology along a gradient of residential development and represents a microcosm of the issues facing cougar managers throughout western North America. Washington has experienced a 30.4% increase in its human population since 1990 (United States Census Bureau 2008), extensive conversion of wildlife habitats (Alberti et al. 2001; Hepinstall et al. 2008; Robinson et al. 2005), and 6,773 cougar–human interaction reports from 1995 to 2008 (Washington Department of Fish and Wildlife 2008).

To better understand the relationship between cougar spatial ecology, demographic characteristics, and interactions with people, we quantified and compared cougar use and interactions with people in a wildland–urban landscape in western Washington. We quantified and compared residential use by different cougar demographic classes to identify segments of the population that are more likely to use residential areas. We hypothesized that males, subadults, and transients would have higher levels of residential use and a greater number of interactions than females, adults, and residents. We investigated reports of cougar–human interaction, compared confirmed interaction levels with reported levels, and estimated interaction rates from observations of marked animals to determine the actual versus perceived risk of cougar presence in residential areas. We used these findings to characterize cougar wildland–urban ecology and crafted recommendations for wildlife managers looking to maintain viable cougar populations in wildland–urban environments while minimizing risks to people in this shared landscape.

MATERIALS AND METHODS

Study site.—We examined cougar wildland–urban ecology and interactions with humans in a 3,500-km^2 study area consisting of wildland and residential portions of King and Snohomish counties, Washington (47°29′N, 121°48′W; Fig. 1). Land ownership was a composite of state, federal, municipal, and private holdings managed for timber production, water resources, multiple use, wilderness, commercial use, and private residential. Major landowners included the Washington Department of Natural Resources, City of Seattle, King County, Hancock Resource Management Group, Fruit Growers Supply Incorporated, and the United States Forest Service. The western portion of the study area (~1,000 km^2) consisted of fragmented forest patches and reserves within a matrix of suburban (2.5–10 residences/ha) and urban (>10 residences/ha) development (Robinson et al. 2005). Remaining urban and suburban development was concentrated along the Interstate 90, United States Highway 2, and Washington State Highway 203 corridors with exurban development (>0–2.5 residences/ha) extending into the Cascade Mountain foothills.

FIG. 1.—Location of the 3,500-km^2 cougar (*Puma concolor*) study area encompassing both wildland and residential portions of western Washington. The wildland–urban interface is depicted by the white line. Urban and residential development occurred across the western one-third of the study area, with residential densities largely increasing from east to west.

Vegetation, physiographic, and topographic characteristics have been described previously at length (Kertson and Marzluff 2010; Kertson et al. 2011a, 2011b). The climate was moderated by the proximity of a mild, maritime environment and temperature extremes were rare. Mean annual precipitation ranged from 142 cm in the west to 257 cm in the east and occurred primarily as rain between 1 October and 1 July (Western Region Climate Center 2009).

Cougars within the study area preyed primarily on black-tailed deer (*Odocoileus hemionus columbianus*), beaver (*Castor canadensis*), elk (*Cervus elaphus*), raccoon (*Procyon lotor*), and mountain beaver (*Aplodontia rufa*—Kertson et al. 2011a). The study area consisted of all, or part, of Washington Department of Fish and Wildlife Game Management Units 454 (Issaquah), 460 (Snoqualmie), 485 (Green River), and 490 (Cedar River). Hunting of cougars within Game Management Unit 490 was prohibited, but low levels of cougar harvest occurred in Game Management Units 454, 460, and 485 with 0–3 individuals removed each year from 2003 to 2008 (Washington Department of Fish and Wildlife 2008). Reported cougar–human interaction within this area was frequently the highest in the state ($\bar{X} = 129$ reports/year, $SD = 21$ reports/year, from 1 January 2006 to 31 December 2008 [Washington Department of Fish and Wildlife 2008]), but per capita report levels were low ($\bar{X} = 0.00016$ reports per person per year, $SD = 0.000058$ reports per person per year, $n = 3$ years).

Capture, collaring, and monitoring.—We attempted to capture cougars >1 year of age present in the study area each year from November 2003 to December 2008. Cougar capture, handling, and collaring have been described in detail elsewhere (Kertson and Marzluff 2010; Kertson et al. 2011a, 2011b), with all techniques performed in accordance with the guidelines of the American Society of Mammalogists for the use of live animals in research (Sikes et al. 2011) and approved by the University of Washington's Institutional Animal Care and Use Committee under protocol 2185-36.

Cougars were aged at the time of capture based on tooth color, wear, and a measurement of gum-line recession (Anderson and Aune 2004; Laundré et al. 2000). Females reach sexual maturity and tend to establish home ranges before males, so we classified females $\leq$2.0 and males $\leq$3.0 years of age as subadults (Sunquist and Sunquist 2002). Cougar social class (i.e., resident versus transient) is dependent upon a number of physiological, behavioral, and ecological factors, so we based classification as a resident or transient on a combination of sex, age, size, spatial overlap with larger (i.e., more dominant) individuals, and observed movements (Hemker et al. 1984; Logan and Sweanor 2001). We monitored reproduction of all females using the global positioning system and very-high-frequency methods of Cooley et al. (2009). We did not separate demographic classes for adult females based on reproductive status because all adult females within our sample were accompanied by dependent offspring for all or a portion of the year(s) they were monitored. Females $\leq$2.0 years old were considered subadult transients until we confirmed reproduction. Males $\leq$3.0 years of age weighing $<$64.0 kg with greater than one-half of their utilization distribution (UD) overlapping the UD of an older, larger male (volume of intersection—Kernohan et al. 2001) were considered subadult transients. Male cougars $>$3.0 years of age weighing $>$64.0 kg were considered adult transients if greater than one-half of their UD overlapped the UD of a larger male or we observed a marked shift in UD location following an interaction with another male.

We programmed global positioning system radiocollars to acquire a satellite location-fix for 180 s every 4 h in an attempt to maximize collar performance (Cain et al. 2005; DeCesare et al. 2005; D'Eon and Delparte 2005; Lewis et al. 2007). We randomly selected and located both global positioning system– and very-high-frequency–collared individuals 1–2 days per week between 0600 h and 2000 h by homing to an estimated 100 m of their position using ground-based radiotelemetry (Mech 1983).

Cougar space use and interactions with humans.—The UD is a probability density function that quantifies an individual's relative use of space (Van Winkle 1975). We estimated fixed-kernel home ranges (Kernohan et al. 2001; Worton 1989) for each cougar monitored at least 3 months with greater than 30 global positioning system or very-high-frequency relocations, or both (Seaman et al. 1999), using the Fixed Kernel Density Estimator in Hawth's Tools (Beyer 2004) in ArcMap 9.3 (Environmental Systems Research Institute 2009). We used the hpi function within the KernSmooth package in program R (R Development Core Team 2008; Wand 2006) to estimate the bivariate plug-in bandwidth values (h_{pi}) for each kernel (Wand and Jones 1995). We selected the bivariate h_{pi} to smooth kernels based on the spatial characteristics of cougar relocation data and the lower tendency of h_{pi} to oversmooth kernels compared to other bandwidth estimators (Gitzen et al. 2006; Kertson and Marzluff 2010). We generated kernels on a 30 × 30-m grid and defined use for cougars as the 99% fixed-kernel boundary with each cell within this area assigned a probability value based on the volume (height) of the UD (Van Winkle 1975; Worton 1989). To facilitate additional comparisons of cougar residential use, we used UDs and Percent Volume Contour in Hawth's Tools (Beyer 2004) to create 99% area polygons (home ranges) for each cougar. For individuals monitored $>$1 year, we considered each calendar year independent because individual space-use patterns changed annually, most likely because of high levels of mortality in the population leading to home-range shifts (Logan and Sweanor 2001), changes in cougar social or reproductive status, and landscape alteration primarily in the form of commercial logging and residential development. We did not include dependent offspring within our analysis because the movements of these individuals are not independent of their mothers.

The wildland–urban interface is the confluence of wildland (0 residences/ha) and residential ($>$0 residence/ha) portions of the landscape (Theobald and Romme 2007). We used the SERGoM version 1 landcover model (Theobald 2005) and ArcMap 9.3 to classify residential and wildland portions of our study area and delineate the location of the wildland–urban interface (Kertson et al. 2011b). Specifically, we used the Year 2000 Rural I-3 projection and ArcMap 9.3 to create a residential development polygon and a line-layer depicting the location of the wildland–urban interface (Kertson et al. 2011b). We used 1.0-m-resolution aerial photographs of the study area (Washington Department of Natural Resources 2008), county tax parcel records, and the Editor tool in ArcMap 9.3 to adjust the location of the wildland–urban interface and reclassify residential density levels as needed to account for mapping errors and residential development that occurred after 2000 (Kertson et al. 2011b).

We measured the proportion of the each cougar's UD volume and area to quantify intensity of use and spatial overlap with residential development. To measure intensity of use, we intersected a point grid containing values of each cougar's UD with the residential polygon using Select by Location in ArcMap 9.3. Because the UD is a probability density function that sums to 1.0 (Van Winkle 1975; Worton 1989), the summed values within the residential polygon represent the proportion of cougar use. To quantify spatial overlap, we used Polygon in Polygon Analysis in Hawth's Tools (Beyer 2004) and the field calculator to measure the proportion of each cougar's 99% home-range area that fell within the residential portion of the landscape. Polygon in Polygon Analysis uses zonal tools within ArcMap to produce an area-based summary of overlap between 2 polygons of interest (Beyer 2004). Subsequently, we estimated the proportion of residential overlap for each cougar using this measure of residential area within the home range divided by total home-range area.

To complement probabilistic and area-based measures of residential use, we examined the proximity of cougars to residential development using the combined global positioning system and very-high-frequency locations of each cougar. We created a 30 × 30-m grid of distances to residential development in King, Pierce, and Snohomish counties using the residential point layer and Spatial Analyst in ArcMap 9.3. We measured the distance of each location to residential development, calculated the average distance for each cougar ($n = 29$), and calculated the proportion of locations of of each individual and of the sample population within 0–500, 501–1,000, 1,001–2,000, 2,001–5,000, and >5,000 m of residential development.

We also calculated daily and distance-based cougar interaction rates to quantify the potential of a cougar interacting with people within the study area. We estimated daily interaction rates by dividing the number of known interactions from marked cougars by the total number of radiodays individuals were monitored. To estimate the distance-based rate, we divided the number of known interactions from marked cougars by the number of global positioning system and very-high-frequency relocations within 500 m of residential development (Kertson et al. 2011a).

We estimated per capita livestock depredation using the number of confirmed depredations and 2007 livestock population estimates for King and Snohomish counties obtained from the National Agricultural Statistics Service (United States Department of Agriculture 2007). Counts of livestock for the study area were not available, so we estimated the count based on the proportion of both counties overlapping the study area (King: ~53%; Snohomish: ~6%). We estimated species-specific per capita depredations for the most common species killed and we excluded cattle from the analysis because cougar depredations on cattle were not observed and most cattle reside on commercial dairy farms located on rural, agricultural lands rarely used by cougars (Kertson et al. 2011a, 2011b).

Cougar report classification and investigation.—We investigated reports of cougar–human interaction received by the Washington Department of Fish and Wildlife in the study area from 1 January 2006 to 31 December 2008. We defined cougar–human interactions and subsequent reports as a sighting (a cougar was observed by a person, but the presence of the person did not alter the behavior of the cougar), an encounter (a cougar was observed by a person from <50 m and the person's presence elicited a behavioral response from the cougar; e.g., prolonged staring, fleeing, or approaching), a depredation (livestock or pets were killed), or an attack (physical contact between a person and cougar). We contacted the reporting party, visited the location the day of the report, and conducted a thorough search for evidence of cougar (tracks, scat, hair, prey carcass, or a combination of these). We did not consider eyewitness accounts without physical evidence verified and we did not consider multiple local reports independent unless timing of incidents, physical evidence, telemetry data, or a combination of these suggested different cougars were involved. We classified report outcomes as confirmed (physical evidence present), probable (no physical evidence, but information provided by the reporting party combined with circumstances of the interaction suggested it was possible), and unconfirmed (physical evidence of other species present or information provided by the reporting party, or both, was not consistent with cougar). We attempted to document the demographic characteristics of the cougar(s) involved in all confirmed reports. To increase sample sizes, we included depredations we investigated dating back to January 2005. For all reports, we recorded forest type (conifer, hardwood, mixed, or residential), understory density (low, medium, or high), Universal Transverse Mercator coordinates for the site using a handheld global positioning system receiver, and whether or not human activity was present. We calculated the percentage of confirmed, probable, and unconfirmed reports as the number in each class divided by the total number of reports. To better understand the potential influences of residential development and forest cover on the risk for cougar–human interactions, we used the methodology of Kertson et al. (2011b) and 1-sided *t*-tests (Zar 1999) to compare mean residential density (residences/km^2) and percent forest cover per square kilometer for locations of confirmed interactions and the study area as a whole.

Statistical analyses.—We used an analysis of variance (ANOVA) fixed-effects model to determine if there were statistical differences between residential use and observed proximity to people of cougars with different sex, age, and social characteristics. We tested for differences between specific demographic classes (e.g., adult male residents versus adult female residents) using a 1-way ANOVA with multiple-comparison procedures controlling for type I error with Tukey's honestly significant difference (Oehlert 2000). We log-transformed UD and home-range area overlap outputs to conform to the assumptions of the ANOVA model (Zar 1999). We tested for differences between the numbers of cougar–human interactions among demographic classes using the chi-square goodness-of-fit test (Zar 1999). We assumed the expected number of interactions from each demographic class to be equal because the sex and age structure of the overall population were unknown. All statistical tests were considered significant at $\alpha \leq 0.05$.

RESULTS

Capture, collaring, and monitoring.—We captured 32 adult and subadult cougars (16 males and 16 females) from November 2003 to December 2008. Cougars were monitored an average of 332 days (*SD* = 300 days) with global positioning system and very-high-frequency collars yielding an average of 477 locations/year (*SD* = 540 locations/year, $n = 42$ cougar years). Cougars were exposed to a variety of anthropogenic mortality sources within the study area and average annual survival was estimated to be 56% (B. Kertson, Washington Department of Fish and Wildlife, pers. comm.). Consequently, only 2 males and 3 females were monitored for >1 year, with 2 of these females transitioning from subadult transient to adult resident classes. One adult resident male was

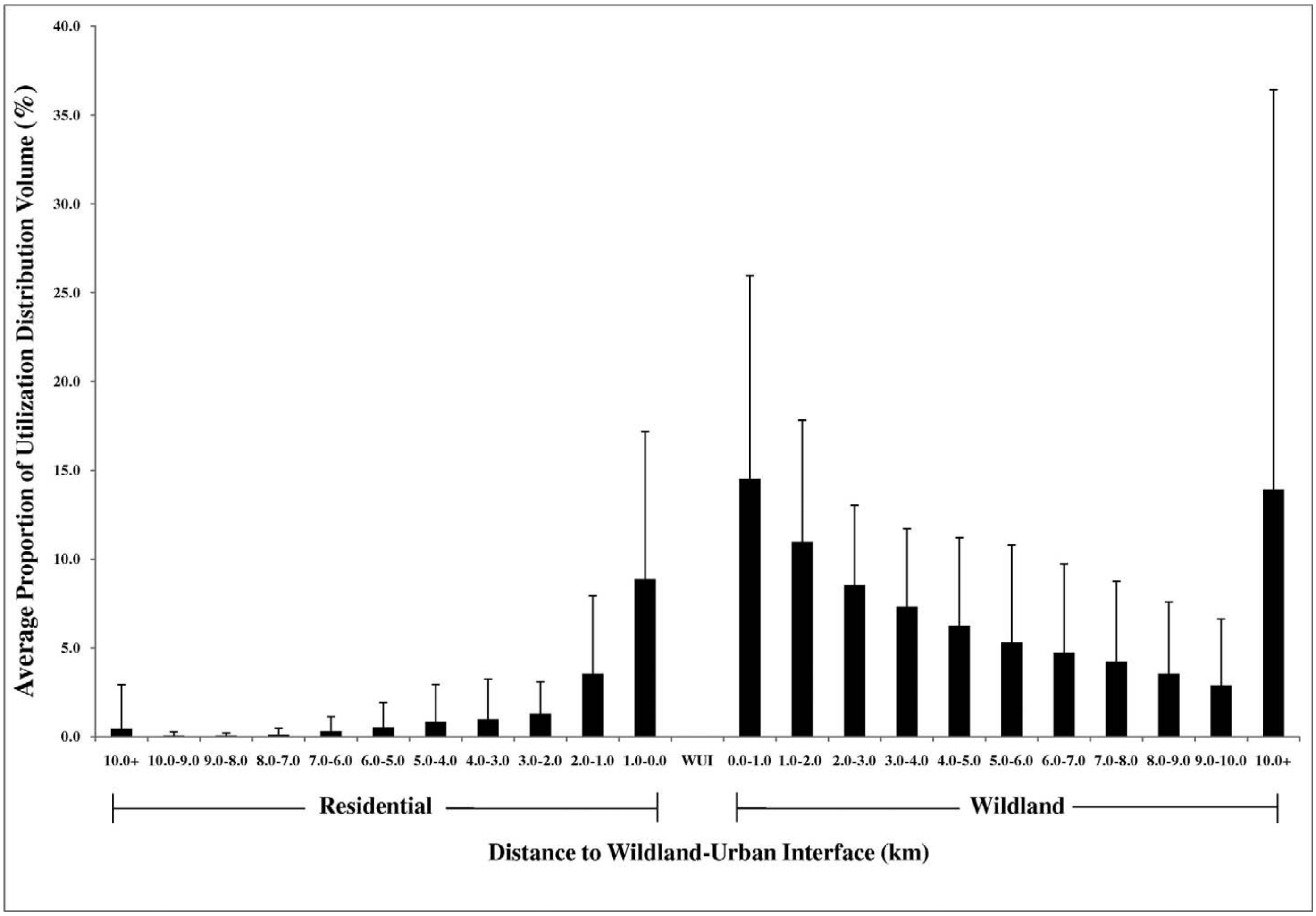

FIG. 2.—Average proportion of utilization distribution (UD) volume in 1-km intervals from the wildland–urban interface (WUI) in wildland and residential portions of western Washington from 2003 to 2008. Averages are derived from 33 UDs ($n = 27$ cougars) and errors bars represent 1 *SD*.

reclassified as an adult transient after he was usurped by another male and he shifted his home range approximately 25 km south.

Cougar space use and interactions with humans.—We estimated 33 UDs for 27 cougars. Male UDs averaged 678.2 km^2 ($SD = 369.4$ km^2, $n = 17$) and female UDs averaged 238.6 km^2 ($SD = 131.3$ km^2, $n = 16$). Subadult male and female UDs averaged 497.9 km^2 ($SD = 310.0$ km^2, $n = 9$) compared to 452.7 km^2 ($SD = 376.0$ km^2, $n = 24$) for adults. Transients' UDs averaged 592.2 km^2 ($SD = 409.9$ km^2, $n = 12$) and residents 392.4 km^2 ($SD = 306.7$ km^2, $n = 21$).

The majority of cougars (91% of UDs, 93% of individuals) had a portion of their UD overlapping residential development. Use of residential areas occurred primarily within 2 km of the wildland–urban interface in areas of exurban development (Fig. 2). Use of suburban settings was less common and largely occurred in forested corridors and patches within the matrix of residential development (Fig. 3). Residential use varied substantially between individuals ranging from 0% to 55.03%, but 93% of individuals spent the majority of their time within wildland areas (i.e., >50% of their UD volume overlapped with wildlands [Fig. 2]). Only 1 adult female and 1 subadult male had >50% of their UD within residential areas. Residential use based on UDs averaged 16.86% ($SD = 17.05\%$, $n = 33$) and home-range area overlap with residential areas averaged 18.35% ($SD = 16.75\%$, $n = 33$; Table 1).

All demographic classes of cougar used residential areas. Subadult and transient cougars had the highest proportions of their UD volume and home-range area overlapping residential development, adults the least, and males and females were essentially equal (Table 1). Cougar age had a significant effect on residential use and area overlap (AGE$_{\mathrm{UD}}$: $F_{1,29} = 7.201$, $P = 0.39$; AGE$_{\mathrm{Area}}$: $F_{1,29} = 6.496$, $P = 0.02$), but the effect of sex, social status, and the interaction of sex and age characteristics were not significant (SEX$_{\mathrm{UD}}$: $F_{1,29} = 0.771$, $P = 0.39$; SEX$_{\mathrm{Area}}$: $F_{1,29} = 2.508$, $P = 0.12$; SOCIAL$_{\mathrm{UD}}$: $F_{1,29} = 0.0003$, $P = 0.99$; SOCIAL$_{\mathrm{Area}}$: $F_{1,29} = 0.0009$, $P = 0.98$; SEX–AGE$_{\mathrm{UD}}$: $F_{1,29} = 0868$, $P = 0.36$; SEX–AGE$_{\mathrm{Area}}$: $F_{1,29} = 1.412$, $P = 0.24$). Transient, subadult males and females were observed with the highest residential overlap followed by adult females; resident, adult males; and transient, adult males (Table 2); the effect of cougar demographic class on residential use and overlap

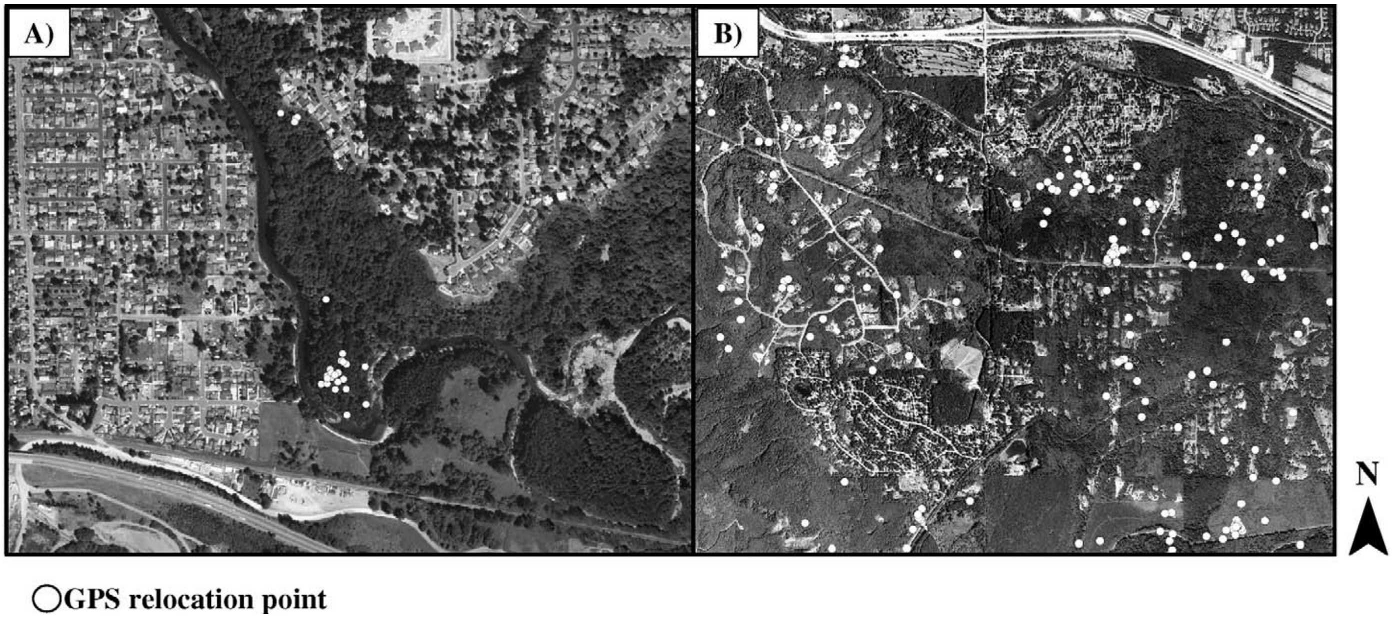

Fig. 3.—Examples of observed cougar (*Puma concolor*) use of suitable habitat in residential portions of the study area in western Washington recorded with global positioning system radiocollars. A) Subadult male M326′s use of the Green River riparian corridor in Auburn, Washington, in 2008. B) Adult female F137's use of forest patches and corridors at the wildland–urban interface of North Bend, Washington, in 2004 and 2005.

approached significance (UD: $F_{4,28} = 2.142$, $P = 0.10$: Area: $F_{4,28} = 2.486$, $P = 0.07$). Multiple comparisons did not yield significant differences between any 2 demographic classes.

Cougars were an average of 3,773 m ($SE = 503$ m, $n = 29$; 19,416 locations) from residential development, with 12.0% of locations occurring within 500 m, 7.3% between 501 and 1,000 m, 11.8% between 1,001 and 2,000 m, 23.6% between 2,001 and 5,000 m, and 45.3% >5,000 m. Subadult and transient individuals were closer to residential development than were adults and residents. Male and female locations were approximately equal distance from residential development (Fig. 4a). Cougar age had a significant effect on distance to residential development ($F_{1,29} = 4.455$, $P = 0.04$), whereas the effects of sex, social status, and the interaction of sex and age were not significant (SEX: $F_{1,29} = 0.001$, $P = 0.98$; SOCIAL: $F_{1,29} = 0.915$, $P = 0.35$; SEX–AGE: $F_{1,29} = 1.082$, $P = 0.31$). Subadult females were observed closest to residential development followed by subadult males, adult male residents, adult females, and adult male transients (Fig. 4b), but the effect of cougar demographic class on observed proximity to development was not significant ($F_{4,29} = 1.613$, $P = 0.20$) and pairwise comparisons did not reveal any significant differences.

Marked cougars were monitored for 10,633 radiodays ($\bar{X} =$ 332 radiodays/individual, $SD = 300$ radiodays/individual, $n =$ 32) and were involved in 17 known interactions for a rate of 1.6 interactions/1,000 radiodays. Excluding 3 individuals that did not use areas with residential development, interaction rates increased to 1.9 interactions/1,000 radiodays. Cougars were documented within 500 m of residential development on 2,323 occasions, but reported interactions occurred in only 0.73% of these observations.

Cougar report classification and investigation.—We investigated 73 reports of cougar–human interaction within the study area between 1 January 2006 and 31 December 2008. Reports originated throughout the developed portions of the study area close to the wildland–urban interface ($\bar{X} = 3.43$ km, $SD = 3.57$ km). Residential densities in areas of confirmed reports were lower ($t_{20} = -2.854$, $P = 0.005$) and the percentage of forest was higher ($t_{20} = 3.750$, $P < 0.001$) than the averages for the residential portion of the study area. Cougar sightings were the most common type of interaction

Table 1.—Comparison of average utilization distribution (UD) volume and 99% fixed-kernel home-range area overlap (%) with residential development (>0 residence/ha) for cougars (*Puma concolor*) with different sex, age, and social characteristics in western Washington from 2003 to 2008.

	Sex				Age				Social			
	Male (n = 17)		Female (n = 16)		Adult (n = 24)		Subadult (n = 9)		Resident (n = 21)		Transient (n = 12)	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
UD volume	16.33	16.13	17.42	18.50	12.69	16.05	27.99	15.19	12.53	16.33	24.44	16.21
Home-range area	20.09	17.43	16.51	16.36	13.90	14.04	30.23	18.38	13.26	13.53	27.26	18.64

TABLE 2.—Comparison of average utilization distribution (UD) volume and 99% fixed-kernel home-range area overlap (%) with residential development (>0 residence/ha) for demographic classes of cougar (*Puma concolor*) in western Washington from 2003 to 2008.

	Subadult male transient (*n* = 5)		Subadult female transient (*n* = 4)		Adult male resident (*n* = 9)		Adult male transient (*n* = 3)		Adult female resident (*n* = 12)	
	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*	$\bar{X}$	*SD*
UD volume	26.89	20.43	29.35	7.38	11.30	11.70	13.79	17.20	13.45	19.57
Home-range area	30.48	24.36	29.92	10.46	14.90	10.56	18.36	20.03	12.04	15.74

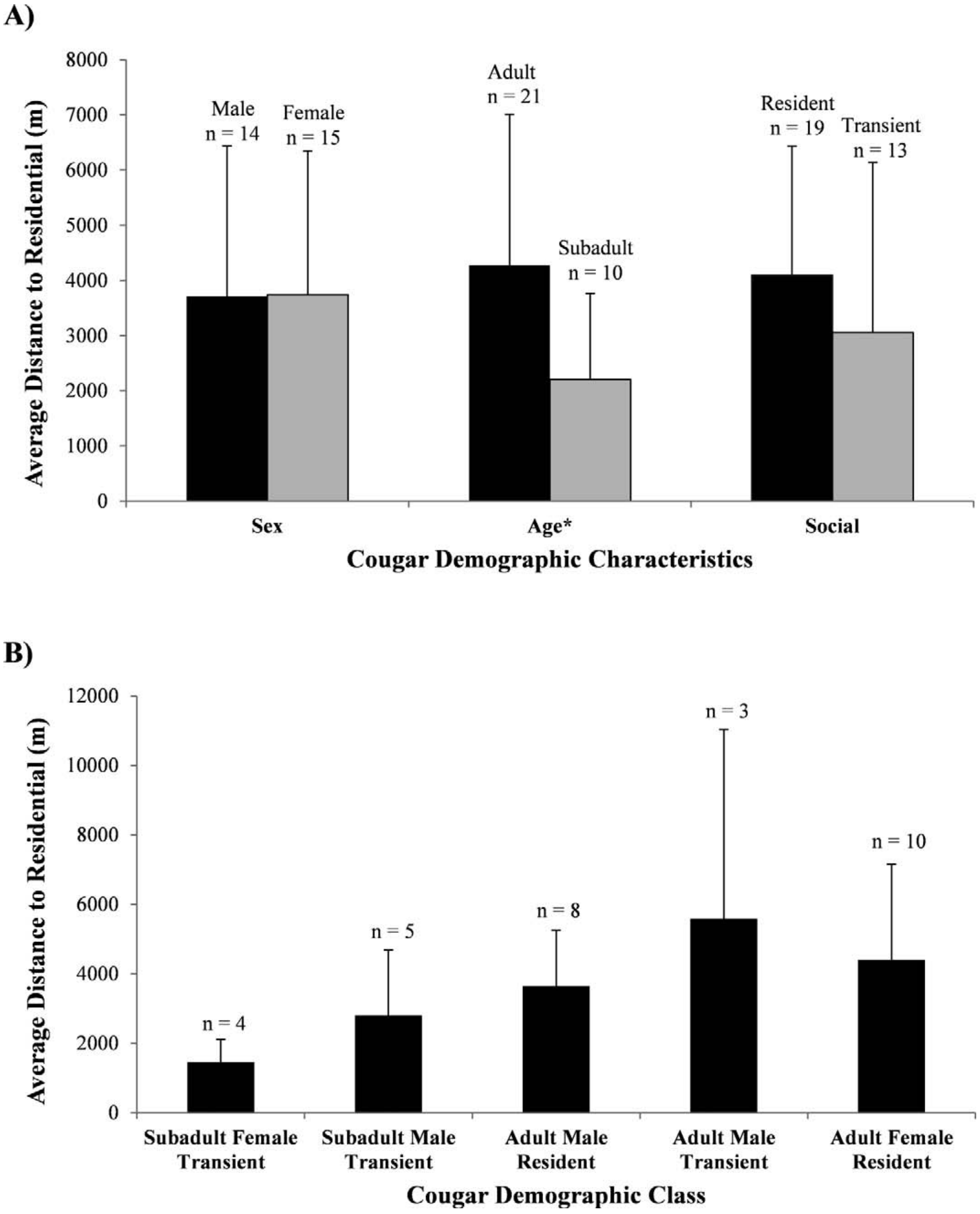

FIG. 4.—Comparison of average distance to residential development for different a) sex, age, and social characteristics; and b) specific demographic classes of cougar (*Puma concolor*) in western Washington from 2003 to 2008. Error bars represent 1 *SE*, sample size is noted above, and an asterisk (*) indicates a statistically significant difference (α = 0.05) between characteristic classes.

Table 3.—Summary of classifications for 73 cougar–human interaction (sightings, encounters, and depredations) reports in western Washington from 1 January 2005 to 31 December 2008.

Report type	No. confirmed	% confirmed	% total	No. probable	% probable	% total	No. unconfirmed	% unconfirmed	% total
Sighting[a]	3	14.28	4.11	11	91.67	15.07	22	55.00	30.14
Encounter[b]	4	19.05	5.48	1	8.33	1.37	3	7.50	4.11
Depredation	14	66.67	19.18				15	37.50	20.55
Total	21		28.77	12		16.44	40		54.79

[a] A cougar was observed by a person, but the presence of the person did not alter the behavior of the cougar.

[b] A cougar was observed by a person from <50 m and the person's presence elicited a behavioral response from the cougar; for example, prolonged staring, fleeing, or approaching.

reported and encounters were the least common (Table 3). Overall confirmation rates were low (29%) and 55% of interaction reports stemmed from domestic dog, coyote, black bear, or bobcat activity. Reports of cougar depredations had the highest level of confirmation and sightings the lowest (Table 3). Bobcats (*Lynx rufus*) were most often mistaken for cougars in sighting ($n = 4$) and encounter ($n = 4$) reports, and coyotes (*Canis latrans*, $n = 7$), bobcats ($n = 2$), and black bears (*Ursus americanus*, $n = 3$) were responsible for most depredations that were not cougar. Sightings of cougars in residential areas rarely correlated with encounters or depredations. One confirmed depredation was associated with 4 sightings of the cougar responsible.

We confirmed 14 depredations from 1 January 2005 to 31 December 2008. Depredations occurred close to the wildland–urban interface ($\bar{X} = 2.10$ km, $SD = 2.26$ km) and most (67%) in areas with residential densities <35 houses/km^2. Horses (*Equus caballus*, $n = 3{,}944$), poultry ($n = 1{,}506$), and alpacas (*Lama glama*, $n = 1{,}281$) were the most common livestock in the study area, followed by sheep (*Ovis* spp., $n = 1{,}038$), goats (*Capra* spp., $n = 781$), and llamas (*L. glama*, $n = 235$). Seventy-nine percent of depredations consisted of sheep (29%), goats (29%), or llamas (21%). Overall per capita depredations were low (1.6 depredations/1,000 livestock), and llamas (1.3 depredations/100 llamas), goats (5.0 depredations/1,000 goats), and sheep (4.0 depredations/1,000 sheep) were most at risk. All depredations occurred at night and 89% involved animals residing unattended in, or immediately adjacent to, heavily forested or riparian habitats.

We documented cougar sex and age in 16 of 21 confirmed reports of interactions. Adult females were the most common demographic class documented ($n = 5$), subadult females and males were equally represented ($n = 4$ each), and adult males ($n = 3$) were documented in the fewest interactions (Table 4). However, these comparisons were confounded by multiple interactions involving the same 10 individuals. Comparisons using unique individuals revealed females were responsible for 60% of interactions; subadults 60%; and adult females, subadult females, and subadult males each generated 30% of interactions (Table 4). The number of observed interactions for specific classes was not different than expected ($X^2_3 = 1.20$, $P = 0.75$).

Discussion

Using a spatially explicit probabilistic approach, we demonstrated widespread, albeit variable, use of exurban and suburban areas by all demographic classes of cougars. High levels of use of residential areas by cougars within all demographic classes reflects a high degree of adaptability and refutes the assumption that use of exurban and suburban habitats is limited to only subadults and transients. Use of residential areas in western Washington appears to be a function of the adaptive and mobile nature of the cougar exploiting suitable habitat and resources within the matrix of residential development. Cougar space-use patterns differed little between wildland and residential environments because individuals used forest corridors and patches in residential areas for hunting, resting, traveling, territorial marking, and procuring resources for offspring (Kertson et al. 2011a, 2011b). Ungulates and other prey are present at the wildland–urban interface and within residential areas (Bender et al. 2004; Happe 1982; McCullough et al. 1997; Prange et al. 2004) and cougars routinely kill a variety of wild prey close to residences (Kertson et al. 2011a; White et al. 2011). High levels of use observed at the wildland–urban interface coupled with documented predation patterns suggest that the wildland–urban interface might function as advantageous edge habitat

Table 4.—Summary of cougar sex and age characteristics for 16 confirmed cougar–human interactions investigated in western Washington from 1 January 2005 to 31 December 2008.

	Subadult female ($n = 3$)		Subadult male ($n = 3$)		Adult male ($n = 1$)		Adult female ($n = 3$)	
Report type	No. reports	%	No. reports	%	No. reports	%	No. reports	%
Sighting[a]			1	6.25			1	6.25
Encounter[b]	1	6.25	1	6.25			2	12.50
Depredation	3	18.75	2	12.50	3	18.75	2	12.50
Total	4	25.00	4	25.00	3	18.75	5	31.25

[a] A cougar was observed by a person, but the presence of the person did not alter the behavior of the cougar.

[b] A cougar was observed by a person from <50 m and the person's presence elicited a behavioral response from the cougar; for example, prolonged staring, fleeing, or approaching.

that allows cougars to exploit prey where they are abundant and vulnerable (Altendorf et al. 2001). Use of residential areas likely also is facilitated by the proximity of development to large, contiguous blocks of high-quality cougar habitat (Kertson et al. 2011b) and the high degree of connectivity between wildland habitat and undeveloped habitat interspersed within residential portions of the landscape. Our observations are consistent with cougars in southern California (Burdett et al. 2010) and bobcats (Donovan et al. 2011; Tucker et al. 2008), black bears (Don Carlos et al. 2009), and coyotes (Gehrt et al. 2009) in wildland–urban environments, suggesting that undeveloped, wildland-like habitats within some developed landscapes function as modified, yet still suitable habitat for many mammalian carnivores.

Our observations of male and female use of residential areas and proximity to people provided limited support for the hypothesis of greater use of residential areas by male cougars. Average use by males and females was approximately equal; however, a portion of UDs for all males overlapped residential development, whereas female use of these areas ranged from none to 55%. Male and female cougars employ different strategies to maximize their fitness and these differences result in significantly larger home ranges for males (Logan and Sweanor 2009; Spencer et al. 2001; Spreadbury et al. 1996). Larger home ranges coupled with extensive residential development along the western slope of the Cascade Mountains makes it more probable that males will encounter some level of residential development. Conversely, female home-range size and space-use patterns translate into variable residential use because females with home ranges far from the wildland–urban interface are unlikely to encounter residential development, whereas females with a home range overlapping the wildland–urban interface have a higher probability of encountering residential development because of localized, intensive use of residential portions of the landscape.

Subadult, transient cougars used developed areas significantly more than did adults, supporting the hypothesis of greater use by this demographic class. Subadult and younger adult transients range over large areas while dispersing and attempting to establish a home range (Beier 1995; Beier et al. 2010; Logan and Sweanor 2001; Maehr et al. 2002; Ruth 1991; Van Dyke et al. 1986). Significantly higher levels of use within, and in closer proximity to, developed areas by these individuals is likely the result of encountering residential development at a higher rate than resident adults while exploring all potentially suitable habitat when attempting to establish a home range. However, the presence of subadults and transients in the study area was very dynamic and the majority of these individuals spent <3 consecutive days in residential areas before returning to wildlands. These results are consistent with observations throughout cougar range (Beier et al. 2010), but the relationship between age and residential use for other mammalian carnivores has not been extensively investigated.

Cougars readily used portions of the landscape with residential development while minimizing their interactions with people, demonstrating a high potential for coexistence. Corridors and forest patches were relatively common and sufficiently large within our study area to support prey and undetected use by a cougar over a short time period (Kertson et al. 2011a). Use of small or isolated, or both, forest patches was mitigated by the presence of dense vegetation and the occurrence of adverse weather conditions (i.e., frequent rain) that provided ample cover and made cougar detection difficult. In areas where corridors were limited or not present, cougars traversed the residential matrix between suitable patches rapidly at night, likely to decrease the probability of encountering people (Kertson et al. 2011b). Although interaction rates reported here are low, our estimates might be conservative because of an inability to locate physical evidence at some report sites where cougars were in fact present and the failure of people to report interactions with cougars.

The majority of confirmed interactions stemmed from cougar depredations on livestock, but livestock were common at the wildland–urban interface and per capita depredation was low for all species. The majority of livestock resided on small, hobby farms at the wildland–urban interface that retained wildland-like habitat characteristics that might encourage cougar use (Kertson et al. 2011b). No depredations involved a cougar entering a livestock-boarding structure and only 2 occurred in higher density suburban environments. The proximity of depredations to wildland habitats and associated circumstances suggest cougars were largely opportunistic in their taking of domestic prey. The prevalence of sheep and goats in confirmed depredations is consistent throughout the Pacific Northwest and cougar range (Beausoleil et al. 2008), demonstrating a high degree of vulnerability for these species because of a small body size, a lack of effective antipredator strategies, and occurrence in high-risk habitats (Inskip and Zimmermann 2009; Odden et al. 2008). However, our observations of greater risk to llamas and limited risk to horses, poultry, and cattle, species of greater risk throughout cougar range (Beausoleil et al. 2008; Bodenchuk 2011), suggest that reported depredation patterns of an adaptable predator are not uniformly applicable across its range.

Comparisons of demographic characteristics of cougars interacting with people across diverse landscapes have failed to yield consistent patterns (Anderson 1991; Aune 1991; Halfpenny et al. 1991; Riley and Aune 1997). Significantly higher use of residential areas by subadults should have increased their probability for interaction, but use levels did not translate into a proportionally higher number of reports. Our interpretation of demographic influences on interaction are limited by small sample sizes, but a lack of population-wide interaction and the presence of repeat offenders in our sample suggests that interactions were most likely a function of individual behaviors (learned or innate) and circumstances. Cougars exhibit a wide variety of behavioral responses to human activity and these responses are not always consistent for individuals within the same demographic class (Sweanor et al. 2005, 2008). We documented interactions stemming from exposure to feline leukemia virus, premature independence (i.e., orphaning), and the social and spatial relationships of females and their offspring. However, higher levels of residential use by younger age classes is relatively consistent throughout cougar range (Beier et al. 2010) and management strategies focused on maintaining an older age structure in local populations may decrease the population's presence in residential areas.

Cougars using residential areas interact with people infrequently and use of interaction reports to guide management is problematic because of low quality. However, interactions do occur and management strategies focused in exurban residential settings and areas close to the wildland–urban interface designed to target problem individuals, educate the public, and improve animal husbandry practices may decrease interactions. Spatially explicit models derived from landscape characteristics and cougar space-use patterns can be used to accurately predict the risk of interactions and should be used as a tool to help guide proactive and reactive management efforts (Kertson et al. 2011b). However, cougars and people appear to coexist better than previously perceived and use of areas close to people is likely to continue if these environments provide ample stalking and security cover, adequate prey resources, and limited human interference. Continued coexistence will require extensive, combined efforts by wildlife managers, landscape planners, and educators to conserve existing wildland resources and improve the public's understanding of cougar ecology, behavior, and the risks associated with living side-by-side with an adaptable large carnivore.

ACKNOWLEDGMENTS

We thank B. Richards, M. White, and the Washington Department of Fish and Wildlife Detachment 10 personnel for invaluable field assistance and B. Maletzke for input on all aspects of our investigation. We also thank the Washington Department of Natural Resources, King County Parks, Seattle Public Utilities, Tacoma Water, Hancock Forest Management, Fruit Growers Supply, and countless private landowners for graciously providing access to their lands. Reviews by R. Beausoleil, G. Koehler, L. Sweanor, and 1 anonymous reviewer greatly improved the quality of the manuscript. Funding and logistical support were provided by the Washington Department of Fish and Wildlife and the University of Washington. Mention of trade names or suppliers does not constitute endorsement by the federal government.

LITERATURE CITED

ALBERTI, M., A. COHEN, AND E. BOTSFORD. 2001. Quantifying the urban gradient: linking urban planning and ecology. Pp. 89–116 in Avian ecology and conservation in an urbanizing world (J. M. Marzluff, R. Bowen, R. McGowan, and R. Donnelly, eds.). Kluwer, New York.

ALTENDORF, K. B., J. W. LAUNDRÉ, C. A. LÓPEZ GONZÁLEZ, AND J. S. BROWN. 2001. Assessing effects of predation risk on foraging behavior of mule deer. Journal of Mammalogy 82:430–439.

ANDERSON, A. E. 1991. Frequency of mountain lion sightings by residents and employees of a housing development. Pp. 19 in Proceedings of the Mountain Lion–Human Interaction Symposium and Workshop (C. S. Braun, ed.). Colorado Division of Wildlife, Denver, Colorado.

ANDERSON, N., AND K. E. AUNE. 2004. Mountain lion aging techniques: a summary of observation on tooth eruption and wear. Montana Fish, Wildlife, and Parks, Helena, Montana.

APKER, J. A., D. UPDIKE, AND D. HOLDERMANN. 2011. Strategies to manage cougar–human interactions. Pp. 145–164 in Managing cougars in North America (J. A. Jenks, ed.). Jack H. Berryman Institute, Utah State University, Logan.

AUNE, K. E. 1991. Increasing mountain lion populations and human–mountain lion interactions in Montana. Pp. 86–94 in Proceedings of the Mountain Lion–Human Interaction Symposium and Workshop (C. S. Braun, ed.). Colorado Division of Wildlife, Denver, Colorado.

BEAUSOLEIL, R. A., D. DAWN, D. A. MARTORELLO, AND C. P. MORGAN. 2008. Cougar management protocols: a survey of wildlife management agencies in North America. Pp. 205–241 in Proceedings of the Ninth Mountain Lion Workshop (D. E. Toweill, S. Nadeau, and D. Smith, eds.). Idaho Department of Fish and Game, Sun Valley.

BEIER, P. 1991. Cougar attacks on humans in the United States and Canada, 1890–1990. Wildlife Society Bulletin 19:403–412.

BEIER, P. 1995. Dispersal of juvenile cougars in fragmented habitat. Journal of Wildlife Management 59:228–237.

BEIER, P., S. P. D. RILEY, AND R. M. SAUVAJOT. 2010. Mountain lions (*Puma concolor*). Pp. 177–189 in Urban carnivores: ecology, conflict, and conservation (S. D. Gehrt, S. P. D. Riley, and B. Cypher, eds.). Johns Hopkins University Press, Baltimore, Maryland.

BENDER, L. C., D. P. ANDERSON, AND J. C. LEWIS. 2004. Annual and seasonal habitat use of Columbian black-tailed deer in urban Vancouver, Washington. Urban Ecosystems 7:41–53.

BEYER, H. 2004. Hawth's Analysis Tools for ArcGIS. http://www.spatialecology.com/htools. Accessed 8 November 2008.

BODENCHUK, M. J. 2011. Population management: depredation. Pp. 135–144 in Managing cougars in North America (J. A. Jenks, ed.). Jack H. Berryman Institute, Utah State University, Logan.

BURDETT, C. L., ET AL. 2010. Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1:4.

CAIN, J. W., P. R. KRAUSMAN, B. D. JANSEN, AND J. R. MORGART. 2005. Influence of topography and GPS fix interval on GPS collar performance. Wildlife Society Bulletin 33:926–934.

CARDILLO, M., A. PURVIS, W. SECHREST, J. L. GITTLEMAN, J. BIELBY, AND G. M. MACE. 2004. Human population density and extinction risk in the world's carnivores. PLoS Biology 2:e197.

COOLEY, H. S., R. B. WIELGUS, H. S. ROBINSON, G. M. KOEHLER, AND B. T. MALETZKE. 2009. Does hunting regulate cougar populations: a test of the compensatory mortality hypothesis. Ecology 90:2913–2921.

COUGAR MANAGEMENT GUIDELINES WORKING GROUP. 2005. Cougar management guidelines. 1st ed. WildFutures, Bainbridge Island, Washington.

DECESARE, N. J., J. R. SQUIRES, AND J. A. KOLBE. 2005. Effect of forest canopy on GPS-based movement data. Wildlife Society Bulletin 33:935–941.

D'EON, R. G., AND D. DELPARTE. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. Journal of Applied Ecology 42:383–388.

DON CARLOS, A. W., A. D. BRIGHT, T. L. TEEL, AND J. J. VASKE. 2009. Human–black bear conflict in urban areas: an integrated approach to management response. Human Dimensions of Wildlife 14:174–184.

DONNELLY, R., AND J. M. MARZLUFF. 2006. Relative importance of habitat quality, structure, and spatial patterns to birds in urbanizing environments. Urban Ecosystems 9:99–117.

DONOVAN, T. M., M. FREEMAN, H. ABOUELEZZ, K. ROYAR, A. HOWARD, AND R. MICKEY. 2011. Quantifying home range requirements for bobcats (*Lynx rufus*) in Vermont. Biological Conservation 144:2799–2809.

ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE. 2009. ArcGIS 9.3 desktop. Environmental Systems Research Institute, Redlands, California.

EWING, R., J. KOSTYACK, D. CHEN, B. STEIN, AND M. ERNST. 2005. Endangered by sprawl: how runaway development threatens America's wildlife. National Wildlife Federation, Smart Growth America, and NatureServe, Washington, D.C.

FITZHUGH, E. L., S. SCHMID-HOLMES, M. W. KENYON, AND K. ETLING. 2003. Lessening the impact of a puma attack on a human. Pp. 89–103 in Proceedings of the Seventh Mountain Lion Workshop (S. A. Becker, D. D. Bjornlie, F. G. Lindzey, and D. S. Moody, eds.). Wyoming Game and Fish Department, Lander, Wyoming.

GEHRT, S. D., C. ANCHOR, AND L. A. WHITE. 2009. Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? Journal of Mammalogy 90:1045–1057.

GEHRT, S. D., S. P. D. RILEY, AND B. L. CYPHER. 2010. Urban carnivores: ecology, conflict, and conservation. Johns Hopkins University Press, Baltimore, Maryland.

GILL, R. B. 2009. To save a mountain lion: evolving philosophy of nature and cougars. Pp. 5–16 in Cougar ecology and conservation (M. G. Hornocker and S. Negri, eds.). University of Chicago Press, Chicago, Illinois.

GITZEN, R. A., J. J. MILLSPAUGH, AND B. J. KERNOHAN. 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. Journal of Wildlife Management 70:1334–1344.

HALFPENNY, J. C., M. R. SANDERS, AND K. A. MCGRATH. 1991. Human–lion interactions in Boulder County, Colorado: past, present, and future. Pp. 10–16 in Proceedings of the Mountain Lion–Human Interaction Symposium and Workshop (C. S. Braun, ed.). Colorado Division of Wildlife, Denver, Colorado.

HANSEN, A. J., ET AL. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications 15:1893–1905.

HAPPE, P. J. 1982. The use of suburban habitats by the Columbian black-tailed deer. M.S. thesis, Oregon State University, Corvallis.

HEMKER, T. P., F. G. LINDZEY, AND B. B. AKERMAN. 1984. Population characteristics and movement patterns of cougars in southern Utah. Journal of Wildlife Management 48:1275–1284.

HEPINSTALL, J. A., M. ALBERTI, AND J. M. MARZLUFF. 2008. Predicting land cover change and avian community responses in rapidly urbanizing environments. Landscape Ecology 23:1257–1276.

HERBERT, D., AND D. LAY. 1997. Cougar–human interactions in British Columbia. Pp. 44–45 in Proceedings of the Fifth Mountain Lion Workshop (W. D. Padley, ed.). California Department of Fish and Game, San Diego, California.

INSKIP, C., AND A. ZIMMERMANN. 2009. Human–felid conflict: a review of patterns and priorities worldwide. Oryx 43:18–34.

JACKSON, P., AND K. NOWELL. 1996. Problems and possible solutions in management of felid predators. Journal of Wildlife Research 1:304–314.

KERNOHAN, B. J., R. A. GITZEN, AND J. J. MILLSPAUGH. 2001. Analysis of animal space use and movements. Pp. 125–166 in Radio tracking and animal populations (J. J. Millspaugh and J. M. Marzluff, eds.). Academic Press, Inc., San Diego, California.

KERTSON, B. N., AND J. M. MARZLUFF. 2010. Improving studies of resource selection by a greater understanding of resource use. Environmental Conservation 38:18–27.

KERTSON, B. N., R. D. SPENCER, AND C. E. GRUE. 2011a. Cougar prey use in a wildland–urban environment in western Washington. Northwestern Naturalist 92:175–185.

KERTSON, B. N., R. D. SPENCER, J. M. MARZLUFF, J. HEPINSTALL-CYMERMAN, AND C. E. GRUE. 2011b. Cougar space use and movements in the wildland–urban landscape of western Washington. Ecological Applications 21:2866–2881.

LAUNDRÉ, J. W., L. HERNÁNDEZ, D. STREUBEL, K. ALTENDORF, AND C. LÓPEZ GONZÁLEZ. 2000. Aging mountain lions using gum-line recession. Wildlife Society Bulletin 28:963–966.

LEWIS, J. S., J. L. RACHLOW, E. O. GARTON, AND L. A. VIERLING. 2007. Effects on habitat on GPS collar performance: using data screening to reduce location error. Journal of Applied Ecology 44:663–671.

LOGAN, K. A., AND L. L. SWEANOR. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C.

LOGAN, K. A., AND L. L. SWEANOR. 2009. Behavior and social organization of a solitary carnivore. Pp. 105–117 in Cougar ecology and conservation (M. G. Hornocker and S. Negri, eds.). University of Chicago Press, Chicago, Illinois.

MAEHR, D. S., D. B. SHINDLE, O. L. BASS, AND T. S. HOCTOR. 2002. Florida panther dispersal and conservation. Biological Conservation 106:187–197.

MATTSON, D. 2007. Managing for human safety in mountain lion range. Pp. 43–56 in Mountain lions of the Flagstaff Uplands: 2003–2006 progress report (D. Mattson, ed.). United States Geological Survey, Southwest Biological Science Center, Flagstaff, Arizona.

MCCULLOUGH, D. R., K. W. JENNINGS, N. B. GATES, B. G. ELLIOTT, AND J. E. DIDONATO. 1997. Overabundant deer populations in California. Wildlife Society Bulletin 25:478–483.

MCKINNEY, T. D. 2011. Cougar research and management need. Pp. 189–200 in Managing cougars in North America (J. A. Jenks, ed.). Jack H. Berryman Institute, Utah State University, Logan.

MECH, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis.

ODDEN, J., I. HERFINDAL, J. D. C. LINNELL, AND R. ANDERSON. 2008. Vulnerability of domestic sheep to lynx depredation in relation to roe deer density. Journal of Wildlife Management 72:276–282.

OEHLERT, G. W. 2000. A first course in design and analysis of experiments. W. H. Freeman and Company, New York.

PICKETT, S. T. A., ET AL. 2001. Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annual Review of Ecology and Systematics 32:127–157.

PRANGE, S., S. D. GEHRT, AND E. P. WIGGERS. 2004. Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. Journal of Mammalogy 85:483–490.

RAY, J. C., K. H. REDFORD, R. S. STENECK, AND J. BERGER. 2005. Large carnivores and the conservation of biodiversity. Island Press, Washington, D.C.

R DEVELOPMENT CORE TEAM. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org. Accessed 16 March 2008.

Riley, S. J., and K. E. Aune. 1997. Mountain lion–human and mountain lion–livestock incidents in Montana. Pp. 91 in Proceedings of the Fifth Mountain Lion Workshop (W. D. Padley, ed.). California Department of Fish and Game, San Diego, California.

Robinson, L., J. P. Newell, and J. M. Marzluff. 2005. Twenty-five years of sprawl in the Seattle region: growth management responses and implications for conservation. Landscape and Urban Planning 71:51–72.

Ruth, T. K. 1991. Mountain lion use of an area of high recreational development in Big Bend National Park Texas. M.S. thesis, Texas A&M University, College Station.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Shuey, M. L. 2005. Land-cover characteristics of cougar/human interactions in and around an urban landscape. Pp. 117–126 in Proceedings of the Eighth Mountain Lion Workshop (R. A. Beausoleil and D. A. Martorello, eds.). Washington Department of Fish and Wildlife, Olympia, Washington.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Spencer, R. D., D. J. Pierce, G. A. Schirato, K. R. Dixon, and C. B. Richards. 2001. Mountain lion home range, dispersal, mortality and survival in the western Cascade Mountains of Washington. Washington Department of Fish and Wildlife, Olympia.

Spreadbury, B. R., K. Musil, J. Musil, C. Kaisner, and J. Novak. 1996. Cougar population characteristics in southern British Columbia. Journal of Wildlife Management 60:962–969.

Sunquist, M., and F. Sunquist. 2002. Puma. Pp. 252–277 in Wild cats of the world (M. Sunquist and F. Sunquist, eds.). University of Chicago Press, Chicago, Illinois.

Sweanor, L. L., K. A. Logan, J. W. Bauer, B. Millsap, and W. M. Boyce. 2008. Puma–human relationships in Cuyamaca Rancho State Park California. Journal of Wildlife Management 72:1076–1084.

Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2005. Puma responses to close approaches by researchers. Wildlife Society Bulletin 33:905–913.

Theobald, D. M. 2005. Landscape patterns of exurban growth in the USA from 1980 to 2020. Ecology and Society 10:32.

Theobald, D. M., and W. H. Romme. 2007. Expansion of the U.S. wildland–urban interface. Landscape and Urban Planning 83:340–354.

Torres, S. G., T. M. Mansfield, J. E. Foley, T. Lupo, and A. Brinkhaus. 1996. Mountain lion and human activity in California: testing speculations. Wildlife Society Bulletin 24:451–460.

Tucker, S. A., W. R. Clark, and T. E. Gosselink. 2008. Space use and habitat selection by bobcats in the fragmented landscape of south-central Iowa. Journal of Wildlife Management 72:1114–1124.

United States Census Bureau. 2008. Annual estimates of the population for counties of Washington. Population Division, United States Census Bureau, Washington, D.C.

United States Department of Agriculture. 2007. National Agricultural Statistics Service. United States Department of Agriculture, Washington, D.C.

Van Dyke, F. G., R. H. Brocke, H. G. Shaw, B. B. Ackerman, T. P. Hemker, and F. G. Lindzey. 1986. Reactions of mountain lion to logging and human activity. Journal of Wildlife Management 50:95–102.

Van Winkle, W. 1975. Comparison of several probabilistic home range models. Journal of Wildlife Management 39:118–123.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science 277:494–499.

Wand, M. P. 2006. KernSmooth: functions for kernel smoothing for Wand and Jones (1995). R package version 2.22-19. Report by Brian Ripley.

Wand, M. P., and M. C. Jones. 1995. Kernel smoothing. Chapman & Hall, London, United Kingdom.

Washington Department of Fish and Wildlife. 2008. 2008 Enforcement Program annual report. Enforcement Program, Washington Department of Fish and Wildlife, Olympia.

Washington Department of Natural Resources. 2008. 2008 statewide aerial imagery. Washington Department of Natural Resources, Olympia.

Western Region Climate Center. 2009. Washington. www.wrcc.dri.edu/summary/Climsmwa.html. Accessed 16 October 2009.

White, K. R., G. M. Koehler, B. T. Maletzke, and R. B. Wielgus. 2011. Differential prey use by male and female cougars in Washington. Journal of Wildlife Management 75:1115–1120.

Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation 3:165–173.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Zar, J. H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, Inc., Englewood Cliffs, New Jersey.

Submitted 1 February 2012. Accepted 10 December 2012.

Associate Editor was I. Suzanne Prange.