

EFFECTS OF ANTHROPOGENIC DISTURBANCE ON
LANDSCAPE ECOLOGY OF COUGARS

By

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Abstract

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Anthropogenic disturbance in the form of hunting and human landscape alterations have extensive effects on cougar populations. I analyzed the effects of hunting and related immigration on the social organization of two independent populations of cougars; a source population with low hunting mortality (11%) and a 12% emigration rate, and a sink population with high mortality (24%) and a 13% immigration rate. I compared home range size, 2-dimensional home range overlap, and 3-dimensional utilization distribution overlap index (UDOI) between annual cougar home ranges. Male cougars in the heavily hunted area had 2-3 times larger home ranges, and 2-dimensional and 3-dimensional UDOI overlap-indicating a difference in the social structure in the high mortality area. Females showed no difference in home range size and overlap of home range areas between study populations.

Traditional closed population methods to estimate density may over-estimate numbers of carnivores. I used cougar home range size and overlap to model total (closed) and proportional (open) densities within the 99% composite female range for two sampling areas in Washington. These simulations suggest that traditional closed population estimates may more than double or triple estimates of density and population size. The proportion of time spent by territorial

animals within a sampling area should be considered when calculating densities of wide-ranging, territorial carnivores.

Understanding the ecology of how cougars respond to human development aids in landscape planning and minimizes negative interactions. I analyzed sex and seasonal differences in use of human occupied areas and identified cumulative percentage of cougar utilization for distance to structures and density of human development. There were no differences in habitat use between sexes. Cougars used lower elevations and steeper slopes during winter, and expanded into higher elevation areas with greater canopy closure during summer. Cougar response to density of human structures was equally negative for both seasons. Only 5% of cougar habitat use occurs in areas where density of human structures exceeds 19.6 structures/km². I found cougars utilized areas > than 240 m from structures 95% of the time in winter, and > 340 m from structures during summer.

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Dedication

This dissertation is dedicated to my parents for their support, encouragement, and love.

I hope I make you proud!

CHAPTER ONE

EFFECTS OF HUNTING ON COUGAR SPATIAL ORGANIZATION

ABSTRACT

Social organization (home range size and overlap) of solitary carnivores may be regulated by three competing hypotheses; intrinsic territoriality (land tenure), food or prey distribution, or prey density for females and territoriality for males. The effects of harvest on social organization of carnivores can be used to test these hypotheses by removing adjacent conspecifics if food is adequate. The food hypothesis predicts that home ranges size and overlap for both males and females should remain the same following removal of conspecifics. The land tenure hypothesis predicts that male and female cougar home range sizes and overlap should increase following removal of conspecifics. The prey density for females and territoriality hypothesis for males predicts that female home range size and overlap should remain constant while male home range size and overlap should increase following removal of conspecifics. I analyzed the effects of hunting and related immigration on the social organization for two independent populations of cougars, a source population with 11% hunting mortality and a 12% emigration rate and a sink population with 24% mortality and a 13% immigration rate. I marked 22 cougars in the lightly hunted population and 20 in the heavily hunted population with GPS collars from 2002 – 2008. I compared home range size, 2-dimensional home range overlap, and 3-dimensional utilization distribution overlap index (UDOI) between annual cougar home ranges. Male cougars in the heavily hunted area had larger home ranges sizes with greater 2-dimensional and UDOI overlap than those in the lightly hunted area. Females showed no difference in size and overlap of home range areas between study populations - suggesting that differences in prey quantity and distribution between study areas did not explain differences in male territoriality. This research supports the food hypothesis for females and territoriality hypothesis for males regulating social organization of solitary carnivores.

INTRODUCTION

Wildlife managers often use the surplus male hypothesis to manage game species in North America (Caughley and Sinclair 1994). For most ungulate species, removal of a portion of the adult male segment of the population may have beneficial or benign effects because of compensatory mortality and reproduction. In addition, ungulates are generally considered to be food or habitat limited (not territorial), so harvest of males may have little effect on home range dynamics (McCullough, 2001, White, 2001). These assumptions may not hold true for carnivores, such as cougars (my animal model), where intra-specific aggression and territoriality helps to structure the population (Hornocker 1969, Siediensticker et al. 1973, Logan and Sweanor 2001).

In Washington, cougars are hunted to provide recreational opportunities and to reduce conflicts with humans and predation on ungulates (Washington Department of Fish and Wildlife 2003). However the effect of high hunter harvest on the social structure of carnivore populations is unknown. Social structure is defined by Logan and Sweanor (2010) as the interaction of individuals with one another in a population and with their environment. Hornocker (1969) hypothesized that the social structure (home range size and overlap) of cougars was determined by a land tenure system or intrinsic territoriality. Pierce et al. (2000) studied primarily female cougars and hypothesized that cougar social structure was determined by abundance and distribution of food resources. Later, Logan and Sweanor (2001) hypothesized that male and female cougars display different social structure to maximize reproductive success. The “reproductive strategies” hypothesis suggests that female cougars are food or prey limited and males are limited by the size of the territory they can defend to maximize the number of breeding females regardless of prey abundance and distribution.

I tested the food and prey, land tenure, and sex specific hypotheses by contrasting home range dynamics for a lightly and heavily hunted population. I analyzed the effects of high mortality on spatial organization of cougars by comparing home range size, 2-dimensional home range overlap and 3-dimensional utilization distribution overlap index (UDOI). The food or prey regulation hypothesis predicts that home ranges size and overlap for both males and females should remain the same following removal of conspecifics. The land tenure hypothesis predicts that male and female cougar home range sizes and overlap should increase following removal of conspecifics. The sex-specific hypothesis predicts that female home range size and overlap should remain constant while male home range size and overlap should increase following removal of conspecifics.

STUDY AREAS

Heavily Hunted Area

The heavily hunted study area is 1,476 km² in size located near Kettle Falls, WA (48°N, 118°W), and includes a patchwork of federal, state, and privately owned lands. The study area is bounded by the Columbia and Kettle Rivers and British Columbia Highway 3. The area is part of a glacially subdued mountainous region (400-2,130 m elevation), and occupies the transition between the East-slope Cascades and Northern Rocky Mountain physiographic province (Bailey et al., 1994). Tree species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), ponderosa pine (*Pinus ponderosa*), western red cedar (*Thuja plicata*), and subalpine fir (*Abies lasiocarpa*). Most of the 46 cm annual precipitation falls as snow from mid-November to mid 31April. Mean annual temperatures ranges from -6°C in January to 21°C in

July. White-tailed deer (*Odocoileus virginianus*) are the most abundant ungulate, but mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*) are also present. Common predator species besides cougar include coyotes (*Canis latrans*), black bears (*Ursus americanus*), and bobcats (*Lynx rufus*). Cougar hunting without the use of hounds was permitted in the study area each year from 1 September to 30 November. Hunting with the aid of hounds occurred from 1 December to 31 March.

Lightly Hunted Area

The lightly hunted study area is 1,652 km² and is located along the east slope foothills of the North Cascades foothills near the town of Cle Elum, WA (47°N, 121°W). The area is bounded by the Cascade Mountains to the west, the Alpine Lakes Wilderness to the north and Kittitas Valley to the south and east. The majority of the study area is a patchwork of U.S. Forest Service, privately owned timber lands, private residential or agricultural areas. Elevation ranges from 462 – 2,279 m. Sagebrush steppe foothills (below 550 m elevation) transition to ponderosa pine (*Pinus ponderosa*) and Douglas fir covered slopes. Sub-alpine fir, Englemann spruce (*Picea engelmannii*), silver fir (*Abies amabilis*), and western hemlock dominate elevations > 1,550 m. Precipitation averages 56.4 cm/yr. Mean annual temperature ranges from –7°C in January to 27°C in July. Elk and mule deer occur throughout the study area, and mountain goats (*Oreamnos americanus*) are present at higher elevations. Common predator species include cougar, coyotes, black bears, and bobcats. Cougar harvest without the use of hounds was permitted in the study area each year from 1 August to 15 March.

Demographic Comparisons of the Study Areas

The heavily hunted area had an overall hunting mortality rate of 0.24 ± 0.05 and a male mortality rate of 0.35. The heavily hunted area had survival-fecundity rate of growth of 0.78, a net immigration rate (mostly males) of 0.11, and a resulting observed growth rate of 0.91. Density was stable or at equilibrium over 5 years at 3.46 cougars / 100 km². Mean age of cougars was 27 months (Cooley et al. 2009b)

The lightly hunted area had an overall hunting mortality rate of 0.11 ± 0.04 and a male mortality rate of 0.16. The lightly hunted area had a survival-fecundity rate of growth of 1.10, a net emigration rate (mostly males) of 0.12 and a resulting observed growth rate of 0.98. Density was stable over 5 years at 3.62 cougars / 100 km². Mean age of cougars was 38 months (Cooley et al., 2009b).

METHODS

Captures and monitoring

I attempted to capture and mark all cougars each year, from 2002 through 2007, by conducting thorough and systematic searches for tracks in winter in each study area. I used hounds to track and tree cougars (Hornocker 1970) and immobilized cougars with ketamine hydrochloride (200 mg/mL) and xylazine hydrochloride (20 mg/mL) at a dosage of 0.4 mL/10 kg of body mass, or with Telazol at a dosage of 6 mg/kg, using a projectile dart (Ross and Jalkotzy 1992, Spreadbury et al. 1996). I determined sex and classified animals as kittens (0–12 months), juveniles (13–24 months), or adults (>25 months) based on physical measurements and gum regression on the canine teeth (Laundre et al. 2000). I fitted each animal with a mortality-sensing Very High Frequency (VHF; Advanced Telemetry Systems, Isanti, Minnesota, USA) or Global

Positioning Satellite collar (GPS; Lotek Wireless, Newmarket, Ontario, Canada and Televilt, Lindesberg, Sweden). GPS collars were programmed to collect locations at 4-hour intervals (six times/day) and data were retrieved using a remote communication unit. I handled all animals in accordance with Washington State University Animal Care (IACUC Permit #3133) and Animal Welfare Assurance Committee (AWAC Permit #A3485-01).

Home range size

I calculated the 99% volume fixed kernel home range for each cougar for each year with more than 70 locations per animal year (Seaman et al., 1999). I used the Adehabitat package (Calenge, 2006) in Program R to calculate the h plug in smoothing parameter (hpi) for the 99% kernel density estimate (Gitzen and Millsaugh, 2003; Gitzen et al., 2006). I entered the hpi value calculated for each cougar into Hawth's tools extension in ArcGIS 9.3 to calculate a kernel density function and the 99% volume contour (Beyer, 2004) and kernel density estimate with 30 m cell size. I calculated the probability density function for each animal utilization distribution by dividing each cell in the density grid (output from the previous step) by the sum of all the cells in each kernel density grid. I then created a 99 % volume contour polygon from the utilization distribution for each cougar and calculated the area in square kilometers.

Homerange overlap

Home range overlap is an effective measure of shared space use for territorial species and is useful as a quantitative measure for assessing the degree of interaction among individuals (Fieberg and Kochanny, 2005, Kernohan et al. 2001, Marzluff et al. 2001, Millsaugh et al. 2004). Home range overlap is an intuitive method, that is used to assess social organization in

several species including jaguars (*Panthera onca*), bobcats (*lynx rufus*), and coyotes (*Canis latrans*) (Rabinowitz and Nottingham, 1986; Nielson and Woolf, 2001; Atwood and Weeks, 2003).

I calculated home range overlap by summing the area shared by two adjacent cougars with the “polygon in polygon” tool function in Hawth’s tools in ArcGIS 9.3. The shared area was divided by the total home range size for each cougar. I averaged the overlap for each individual cougar with all other adjacent cougars.

Two dimensional polygon space use does not consider the internal anatomy of the home range (Kernohan et al., 2001). Utilization distribution overlap index (UDOI) compares the 3-dimensional utilization distribution for overlapping home ranges (Kernohan et al., 2001; Fieberg, 2005). I used UDOI for quantifying overlap in terms of shared space-use of utilization distribution estimates (Fieberg 2005). I used the “kerneloverlap” function in Adehabitat (Calenge, 2006) in Program R to calculate the UDOI (Fieberg and Kochanny, 2005). The equation for the UDOI is:

$$UDOI = \frac{A_{1,2}}{A_1 + A_2} \iint_{-\infty}^{\infty} \widehat{UD}_1(x, y) \times \widehat{UD}_2(x, y) dx dy$$

Where UD_1 is the estimated utilization distribution for animal 1, UD_2 is the estimated utilization distribution for animal 2, and $A_{1,2}$ is the area of overlap between the two utilization distributions.

Statistical Analysis

I used a factorial analysis of variance (Zar 1996) to test for differences between study areas, sexes, and interactions of study area by sex for home range size, 2-dimensional home range overlap, and 3-dimensional UDOI. I used a log-transformation to normalize the data for home range size, and Arc-sin square root transformation to approach normality for the 2-

dimensional overlap and UDOI data. I used Fishers Least-significant-difference post hoc tests with a Holm-Bonferroni adjustment to control the family-wise error rate for home range size, 2-dimensional overlap and UDOI (Holm 1979).

RESULTS

I captured, collared, and monitored 22 (13 males, 9 females) cougars in the lightly hunted area from December 2001 - 2008 and 20 (7 males, 13 females) cougars in the heavily hunted area from December 2004 - 2007. Each cougar had 760 ± 418 GPS acquisitions per year.

Homerange size

There were significant effects for sex, study area and sex by study area interactions for home range size (Table 1.1). Male home range sizes were twice as large (753 km^2 vs 348 km^2) ($P < 0.01$) in the heavily hunted area but there were no differences (249 km^2 vs 199 km^2) in home range sizes for females ($P = 0.53$) between areas (Table 1.2).

Homerange overlap

There were significant effects for sex, study area, and sex by study area interactions (Table 1.3). There was a higher 2-dimensional overlap ($P < 0.05$) in the heavily hunted study area for males, but no differences in female to female, female to male, or male to female overlap between the two areas (Table 1.4).

There were significant effects for sex by study area interaction for 3-dimensional UDOI overlaps (Table 1.5). The heavily hunted area had higher UDOI values for males than the lightly

hunted area (0.38 vs 0.16, $P < 0.01$) indicating more shared space use, but there were no differences in the female to female, female to male, and male to female UDOI (Table 1.6).

DISCUSSION

Our data suggests a difference in male, but not female cougar social organization after removal of conspecifics. These results support the sex-specific food (females) and territoriality (male) hypothesis proposed by Logan and Sweanor (2001); whereby male home range size and overlap is regulated through breeding territoriality and females are regulated by prey density. Home range size, 2-dimensional overlap, and 3-dimensional UDOI overlaps for males were 2-3 times greater in the heavily hunted area. This contrasts to the lightly hunted area, where high use areas (UDOI) were mutually exclusive between resident males. Male cougars in the lightly hunted population had numerous apparent facial and body scars in contrast to the heavily hunted population where male cougars had notably fewer scarring or wounds observed during captures (Maletzke, unpublished data). These scars may be a result of increased territorial defense in the lightly hunted area. Kill rates (6.68 vs 7.04 days/kill), and home range size of females (240 ± 103 vs 198 ± 42 km²) were similar among areas suggesting that differences in prey availability did not explain the differences in male home range size and overlap between areas (Cooley 2009b, Cooley 2008; White 2009). Female home range size was not different, but female 2-dimensional and 3-dimensional overlap appeared higher in the heavily hunted area however this difference was not statistically different (Table 1.4).

In the heavily hunted area, home range boundaries of male cougars overlapped significantly, although areas of high use (shown by peaks in the UD, Figure 1.2) were discreet among males with little or no overlap. Males are believed to increase their reproductive success

by defending a territory with as many females as possible (Sandell, 1989). If adjacent resident males are killed, those territorial boundaries are no longer defended allowing for home range expansion into those former areas, as seen here.

Females rear kittens by themselves and their reproductive success is closely related with the amount of food they can capture (Sandell, 1989). Females may increase their reproductive success by occupying areas where the distribution of prey is sufficient and where they can establish familiarity with the landscape to capture prey (Pierce et al., 2000). Therefore, females are better off maintaining a stable home range of sufficient size where prey is adequate to support requirements for rearing young. Similar differences in male and female home range sizes was demonstrated for leopards (*Panthera pardus*, Mizutani, 1998) Female leopards appeared to move the minimum distance required to obtain prey and rear young, while for males, maintaining territory and locating mates probably accounted for moving greater distances (Mizutani, 1998).

It appears that social organization of solitary female carnivores is regulated by food and will limit their home range size and overlap sufficient to provide necessary resources for themselves and their offspring. Solitary male carnivores appear to be limited by male conspecifics and will expand their home range size and overlap to maximize breeding opportunities.

Carnivores are hunted for trophies, to protect livestock, and to manage for public safety. Cougar populations are open populations with compensatory immigration occurring in areas of heavy harvest. (Robinson et al. 2008, Cooley et al. 2009a, Cooley et al. 2009b). The hypothesis that food regulates cougar home range size and overlap and that hunting does not have an effect social organization does not hold because of the increases found in male home range size and

overlap associated with heavy harvest. If home ranges are larger and overlap is greater for male cougars in a heavily hunted population, then more individual males may encounter humans, their residences, and their livestock, increasing probabilities for encounters at any given location. This research suggests that high mortality may result in increased, not decreased encounter probabilities between humans and cougars (Maletzke, unpublished data).

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Table 1.1. Analysis of Variance tests for Log transformed home range areas for male and female cougars near Cle Elum, WA (Lightly hunted) and Kettle Falls, WA (Heavily Hunted) areas in

Washington State from 2001 -2008. Lilliefors K-S Normality test = 0.122, $P = 0.115$.

Source	Type III SS	Df	Mean Sq	F-ratio	<i>P</i> -value
Sex	6.789	1	6.789	42.31	<0.01
Study area	1.892	1	1.892	11.79	<0.01
Sex*Study area	1.053	1	1.053	6.57	0.01
Error	6.097	38	0.160		

Table 1.2. Area of a 99% volume contour from annual fixed kernel home ranges and the average number of locations per homerange for cougars near Cle Elum (Lightly hunted) and Kettle Falls (heavily hunted), Washington from 2002-2008.

Sex	n	Lightly Hunted		Heavily Hunted			^a P-value	^b α/k
		\bar{x} (km ²)	SD	n	\bar{x} (km ²)	SD		
♂	13	347.5	134.4	7	752.5	337.5	<0.01	0.025
♀	9	198.9	42.9	13	240.2	103.7	0.53	0.05

^a Fisher's Least-significant difference post hoc test

^b Holm-Bonferroni adjusted alpha value where $\alpha = 0.05$ and k is the number of pairwise comparisons.

Table 1.3. Analysis of Variance tests of the area of overlap (Arc-sin square root transformed) for male and female cougars near Cle Elum, WA (Lightly hunted) and Kettle Falls, WA (Heavily Hunted) areas in Washington State from 2001 -2008. Lilliefors K-S Normality test = 0.076, $P = 0.04$.

Source	Type III SS	Df	Mean Sq	F-ratio	<i>P</i> -value
Sex	2.863	3	0.954	18.23	<0.01
Study area	0.258	1	0.258	4.93	0.03
Sex*Study area	0.539	3	0.180	3.44	0.02
Error	7.015	134	0.052		

Table 1.4. Two dimensional overlap between adjacent cougars averaged per individual in Cle Elum (Lightly Hunted) and Kettle Falls (Heavily Hunted), Washington from 2001-2008.

Sex	n	<u>Lightly Hunted</u>		<u>Heavily Hunted</u>			^a P-value	^b α/k
		Overlap	SD	n	Overlap	SD		
♂	19	0.17	0.11	9	0.41	0.23	<0.01	0.01
♀	24	0.20	0.15	19	0.31	0.18	0.03	0.02
♂ - ♀	20	0.26	0.18	9	0.16	0.06	0.22	0.03
♀ - ♂	29	0.51	0.26	13	0.57	0.19	0.55	0.05

^a Fisher's Least-significant difference post hoc test

^b Holm-Bonferroni adjusted alpha value to control for familywise error rates where $\alpha = 0.05$ and

k is the number of pairwise comparisons.

Table 1.5. Analysis of Variance tests of the utilization distribution overlap index (Arc-sin square root transformed) for male and female cougars near Cle Elum, WA (Lightly Hunted) and Kettle Falls, WA (Heavily Hunted) areas in Washington State from 2001 -2008. Lilliefors K-S Normality test = 0.0042, $P = 0.718$.

Source	Type III SS	Df	Mean Sq	F-ratio	<i>P</i> -value
Sex	0.429	3	0.14	2.259	0.08
Study area	0.104	1	0.10	1.650	0.20
Sex*Study area	0.687	3	0.23	3.622	0.02
Error	8.539	135	0.06		

Table 1.6. Three dimensional overlap calculated using the utilization distribution overlap index (UDOI) for cougars in a Cle Elum (Lightly Hunted) and Kettle Falls, Washington from 2001 - 2008.

Sex	<u>Lightly Hunted</u>			<u>Heavily Hunted</u>			<i>a</i> P-value	<i>b</i> α/k
	n	Overlap	SD	n	Overlap	SD		
♂	19	0.16	0.15	9	0.38	0.27	0.01	0.01
♀	26	0.12	0.14	19	0.27	0.29	0.04	0.02
♂ - ♀	21	0.30	0.25	9	0.19	0.08	0.36	0.03
♀ - ♂	29	0.32	0.30	13	0.19	0.11	0.30	0.05

a Fisher's Least-significant difference post hoc test

b Holm-Bonferroni adjusted alpha value to control for familywise error rates where $\alpha = 0.05$ and *k* is the number of pairwise comparisons.

Figure 1.1. Two dimensional overlap of two male cougar in Cle Elum, WA (Lightly hunted area) in 2002. The larger home range size was 501 km² with an area of overlap of 13 % and the smaller home range was 298 km² with a 31% overlap.

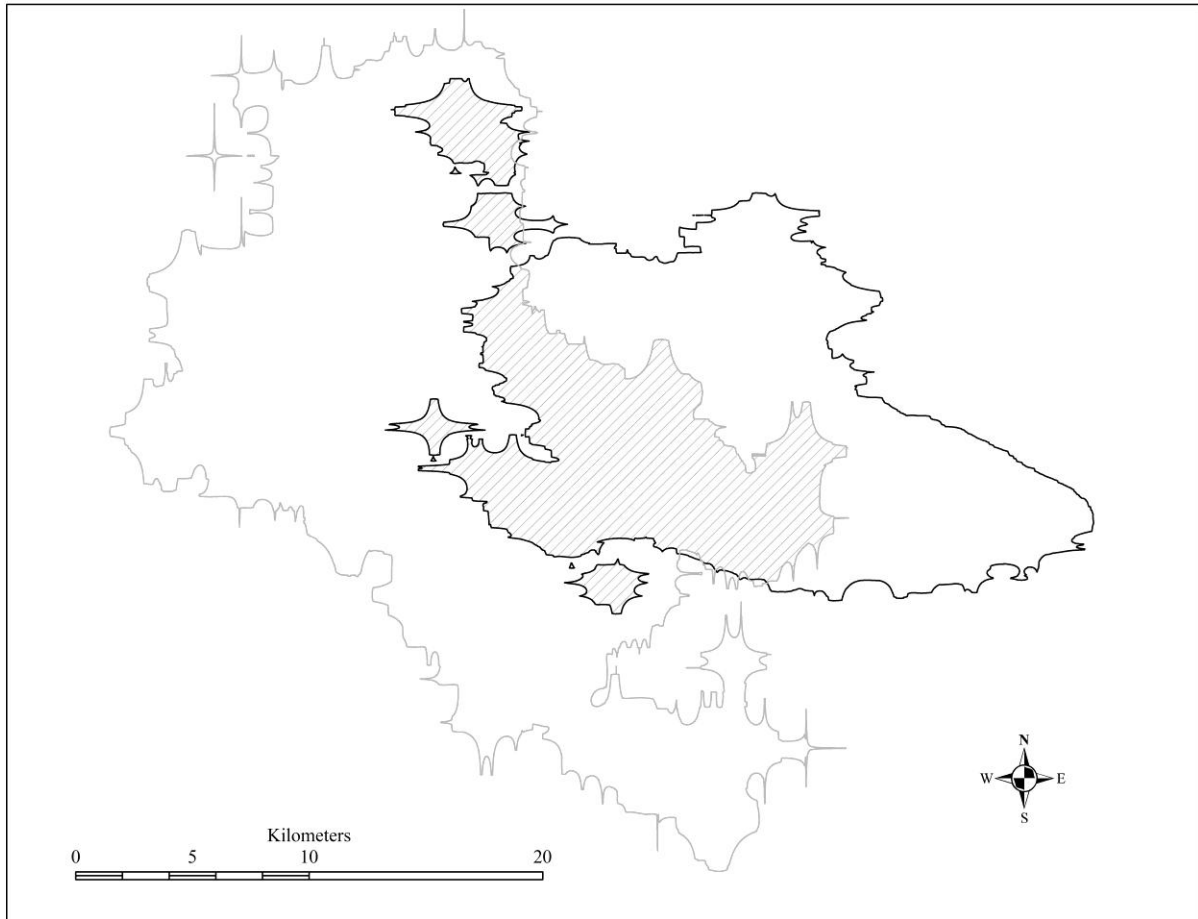
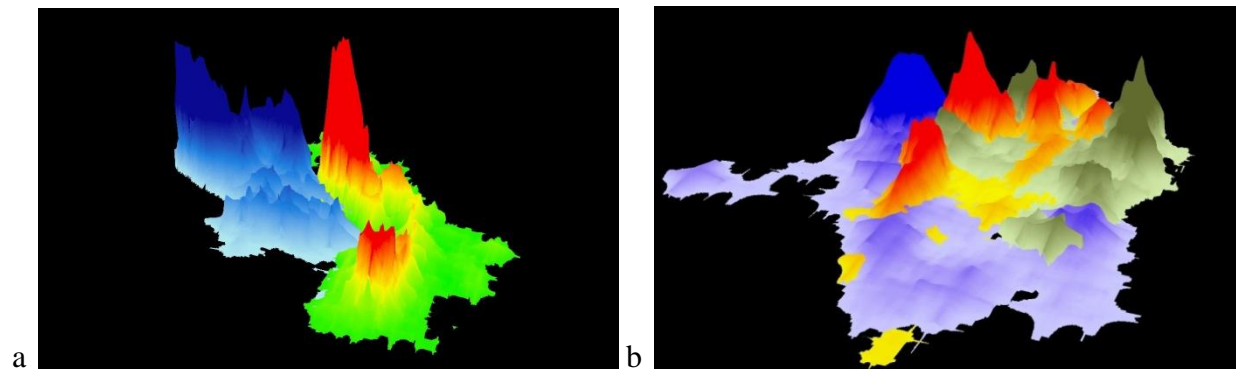


Figure 1.2. Utilization distribution for two cougars (a) in the lightly hunted area near Cle Elum, WA and the three cougars (b) in the heavily hunted area near Kettle Falls Washington, 2007. The color ramps (blue to white, red to green, and green to white) are individual cougars and the peaks represent areas of high probability of use.



CHAPTER TWO

ESTIMATING DENSITIES OF A SOLITARY CARNIVORE

ABSTRACT

Traditional closed population methods to estimate density may over-estimate numbers of territorial, solitary carnivores. However, Global Positioning Systems may improve estimates by defining animal-based area boundaries, thereby accounting for animal movements outside sampling areas. I used cougar home range size and overlap to model total (closed) and proportional (open) densities within a 99% composite female range, for two sampling areas in Washington. These simulations suggest that traditional closed population estimates may more than double estimates of density and population size. Estimates based on closed population models may result in setting high harvest quotas with potential overharvest of carnivore populations. The proportion of time spent by territorial animals within a sampling area should be considered when calculating densities of wide-ranging, territorial carnivores.

INTRODUCTION

Wildlife managers depend on accurate and comparable density estimates to interpret population status and trends. Traditional area-based estimates may not accurately reflect densities and/or be comparable among areas because sampling areas vary by size and scale (Blackburn and Gaston 1997, Smallwood and Schonewald 1988, Smallwood 1997). More importantly, density estimates that do not account for the proportion of time animals spend outside a sampling area can result in overestimates (McLellan 1989). For example, some estimators give equivalent weights to animals that may spend 10% or 100% of the time in a study area. If I sampled or extrapolated these estimates to adjacent areas, the same animal would count as 2 independent animals (the animal would be counted in each area that they spend time in). For any animal not present 100% of the time in the sample area, this method leads to density overestimates. Global Positioning System (GPS) collars can improve effectiveness of density estimates by defining biologically meaningful boundaries from re-location data and accounting for the time animals spend outside the boundary.

Several methods have been used to estimate densities of solitary carnivores, cougars (*Puma concolor*) being my animal model. A common method estimates densities from the number of animals observed and located within a subjective predefined sampling area, often established by physiographic and human imposed boundaries such as administrative boundaries, highways, etc. Carnivore studies that attempt to count all animals commonly use this method to detect changes in density over time (Robinson et al. 2008, Stoner et al. 2006, Logan and Swenor 2001, Ross and Jalkotzy 1992, Servheen 1983).

A second method derives density estimates that may be more ecologically based, using the 95% composite range for females as the study area boundary (Wielgus et al. 1994, Wielgus

and Bunnell 2000, Hellgren et al. 2005, Lambert et al. 2006, Cooley 2008). This method still typically counts males as whole animals despite the fact that males may spend significant time outside the sample area.

Cooley et al. (2008) proposed a method that accounted for animal movements beyond the composite home range of females and estimated densities based on the proportional number of GPS locations for each animal that occurred within that boundary; not the whole number of animals inside the study area boundary. This method yielded adult (≥ 25 months) cougar densities of 1.36 ± 0.27 and 1.31 ± 0.20 adult cougars /100 km² for two study areas (Cooley et al. 2009). In comparison, using the whole number of cougars inside an annual 95% composite home range of collared females yielded density estimates: 2.65 ± 0.52 and 2.07 ± 0.37 adult cougars / 100km² for the two areas, respectively.

To test the overall effectiveness and generalizability of Cooley et al's (2008) proportional use method, I simulated potential maximum density estimates for two independent populations of GPS-collared cougars in Washington from 2002 - 2008. I estimated home range size and average overlap of adjacent cougars in these two populations. I used these averages and their 95% confidence intervals to simulate cougar home ranges and compared density estimates from the total and proportional number of cougars. I hypothesized that traditional carnivore density estimation methods that do not account for the proportion of time animals spend in a designated sampling area would result in over-estimating the density of carnivores and population size.

STUDY AREAS

I monitored two cougar populations in study areas > 250 km apart and managed under different hunting strategies (Figure 2.1). The Northeast Washington study area, where hunting

with the aid of hounds resulted in 24% harvest mortality of cougars, was defined as heavily hunted. The second study area in the Central Washington, where the use of hounds was not permitted - resulted in 11% harvest mortality of cougars (via hunters on foot) and was defined as lightly hunted (Cooley et al 2009).

Heavily hunted area

The 1,476 km² study area lies north of the town of Kettle Falls, WA (48°N, 118°W), and includes a patchwork of federal, state, and privately owned lands. The study area is bounded on the southeast and southwest by the Columbia and Kettle Rivers. On the north it ranges into British Columbia, Canada and is bordered by the Columbia River and Highway 3. The area is 400-2,130 m elevation and includes the East-slope of the Cascades and Northern Rocky Mountain physiographic province (Bailey et al. 1994). Tree species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), ponderosa pine (*Pinus ponderosa*), western red cedar (*Thuja plicata*), and subalpine fir (*Abies lasiocarpa*). Precipitation is 46 cm / year and primarily snow during mid-November to mid 31 April. Mean annual temperatures ranges from -6°C in January to 21°C in July. White-tailed deer (*Odocoileus virginianus*) are the most abundant ungulate, but mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*) are also present. Common predator species besides cougar include coyotes (*Canis latrans*), black bears (*Ursus americanus*), and bobcats (*Lynx rufus*). Cougar harvest without the use of hounds was permitted in the study area each year from 1 September to 30 November. Harvest with the aid of hounds occurred 1 December to 31 March or until a female quota was attained for each cougar management zone.

Lightly hunted area

The study area is 1,652 km² and is located along the east slope foothills of the North Cascades Mountains near the town of Cle Elum, WA (47°N, 121°W). It is bounded by the crest of the Cascade Mountains on the west, the Alpine Lakes Wilderness on the north and agricultural lands of the Kittitas Valley to the south and east. The majority of the study area is a patchwork of U.S. Forest Service, privately owned timber lands, and private residential or agricultural areas. The elevation ranges from 462 – 2,279 m. Sagebrush steppe foothills (below 550 m elevation) transition upwards to ponderosa pine and Douglas-fir covered slopes. Forest cover at middle elevations is composed of Douglas-fir, grand fir (*Abies grandis*), and western larch (*Larix occidentalis*) with a variety of other conifers and broadleaf trees. Subalpine fir, Engelmann spruce (*Picea engelmannii*), Pacific silver fir (*Abies amabilis*), and western hemlock dominate elevations > 1,550 m. Precipitation averages 56.4 cm/yr, primarily as snowfall during winter. Mean annual temperature ranges from –7°C in January to 27°C in July. Elk and mule deer occur throughout the study area, and mountain goats (*Oreamnos americanus*) are present at higher elevations. Common predator species include cougar, coyotes, black bears, and bobcats. Cougar harvest without the use of hounds was permitted in the study area each year from 1 August to 15 March.

METHODS

Captures

Cougars were captured using large box traps or treed with the aid of hounds (Hornocker 1970). Captures primarily occurred during the winter (November to March) when I could use

snow to locate cougar tracks. I systematically searched the roads and trails by 4x4 truck and snowmobiles for tracks. In riparian areas or drainages inaccessible to motorized vehicles I used snowshoes to hike transects to search for tracks.

Immobilization

I immobilized cougars with a combination of Ketamine hydrochloride (100mg/ml ~ anesthesia 5 mg/kg) and Xylazine hydrochloride (100mg/ml ~ sedative 0.5 mg/kg) or with Telazol at a dosage of 6 mg/kg and fitted them with GPS4400 Lotek (Lotek Wireless Inc., Newmarket, Ontario Canada), Simplex, Tellus, or Posrec (Televilt International, Lindesberg, Sweden) GPS collars. All procedures for capture, handling, and monitoring of cougars were approved by a Washington State University Animal Care Committee Permit (WSU-LARC/IACUC #3133). I programmed the collars to acquire a GPS location at 4 or 6 hour intervals throughout the year and to transmit GPS data remotely to a receiver at 2 - 6 week intervals.

Home range size

I calculated a 99% volume fixed kernel home range estimate for each cougar for each year. Simulations indicated that 99 % contours reflected a biologically realistic representation based on a large sample of locations used to estimate and depict a home range. Annual home ranges were calculated with an average of more than 500 locations per animal (Seaman et al., 1999). I used the Adehabitat package in Program R to calculate the “plug in” X and Y axis smoothing parameters for the kernel density grid (Calenge, 2006; Gitzen and Millsbaugh, 2003; Gitzen et al., 2006). I entered the plug-in X and Y smoothing parameter values calculated for

each cougar into Hawth's tools extension in ArcGIS 9.3 to calculate a kernel density function and a 99% volume contour (Beyer, 2004). I calculated the area of overlap by averaging each combination of adjacent overlapping cougar home ranges with the polygon tool function in Hawth's tools in ArcGIS 9.3. I estimated area of overlap within genders and averaged all overlaps for each individual among females and among males. Male and female home ranges overlapped completely and were not a biologically meaningful measure for comparisons.

Density estimates

I used average home range size and area of overlap to simulate 2 different estimates of cougar densities for both study areas: density considering the whole number of cougars inside the study area, and density considering only the proportional number of GPS locations inside the study area. I simulated home ranges as circles to reduce complexity of shape and the number of input metrics and to allow generalizability to other species and areas. I used the average home range size and area of overlap of adjacent cougars with a 95% confidence interval for each sex in each study area. I derived the radius [$r = \text{square root} (\text{Area}/\pi)$] of the simulated circles from the average home range area (km^2). I spaced the centroids for circular home ranges to adjust the overlap for each combination of the lower and upper 95% CI and averages for females and males in each study area. I combined densities for males and females to derive total density estimates for adult resident cougars for each study area.

I compared density estimates derived from counting the 'whole animal' that intersected the 99% composite range of females to that derived from the 'proportion' of time each animal spent within the 99% composite range of females. I divided the count of simulated circular home ranges by the total area of the 99% composite range of females and multiplied by 100 to

calculate cougars /100 km². I calculated the proportional density for the time spent within the study area by intersecting the simulated home ranges by the 99% cougar composite range of females. I summed the home range areas contained inside the study boundary. I divided this total sum by the area of one simulated home range, and multiplied by 100 for scale to cougars per 100 km². I calculated these density estimates from two correlated variables, home range size and overlap. If this method is used to calculate actual cougar densities, the resulting interval will be an approximate 95% confidence interval for the total population density.

RESULTS

Home range size and overlap

I captured and collared 22 adult (≥ 25 months) cougars with GPS collars in the lightly hunted area (13 males, 9 females) from December 2001 - 2008 and 20 adult cougars in the heavily hunted area (7 males, 13 females) from December 2004 - 2007. Areas (km²) \pm standard deviation for 99% volume contours from annual fixed kernel home ranges in the lightly hunted population were 205.1 ± 79.1 km² for females and 388.4 ± 162.9 km² for males. Home range areas in the heavily hunted area were 259.2 ± 120.0 km² for females and 689.8 ± 356.7 km² for males. Average two dimensional overlap between females for the lightly hunted area was $20 \pm 15\%$, and $31 \pm 18\%$ for the heavily hunted area. Mean overlap between adjacent males for the lightly and heavily hunted areas were $17 \pm 11\%$ and $41 \pm 23\%$, respectively.

Density estimates

The mean number for counts of whole animals (where each animal counts as one) that overlapped the lightly hunted study area (Table 2.1) was 56 for an estimated density of 4.0 cougars/100 km², whereas the estimate based on the proportion of home range within the study areas was 22.8 animal home ranges for an estimated density of 1.38 cougars/100 km². For the heavily hunted study area (Table 2.2) the mean number of counts of whole animals overlapping the study area was 64 cougar home ranges for an estimated density of 4.34 cougars/100 km². This compares to an estimate using proportional cougar home ranges of 24.0 cougars for an estimated density of 1.63 cougars/100 km². Density estimates based on total counts of whole cougars were two to three times greater than estimates based on that of the proportion of home ranges (Figure 2.2).

DISCUSSION

Our simulations demonstrate that traditional methods that count total animals within a study area may over-estimate densities by not considering territorial spacing, large home ranges, and movement outside the study area for cougars, and perhaps other carnivores. The smaller the sampling area, and the larger the animals' movements, the more bias this may have on densities and numbers of animals. This is related to one of the scale issues of observation identified by O'Neill et al. (1996), wherein the extent of analysis truncates observations, thus biasing landscape-scale estimates without appropriate corrective procedures.

Ungulate densities and numbers are typically determined from aerial and ground surveys corrected by sight ability models (Rice et al 2009, Anderson et al 1998), line transects (Focardi et al 2002), or pellet transects (Forsyth et al 2005) - because these animals are usually visible and

relatively abundant on the landscape. These survey methods appear adequate when fundamental statistical aspects of random sampling and bias corrections are applied (Mason et al 2006).

Numbers of small mammals are often determined from mark-recapture techniques, assuming population closure (Hammond and Anthony 2006, Grenier et al 2008). This also appears adequate because of the ability to obtain sufficient sample sizes and the small mammals typically have relatively small home range sizes completely encompassed by most study areas boundaries.

Unlike ungulates or small mammals, density estimates are difficult to assess for carnivores because of their secretive nature, low numbers, and high mobility. Non-invasive methods to assess densities of carnivores include camera traps, track counts, following track to collect DNA, hair snares, and scat collection dogs – all which assume a closed population (McCarthy et al 2008, McKelvey et al 2006, Wasser et al 2004). Similarly, density estimates using telemetry attempt to count all the animals located within a closed study area (Robinson et al 2008, Stoner et al 2006, Logan and Sweanor 2001, Ross and Jalkotzy 1992, Servheen 1983) without accounting for high mobility and large home ranges of carnivores. These estimates produce a density where there is no accountability of the proportion of use outside the defined study area.

Natural barriers can influence movements and density estimates for carnivores (Smallwood and Schonewald 1988, Smallwood 1997). The lightly hunted area was surrounded by forested habitat that did not present a barrier to animal movements and should be considered an open population. Home ranges of several cougars straddled the boundary of the study area and traditional estimates resulted in a 3-fold increase for density and numbers. In contrast, the heavily hunted area that was bounded on two sides by large rivers, which did not transect male home ranges and resulted in only a two-fold increase of estimated density and numbers.

Such errors in density may have significant consequence for management of carnivore populations. Managers often estimate state-wide populations and corresponding sustainable harvest based on density estimates from isolated studies (Cooley et al., 2009). Estimates of carnivore densities based on traditional methods that assume population closure (counting whole animals) may over-estimate numbers and incorrectly justify a hunter harvest 2-3 times greater than what is biologically appropriate. For example, a game management unit of 5,000 km² with a proportional density of 1.6 cougars/100 km² resulted in an estimate of 80 cougars and perhaps 20 allowable kills. In contrast, estimates based on the whole number of animals resulted in densities of 4.0 cougars/100 km², for an estimate of 200 cougars and an allowable kill of 50 cougars – almost as large as the actual population. Harvest quotas based on whole animal counts may unintentionally result in over-harvest and population declines. Management for solitary low density populations of carnivores requires greater precision of estimates for sustainable harvest levels. I encourage researchers and managers to consider these differences when calculating densities and establishing quotas for solitary, territorial carnivores with large home ranges and movements. I recommend that the proportional density estimator for telemetry or detection probability for mark-recapture studies be incorporated (Cooley 2008, Gardner 2009).

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Table 2.1. Simulated total number and proportional number of cougars and densities calculated from a 95% confidence interval and mean of the home ranges size and area of overlap based on empirical data from a population of cougars in central Washington 2002-2008.

Sex	Home range (km ²)	Overlap	Total Number	Total Density _d	Proportional Number	Proportional Density _d
Females	174.372 _a	0.13 _a	34	2.06	14.9	0.90
		0.20 _b	39	2.36	18.1	1.09
		0.26 _c	52	3.15	22.2	1.35
	205.058 _b	0.13 _a	30	1.82	12.6	0.76
		0.20 _b	35	2.12	15.4	0.93
		0.26 _c	45	2.72	19.0	1.15
	235.744 _c	0.13 _a	27	1.63	10.8	0.66
		0.20 _b	35	2.12	13.5	0.81
		0.26 _c	38	2.29	16.4	1.00
Males	317.964 _a	0.12 _a	21	1.27	7.7	0.46
		0.17 _b	26	1.57	9.2	0.56
		0.23 _c	29	1.76	10.9	0.66
	388.421 _b	0.12 _a	18	1.09	6.5	0.39
		0.17 _b	21	1.27	7.4	0.45
		0.23 _c	25	1.51	8.9	0.54
	458.879 _c	0.12 _a	15	0.91	5.5	0.33
		0.17 _b	18	1.09	6.5	0.40
		0.23 _c	23	1.39	7.5	0.46
Total Resident Cougars	+ 95% CI	- 95% CI	42	2.54	16.3	0.99
	Mean	Mean	56	4.00	22.8	1.38
	- 95% CI	+ 95% CI	81	4.90	33.1	2.00

_a Mean – (width of 95% confidence interval/2)

_b Mean

_c Mean + (width of 95% confidence interval/2)

_d Density units are cougars /100km²

Table 2.2. Simulated total number and proportional number of cougars and densities calculated from a 95% confidence interval and mean of the home ranges size and area of overlap based on empirical data from a population of cougars in northeast Washington, 2004-2008.

Sex	Home range (km ²)	Overlap	Total Number	Total Density _d	Proportional Number	Proportional Density _d	
Female	199.552 _a	0.22 _a	32	2.16	15.4	1.04	
		0.31 _b	45	3.05	20.3	1.37	
		0.40 _c	59	4.00	27.8	1.89	
	259.248 _b	0.22 _a	28	1.90	11.6	0.79	
		0.31 _b	37	2.51	15.6	1.05	
		0.40 _c	48	3.25	21.2	1.44	
	318.944 _c	0.22 _a	22	1.49	9.6	0.65	
		0.31 _b	30	2.03	12.8	0.87	
		0.40 _c	42	2.85	17.3	1.17	
	Male	415.634 _a	0.23 _a	19	1.29	7.8	0.53
			0.41 _b	36	2.44	13.9	0.94
			0.59 _c	78	5.28	29.9	2.03
689.811 _b		0.23 _a	14	0.95	4.5	0.31	
		0.41 _b	27	1.83	8.4	0.57	
		0.59 _c	57	3.86	18.0	1.22	
963.988 _c		0.23 _a	11	0.75	3.2	0.22	
		0.41 _b	21	1.42	6.0	0.40	
		0.59 _c	48	3.25	12.9	0.88	
Total Resident Cougars		+ 95% CI	- 95% CI	33	2.24	12.8	0.87
		Mean	Mean	64	4.34	24.0	1.63
		- 95% CI	+ 95% CI	137	9.28	57.7	3.91

_a Mean – (width of 95% confidence interval/2)

_b Mean

_c Mean + (width of 95% confidence interval/2)

_d Density units are cougars /100km²

Figure 2.1. Central Washington study area and Northeast Washington U.S.A. study area.

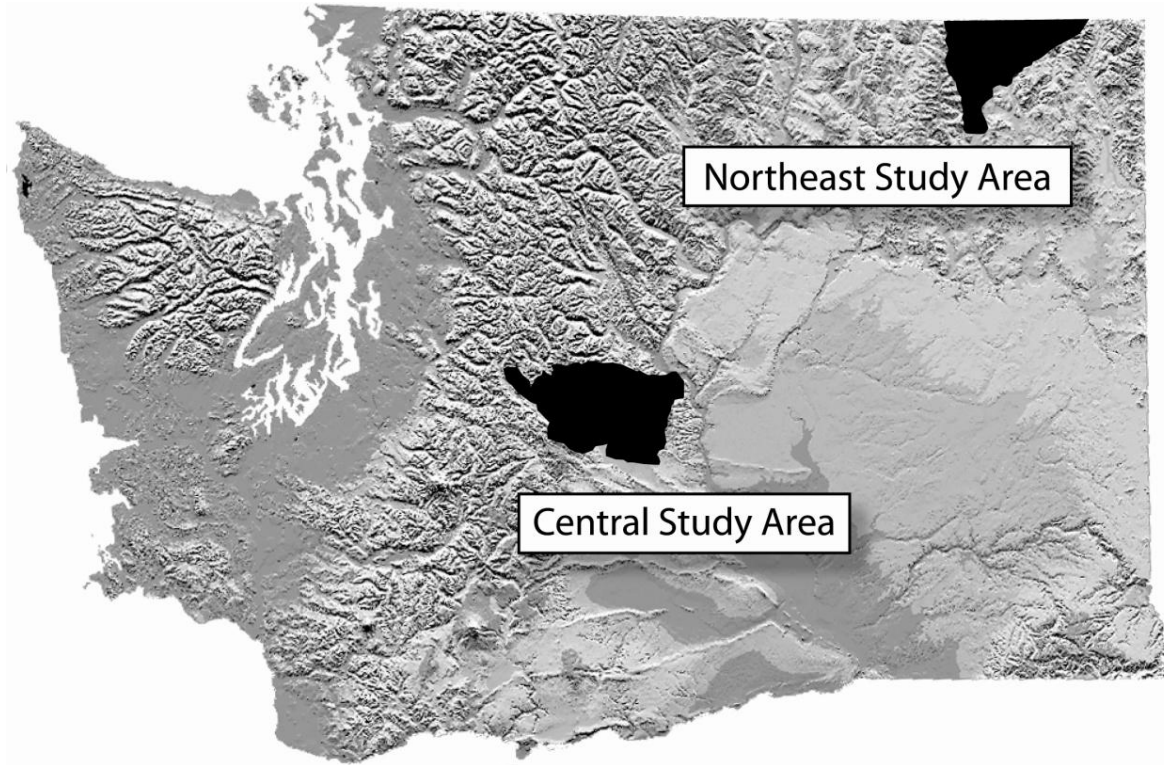
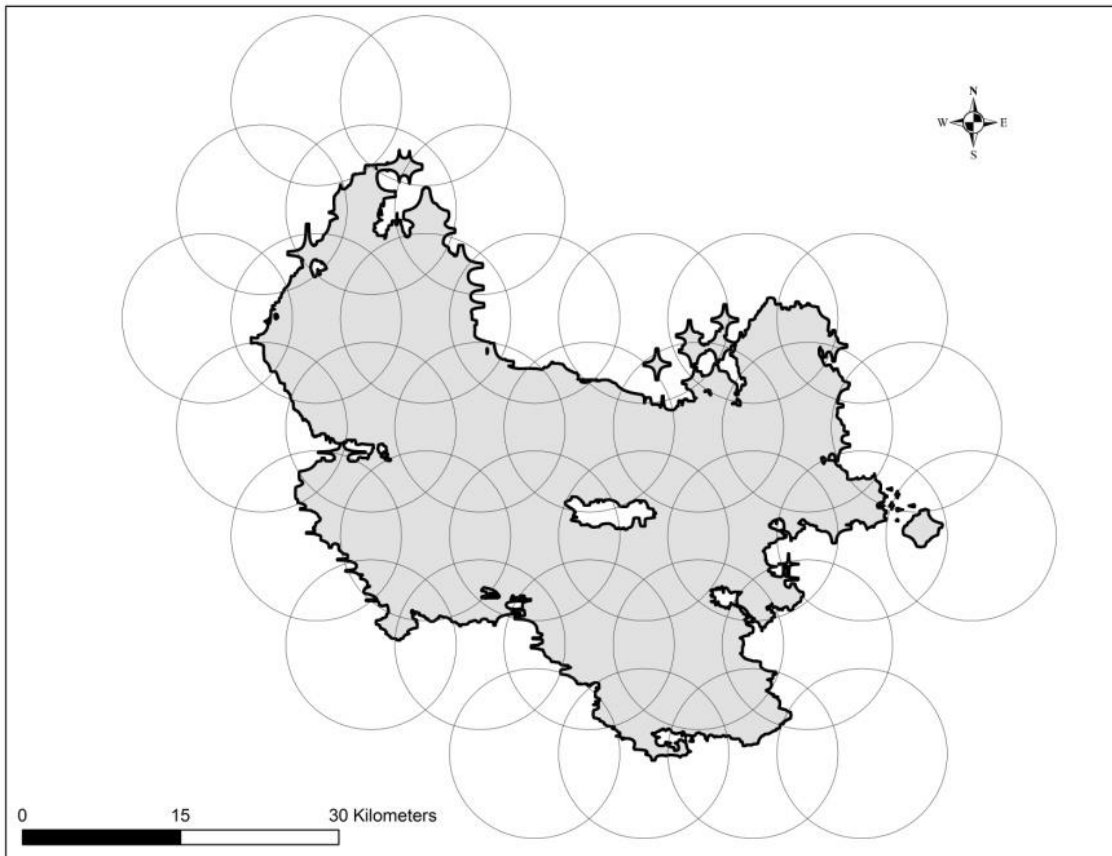


Figure 2.2. Female home range simulation (circles) based on average 99% fixed kernel home range size and overlap of adjacent female based on GPS collared cougars in Cle Elum Washington from 2001-2008. The boundary (gray) is defined by a 99% composite Kernel home range for all female cougars within the study area.



CHAPTER THREE
COUGAR SEASONAL HABITAT USE AND
RESPONSE TO HUMAN DEVELOPMENT

ABSTRACT

Human development continues to expand in many places across North America and interactions between people and wildlife are increasing. Understanding wildlife response to such development aids landscape planning and could minimize negative wildlife human interactions. I analyzed habitat use from 15 cougars to identify sex and seasonal differences and identify distance to structures and density of human development that may impede cougar habitat use. I created habitat models with elevation, slope, canopy closure, and density of human structures to identify differences for sex and season by cougars. There were no differences in habitat use between sexes. Cougars used lower elevations and steeper slopes during winter and expanded into higher elevations with higher canopy closure during the summer. However, cougar response to density of human structures was equally negative for both seasons. Areas where density of structures exceeded 19.6 structures / km² accounted for less than 5% of cougar use within home ranges. Seventy six percent of cougar use occurred in areas with < 1 human structure/km². Cougars used areas > than 240 m from structures 95% of the time in the winter and > 340 m from structures during the summer. These metrics can be used to guide future development and maintain connectivity for this large wide-ranging carnivore and minimize human/cougar interactions across the landscape.

INTRODUCTION

Residential and commercial development of the human-wildland interface is occurring across North America and in many places around the world (Theobald, 2005). Human-wildlife interactions are increasing (Torres et al., 1996) and landscape connectivity for remaining wild land areas is rapidly diminishing due to human encroachment of development (Morrison and Boyce, 2008). Landscape connectivity and genetic exchange across a landscape have been at the forefront of research in recent years (Sanderson et al., 2002; Maehr and Deason, 2002; Fahrig, 2007). New proposals to sub-divide wild lands into residential and commercial areas or expand highways and freeways may continue to decrease landscape connectivity for organisms and their genetic flow (Trombulack and Frissell, 2000; Epps et al., 2005). For example, carnivores typically avoid areas near human development (Hebblewhite et al., 2005, Clevenger and Waltho, 2000); however, few studies sought to identify the density of human development at which habitat utilization is impacted.

The cougar (*Puma concolor*) is a keystone predator across much of South and Western North America (Beschta, and Ripple, 2009). Research on cougars may provide a model for other solitary felids and wide ranging carnivores. Because cougars are highly mobile and relatively sensitive to human development, modeling habitat utilization of this species may assist in protecting the habitat and connectivity for many other species (Beier, 1993). In addition, male cougars are believed to cause more negative cougar/human interactions than females (Beier, 1991).

I analyzed habitat utilization of cougars fitted with global positioning system collars using resource utilization functions. I tested whether male cougars use human-occupied areas more than females and assessed whether cougars responded to habitat and human development

parameters differently during winter and summer. Specifically, I hypothesized that cougars would use areas near human development less in the summer as they followed prey movements to higher elevations during the snow free months (McCorquedale, 2003).

One year after the project initiated, construction began for a 24.3 km² residential development and resort for recreation and golf began in the study area. Concurrently, several others smaller developments occurred in the area during the eight year study. I analyzed the spatial response of cougars to development by separating cougar use on an annual and seasonal basis.

Previous research has focused on a patch mosaic approach to modeling, where a polygon is classified as either residential or wild land (Carrol et al., 2001; Sanderson et al., 2001; Urquiza-Haas et al., 2009) and relatively few studies have used gradient analysis on mammals (McDonnell and Hahs, 2008). The gradient process can often yield more information than a patch mosaic approach alone (MacGarigal and Cushman, 2005).

To approach human development as a gradient, I fit a Weibull equation to the cumulative distribution functions for collared cougars based on their utilization distributions. I determined the average model equation capable of predicting how much of the cougar's cumulative distribution occurs at a given housing density and Euclidean distance to houses. These models can predict thresholds of housing density or Euclidean distance to structures based on the percentage of the cumulative distribution function of the cougar utilization distribution. Understanding the effects of human development on cougar utilization distributions may provide land managers, developers, and conservation organizations tools to identify areas where connectivity still exists and areas of concern which may require action to protect, or manage to minimize cougar-human interactions.

STUDY AREA

The study area is 1,652 km² and is located along the east slope foothills of the North Cascades mountains near Cle Elum, WA (47°N, 121°W). The boundaries consist of the Cascade Mountains to the west, the Alpine Lakes Wilderness to the north, and the agricultural lands of the Kittitas Valley to the south and east. The majority of the study area is a patchwork of U.S. Forest Service, privately owned timber lands, private residential or agricultural areas. Elevation ranges from 462 – 2,279 m. Sagebrush steppe foothills (below 550 m elevation) transition to ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*). Sub-alpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea engelmannii*), Pacific silver fir (*Abies amabilis*), and western hemlock (*Tsuga heterophylla*) dominate at elevations > 1,550 m. Precipitation averages 56.4 cm/yr, mostly as snow during winter with substantially higher amounts at greater elevations. Mean annual temperature ranges from –7°C in January to 27°C in July. Elk (*Cervus Canadensis*) and mule deer (*Odocoileus hemionus*) occur throughout the study area, and mountain goats (*Oreamnos americanus*) are present at higher elevations. Common predator species include cougar, coyotes (*Canis latrans*), black bears (*Ursus americanus*), and bobcats (*Lynx rufus*). Cougar harvest without the use of hounds occurs in the study area each year from 1 August to 15 March. Total adult cougar densities were 1.87 ± 0.42 (Cooley et al. 2009) with female kill rates of 7.04 days/kill (K. White, unpublished data).

METHODS

Captures and monitoring

I attempted to capture and mark all cougars each year, from January 2002 through December 2008, by conducting thorough and systematic searches of each study area during winter when tracks can be detected in snow. I used hounds to track and tree cougars (Hornocker 1970). I immobilized treed cougars with a mixture of ketamine hydrochloride (200 mg/mL) and xylazine hydrochloride (20 mg/mL) at a dosage of 0.4 mL/10 kg of body mass, using a projectile dart shot into the hindquarter (Ross and Jalkotzy 1992, Spreadbury et al. 1996). I determined sex and classified animals as kittens (0–12 months), juveniles (13–24 months), or adults (>25 months) based on physical measurements and gum regression of canine teeth (Laundre et al. 2000). I fitted each animal with a mortality-sensing Very High Frequency (VHF; Advanced Telemetry Systems, Isanti, Minnesota, USA) or Global Positioning System collar (GPS; Lotek Wireless, Newmarket, Ontario, Canada and Televilt, Lindesberg, Sweden). GPS collars were programmed to collect locations at 4-hour intervals (six times/day). The data were retrieved using a remote communication unit. I handled all animals in accordance with Washington State University Animal Care (IACUC Permit #3133) and Animal Welfare Assurance Committee (AWAC Permit #A3485-01).

Habitat coverages

I incorporated 4 uncorrelated ($r < 0.5$) parameters into the habitat model including: elevation, slope, canopy closure, and density of human structures. Elevation was derived from a 30m-resolution Digital Elevation Model (U.S. Geological Survey, Department of Interior, USA). I derived slope in degrees from the 30m-Digital Elevation Model using a slope function in the

ArcGIS-geospatial environment. I used the GNN layer developed from a 2006 Landsat image to estimate canopy closure in the study area (Ohmann, 2009).

I created a human structures density layer (structures / km²) using county tax parcel data for Kittitas County, Washington. I used the “year built” field in the county attribute files to assign a year in which houses were developed on each tax parcel. I selected each tax parcel with structure and created centroids for those parcels. Using the simple density function with a circular roving window analysis in spatial analyst, I created a density grid (30m-resolution) of houses per km². To test for multi-scale differences in cougar responsiveness, I used Euclidean distance to structures and three different window sizes (0.25 km², 0.5 km², and 1 km²) for density of human structures on the landscape.

Calculating seasonal utilization distributions

I defined the winter periods as December 1st - April 30th and summer as May 1st – November 30th (Maletzke, 2004). I calculated a 99% volume fixed kernel home range estimate for each cougar. Seasonal home ranges were calculated with an average of more than 650 locations per cougar per season (Seaman et al., 1999) and only cougars with locations for both seasons were used in the analysis. I used the Adehabitat package (Calenge, 2006) in Program R to calculate the “plug in” X and Y axis smoothing parameters for the kernel density grid (Gitzen and Millspaugh, 2003; Gitzen et al., 2006). I entered the plug in X and Y smoothing parameter values calculated for each cougar into the Hawth’s Tools extension (Beyer, 2004) in ArcGIS 9.3 to calculate a Kernel density function grid. To convert the kernel density function to a utilization distribution for each cougar I divided each grid by the sum of all the values in the

kernel density grid. I clipped the kernel density grid by a 99% volume contour and re-scaled the utilization distribution to values from 1 – 99 for inclusion in the regression analysis.

Resource Utilization Function Analysis

I used the package ‘ruf’ in Program R to run the regression analysis using the utilization distribution as the dependent variable and the habitat variables as independent parameters (Handcock, 2004). I used paired *t*-tests to assess differences in beta coefficients of the resource utilization functions between sexes and seasons (Zar, 1999). I used analysis of variance to test for significant differences in the standardized coefficients for the three scales (0.25 km², 0.5 km², and 1 km²) for density of structures. I compared the standardized coefficients between sexes and seasons and to determine relative strength of the parameters in the model. The unstandardized coefficients were used to model and map relative habitat use by cougars by season. The variability was determined by subtracting the variance due to estimating the individual coefficients ($Var\left(\frac{\hat{\beta}_j}{\beta_j^*}\right) = \frac{1}{n^2} \sum_{i=1}^n SE^2 \hat{\beta}_{ij}^*$) from the total variance ($Var\left(\frac{\hat{\beta}_j}{\beta_j^*}\right) = \frac{1}{n-1} \sum_{i=1}^n (\hat{\beta}_{ij} - \frac{\hat{\beta}_j}{\beta_j^*})^2$ where $\left(\frac{\hat{\beta}_j}{\beta_j^*}\right)$ is an average resource utilization function (Marzluff et al. 2004).

Determining avoidance thresholds for residential development

I separated cougar annual home ranges by calendar year (January 1st – December 31st) and created the utilization distribution with the same methods as for the seasonal home ranges. A density grid of houses per km² for each consecutive year was created to account for new houses and to address temporal patterns of cougar behavior associated with residential

development. This density grid was created with a moving window analysis counting all houses within a 1 km² circular window for each grid.

I used a two-parameter Weibull equation to approximate the cumulative distribution functions of the utilization distribution values from each cougar over human structures per km². The Weibull distribution is an extremely flexible family of probability distribution functions with the ability to approximate exponential and sigmoidal functions. I used a nonlinear least squares convergence to determine the parameters of the Weibull equation. Shape and scale parameter values derived from the Weibull distribution can be used to test hypotheses about wildlife spatial behavior (Broseth et al. 2005, Metsaranta, 2008). I used Weibull-derived parameter values to test cougar spatial responses to development between different groups (e.g., males vs. females) and to identify thresholds of maximum housing densities that inhibit cougar movements on through the landscape. I averaged the Weibull parameters for each cougar if there were multiple years for one individual so that each cougar accounted for one sampling unit.

I constructed empirical cumulative distribution functions of the utilization distribution for each cougar using a summation function for each consecutive housing density value from 1 house per km² to the maximum observed within each cougar's utilization distribution. A two-parameter Weibull cumulative distribution function was fitted to the empirical cumulative distribution function with the following formula: $f(x) = 1 - \exp\left(-\left(\frac{x}{a}\right)^b\right)$ where (a) is the scale parameter and (b) is the shape parameter as a function of x, the housing density.

For each cougar, I also created a null model for Euclidean distance to human structures where I converted the utilization distribution into a homogenous grid, whereby each pixel had the same value for inclusion in the cumulative distribution function. This null model allows the creation of a Weibull cumulative distribution function assuming that cougars are not responsive

the distance to houses within their home ranges. A paired t-test with a Bonferroni adjustment for multiple comparisons was used to determine differences between the shape and scale parameters for the empirical Weibull function and the null Weibull function (Zar, 1999).

RESULTS

I captured and monitored 15 (7 females, 8 males) cougars from December 2001 - 2008. GPS acquisitions per cougar per season used to calculate home ranges were 976 ± 770 (mean \pm SD) in summer and 649 ± 576 in winter.

Seasonal resource utilization functions

I found no difference comparing the elevation ($T=-0.37$, $df=9.3$, $P=0.72$), slope ($T=0.29$, $df=11.9$, $P=0.77$), canopy closure ($T=0.55$, $df=9.9$, $P=0.59$), or density of human structures ($T=0.021$, $df=11.6$, $P=0.98$) between male and female cougars. Also, no significant ($F=0.22$, $P=0.88$) variation occurred when testing for multi-scale differences in responses from cougars at 0.25 km^2 , 0.5 km^2 , and 1 km^2 levels of densities of human structures. By interpreting the standardized coefficients, I found elevation was the best overall predictor of habitat use for cougars. Density of human structures was the second best predictor of habitat use by cougars for winter and summer (Table 3.1). During winter, slope was a better predictor than percent canopy closure, however during summer; canopy closure was a stronger predictor than slope. Density of houses (per km^2) and elevation (m) were negatively associated with cougar habitat use for both winter and summer. Slope was positively correlated with cougar habitat use in both seasons, but it was a stronger predictor variable during the winter. Percent canopy closure was positive for both seasons; however, the effect was not significant during winter.

The average unstandardized RUF equation for the cougar population in the winter was:
 $f(x) = 24.02 + 0.0132 (\text{Canopy}) - 0.1115 (\text{House Density} / \text{km}^2) - 0.0173 (\text{Elevation}) + 0.0748$
 (Slope). The average unstandardized RUF equation for the cougar population in summer was:
 $f(x) = 0.79 + 0.0334 (\text{Canopy}) - 0.1110 (\text{House Density} / \text{km}^2) - 0.0077(\text{Elevation}) + 0.0710$
 (Slope).

Residential development threshold

Cumulative distribution functions for cougar utilization distributions were plotted against density of structures (Figure 3.1). I also found no difference in the Weibull parameters (scale parameter was $P=0.1$, shape parameter was $P=0.12$) between winter and summer for density of structures (Figure 3.2). The population average annual Weibull equation (Figure 3.3) for the density of structures was: $f(x) = 1 - \exp\left(\frac{(\text{housing density})}{0.410}\right)^{0.284}$. For this study area and during this period, I predicted the 95% cumulative distribution for housing density was 19.6 structures per km^2 (approximate 95% confidence interval = 3.6 – 76.2) beyond which areas with densities of human structures > 19.6 were rarely ever used. The y-intercept showed that 76% of the use occurred below 1 human structure / km^2 .

Euclidean Distance to structures

Using the same approach as with density of structures, I fit a two parameter Weibull functions to the cumulative distribution function of the Euclidean distance to structures within a cougar home range calculated using the utilization distribution values and again with a homogeneous values (a null model) across the same home range (Table 3.2). I found a difference between the Weibull scale ($T=-3.57$, $df=14$, $P<0.01$) parameter, but no difference in

the shape parameter ($T=0.03$, $df=14$, $P=0.03$; $\alpha=0.025$ with Bonferroni correction) for both winter and summer. A significant difference ($T=-5.11$, $df=14$, $P<0.01$) in the scale parameter between winter and summer indicates a higher proportion of the cumulative distribution function was nearer to houses during the winter than during the summer (Figure 3.4). During the winter, 95% of the cumulative distribution occurred greater than 240 m (approximate 95% confidence interval = 87 – 467 m) from human structures. The 95% cumulative distribution for distance to structures increased to greater than 345 m (approximate 95% confidence interval = 165 – 592) during the summer.

DISCUSSION

Contrary to expectations (Beier, 1991), male cougars did not avoid human structures less than females in this study area. Different responses to landscape variables such as elevation and density of human structures were not detected between males and females. Prey use differed between male and female cougars (White et al. in press) but no habitat use differences were detected for the parameters analyzed. My results suggests that prey selection is independent of landscape-driven spatial behavior, and as White et al. (in press) suggest, may be dependent on gender-specific traits such as body size.

Cougars depicted a much stronger affinity for lower elevations during the winter. Deer and elk migrate during winter from higher elevation areas to lower elevation areas near valley bottoms (McCorquedale, 2003). During the summer, cougars shifted movement patterns to utilize portions of their home range with higher elevations. The vegetation gradient goes from sub-alpine fir zones at higher elevations to shrub-steppe habitat at lower elevation and eastern portions of the study area. With the shift to lower areas in winter, cougars utilize areas with open

douglas-fir, ponderosa pine, or shrub steppe habitats. The coefficients for canopy cover reflect these shifts in habitat preferences with non-significance of canopy cover during the winter, but positive selection for canopy cover during the summer. Coefficients for slope were positive during both seasons indicating the preference for steeper terrain. Slope may be a proxy for a cougar's ability to ambush prey using the vertical relief as stalking advantage. Utilization distribution values were equally negatively correlated with density of human structure on the landscape during both seasons. Several large carnivore species have shown similar responses toward human development (Beier, 1993, Randa and Yunker 2006, Urquiza-Haas et al. 2009). Cougars responded with similar avoidance levels during the winter as they do during the summer. Human structures in the study area primarily occur in the valley bottoms and at lower elevations. Cougars are concentrated along the margins of developed areas based on Euclidean distance to structures, but within their winter ranges are displaying avoidance behavior toward human development when scale is based on density of structures. This underlines the importance of analyzing natural phenomena at multiple scales to clarify apparently contradictory patterns (Levin 1992).

Movement thresholds to human development

The average y-intercept or 76% of the cougar utilization distribution occurred where densities of human structures was < 1 , suggesting that the majority of cougar movements were in areas with no human development (table 3.2). My results suggest that cougars almost completely avoid areas with a development of 19.6 structures per km^2 and may retract or shift home ranges if density of human structures exceeds this level. This retraction of the home range of male and female cougars can be seen visually (Figure 3.5) near an area of residential

development that occurred during the study between 2003 and 2008. Beier (1993) identified similar shifts or home range retractions in the Santa Ana Mountains where cougar were excluded in areas after human development blocked corridors connecting habitat patches.

I also found a seasonal effect when analyzing the Euclidean distance to houses (Figure 3.4). Cougar movements were farther from human structures on the landscape during summer than in winter. This may result from the seasonal movements of cougars expanding into summer range to follow prey to higher elevations (McCorquedale 2003). During the winter I found a significant difference in the scale parameters between the Weibull equation based on utilization distributions and the homogeneous Weibull. This suggests that during the winter cougars may be forced to use areas on the landscape nearer to houses than what is available to them. This could be explained by snow accumulation restricting cougars to low elevation areas near residences, which are primarily located in the flatter valley bottoms and low elevation areas. During the summer I found no difference between the utilization distribution and null model equations. This may be due to cougars utilizing their entire home range in the summer months without restrictions from snow accumulation or prey concentrations. Despite cougar use of areas closer to human structures in the winter, the density of human structures on the landscape still negatively impacts cougar use of these areas.

Management Implications

The cougar is an adaptable species with a range spanning two continents, but there is a limit to the amount of human development it will tolerate within a landscape. For example, from 2001-2008, my results suggest cougars used areas with less than 19.6 human structures / km². These results could be used as guidelines for landscape planning agencies or developers to

maintain connectivity on the landscape and to maintain movement corridors between habitat patches. They can be used to prioritize land acquisitions and triage where to allocate funds to preserve connectivity or corridors for wildlife.

On the east slopes of the Cascade crest, cougars are restricted to low elevations and compete for space with human development. Our results suggest that during the winter cougars are forced to use low elevations areas near human structures where development is targeted because snow accumulation is less and mild slopes favor construction. My results suggests a need to prioritize areas for protection in winter ranges for cougars and redirect human development toward summer range areas for cougars where more space is available for both humans and cougars.

Developers could use this knowledge to assist in designing new subdivisions on the landscape while maintaining the connectivity for wildlife. By clustering development > 19.6 human structures / km², more habitats remain intact as larger undeveloped spaces. If landscape planning agencies subdivide areas so that human development occurs at densities > 19.6 human structures/km² then cougars may still utilize those areas, however cougar/human encounter rates may increase. With forethought and a landscape approach to human development perhaps large carnivores and humans will be able to coexist with fewer interactions.

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Table 3.1. Estimates of standardized parameter coefficients (β) for 15 cougars (7 females and 8 males) near Cle Elum, WA from 2001-2008. Seasons represent snow on and snow free periods.

Winter (December 1st – April 30th)

Resource Attribute	Mean standardized β	95% Confidence interval	$P(\beta = 0)$	No. of cougars with use significantly associated with attribute	
				+	-
Forest Canopy	0.17	-0.08 - 0.55	0.39	7	4
House Density / km ²	-1.08	-1.52 - -0.63	0.01	2	13
Elevation	-3.30	-3.69 - -2.91	< 0.01	0	15
Slope (degrees)	0.83	0.49 - 1.16	0.04	9	3

Summer (May 1st- November 30th)

Resource Attribute	Mean standardized β	95% Confidence interval	$P(\beta = 0)$	No. of cougars with use significantly associated with attribute	
				+	-
Forest Canopy	0.98	0.59 – 1.36	< 0.01	11	1
House Density / km ²	-1.00	-1.37 - -0.63	0.01	1	14
Elevation	-1.85	-2.77 - -0.93	< 0.01	4	10
Slope (degrees)	0.68	0.33 – 1.03	0.03	8	3

Table 3.2. Parameter coefficients for a Weibull equation determined through fitting a nonlinear least squares convergence to empirical cumulative distribution functions for Euclidean distance to structures based on the utilization distribution (Empirical) and a homogenous landscape (Null) for 15 cougars.

Season	Parameter	N	Empirical Model		Null Model		^a Paired T-test <i>P</i>
			Mean	SE	Mean	SE	
Winter	Scale	15	1638.8	270.1	2010.8	303.0	<0.01
	Shape	15	1.6	0.2	1.3	0.1	0.03
Summer	Scale	15	2853.8	419.5	2947.7	421.8	0.38
	Shape	15	1.4	0.1	1.3	0.1	0.03

^a Alpha value corrected with a Bonferroni adjustment due to the Weibull model including two parameters ($\alpha = 0.025$).

Figure 3.1. Weibull function curve (solid black line) based on the average coefficients derived from non linear least squares convergence on the empirical cumulative density functions (CDF, dotted lines) for each cougar's utilization distribution values in relation to housing density.

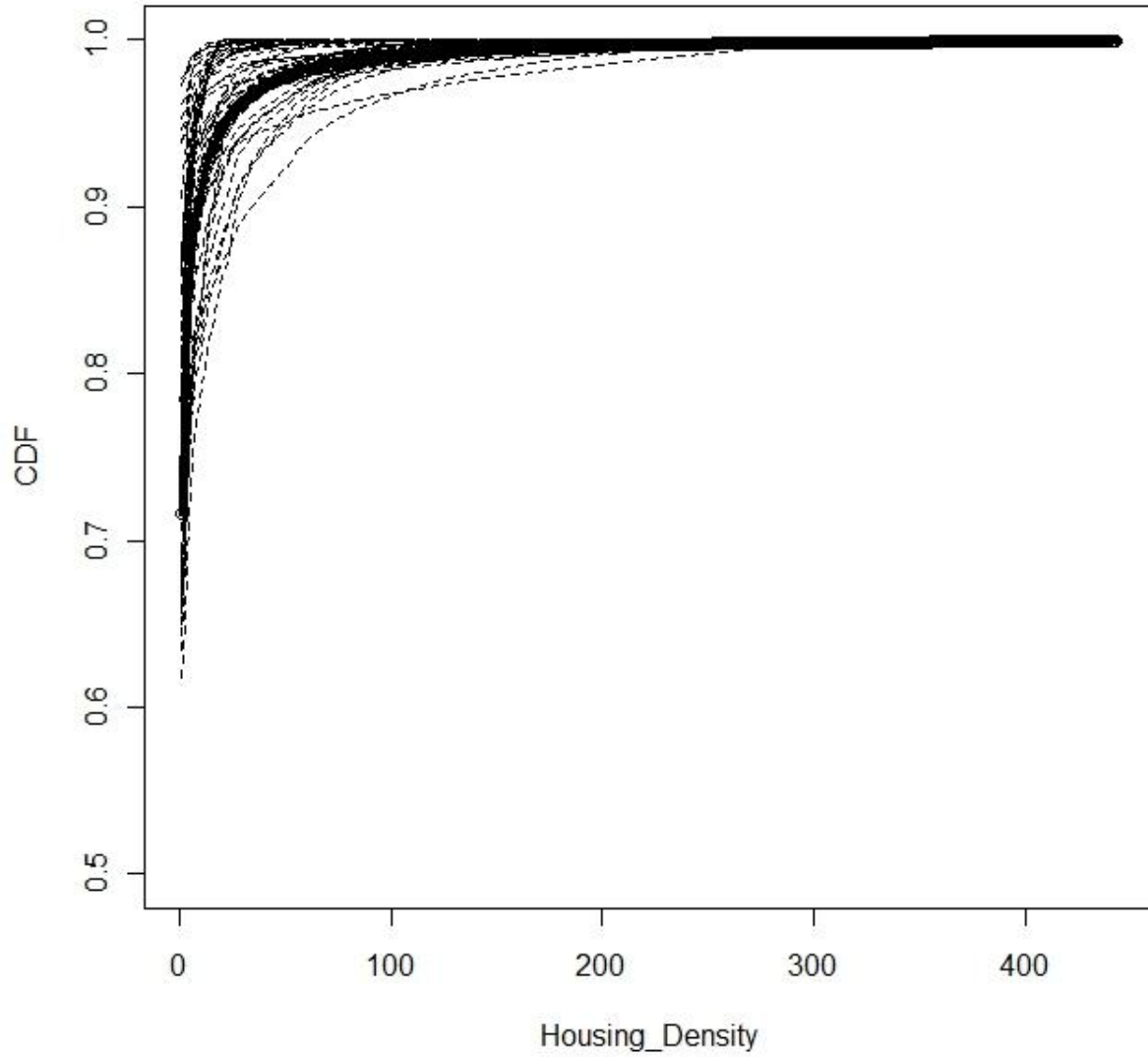


Figure 3.2. Comparison of Average Weibull function fit on density of structures for cumulative distribution function (CDF) based on the utilization distribution for each cougar (7 females and 8 males) near Cle Elum, WA from 2001 – 2008.

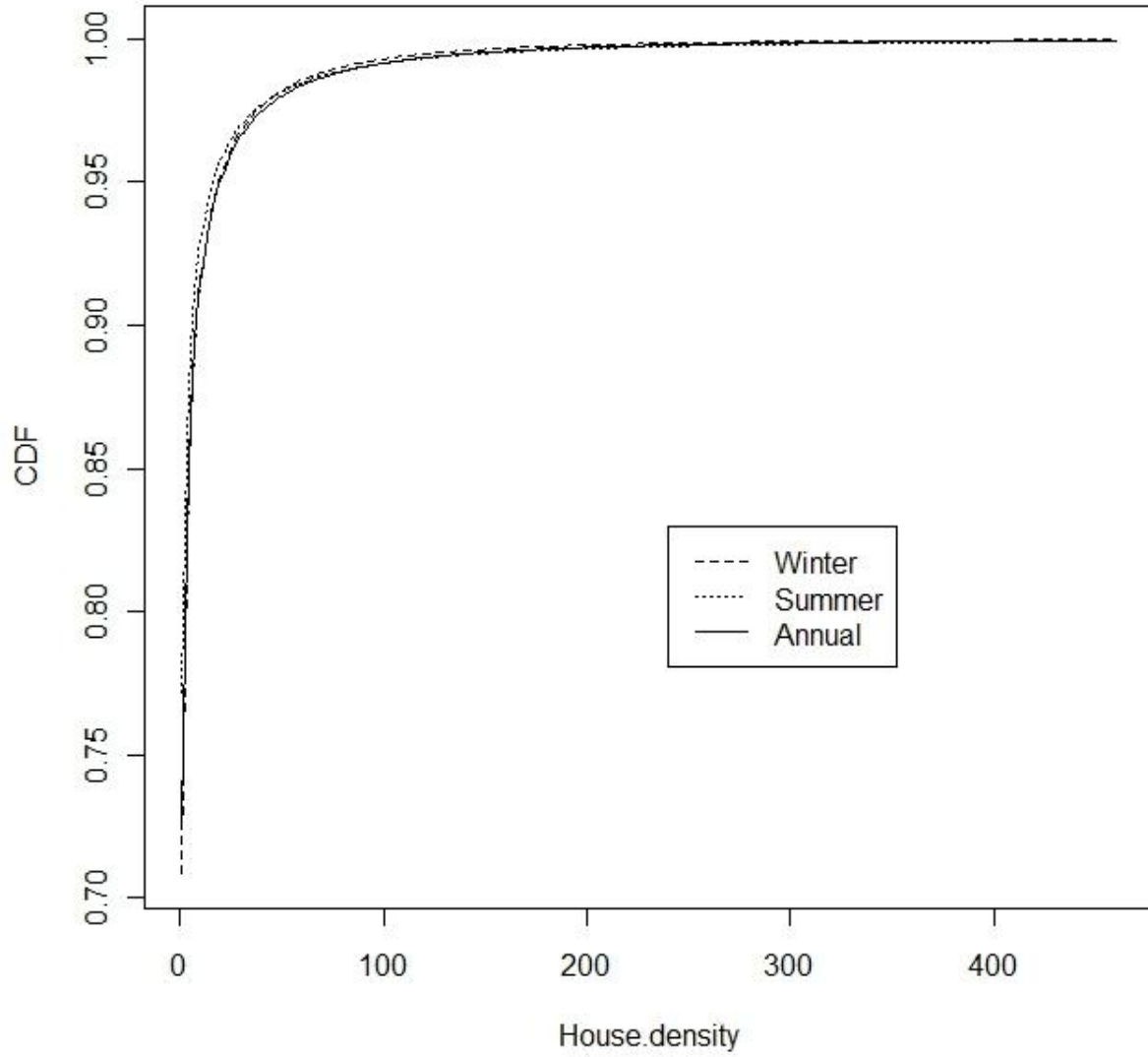


Figure 3.3. Approximate 95% confidence interval for the shape and scale parameters fit to empirical cougar cumulative distribution functions (CDF) for housing density per km².

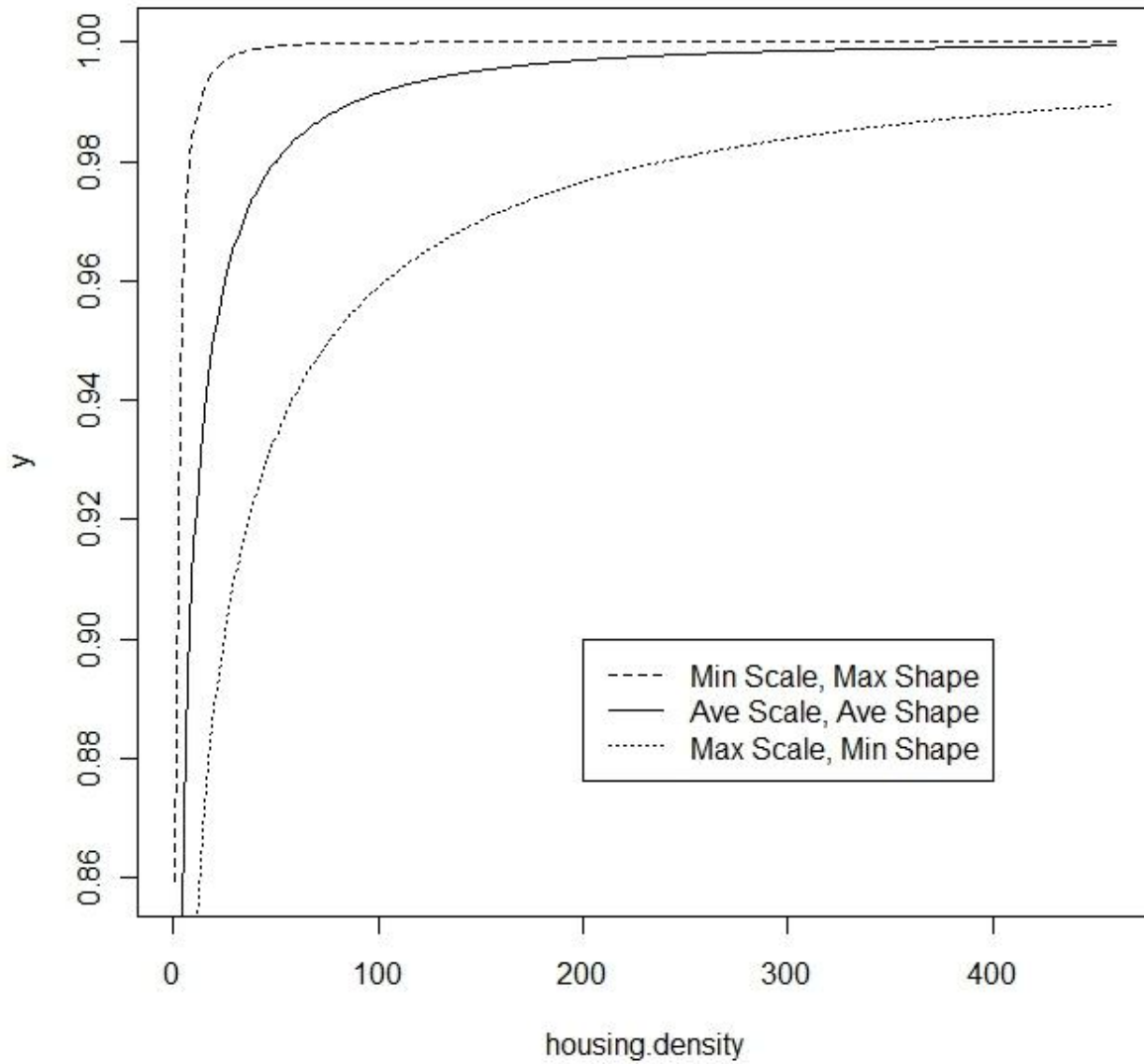


Figure 3.4. Comparison of Average Weibull function fit on Euclidean distance to houses for cumulative distribution function (CDF) based on the utilization distribution for each cougar (7 females and 8 males) near Cle Elum, WA from 2001 – 2008.

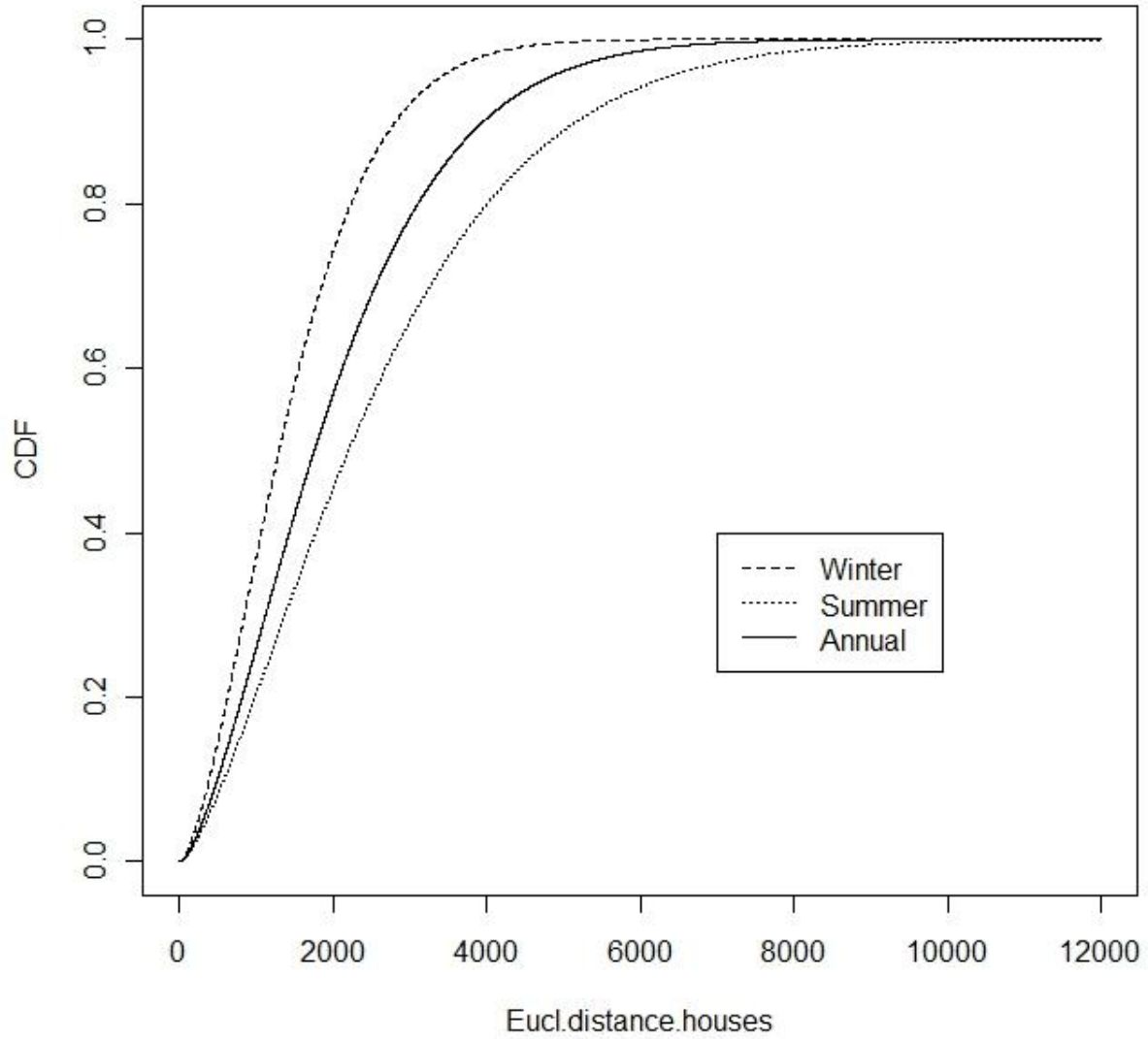


Figure 3.5. Cougar locations from 2003(a) and 2008 (b) display a retraction of home ranges in response to density of human structures. Dark gray circles indicate GPS locations from male cougars, while light gray circles indicate female cougar locations. The grayscale shading indicates structure density on the landscape with darker shading denoting higher densities of structures (Arrows indicate areas of high density development during the study).

