Home range characteristics of a subordinate predator: selection for refugia or hunt opportunity?

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Abstract

Cougars *Puma concolor* are described as 'habitat generalists', but little is known about which ecological factors drive their home range selection. For example, how do resource distributions and inter-species competition with dominant competitors (i.e. wolves, *Canis lupus*) over such resources, influence the distributions of cougars on the landscape? We tracked cougars using *Very High Frequency* (VHF; 2001 to 2005) and *Global Positioning System* (GPS; 2006 to 2011) technology in the Southern Yellowstone Ecosystem (SYE) in northwestern Wyoming, USA. We tested whether data type (VHF vs. GPS), cougar sex, access to forests (refugia) or hunt opportunity explained the size of 50% and 95% kernel density estimator (KDE) home ranges. Second, we quantified attributes of cougar home ranges and tested whether they were different from attributes of the overall study area, to address the ecological question: Do cougars select home ranges based on the availability of refugia, hunt opportunity or some combination of the two? Cougar sex and data type proved significant predictors of home range size for both 95% and 50% KDEs, and the amount of forest partly explained the size of 50% KDEs. Cougar home ranges derived from VHF data were 1.4–1.9 times larger than home ranges derived from GPS data; however, home range attributes determined from VHF and GPS data were remarkably equivalent. Female cougars selected home ranges with higher hunt opportunity than males, supporting the assumption that females primarily select home ranges with suitable prey to sustain themselves and their young. All cougars selected home ranges further from known wolf packs, providing evidence for newly established competition between resident cougars and recolonizing wolves, but did not select home ranges with greater access to landscape refugia. Our results provided evidence that cougars in the SYE select home ranges that provide high hunting opportunity and a spatial buffer that mitigates potential conflicts with a dominant competitor.

Introduction

That individual animals restrict their movements to home ranges has been an area of interest to ecologists for well over a century (Darwin, 1859; Seton, 1909). A home range defines the area traversed by an animal in its normal behavioural activities of foraging, seeking shelter, reproduction and maximizing fitness (Burt, 1943; Powell, 2012). Animal home ranges betray species ecology, if approached with appropriate questions (Powell & Mitchell, 2012). Outlining the area within which an individual moves is but the first step in understanding home ranges within an ecological perspective. For example, how do resource distributions and intra- and inter-species competition over such resources influence the distributions of animals on the landscape?

Many ecosystems have multiple predator species that not only compete for shared resources, but also pose direct and indirect threats to each other (Creel, Spong & Creel, 2001; Kortello, Hurd & Murray, 2007; Vanak *et al.*, 2013). Even so, behavioural mechanisms for coexistence of multiple carnivore species remain poorly understood. Predators have been observed to select home ranges based upon prey distributions and availability (e.g. cougars in Grigione *et al.*, 2002; Elbroch & Wittmer, 2012), while prey species should select home ranges dependent upon the availability of adequate refugia (Fisher, 2000). In systems with multiple predators, subordinate predators may need to secure a balance between prey availability and adequate refuge to reduce the risk of intraguild competition. For example, in African savannas, cheetahs *Acinonyx jubatus* and African wild dogs *Lycaon*

pictus are subordinate to African lions *Panthera leo* and spotted hyenas *Crocuta crocuta*. Cheetahs and wild dogs suffer reduced access to high-resource areas, kleptoparasitism of their kills, and increased mortality from exploitation competition (Creel *et al.*, 2001).

The cougar *Puma concolor* is a large, solitary carnivore with the largest distribution of any terrestrial mammal in the western hemisphere (Sunquist & Sunquist, 2002). Cougars are described as 'habitat generalists' and utilize a wide diversity of habitats and landscapes across the full extent of their range (Sunquist & Sunquist, 2002). In the US, cougars are expanding east into areas where they were previously extirpated, even while they may be declining in Central and South America (Caso *et al.*, 2008). Quantifying and describing home range characteristics of this cryptic, wide-ranging species poses many challenges, and thus, little is known about which ecological factors drive cougar home range selection (Grigione *et al.*, 2002; Elbroch & Wittmer, 2012).

Numerous field studies have confirmed that male cougars have larger home ranges than females. The biological assumption is that males select larger home ranges that provide access to sufficient females for mating opportunities (Seidensticker *et al.*, 1973; Logan & Sweanor, 2001, 2010; Laundré & Loxterman, 2007), whereas we assume adult female cougars select smaller home ranges that provide the necessary prey to sustain themselves and their dependent offspring. Alternatively, male home ranges may provide greater access to prey to match their increased metabolic requirements over females because of their larger size. These assumptions, however, are difficult to test because of the difficulty in quantifying prey numbers at the scale of cougar home ranges, or more specifically, actual prey 'availability' for hunting cougars.

We tracked cougars using *Very High Frequency* (VHF; 2001 to 2005) and *Global Positioning System* (GPS; 2006 to 2011) technology in the Southern Yellowstone Ecosystem (SYE) in northwestern Wyoming, USA. Our long-term study provided the unique opportunity to compare cougar home ranges and their attributes, as derived from VHF and GPS data. First, we tested whether data type (VHF vs. GPS), cougar sex, access to forests (refugia) or hunt opportunity explained cougar home range sizes at both the core, defined as the 50% fixed-kernel home range (Dickson & Beier, 2002), and 95% kernel density estimator (KDE) home ranges. Following our assumptions about cougar ecology, we predicted female cougars in the SYE would utilize smaller home ranges than males (Grigione *et al.*, 2002; Elbroch & Wittmer, 2012), and that the greater accuracy of locations acquired by GPS collars would result in smaller home ranges than home ranges derived from VHF data. Because cougars are subordinate competitors to wolves *Canis lupus* and bears *Ursus* spp. (Kortello *et al.*, 2007; Ruth & Murphy, 2010), we also hypothesized that cougars would require access to structured habitats (forests) to keep themselves safe, especially in core home ranges.

Next, we quantified attributes of cougar home ranges by assessing point attributes selected randomly from within core and 95% fixed-kernel home ranges and then tested whether they were statistically different from attributes of the study area as a whole. We hypothesized that home range attributes would vary between home ranges derived from VHF and GPS data, between home ranges of males and females, and between core and 95% KDEs. We hypothesized that cougar core areas derived from GPS data would identify areas with higher hunting opportunity (areas in which cougars were more likely to kill prey) and lower safety attributes (terrain ruggedness, complex vegetation classes) than core areas derived from VHF data.

Ultimately, we employed home range attribute data to address the following ecological question: Do cougars select home ranges based on the availability of refugia (terrain ruggedness, complex vegetation classes, longer distances from roads and known wolf packs), hunt opportunity, or some combination of the two? Because of the difficulty in quantifying prey numbers at the scale of cougar home ranges and determining what prey is truly available, we used 'hunt opportunity' as a proxy for prey availability, which we defined as areas in which cougars were likely to kill prey, quantified with a resource selection function analysis of verified cougar kills located in the field (Elbroch *et al.*, 2013; Kunkel *et al.*, 2013). We hypothesized females would select home ranges with higher hunting opportunities and greater access to refugia than males (Seidensticker *et al.*, 1973; Logan & Sweanor, 2001, 2010). Because cougars are subordinate competitors and a trophy species in Wyoming subject to human hunting, we also hypothesized both male and female cougars would select for home ranges with more rugged terrain and complex vegetation classes (escape terrain and concealment), and further from roads and known wolf packs than expected when compared with characteristics of the study area as a whole (Kortello *et al.*, 2007).

Material and methods

Study area

Our study area encompassed approximately 2300 km² of the SYE in southern Teton County, Wyoming (Fig. 1). Elevations in the study area ranged from 1800 m in the valleys to >3600 m in the mountains. The area was characterized by short, cool summers and long, cold winters with frequent snowstorms. Average summer temperatures were 6.9°C, and average winter temperatures were −7.2°C (Gros Ventre SNOTEL weather station). Precipitation occurred mostly as snow, and maximum snow depths ranged from 100 cm at lower elevations to >245 cm at intermediate and higher elevations (2000 m +).

Habitats included foothill grasslands, big sagebrush *Artemisia tridentate* dominated shrub-steppe, Douglas-fir forests, aspen *Populus tremuloides* forests and higher elevation coniferous forests, composed of lodge pole pine *Pinus contorta*, subalpine fir *Abies lasiocarpa*, Engelmann spruce *Picea engelmannii* and white bark pine *P. albicaulis*. Riparian corridors were dominated by cottonwood *Populus* spp. and willow *Salix* spp. communities (Marston & Anderson, 1991).

In addition to cougars, the SYE was inhabited by numerous other carnivores, including brown bears *Ursus arctos*, American black bears *U. americana*, wolves, coyotes *C. latrans* and
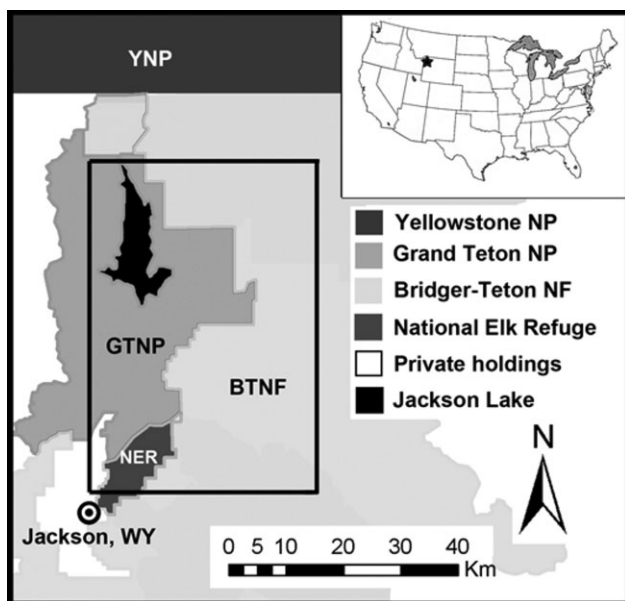
Figure 1 Location of the study area in north-west Wyoming, USA and a close-up of land ownership within the area of focus. The smaller rectangle delineated by a black line was the area in which we focused capture efforts and our interaction study using marked individuals (Elbroch *et al.*, 2013).

red foxes *Vulpes vulpes*. Ungulates included elk *Cervus elaphus*, mule deer *Odocoileus hemionus*, white-tailed deer *O. virginianus*, Shiras moose *Alces alces shirasi*, bighorn sheep *Ovis canadensis* and North American pronghorn *Antilocapra americana*.

Cougar capture

Each year from November through March, we employed trailing hounds to force cougars to retreat to a tree or rocky outcrop where we could safely approach them; trailing hounds are the most common method to capture cougars for research in North America. Cougars were immobilized with ketamine (2.5–3.0 mg kg⁻¹) and medetomidine (0.075 mg kg⁻¹) delivered by a CO_2 Dan-Inject rifle (DanWild LLC, Austin, TX, USA), before they were processed. We recorded age using tooth condition (Heffelfinger, 2010) or gum line recession (Laundré *et al.*, 2000), sex, weight and standardized body measurements. Cougars were fitted with either a VHF (Telonics, Mesa, AZ, USA) or GPS collar (Telonics; Televilt, Bandygatan, Sweden; or Vectronics, Berlin, Germany). GPS collars were programmed to acquire location data between four and eight times per day. All collars were equipped with mortality sensors that activated after 8 h of inactivity. Our capture protocols for cougars followed those outlined in Quigley (2000), adhered to the guidelines outlined by the American Society of Mammalogists (Sikes *et al.*, 2011) and were approved by the Jackson Institutional Animal Care and Use Committee (Protocol 027-10EGDBS-060210).

Home range calculations

We calculated 50% (core area) and 95% annual fixed-kernel home ranges for marked, adult cougars resident in the study area from 2001 to 2011. We quantified KDEs (Worton, 1989; Kie *et al.*, 2010), isopleths and area (km) in the Geospatial Modeling Environment (GME, Beyer, 2009–2012). Annual home ranges were calculated for cougars wearing VHF collars for which we had gathered a minimum of 30 independent locations (Seidensticker *et al.*, 1973; Grigione *et al.*, 2002) across a minimum of 10 months, and for cougars wearing GPS collars, data spanning a minimum of 10 months. Cougars with VHF collars were triangulated in the field, either from fixed wing aircraft or on the ground, and all location data with an error ellipse less than 4000 m² were retained for analyses (Program LOAS, Ecological Software Solutions, Sacramento, CA, USA). The smoothing factor *(h)* for VHF data was determined through least squares cross-validation (Worton, 1989), and for GPS data, using the plug-in method (Loader, 1999) in the GME. For cougars that were sampled for multiple years, we calculated an average home range size before including it in further analyses. After home ranges were determined for each individual cougar, we then defined the spatial extent of our study area as the minimum convex polygon (MCP, Mohr, 1947; GME) encompassing all cougar location data.

Defining point attributes to determine home range attributes

In ArcGIS 10, we assigned 200 random points within 50% core areas, 400 random points within 95% home ranges and 2000 random points within the MCP defining the extent of the study area. When a cougar was sampled for multiple years, resulting in multiple home ranges and additional points, we randomly subsampled 200 and 400 points at the 50% and 95% KDEs from across years for each cougar to include in further analyses. We then assigned the following attributes to each random point: cougar ID; cougar sex and weight; data type (GPS or VHF); terrain ruggedness (vector ruggedness measure, VRM); vegetation type; hunt opportunity; distance to nearest road; and centre of each wolf pack territory.

We derived VRM from the digital elevation model (http://datagateway.nrcs.usda.gov/) following the method of Sappington, Longshore & Thompson (2007). We reclassified 87 land cover classes described in a Gap Analysis Program land cover (gapanalysis.usgs.gov/gaplandcover) at 30 m resolution, into five general land cover classes: (1) open meadows or crop lands, (2) barren habitats and open-water bodies, (3) shrub-steppe, (4) forest (5) and riparian zones.

Based on results of earlier seasonal resource selection function analyses (Elbroch *et al.*, 2013), we calculated the relative probability of a cougar making a kill in any location in the study area. The resulting odds ratio expression for a given landscape location was calculated using the spatial distribution of actual cougar kills to generate a probability surface that then served as a template to identify landscape heterogeneity (Kauffman *et al.*, 2007; Kunkel *et al.*, 2013); cells with a higher value indicated a higher relative probability of kill

occurrence. Contributing point attributes included in this analysis were distance to forest edge (m), distance to nearest water (m), aspect (transformed to north, east, south, west), slope (%) and elevation (m) (Elbroch *et al.*, 2013). Because kill sites were analysed on a seasonal basis and home ranges were delineated as year-round occupancy, we combined values from each seasonal output (summer, winter) to create a value we defined as 'hunt opportunity', a quantitative assessment of the likeliness that a cougar would kill prey in a given location.

In collaboration with the US Fish and Wildlife Service and Wyoming Game and Fish Department, we obtained MCPs of marked wolf packs in the study area for each year. We determined the centroid of each MCP and used this location from which we quantified distance to the nearest wolf pack (m).

Determining explanatory variables associated with home range size

Prior to any statistical analyses, we used a correlation matrix to evaluate collinearity ($|r| > 0.7$) among predictor variables: cougar sex, cougar weight, data type (VHF vs. GPS), hunt opportunity (as a proxy for availability) and the percentage of forested habitat. Cougar weight and sex were highly correlated ($|r| = 0.80$), so we removed cougar weight from further analyses. The remaining predictor variables were not correlated (all $|r| < 0.50$) and were retained for analysis. We employed generalized linear models and likelihood ratio statistics based on their asymptotic chi-square distributions (JMP 10, SAS Institute Inc., Cary, NC, USA), to conduct a multivariate regression of cougar sex, data type, hunt opportunity and percentage of forested habitat on home range size. This process was conducted for 95% and 50% KDEs.

Comparing home range attributes with the larger study area

Following our analysis identifying predictor variables significant in determining a cougar's home range size, we created four categories with which to compare home range attributes with the study area as a whole: VHF males, GPS males, VHF females and GPS females. We employed separate analyses of variances (ANOVAs) and post-hoc Tukey's honestly significant difference (HSD) tests to determine whether the following mean home range attributes, hunting opportunity, terrain ruggedness, distance to nearest road and wolf pack, and percentage of land cover class, statistically differed from each other and from the study area as a whole at both the 50% core area and 95% fixed-kernel home range. Prior to any statistical tests, we tested whether data met the assumptions of ANOVA (Steel, Torrie & Dickey, 1997). To meet these assumptions, we applied root transformations to VRM, distance to roads and distance to water, and a $\log_{10}$ transformation to distance to wolf pack.

Results

From 2001 to 2011, we quantified 67 annual home ranges for 28 individual cougars. Nine individual female cougars and five males were fitted with GPS collars, and 16 females and five males were fitted with VHF collars. Seven cougars were equipped with both collar types in alternating years producing both GPS and VHF derived home ranges.

Explanatory variables associated with home range size

Cougar sex and data type explained the size of a cougar's home range for both the 95 ($\chi^2_{1,4} = 6.59$, $P = 0.01$; $\chi^2_{1,4} = 6.20$, $P = 0.01$) and core (50%) ($\chi^2_{1,4} = 9.37$, $P < 0.01$; $\chi^2_{1,4} = 5.99$, $P = 0.01$) KDEs. The percentage of forested habitat within a home range partially explained the size of core KDEs ($\chi^2_{1,4} = 5.08$, $P = 0.02$). Hunt opportunity did not explain home range size at either scale (both $P > 0.10$). Male home ranges were 1.9–3.3 times larger than female home ranges ($P < 0.01$), and home ranges derived from VHF data were 1.4–1.9 larger than those created using GPS data ($P < 0.01$; Fig. 2a,b, Table 1).

Home range attributes

The MCP for the study area we employed to compare home range attributes was 7012 km². The number of attributed points used in analyses equalled 22 400: 1800 for GPS females, 1000 for GPS males in 50% KDEs; 3600 for GPS females, 2000 for GPS males in 95% KDEs; 3000 for VHF females, 1000 for VHF males in 50% KDEs; 6000 for VHF females, 2000 for VHF males in 95% KDEs and 2000 across the study area. Results of the various Tukey's pairwise comparison tests can be found in Table 1. Hunt opportunity was highest in GPS female core areas and lowest in GPS male 95% KDEs ($F_{8, 22,399} = 61.40$, $P < 0.01$; Fig. 2c, Table 1). Both VHF and GPS female home ranges had higher hunt opportunity than the average of the study area, which was statistically equivalent to GPS male home ranges at the 95% KDE ($P < 0.01$; Table 1). All cougar home ranges were further from the centroid of known wolf pack territories than expected when compared with the study area ($F_{4, 10,399} = 425.19$, $P < 0.01$; Fig. 2d, Table 1). 95% KDE home ranges of male cougars were further from roads than 95% KDE female home ranges, though all home ranges were closer to roads than expected when compared to the study area ($F_{8, 22,399} = 191.83$, $P < 0.01$; Table 1). Terrain ruggedness (VRM) did not differ between 50% and 95% KDEs, between males and females, or between home ranges derived from VHF or GPS data, but were slightly higher than the study area in some instances ($F_{8, 22,399} = 2.16$, $P = 0.03$; Table 1).

In general, cougars selected home ranges with proportionate representation of land cover classes existing in the SYE (Table 2), with a few exceptions. Female core home ranges derived from VHF data had a higher percentage of forested habitat than the study area ($F_{8, 167} = 2.06$, $P = 0.04$; Table 2). There were no differences when comparing riparian habitat between the home ranges and the study area, although, core male home ranges derived from VHF data had a higher percentage of riparian habitat than female 95% KDEs derived
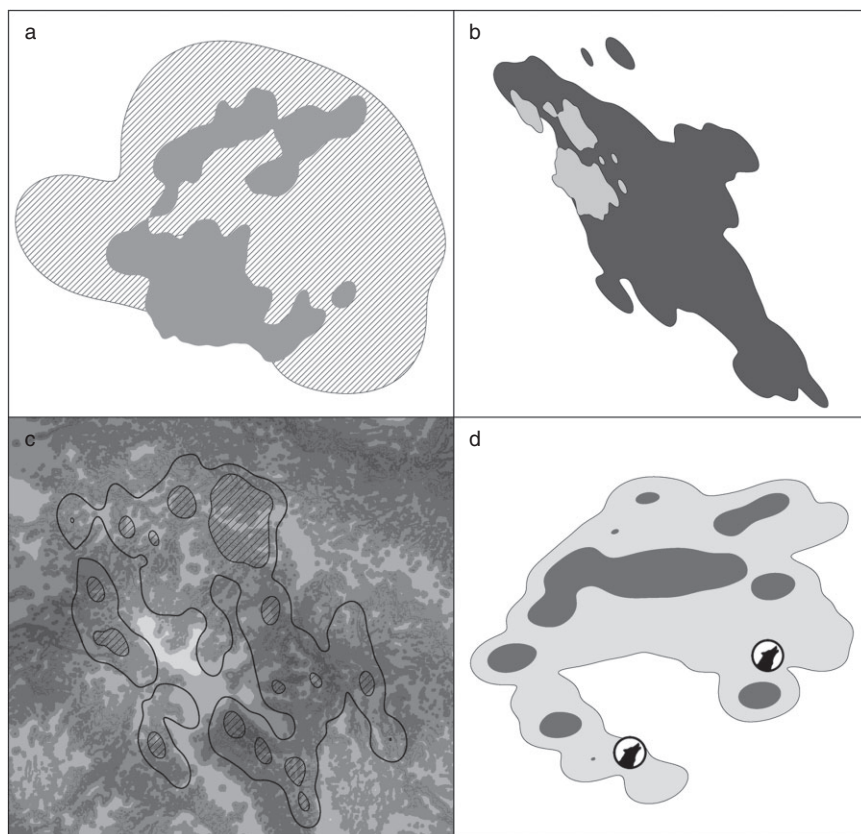
Figure 2 Examples of cougar home ranges in the Southern Yellowstone Ecosystem: (a) home ranges derived from VHF telemetry (larger, cross-hatch fill) and GPS telemetry (smaller, solid grey) from the same female in sequential years; (b) overlapping smaller female (light grey) and larger male (dark grey) home ranges from GPS telemetry; (c) 95% KDE (black outline) and 50% core (cross-hatch fill) home ranges overlaid on our 'hunt opportunity' map, darker colours indicate a greater likeliness that a cougar would kill prey there; (d) 95% KDE (light grey) and 50% core (dark grey) home ranges for a single cougar in relation to known wolf pack centroids (wolf heads).

from GPS data ($F_{8, 165} = 2.44$, $P = 0.02$; Table 2). Additionally, all cougar home ranges encompassed less meadow than expected compared with the study area ($F_{8, 167} = 67.77$, $P < 0.01$), and female home ranges had less barren habitat than males ($F_{8, 121} = 13.90$, $P < 0.01$; Table 2). With the exception of male home ranges derived from VHF data, all home ranges contained more shrub habitats than the study area ($F_{8, 167} = 22.83$, $P < 0.01$; Table 2).

Discussion

Understanding why carnivores select the home ranges they do is an important aspect of ecological research and conservation (Nilsen, Herfindal & Linnell, 2005), and measuring home range sizes and describing home range attributes remains an evolving field of interest. Nevertheless, the lack of standardization in sampling method, sampling scheme and sample size have led to great variation in the estimation of home range sizes, even within species (Gula & Theuerkauf, 2013). In support of our hypothesis, cougar home ranges in the SYE derived from VHF data were 1.4–1.9 times larger than home ranges derived from GPS data, likely due to the increased accuracy and sheer volume of locations acquired with GPS technology (Kie *et al.*, 2010). Unlike our observations, previous studies have observed similar size and shape of home ranges derived from GPS and VHF collars when a high enough frequency of data acquisition is collected from VHF

collars (1–3 locations/week, Börger *et al.*, 2006; Kochanny, Delgiudice & Fieberg, 2009), further emphasizing the need for standardization in sampling methods (Gula & Theuerkauf, 2013). In contrast to home range size, home range attributes determined from VHF and GPS home ranges were remarkably equivalent (*sensu* Land *et al.*, 2008), lending support for earlier cougar research dependent upon only VHF technology.

As has been reported by numerous cougar studies in western North America (Dickson & Beier, 2002; Grigione *et al.*, 2002; Nilsen *et al.*, 2005), our data affirmed our prediction that male home ranges were larger than female home ranges. GPS male 95% KDEs were approximately 2.7 times larger than those of GPS females. VHF male home ranges were approximately 2.0 times larger than female home ranges. Contrary to our third prediction, we did not detect a change in home range size based on hunt opportunity at either scale. Cougars did, however, select home ranges with higher hunting opportunity than expected given mean hunting opportunity across the study area. Thus, hunt opportunity explained where cougar home ranges were placed within the study area, but not the size of cougar home ranges. Further, female home ranges, in general, had higher hunting opportunities than male home ranges, corroborating the long-standing assumption that females primarily select home ranges with suitable prey to sustain themselves and their dependent young (Laundré & Loxterman, 2007; Logan & Sweanor, 2010).

Table 1 Descriptive statistics of cougar home ranges in the Southern Yellowstone Ecosystem from 2001 to 2011, and results of Tukey's HSD tests to determine differences in home range size, hunting opportunity, distance to roads, terrain ruggedness (VRM) and distance to nearest wolf pack between GPS males, VHF males, GPS females, VHF females and the study area as a whole in 95% and 50% KDEs

Parameter	Collar type	Sex	KDE	Mean	Tukey's	SD	Min	Max
Size (km²)	VHF	Male	95	1028.83	A	449.35	403.85	1827.12
	GPS	Male	95	567.17	B	184.28	357.19	914.97
	VHF	Female	95	543.89	C	507.11	34.10	1892.27
	VHF	Male	50	266.40	D	113.14	109.27	457.75
	GPS	Female	95	209.58	E	139.02	67.13	587.58
	GPS	Male	50	123.07	F	51.44	63.60	253.51
	VHF	Female	50	130.67	G	119.63	6.25	465.41
	GPS	Female	50	38.21	H	26.49	11.67	105.72
Hunt Opp	GPS	Female	50	9.56	A	1.58	4.03	15.28
	VHF	Female	50	9.52	A	1.82	3.55	17.68
	VHF	Female	95	9.42	A B	1.88	3.04	16.91
	GPS	Female	95	9.32	B C	1.66	3.18	16.77
	VHF	Male	50	9.25	B C	1.69	3.34	13.93
	GPS	Male	50	9.23	C	1.55	4.64	13.78
	VHF	Male	95	9.18	C	1.85	3.26	15.35
	GPS	Male	95	8.82	D	1.70	3.22	15.24
	Study area			8.76	D	2.15	2.46	18.22
Roads (m)	VHF	Female	50	2866.89	A	3083.45	0.13	15514.30
	VHF	Female	95	3128.99	B	3318.19	0.05	21952.00
	GPS	Female	50	3202.42	B	2952.78	1.14	13650.40
	GPS	Female	95	3225.68	B	3147.38	1.11	14543.10
	VHF	Male	50	3676.65	C	3067.56	3.80	13138.90
	VHF	Male	95	3854.81	C	3304.34	2.43	14002.10
	GPS	Male	50	4224.62	B	9098.92	0.26	56267.80
	GPS	Male	95	5431.39	D	8415.82	2.02	58019.20
	Study area			6946.45	E	5583.41	0.73	28010.80
VRM	VHF	Male	95	0.16	A	0.18	0.00	0.95
	VHF	Female	50	0.17	A	0.19	0.00	0.96
	VHF	Male	50	0.16	A B	0.19	0.00	0.97
	GPS	Male	50	0.16	A B	0.19	0.00	0.92
	GPS	Male	95	0.16	A B	0.18	0.00	0.96
	GPS	Female	50	0.16	A B	0.17	0.00	0.89
	VHF	Female	95	0.16	A B	0.18	0.00	0.98
	GPS	Female	95	0.16	A B	0.18	0.00	0.96
	Study area			0.15	B	0.18	0.00	0.97
Wolves (m)	GPS	Male	95	13722.9	A	6627.32	110.27	39346.10
	GPS	Male	50	13338.8	A	5879.04	739.29	37739.40
	GPS	Female	50	11731.4	B	5929.12	499.57	92945.00
	GPS	Female	95	11750.7	B	5820.89	208.56	36624.50
	VHF	Male	50	n/a	n/a	n/a	n/a	n/a
	VHF	Male	95	n/a	n/a	n/a	n/a	n/a
	VHF	Female	50	n/a	n/a	n/a	n/a	n/a
	VHF	Female	95	n/a	n/a	n/a	n/a	n/a
	Study area			7251.68	C	3686.87	215.98	20483.50

GPS, Global Positioning System; KDE, kernel density estimator; SD, standard deviation; VHF, Very High Frequency; VRM, vector ruggedness measure.

We found mixed support for our predictions that the percentage of forested habitat would influence home range size, or that cougars would select home ranges with greater refugia than expected as compared with the study area. Unlike in the open landscapes of Patagonia where forests are scarce, cougars primary hunt open grasslands, and cougars lack dominant competitors (Elbroch & Wittmer, 2012), we did not find forests influenced cougar home range size for 95% KDEs in the SYE. However, the percentage of forest did partly explain the size of 50% core areas. Neither did we find support for our hypothesis that GPS core areas would include less refugia than VHF core areas; they proved

Table 2 Percentage land cover classes of cougar home ranges in the Southern Yellowstone Ecosystem from 2001–2011, and results of Tukey's HSD tests to determine differences in proportions of land cover classes between GPS males, VHF males, GPS females, VHF females and the study area as a whole in 95% and 50% KDEs

Collar type	Sex	KDE	Barren		Meadow		Shrub		Forest		Riparian	
VHF	Male	95	3.00	A B	15.85	A	26.00	A B C D	52.30	A B	4.65	A B
VHF	Female	95	1.20	A	13.43	A	29.10	A B C	51.73	A B	5.33	A B
VHF	Female	50	2.50	A	11.26	A B	27.03	B C	55.80	A	5.40	A B
GPS	Male	95	3.08	A B	13.15	A B	28.95	A B C	52.45	A B	3.60	A B
GPS	Female	95	1.08	A	12.19	A B	32.52	A B C	51.61	A B	3.30	A
VHF	Male	50	2.25	A B	13.50	A B	22.30	C D	57.30	A B	7.50	B
GPS	Female	50	1.75	A	8.77	B	35.72	A	51.61	A B	3.93	A B
GPS	Male	50	1.75	A	7.90	B	35.80	A B	51.00	A B	4.60	A B
	Study area		4.51	B	23.56	C	17.06	D	50.69	B	4.16	A B

GPS, Global Positioning System; KDE, kernel density estimator; VHF, Very High Frequency.

equivalent. This may be reflective of the fact that the SYE includes a greater availability of refugia for cougars, or different prey, or some other ecological factor we overlooked.

Overall, cougars selected home ranges with only one safety attribute: distance from wolves. Although cougars selected home ranges further from known wolf packs, they selected home ranges closer to roads than expected, where we assumed they were more vulnerable to human hunters. Male home ranges were even further from wolves than were females. Female home ranges, however, were more reflective of higher hunting opportunity, and these areas may provide hunting habitat for wolves as well. Kunkel & Pletscher (2001) reported that wolves focused their activity in areas where prey were most abundant, and therefore, female cougars selecting better hunting areas for themselves may in fact be decreasing their distances to wolves seeking the same resources. The same behavioural tactics have been observed in African systems, where dominant carnivores often reside in areas with the highest prey availability, hence, the greatest cost for subordinate carnivores (intra-guild predation) is also coupled with the highest potential benefit of resource acquisition (Vanak *et al.*, 2013). Female cougar home ranges were closer to roads than home ranges of males, but all cougars selected home ranges closer to roads than expected when compared with mean distances to roads across the study area. In the SYE, the major road networks follow water systems at lower elevations, where prey congregate, especially in winter when ungulates migrate to lower elevations (Elbroch *et al.*, 2013).

In conclusion, cougar home range selection in the SYE reflects an awareness of prey availability and mitigating risks of interactions with dominant competitors (wolves). Our work highlighted likely competition scenarios between re-established wolves and resident cougars, as evidenced by cougars selecting home ranges away from known wolf packs. Spatial displacement between wolves and cougars has been noted in other studies (Kortello *et al.*, 2007; Kunkel *et al.*, 2013). This, no doubt, limits the availability of quality habitat in the SYE, which has implications for juvenile cougar survival, juvenile dispersal success and overall cougar population dynamics.

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