

Spatial overlap in a solitary carnivore: support for the land tenure, kinship or resource dispersion hypotheses?

L. Mark Elbroch^{1*}, Patrick E. Lendrum¹, Howard Quigley¹ and Anthony Caragiulo²

¹*Panthera*, 8 West 40th Street, 18th Floor, New York, NY 10018, USA; and ²*Sackler Institute for Comparative Genomics, American Museum of Natural History, 79th Street at Central Park West, New York, NY 10024, USA*

Summary

1. There are several alternative hypotheses about the effects of territoriality, kinship and prey availability on individual carnivore distributions within populations. The first is the land-tenure hypothesis, which predicts that carnivores regulate their density through territoriality and temporal avoidance. The second is the kinship hypothesis, which predicts related individuals will be clumped within populations, and the third is the resource dispersion hypothesis, which suggests that resource richness may explain variable sociality, spatial overlap or temporary aggregations of conspecifics.

2. Research on the socio-spatial organization of animals is essential in understanding territoriality, intra- and interspecific competition, and contact rates that influence diverse ecology, including disease transmission between conspecifics and courtship behaviours.

3. We explored these hypotheses with data collected on a solitary carnivore, the cougar (*Puma concolor*), from 2005 to 2012 in the Southern Yellowstone Ecosystem, Wyoming, USA. We employed 27 annual home ranges for 13 cougars to test whether home range overlap was better explained by land tenure, kinship, resource dispersion or some combination of the three.

4. We found support for both the land tenure and resource dispersion hypotheses, but not for kinship. Cougar sex was the primary driver explaining variation in home range overlap. Males overlapped significantly with females, whereas the remaining dyads (F–F, M–M) overlapped significantly less. In support for the resource dispersion hypothesis, hunting opportunity (the probability of a cougar killing prey in a given location) was often higher in overlapping than in non-overlapping portions of cougar home ranges. In particular, winter hunt opportunity rather than summer hunt opportunity was higher in overlapping portions of female–female and male–female home ranges.

5. Our results may indicate that solitary carnivores are more tolerant of sharing key resources with unrelated conspecifics than previously believed, or at least during periods of high resource availability. Further, our results suggest that the resource dispersion hypothesis, which is typically applied to social species, is applicable in describing the spatial organization of solitary carnivores.

Key-words: Greater Yellowstone Ecosystem, home range, migratory prey, *Puma concolor*, spatial organization, territoriality

Introduction

Determining what ecological factors drive patterns in animal distributions remains a central question of ecology (Emlen & Oring 1977). Both the distributions of carnivore populations and individual carnivore territories, for

example, are primarily explained by the availability of key resources (i.e. prey availability for both sexes of carnivores; Burt 1943; Schaller 1972; Maher & Lott 2000; McLoughlin, Ferguson & Messier 2000; and female availability for male carnivores, Caro 1989; Schmidt, Jedrzejewski & Okarma 1997). Nevertheless, the spatial distributions of carnivore populations, as well as the individuals within these populations, are also influenced by

*Correspondence author. E-mail: melbroch@panthera.org

intraspecific (Macdonald 1983) and interspecific competition (Vanak *et al.* 2013; Lendrum *et al.* 2014).

Most carnivores are classified as solitary (Sandell 1989), a life-history strategy characteristic of non-cooperative species living in habitat with complex structure where competition exists for dispersed patches of prey (Sandell 1989; Logan & Sweanor 2001). Thirty-five of 37 wild felid species do not hunt or defend resources as a team, or cooperatively raise their young (Caro 1989; Sandell 1989; Lopez-Bao, Rodriguez & Ales 2008). Nevertheless, there are contradictory observations on how felids interact in the literature. For example, Packer (1986) stated that solitary female felids are intolerant of conspecifics, whereas Hornocker (1969) and Seidensticker *et al.* (1973) did not observe territoriality among solitary female felids.

Consequently, there are several alternative hypotheses about the effects of territoriality, kinship and prey availability on solitary carnivore distributions within populations. The 'land-tenure' hypothesis proposes that carnivores exhibit low densities because of territorial behaviours that result in minimal spatial overlap among conspecifics, and where animals do overlap, temporal avoidance of conspecifics (Hornocker 1969, 1970; Seidensticker *et al.* 1973; Ferreras *et al.* 1997; Diefenbach *et al.* 2006). In a land-tenure system, resident males aggressively defend their territories against male intruders, whereas females may overlap more with conspecifics, but express mutual avoidance (Ross & Jalkotzy 1992; Logan & Sweanor 2001). Evidence supporting the land-tenure hypothesis includes the polygynous mating system of most felids, in which males generally hold exclusive territories overlapping several females (Logan & Sweanor 2001, 2010; Lopez-Bao, Rodriguez & Ales 2008), and the fact that interactions between adult solitary felids occur primarily during the breeding season or randomly to determine territorial disputes (Kleiman & Eisenberg 1973; Lopez-Bao, Rodriguez & Ales 2008; Mattisson *et al.* 2013; Elbroch, Quigley & Caragiulo 2014). Spatially, the land tenure hypothesis predicts that male carnivores will overlap substantially with female conspecifics, but not other males, and that female carnivores will overlap primarily with male conspecifics, but may overlap to some degree with other females.

The kinship hypothesis (Hamilton 1964; Griffiths & Armstrong 2001) suggests that there are fitness benefits for individual animals that tolerate or even cooperate with related conspecifics. Individual fitness is enhanced through inclusive benefits shared with relatives, and this inclusive fitness increases the chances of ensuring the continuation of their shared genetic lineage. The kinship hypothesis predicts for aggregations of related individuals rather than the random distribution of individuals in populations, and has found support through research on the spatial organization of salmonids (*Oncorhynchus* spp.), Anuran amphibians, bears (*Ursus* spp.) and woodrats (*Neotoma* spp.) (Caro 1989; Blaustein & Waldman 1992; Brown & Brown 1993; Paetkau *et al.* 1998; Innes *et al.* 2012).

The resource dispersion hypothesis (Macdonald 1983) was developed to explain variable sociality within and across social species; however, it is potentially applicable to solitary species as well (Wagner, Frank & Creel 2008). The resource dispersion hypothesis predicts that higher resource richness, which varies in time and across space, reduces 'the resource-based cost of sharing a territory with conspecifics' (Johnson *et al.* 2002). Such resource fluxes can explain spatial grouping or other social behaviours that do not result in any apparent benefits for the individuals involved (Johnson *et al.* 2001). If applied to solitary species, the resource dispersion hypothesis predicts that territorial species may overlap where resource richness is highest even while individuals remain behaviourally solitary (Wagner, Frank & Creel 2008). For example, tigers (*Panthera tigris*), cougars (*Puma concolor*), jaguars (*Panthera onca*) and cheetahs (*Acinonyx jubatus*) are territorial species known to aggregate at kills made by conspecifics for short time periods (Schaller 1967; Seidensticker *et al.* 1973; Caro 1989; Guilder *et al.* 2015). In fact, intraspecific associations and interactions are increasingly being documented in what were assumed to be solitary species (e.g. Elbroch, Quigley & Caragiulo 2014; Quaglietta *et al.* 2014; Guilder *et al.* 2015), increasing the potential applicability of the resource dispersion hypothesis in explaining variable social organization of solitary species as well.

The cougar is a well-studied, solitary felid with the broadest geographic range of any terrestrial mammal in the Western Hemisphere (Sunquist & Sunquist 2002), and a species that exemplifies these competing hypotheses. Most research suggests that cougars are a land-tenure species and that they are regulated by density dependence, mutual avoidance and indirect signalling via scent marking and scraping (Hornocker 1969, 1970; Seidensticker *et al.* 1973; Hemker, Lindzey & Ackerman 1984; Logan & Sweanor 2001). Female cougars utilize smaller home ranges that provide the necessary resources to sustain themselves and their kittens, while males utilize home ranges that provide access to numerous females for mating opportunities (Seidensticker *et al.* 1973; Sandell 1989; Lendrum *et al.* 2014). Cougar interactions are considered rare and to be primarily explained by breeding behaviour (Seidensticker *et al.* 1973; Logan & Sweanor 2001; Elbroch, Quigley & Caragiulo 2014).

Cougar populations also exhibit matrilineal social structures (Logan & Sweanor 2001), implying support for the kinship hypothesis: local cougar populations are expected to be composed of groups of genetically more closely related females and unrelated males that arrived to the area from elsewhere. Most subadult female cougars exhibit philopatry, establishing adult territories in or adjacent to their mothers' ranges, and most subadult males disperse from their natal areas to avoid inbreeding and competition for mating opportunities with resident males (Sweanor, Logan & Hornocker 2000; Logan & Sweanor 2001; Landré & Hernandez 2003).

Cougar home range selection, however, is also influenced by prey availability (Grigione *et al.* 2002; Elbroch & Wittmer 2012; Lendrum *et al.* 2014), suggesting the resource dispersion hypothesis may also be applicable in explaining the spatial organization of cougars. In fact, Pierce, Vernon & Bowyer (2000) reported that territorial overlap between cougars in the Sierra Mountains of California was better explained by prey distributions than social behaviours. Further, Elbroch, Quigley & Caragiulo (2014) suggested that seasonal variation in intraspecific contact rates in northern cougar populations was likely partially explained by seasonal variation in prey distributions rather than breeding opportunities alone. Thus, the spatiotemporal distributions of prey may explain, at least in part, breaches in territoriality in this solitary species.

We tracked cougars from 2005 to 2012 with Global Positioning System (GPS) technology in the Southern Yellowstone Ecosystem (SYE) in north-western Wyoming, USA, and compared the percentage of overlap between simultaneous female–female, female–male and male–male home ranges. Our objective was to determine whether the per cent overlap between two cougars was better explained by the land tenure, kinship or resource distribution hypotheses, or some combination of the three (Table 1).

Materials and methods

STUDY AREA

Our study area encompassed approximately 2300 km² of the Southern Yellowstone Ecosystem (SYE) in southern Teton County, Wyoming (Fig. 1). Teton County includes Yellowstone National Park, Grand Teton National Park, the National Elk Refuge and several National Forests and is 97.9% public lands (Teton Conservation District 2013). 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 +). Plant and animal communities in our study area are described in the study by Elbroch *et al.* (2013).

COUGAR CAPTURE

We captured cougars during winters when determining the presence of a cougar was facilitated by snow. We used trailing hounds to force them to retreat to a tree or rocky outcrop where we could safely approach them. Cougars were immobilized with ketamine (2.5–3.0 mg kg⁻¹) and medetomidine (0.075 mg kg⁻¹), before they were processed. We recorded age using tooth condition (Heffelfinger 2010) or gum line recession (Laundré *et al.* 2000), gender, weight and standardized body measurements. Cougars were fitted with either a Very High Frequency (VHF; Telonics, Mesa, AZ) or Global Positioning System collar (GPS; Telonics, Mesa, AZ, Televilt, Bandygatan, Sweden, Vectronics, Berlin, Germany). GPS collars were programmed to acquire loca-

Table 1. Hypotheses, specific predictions we tested in our study of home range overlap in cougars in the Southern Yellowstone Ecosystem, references and whether or not we found support in our results

Hypothesis	Prediction	References	Support
Land tenure	Cougar sex would explain home range overlap. Highest overlap would be between males and females	Seidensticker <i>et al.</i> (1973), Logan & Sweanor (2001) and Lendrum <i>et al.</i> (2014)	Yes
Kinship	Because of matrilineal lineages, related females would overlap more than un-related females. Male–male overlap would be between unrelated males	Sweanor, Logan & Hornocker (2000), Logan & Sweanor (2001) and Laundré & Hernandez (2003)	No/Yes
Resource dispersion	Hunting opportunities would be higher in areas of home range overlap. Because of winter prey aggregations, winter hunting opportunities would be higher than summer hunting opportunities in areas where cougar home ranges overlapped	Maher & Lott (2000) and Elbroch <i>et al.</i> (2013)	Yes

tion data between 4 and 8 times per day. All collars were equipped with mortality sensors that activated after 8 h of inactivity. Our capture protocols followed those outlined in Quigley (2000), adhered to the guidelines outlined by the American Society of Mammalogists (Sikes & Gannon 2011), and were approved by the Jackson Institutional Animal Care and Use Committee (Protocol 027-10EGDBS-060210).

GENETIC METHODS TO DETERMINE RELATEDNESS

Blood and tissue samples were collected during cougar captures. DNA was extracted, and 21 cougar-specific microsatellite loci were amplified and analysed using primers developed by Kurushima *et al.* (2006). Detailed laboratory methods were described in Elbroch, Quigley & Caragiulo (2014). CERVUS software determined the polymorphic information content (PIC) of each locus. A high PIC value indicated sufficient allelic variation to inform whether the locus was useful for distinguishing among individuals in the population (Botstein *et al.* 1980; Kalinowski 2005).

Relatedness (r) among all individuals was calculated using both ML-RELATE (Kalinowski, Wagner & Taper 2006) and MARK v 3.1 (Ritland 1996b; Ritland & Travis 2004) and described on a scale of 0 to 1 : 0 representing completely unrelated individuals, 0.15 a typical half-sibling relation, 0.5 a typical parent–offspring relation, 0.75 a typical full sibling relation and 1.0 representing

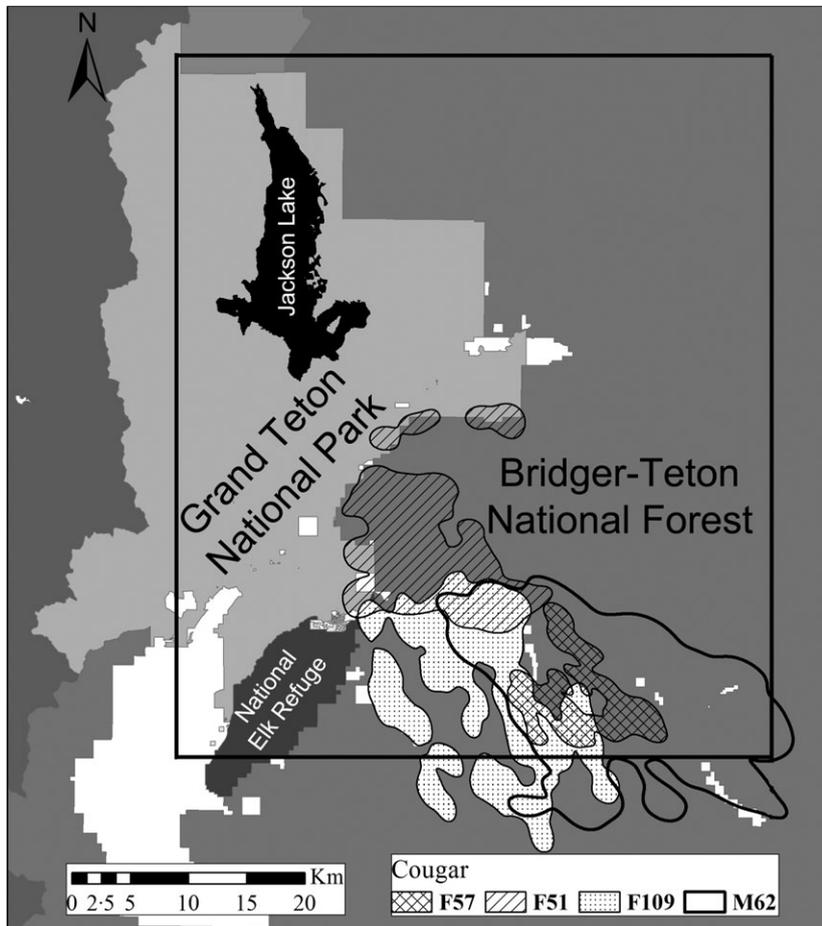


Fig. 1. Location of the study area in northwest Wyoming, USA, and a close up including land ownership/management. The smaller rectangle delineated by a black line was the area in which we focused cougar capture efforts and our home range overlap study between individuals wearing GPS collars. We included 95% KDE home ranges for four cougars, one male and three females, to illustrate the size of male vs. female home ranges and overlaps between the various dyads. As our study system is a hunted population, we selected deceased cougars to illustrate, so as not to reveal their whereabouts.

an individual's complete relatedness to itself. ML-RELATE calculated maximum likelihood estimates of relatedness and relationships by simulating which relationships were consistent with genotype data and comparing putative relationships with alternatives (Kalinowski, Wagner & Taper 2006). MARK estimated pairwise relatedness using four methods to allow for the best model to be chosen for the data (Queller & Goodnight 1989; Ritland 1996b; Lynch & Ritland 1999; Wang & Whitlock 2003). The Ritland (1996a) methodology best fit the data, and relatedness outputs from both ML-RELATE and MARK were checked for corroboration.

HOME RANGE AND HOME RANGE OVERLAP CALCULATIONS

We calculated 50% ('core area') and 95% annual fixed-kernel home ranges for adult cougars marked with GPS technology and resident in the study area between 2005 and 2012. We decided not to include cougars marked with VHF technology in these analyses, because home ranges created from telemetry data proved more amorphous and 1.4–1.9 times larger than those created with GPS data (Lendrum *et al.* 2014); thus, the size of home range overlap determined with VHF data differed significantly from that determined with GPS data. Although removing home ranges derived from VHF data (primarily collected from 2001 to 2005) reduced our sample size and did remove several ranges of overlap during the years included in this analysis, it also greatly

reduced the noise associated with inaccurate home ranges that may have distorted our findings.

We quantified kernel density estimators (KDE, Worton 1989; Kie *et al.* 2010) and isopleths in the Geospatial Modeling Environment (GME, Beyer 2009–2012). Schuler *et al.* (2014) found that the relative bias in home range size determined with GPS data decreased below 5% at a minimum of 200 locations/animal for 95% contours. Our own exploratory analysis assessing the correlation between home range size and the number of GPS fixes revealed that variation in home range sizes stabilized with a minimum of 300–400 locations. Thus, we calculated annual home ranges for cougars fitted with GPS collars that acquired data spanning a minimum of 10 months and that collected a minimum of 350 different GPS locations. We calculated the smoothing factor (h) using the plug-in method (Loader 1999) in the GME.

Home range overlap between individual cougars was determined by overlaying the home ranges of each dyad, then subtracting the portion of overlap with the overlay tool in ArcGIS. We then calculated the area of the overlapping portion (km^2) and divided this by the total home range size of each individual to determine the per cent overlap for each dyad.

TESTING SUPPORT FOR THE LAND TENURE AND KINSHIP HYPOTHESES

We employed generalized linear models to test whether the type of dyad (female–female, female–male or male–male) or the relatedness

coefficient (r) of each cougar pairing explained variation in the amount of home range overlap between cougar dyads at both the 50 and 95% KDEs. First, we tested for the influence of dyad type on differences in mean home range overlap, and then, we tested for the effect of (r) on home range overlap in a series of separate tests within each dyad type with generalized linear mixed models (GLIMMIX; SAS 9.3, SAS Institute Inc., Cary, NC, USA). Cougar dyad was included as a random effect in all tests to account for sampling of some dyads across multiple years.

TESTING SUPPORT FOR THE RESOURCE DISPERSION HYPOTHESIS

Whereas habitat is commonly used as a proxy for resource richness (e.g. Johnson, Macdonald & Morecroft 2001), we estimated 'hunt opportunity' instead, which we defined mathematically as the probability that a cougar would kill prey in a given location as determined with resource selection analyses (RSF) of verified cougar kills (Elbroch *et al.* 2013; Lendrum *et al.* 2014). Hunting opportunity better captured spatiotemporal variation in prey distributions as well as some variation in prey vulnerability, to better reflect which prey were truly available to cougars.

We conducted site searches of areas where triangulation of cougars wearing VHF collars revealed that they had not moved for 24 + hours, or spatially aggregated GPS points indicated a cougar had remained in place for 8 + hours to record prey data for marked cougars (Elbroch *et al.* 2013). Prey remains, including hair, skin, rumen (stomach) and bone fragments, were used to identify prey species. We then identified 7 landscape variables as potentially important predictors of cougar kill sites: elevation (m), slope (%), aspect (transformed into categories of North, East, South, West), terrain ruggedness (vector ruggedness measure; VRM), vegetation type, distance to water and distance to edge habitat (details on data sources and specifics in preparing these data are found in Elbroch *et al.* 2013). Prior to modelling, we used a correlation matrix to evaluate collinearity ($|r| > 0.7$) among predictor variables. No predictor variables were correlated ($|r| < 0.50$), and therefore, all variables remained in the modelling process. We then modelled all possible combinations of the 7 predictor variables. For the categorical variable of aspect, we used southerly aspect as a reference category because southerly aspects are commonly used by prey species (Stewart *et al.* 2010).

We estimated RSFs for summer and winter separately; we employed conditional logistic regression (Boyce 2006) to compare kill sites with random locations, located 2 km from the kill site along each cardinal direction. Each cougar was considered a stratified variable to control for variation among individuals (i.e. individuals were sampling units), and the logistic model was made condition upon that variable (Long *et al.* 2009; Lendrum *et al.* 2012). We calculated Akaike's information criterion adjusted for small sample size (AIC_c), ΔAIC_c , and Akaike weights (w_i) for each model (Burnham & Anderson 2002). We considered models with ΔAIC_c values > 2.0 to measurably differ in information content and then used model-averaged parameter estimates and unconditional standard errors (SE) to assess the influence of each predictor variable on resource selection from the top models (Burnham & Anderson 2002). To evaluate predictive strength of the resource selection functions for kill sites for each season, we used k -fold cross-validation (Boyce *et al.* 2003). We partitioned kill sites into five equal sets, and models were fit to 80% partition of the data, while the remaining 20% of the data

were used as test data (Kauffman *et al.* 2007; Kunkel *et al.* 2013). We used RSF scores to rank the observed location of each stratum against the test data. We then regressed the number of locations from the observed data set in each bin against the median RSF value of the test data and recorded the coefficient of determination (r^2). Additionally, we calculated a Spearman's rank correlation (r_s) as an additional metric of predictive strength. Values with a high r^2 and r_s were indicative of models with high predictive strength (Boyce *et al.* 2003).

Based on our seasonal RSF results, and with respect to a reference vector, defined as the set of mean values for each variable within the domain of availability, we then calculated the relative probability of a cougar killing prey across the landscape in ArcGIS 10 (Kauffman *et al.* 2007; Kunkel *et al.* 2013). We converted parameter estimates to odds ratios by exponentiation for simplicity of interpretation. Therefore, if the 95% confidence interval around an odds ratio contained 1, then that variable was considered not significant (Kauffman *et al.* 2007; Lendrum *et al.* 2012). The resulting odds ratio expression for a given landscape location was then calculated using the spatial distribution of cougar kills to generate a probability surface that 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 a cougar killing prey in that location.

To quantify hunt opportunity within the overlapping and non-overlapping portions of home ranges, we assigned attributes of the hunting opportunity layer to random points assigned by the GME. Six hundred random points were allocated across each 95% KDE and 300 random points were allocated across each 50% KDE, which provided relatively full coverage across KDEs. We tested whether overlapping portions of cougar home ranges had higher 'hunting opportunity' than the portions of their home ranges that did not overlap other marked individuals. We assessed overlap for both 50 and 95% KDEs. In contrast to cougar dyads, the non-overlapping portion of the home range was defined as the portion of home range that did not overlap with any other marked cougar of the same sex as the dyad in question, that is non-overlap with any other female cougar in a F-F dyad. In some years, additional cougars were marked with VHF collars and there were also unmarked cougars in the area; thus, this protocol was our best effort to identify the portion of each cougar's home range that truly did not overlap with other cougars, with full knowledge that this would not always be the case.

Based on average percentage of overlap among M-F and F-F dyads, we scaled down our initial number of random points allocated in the KDE (M-M dyads were too few to analyse). Of the 600 random points in 95% KDEs, we assigned 300 random points in the overlapping portion of M-F dyads, but only 120 random points in the overlapping portions of F-F dyads; we based this upon mean overlap for each dyad type (see Results) and in the interest of maintaining an even distribution of points across entire KDEs. Of the 300 random points in 50% KDEs, we assigned 90 random points in the overlapping portion of M-F dyads, and 30 random points in the overlapping portions of F-F dyads. Then, we assigned the values for winter and summer hunt opportunities to all points and employed a generalized linear model with a binomial distribution and logit link function to determine whether mean hunt opportunity differed between overlapping and non-overlapping portions of cougar home ranges.

Results

COUGARS, GENETICS AND HOME RANGE OVERLAP

Between 2005 and 2012, we calculated 27 annual home ranges (20 female and seven male) for nine adult female cougars and four adult males marked with GPS collars (Table 2). We recorded 64 occurrences of home range overlap at the 95% KDE, and 48 at the 50% KDE (Table 3). Sixty-eight individuals were genotyped using the 21 cougar-specific microsatellite primer sets. The mean number of alleles per locus was 4.14 (ranged from 2 to 8), and the mean polymorphic information content was 0.48 (ranged from 0.112 to 0.694). The matrix of pairwise relatedness coefficients between individuals is presented in Appendix S1, in which we highlight the individuals included in our analyses of home range overlap.

TESTING SUPPORT FOR THE LAND TENURE AND KINSHIP HYPOTHESES

Home range overlap varied with dyad type (F–F, M–F, F–M and M–M) at the 95% KDE ($F_{3,25} = 9.30$, $P < 0.001$) and the 50% KDE ($F_{3,17} = 5.86$, $P < 0.001$; Table 3). The greatest overlaps were among F–M dyads, meaning the amount of female home ranges overlapped

Table 2. Individual cougars, sex, number of GPS locations gathered per year and the resulting 95% and 50% KDE home ranges calculated from the data

CatID_Year	Sex	No. Locations	95% KDE (km ²)	50% KDE (km ²)
F013_2005	F	910	587.6	105.7
F104_2005	F	1488	196.9	30.3
M101_2005	M	936	541.2	127.6
F018_2006	F	1077	93.1	15.3
F013_2007	F	1500	440.0	74.8
M070_2007	M	478	408.0	105.5
M101_2007	M	583	915.0	253.5
F057_2008	F	826	75.3	17.9
F101_2008	F	1593	241.9	43.2
M021_2008	M	530	830.9	148.3
M028_2008	M	1807	596.0	128.0
F013_2009	F	1500	136.7	37.4
F069_2009	F	926	456.7	95.0
F101_2009	F	970	202.6	38.5
F109_2009	F	825	130.9	34.4
M021_2009	M	547	670.7	104.3
F069_2010	F	979	381.4	82.6
F109_2010	F	830	138.5	24.6
F047_2011	F	1560	280.8	33.3
F051_2011	F	1308	78.5	11.7
F057_2011	F	863	67.1	13.3
F109_2011	F	1111	142.6	28.6
M062_2011	M	534	357.2	63.6
F051_2012	F	986	165.1	26.7
F061_2012	F	1550	86.6	18.3
F109_2012	F	1425	228.7	38.4
M062_2012	M	636	384.8	81.3

Table 3. Mean home range overlap (% of home range) among the different dyad types at both the 95% and 50% KDEs. The results of our post hoc Tukey's tests are represented by capital letters. Those that share the same letters were statistically equivalent. Note that our results for M–M dyads were based on a small sample and should be interpreted with caution. Female–male indicated the amount of a female's home range that was overlapped by a male's and the inverse for male–female

Dyads	n	Mean	SE	95% CI	
				Lower	Upper
GPS 95% KDE					
Female–female	30	18.8 ^A	3.48	11.7	25.9
Female–male	15	47.7 ^B	6.32	34.1	61.3
Male–female	15	18.8 ^A	3.38	11.6	26.1
Male–male	4	17.6 ^A	7.32	–5.7	40.8
GPS 50% KDE					
Female–female	18	9.6 ^A	3.14	3.6	15.6
Female–male	14	28.5 ^B	3.55	17.9	39.1
Male–female	14	10.9 ^A	3.55	6.1	15.8
Male–male	2	19.6 ^{AB}	9.41	–4.9	44.2

by males. Overlap between other dyads were less than F–M and statistically equivalent. (Table 3).

Genetic relatedness (r) among female and male cougars in the study area was low ($r = 0.09$, $r = 0.10$). Relatedness was not influential in explaining variation in F–F overlap at either the 95 ($F_{1,9} = 0.04$, $P = 0.85$) or 50% KDE ($F_{1,5} = 2.66$, $P = 0.16$), or in explaining variation in M–F overlap at either the 95 ($F_{1,14} = 0.38$, $P = 0.55$) or 50% KDE ($F_{1,10} = 2.42$, $P = 0.15$). There were two overlapping pairs of male home ranges for 95% KDEs, one between half-siblings ($r = 0.13$) and one between unrelated males ($r = 0.0$). Only the related males had overlapping home ranges at 50% KDE. The half-siblings overlapped 25 and 34% of their home ranges with one another, while the unrelated male cougars overlapped by 4 and 6%.

TESTING SUPPORT FOR THE RESOURCE DISPERSION HYPOTHESIS

We documented 239 prey killed by cougars in summer and 411 prey killed in winter to use in our resource selection function analyses. In winter, the relative probability that a hunting cougar would kill prey at a particular place on the landscape increased as (i) elevation decreased ($\beta = -0.005115$), (ii) distance to edge habitat decreased ($\beta = -0.00633$), (iii) distance to large bodies of water and rivers decreased ($\beta = -0.00069$) and (iv) steepness increased ($\beta = 0.09395$). (Table 4). During summer, cougars were more likely to make a kill in areas with (i) decreasing elevation ($\beta = -0.000865$), (ii) decreasing distance to edge habitat ($\beta = -0.00495$) and (iii) increasing distance from large bodies of water and rivers ($\beta = 0.000616$; Table 4). We used our model-averaged parameter estimates to map the probability surface of cougars successfully killing prey across the landscape

Table 4. Odds ratios for top ranked resource selection function model of seasonal kill sites by cougars. For categorical variables (aspect and habitat type), south aspects and sagebrush steppe were used as the reference category

Parameter	Winter			Summer		
	Point estimate	95% CI		Point estimate	95% CI	
		Lower	Upper		Lower	Upper
Elevation	0.995	0.994	0.996	0.999	0.998	1.000
Distance to edge	0.994	0.992	0.995	0.996	0.994	0.997
Distance to water	0.999	0.999	1.000	1.001	1.000	1.001
Slope	1.100	1.082	1.119			
North	0.622	0.412	0.939			
East	0.553	0.394	0.775			
West	0.757	0.566	1.013			
Meadow	0.473	0.287	0.779			
Barren	n/a	n/a	n/a			
Forested	0.909	0.694	1.191			
Riparian	0.764	0.450	1.298			

(Fig. 2). Further details about these results are found in Elbroch *et al.* (2013).

Winter hunt opportunity was significantly higher in overlapping portions than in non-overlapping portions of F–F 95% KDE home ranges ($F_{1,3597} = 26.99$, $P < 0.001$), but there was no difference in winter hunt opportunity between overlapping and non-overlapping portions in 50% KDEs ($F_{1,1647} = 0.20$, $P = 0.65$, Fig. 3). Summer hunt opportunity, in contrast, was not different between areas of home range overlap and non-overlapping portions of female home ranges at either the 95% KDE ($F_{1,3597} = 2.69$, $P = 0.10$) or 50% KDE ($F_{1,1647} = 0.01$, $P = 0.94$).

Winter hunt opportunity was also significantly higher in the overlapping portions than in non-overlapping portions of both M–F 95% KDE ($F_{1,5397} = 111.91$, $P < 0.001$) and 50% KDE home ranges ($F_{1,2337} = 41.01$, $P < 0.001$) (Fig. 3). Summer hunt opportunity, however, was not significantly higher in the overlapping portions than in non-overlapping portions of M–F 95% KDE home ranges ($F_{1,5397} = 2.30$, $P = 0.13$); summer hunt opportunity values were equivalent in overlapping and

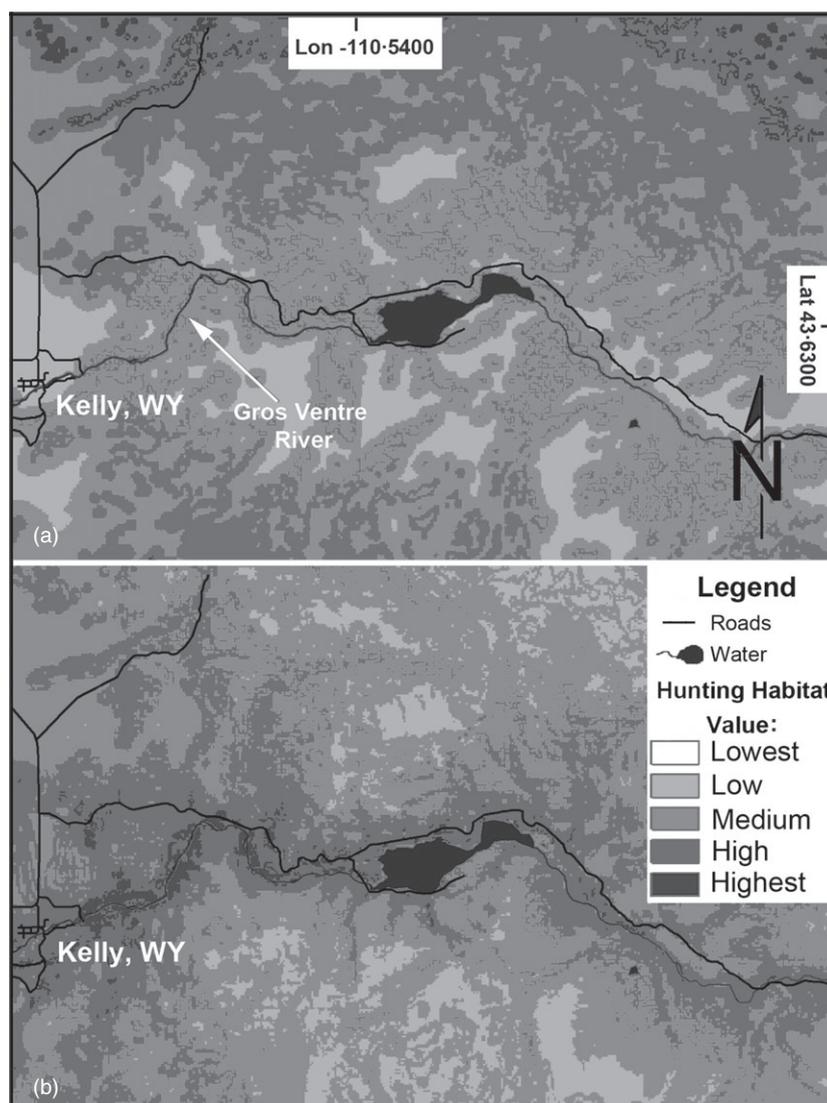


Fig. 2. Seasonal hunting opportunity for cougars. A comparison between summer (a) and winter (b) hunting opportunity for the same section of the study area based upon outputs from our resource selection function analyses. Note the position of the Gros Ventre River, which we highlighted to emphasize the influence of 'distance to water' in different seasonal hunting opportunity.

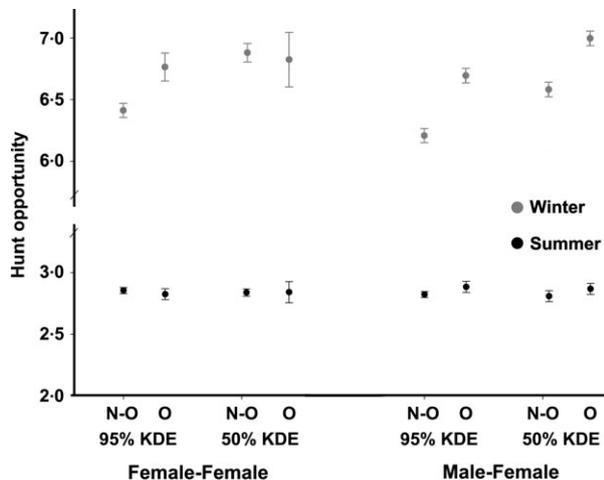


Fig. 3. Differences in winter and summer hunt opportunity in overlapping and non-overlapping portions of F-F and M-F 95% and 50% KDE home ranges.

non-overlapping portions of 50% KDE home ranges ($F_{1,2337} = 0.01$, $P = 0.93$) (Fig. 3).

Discussion

Our results from the SYE suggested that home range overlap in a solitary carnivore was best explained by both the land tenure and resource dispersion hypotheses. This supports earlier work (e.g. Maher & Lott 2000) that proposed these two hypotheses were not necessarily competitors, but complementary in explaining the distributions of carnivores in natural systems. In support for the land-tenure hypothesis, cougar sex was the primary driver explaining variation in home range overlap. Males overlapped significantly with females, as is predicted for territorial species in which males wander larger territories in which females are defensible resources (Caro 1989; Logan & Sweanor 2001). In contrast, females overlapped much less with each other, as also is expected for female solitary carnivores defending territories with sufficient resources to maintain themselves, their dependent young and only fractions of their additional male users (Carr & Macdonald 1986; Logan & Sweanor 2010).

We did not find support for the kinship hypothesis or that more closely related female cougars overlapped more in space than unrelated individuals. This was unexpected given that past research indicated that up to 50% of subadult female cougars establish adult home ranges in or adjacent their natal areas (Sweanor, Logan & Hornocker 2000). In fact, our long-term study following family lineages over time did record several cougar matrilineal lines in the study system, but we also recorded females that immigrated into the study area from elsewhere and then became resident (Elbroch, Quigley & Caragiulo 2014). Nicholson, Krausman & Munguia-Vega (2011) did not find evidence that genetic relatedness explained home range overlap in cougars as well. Our findings could serve to strengthen arguments that relatedness fails to influence

the spatial organization of individuals in carnivore populations (Schenk, Obbard & Kovacs 1998; Nicholson, Krausman & Munguia-Vega 2011), or alternatively, our results may have been biased by pressures of human hunting, which is permissible within our study area. Beausoleil *et al.* (2013) report that territorial boundaries are diminished in hunted cougar populations, and Stoner *et al.* (2013) showed that hunted populations see an increase in female immigration, undermining matrilineal lineages expected in natural cougar populations.

In support for the resource dispersion hypothesis, we found that hunting opportunity in winter was often higher in areas of home range overlap than in non-overlapping portions of cougar home ranges. Our findings also support suppositions made by Pierce, Vernon & Bowyer (2000) that cougars may overlap more where migratory prey are aggregated. Research has shown that female cougars select home ranges with sufficient prey availability (Lendrum *et al.* 2014), and thus, it was not surprising that the areas of male home ranges that overlapped with females would yield higher hunting opportunity than the areas males travelled in between females; this would also support the land-tenure hypothesis. However, areas of female–female overlap also yielded higher hunt opportunity than the remainder of their home ranges, but again, only in winter, and only at the 95% KDE.

McLoughlin, Ferguson & Messier (2000) and Maher & Lott (2000) predicted that carnivore territoriality may diminish when resources are high, and in many northern ecosystems, ungulate prey are migratory and aggregate in lower elevations in winter, increasing their densities over smaller ranges (Sawyer, Lindzey & McWhirter 2005; Smith 2007). This fact is exacerbated in the SYE by supplemental winter feeding of elk, which subsidizes elk numbers and increases their density at smaller spatial scales (Smith 2007). The winter diet of SYE cougars is also dominated by elk (Elbroch *et al.* 2013), large prey sufficient to support the formation of temporary feeding groups (Hornocker 1969); large prey and food patches have been shown to support temporary feeding groups in diverse carnivore species (e.g. spotted hyenas, *Crocuta crocuta*, Kruuk 1972, kinkajous, *Potos flavus*, Kays and Gittleman 2001, jaguars, Guilder *et al.* 2015). Our results also supported the predictions by Elbroch, Quigley & Caragiulo (2014) that cougar spatial associations in winter in the Northern Rocky Mountains, USA, may be explained by both courtship behaviours and winter prey distributions.

In conclusion, we found support for both land tenure and resource dispersion influencing the spatial organization of a large, solitary carnivore. The territoriality exhibited by males defending females and females defending food resources, common among carnivores, was evident in the overall spatial organization of cougars in the SYE; human hunting or other variables, however, may be undermining spatial patterns predicted by the kinship hypothesis, as may be typical of natural cougar popula-

tions and other solitary carnivores. In addition, increased resource density over smaller spatial extents in winter appeared to explain spatial overlap between cougars, especially between adult females. The fact that kinship neither explained patterns of spatial overlap reported here, nor spatial associations in Elbroch, Quigley & Caragiulo (2014), may indicate that cougars and other solitary carnivores may be more tolerant of sharing key resources with unrelated conspecifics than previously believed, or at least during periods of high resource availability. Associations and spatial overlap between unrelated carnivores in areas and at times when prey are aggregated provide strong support for the application of the resource dispersion hypothesis to solitary carnivores.

Acknowledgements

We thank our collaborators, including K. Murphy (Bridger-Teton NF), S. Cain (Grand Teton NP), T. Fuchs (WY Game and Fish) and E. Cole (National Elk Refuge) and our supportive funders, the Summerlee Foundation, The Richard King Mellon Foundation, The Charles Engelhard Foundation, National Geographic Society, The Norcross Wildlife Foundation, Inc., Earth Friends Conservation Fund, The Bay Foundation, Michael Cline Foundation, Eugene V. & Clare E. Thaw Charitable Trust, Connemara Fund, Hogan Films, Community Foundation of Jackson Hole, The Oregon Zoo Foundation, Mr. and Mrs. L. Folger, Mr. and Mrs. G. Ordway, Mr. and Mrs. N. Jannotta, Mr. L. Westbrook, Mr. and Mrs. S. Robertson and several anonymous foundation and individual donors. Thank you also to J.M. Gaillard, Editor, our Associate Editor, and two anonymous reviewers for critical feedback that strengthened and refined our manuscript.

Data accessibility

Cougar location data with which we created home ranges and measured home range overlap are archived with Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.vf85j> (Elbroch *et al.* 2015).

References

Beausoleil, R.A., Koehler, G.M., Maletzke, B.T., Kertson, B.N. & Wielgus, R.B. (2013) Research to regulation: Cougar social behavior as a guide for management. *Wildlife Society Bulletin*, **37**, 680–688.

Beyer, H.L. (2009–2012) Geospatial Modelling Environment (Version 0.7.2.1) (software) <http://www.spatial-ecology.com/gme/>.

Blaustein, A.R. & Waldman, B. (1992) Kin recognition in anuran amphibians. *Animal Behaviour*, **44**, 207–221.

Botstein, D., White, R., Skolnick, M. & Davis, R. (1980) Construction of a genetic linkage map in man using restriction fragment length polymorphisms. *American Journal of Human Genetics*, **32**, 314–331.

Boyce, M.S. (2006) Scale for resource selection functions. *Diversity and Distributions*, **12**, 269–276.

Boyce, M.S., Mao, J.S., Merrill, E.H., Fortin, D., Turner, M.G., Fryxell, J. *et al.* (2003) Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience*, **10**, 421–431.

Brown, G.E. & Brown, J.A. (1993) Do kin always make better neighbours?: the effects of territory quality. *Behavioral Ecology and Sociobiology*, **33**, 225–231.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information Theoretic Approach*, 2nd edn. Springer-Verlag, Berlin, Germany.

Burt, W.H. (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, **24**, 346–352.

Caro, T.M. (1989) Determinants of asociality in felids. *Comparative Socioecology: the Behavioral Ecology of Humans and Other Mammals* (eds V. Staden & R.A. Foley), pp. 41–74. Blackwell Press, Oxford, UK.

Carr, G.M. & Macdonald, D.W. (1986) The sociality of solitary foragers: a model based on resource dispersion. *Animal Behaviour*, **34**, 1540–1549.

Diefenbach, D.R., Hansen, L.A., Warren, R.J. & Conroy, M.J. (2006) Spatial organization of a reintroduced population of bobcats. *Journal of Mammalogy*, **87**, 394–401.

Elbroch, L.M., Quigley, H. & Caragiulo, A. (2014) Spatial associations in a solitary predator: using genetic tools and GPS technology to assess cougar social organization in the Southern Yellowstone Ecosystem. *Acta Ethologica*, **18**, 127–136.

Elbroch, L.M. & Wittmer, H.U. (2012) Puma spatial ecology in open habitats with aggregate prey. *Mammalian Biology*, **77**, 377–384.

Elbroch, L.M., Lendrum, P.E., Newby, J., Quigley, H. & Craighead, D. (2013) Seasonal foraging ecology of non-migratory cougars in a system with migrating prey. *PLoS One*, **8**, e83375.

Elbroch, L.M., Lendrum, P., Quigley, H. & Caragiulo, A. (2015) Data from: Spatial overlap in a solitary carnivore: support for the land-tenure, kinship, or resource dispersion hypotheses? *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.vf85j>.

Emlen, S.T. & Oring, L.W. (1977) Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.

Ferreras, P., Beltrán, J.F., Aldama, J.J. & Delibes, M. (1997) Spatial organization and land tenure system of the endangered Iberian lynx (*Lynx pardinus*, Temminck, 1824). *Journal of Zoology*, **243**, 163–189.

Griffiths, S.W. & Armstrong, J.D. (2001) The benefits of genetic diversity outweigh those of kin association in a territorial animal. *Proceedings of the Royal Society of London B*, **268**, 1293–1296.

Grigione, M.M., Beier, P., Hopkins, R.A., Neal, D., Padley, W.D., Schenewald, C.M. *et al.* (2002) Ecological and allometric determinants of home-range size for mountain lions (*Puma concolor*). *Animal Conservation*, **5**, 317–324.

Guilder, J., Barca, B., Arroyo-Arce, S., Gramajo, R. & Salom-Pérez, R. (2015) Jaguars increase kill utilization rates and share prey in response to seasonal fluctuations in nesting green turtle abundance in Tortuguero National Park, Costa Rica. *Mammalian Biology*, **80**, 65–72.

Hamilton, W.D. (1964) The genetical evolution of social behavior. *Journal of Theoretical Biology*, **7**, 1–52.

Heffelfinger, J. (2010) Age criteria for Southwestern game animals. Special Report #19. Arizona Game and Fish Department.

Hemker, T.P., Lindzey, F.G. & Ackerman, B.B. (1984) Population characteristics and movement patterns of cougars in southern Utah. *Journal of Wildlife Management*, **48**, 1275–1284.

Hornocker, M.G. (1969) Winter territoriality in mountain lions. *Journal of Wildlife Management*, **33**, 457–464.

Hornocker, M.G. (1970) An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. *Wildlife Monographs*, **21**, 1–39.

Innes, R.J., McEachern, M.B., Van Vuren, D.H., Eadie, J.M., Kelt, D.A. & Johnson, M.L. (2012) Genetic relatedness and spatial associations of dusky-footed woodrats (*Neotoma fuscipes*). *Journal of Mammalogy*, **93**, 439–446.

Johnson, D.D.P., Macdonald, D.W. & Morecroft, M.D. (2001) An analysis of social spacing in the European badger (*Meles meles*) in the UK. *Wiss Mitt Niederoö Sterr Landesmuseum*, **14**, 161–170.

Johnson, D.D.P., Macdonald, D.W., Newman, C. & Morecroft, M.D. (2001) Group size versus territory size in group-living badgers: a large-sample field test of the Resource Dispersion Hypothesis. *Oikos*, **95**, 265–274.

Johnson, D.D.P., Kays, R., Blackwell, P.G. & Macdonald, D.W. (2002) Does the resource dispersion hypothesis explain group living? *Trends in Ecology & Evolution*, **17**, 563–570.

Kalinowski, S.T. (2005) Do polymorphic loci require large sample sizes to estimate genetic distances? *Heredity*, **94**, 33–36.

Kalinowski, S., Wagner, A.P. & Taper, M. (2006) ML-RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. *Molecular Ecology Notes*, **6**, 576–579.

Kauffman, M.J., Varley, N., Smith, D.W., Stahler, D.R., MacNulty, D.R. & Boyce, M.S. (2007) Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters*, **10**, 690–700.

Kays, R. & Gittleman, J. (2001) The social organization of the kinkajou *Potos flavus* (Procyonidae). *Journal of Zoology*, **253**, 491–504.

Kie, J.G., Matthiopoulos, J., Fieberg, J., Powell, R.A., Cagnacci, F., Mitchell, M.S. *et al.* (2010) The home-range concept: are traditional

- estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society B*, **365**, 2221–2231.
- Kleiman, D.G. & Eisenberg, J.F. (1973) Comparisons of canid and felid social systems from an evolutionary perspective. *Animal Behaviour*, **21**, 637–659.
- Kruuk, H. (1972) *The Spotted Hyena*. University of Chicago Press, Chicago, IL, USA.
- Kunkel, K.E., Ruth, T.K., Atwood, T.C., Pletscher, D.H. & Hornocker, M.G. (2013) Assessing wolves and cougars as conservation surrogates. *Animal Conservation*, **16**, 32–40.
- Kurushima, J.D., Collins, J.A., Well, J.A. & Ernest, H.B. (2006) Development of 21 microsatellite loci for puma (*Puma concolor*) ecology and forensics. *Molecular Ecology Notes*, **6**, 1260–1262.
- Laundré, J.W. & Hernandez, L. (2003) Factors affecting dispersal in young male pumas. *Seventh Mountain Lion Workshop*, (eds D.D. Becker, F.G. Lindzey & D.S. Moody), pp. 151–160. Wyoming Game and Fish Department, Jackson, WY, USA.
- Laundré, J.W., Hernández, L., Streubel, D., Altendorf, K. & González, C.L. (2000) Aging mountain lions using gum-line recession. *Wildlife Society Bulletin*, **28**, 963–966.
- Lendrum, P.E., Anderson, C.R., Long, R.A., Kie, J.G. & Bowyer, R.T. (2012) Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development. *Ecosphere*, **3**, art82.
- Lendrum, P.E., Elbroch, M., Quigley, H., Thompson, D.J., Jimenez, M. & Craighead, D. (2014) Home range characteristics of a subordinate predator: selection for refugia or hunt opportunity? *Journal of Zoology*, **294**, 59–67.
- Loader, C.R. (1999) Bandwidth selection: classical or plug-in? *Annals Statistics*, **27**, 415–438.
- Logan, K.A. & Sweanor, L.L. (2001) *Desert Puma: Evolutionary Ecology and Conservation of an Enduring Carnivore*. Island Press, Washington, DC, USA.
- Logan, K.A. & Sweanor, L.L. (2010) Behavior and social organization of a solitary carnivore. *Cougar: Ecology and Conservation*, (eds M. Hornocker & S. Negri), pp. 105–117. University of Chicago Press, Chicago, IL, USA.
- Long, R.A., Kie, J.G., Bowyer, R.T. & Hurley, M.A. (2009) Resource selection and movements by female mule deer: effects of reproductive stage. *Wildlife Biology*, **15**, 288–298.
- Lopez-Bao, J.V., Rodriguez, A. & Ales, E. (2008) Field observation of two males following a female in the Iberian lynx during the mating season. *Mammalian Biology*, **73**, 404–406.
- Lynch, M. & Ritland, K. (1999) Estimation of pairwise relatedness with molecular markers. *Genetics*, **152**, 1753–1766.
- Macdonald, D.W. (1983) The ecology of carnivore social behavior. *Nature*, **301**, 379–384.
- Maher, C.R. & Lott, D.F. (2000) A review of ecological determinants of territoriality within vertebrate species. *American Midland Naturalist*, **143**, 1–29.
- Mattisson, J., Segerström, P., Persson, J., Aronsson, M., Rune, G., Same-lius, G. et al. (2013) Lethal male-male interactions in Eurasian lynx. *Mammalian Biology*, **78**, 304–308.
- McLoughlin, P.D., Ferguson, S.H. & Messier, F. (2000) Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evolutionary Ecology*, **14**, 39–60.
- Nicholson, K.L., Krausman, P.R. & Munguia-Vega, A. (2011) Spatial and temporal interactions of sympatric mountain lions in Arizona. *European Journal of Wildlife Research*, **57**, 1151–1163.
- Packer, C. (1986) The ecology of sociality in felids. *Ecological Aspects of Social Evolution* (eds D.I. Rubenstein & R.W. Wrangham), pp. 429–451. Princeton University Press, Princeton, NJ, USA.
- Paetkau, D., Waits, L.P., Clarkson, P.L., Craighead, L., Vyse, E., Ward, R. et al. (1998) Variation in genetic diversity across the range of North American brown bears. *Conservation Biology*, **12**, 418–429.
- Pierce, B.M., Vernon, C.B. & Bowyer, R.T. (2000) Social organization of mountain lions: does a land-tenure system regulate population size? *Ecology*, **81**, 1533–1543.
- Quaglietta, L., Fonseca, V.C., Mira, A. & Boitani, L. (2014) Sociospatial organization of a solitary carnivore, the Eurasian otter (*Lutra lutra*). *Journal of Mammalogy*, **95**, 140–150.
- Queller, D.C. & Goodnight, K.F. (1989) Estimating relatedness using genetic markers. *Evolution*, **43**, 258–275.
- Quigley, K. (2000) *Immobilization and Biological Sampling Protocols*. Hornocker Wildlife Institute/Wildlife Conservation Society, Moscow, ID, USA.
- Ritland, K. (1996a) Estimators for pairwise relatedness and individual inbreeding coefficients. *Genetics Research*, **67**, 175–185.
- Ritland, K. (1996b) A marker-based method for inferences about quantitative inheritance in natural populations. *Evolution*, **50**, 1062–1073.
- Ritland, K. & Travis, S. (2004) Inferences involving individual coefficients of relatedness and inbreeding in natural populations of *Abies*. *Forest Ecology and Management*, **197**, 171–180.
- Ross, P.I. & Jalkotzy, M.G. (1992) Characteristics of a hunted population of cougars in southwestern Alberta. *Journal of Wildlife Management*, **56**, 417–426.
- Sandell, M. (1989) The mating tactics and spacing patterns of solitary carnivores. *Carnivore Behavior, Ecology, and Evolution* (ed J.L. Gittleman), pp. 164–182. Cornell University Press, Ithaca, NY, USA.
- Sawyer, H., Lindzey, F. & McWhirter, D. (2005) Mule deer and pronghorn migration in western Wyoming. *Wildlife Society Bulletin*, **33**, 1266–1273.
- Schaller, G.B. (1967) *The Deer and the Tiger: A Study of Wildlife in India*. University of Chicago Press, Chicago, IL, USA.
- Schaller, G.B. (1972) *The Serengeti Lion: A Study of Predator–Prey Relations*. University of Chicago Press, Chicago, IL, USA.
- Schenk, A., Obbard, M.E. & Kovacs, K.M. (1998) Genetic relatedness and home-range overlap among female black bears (*Ursus americanus*) in northern Ontario, Canada. *Canadian Journal of Zoology*, **76**, 1511–1519.
- Schmidt, K., Jedrzejewski, W. & Okarma, H. (1997) Spatial organization and social relations in the Eurasian lynx population in Bialowieza Primeval Forest. *Acta Theriologica*, **42**, 289–312.
- Schuler, K.L., Schroeder, G.M., Jenks, J.A. & Kie, J.G. (2014) Ad hoc smoothing parameter performance in kernel estimates of GPS-derived home ranges. *Wildlife Biology*, **20**, 259–266.
- Seidensticker, J.C.J., Hornocker, M.G., Wiles, W.V. & Messick, J.P. (1973) Mountain lion social organization in the Idaho primitive area. *Wildlife Monographs*, **35**, 1–60.
- Sikes, R.S., Gannon, W.L. & the Animal Care and Use Committee of the American Society of Mammalogists (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, **92**, 235–253.
- Smith, B.L. (2007) Migratory behavior of hunted elk. *Northwest Science*, **81**, 251–264.
- Stewart, K.M., Bowyer, R.T., Kie, J.G. & Hurley, M.A. (2010) Spatial distributions of mule deer and North American elk: resource partitioning in a sage-steppe environment. *American Midland Naturalist*, **163**, 400–412.
- Stoner, D.C., Wolfe, M.L., Rieth, W.R., Bunnell, K.D., Durham, S.L. & Stoner, L.L. (2013) De facto refugia, ecological traps and the biogeography of anthropogenic cougar mortality in Utah. *Diversity and Distributions*, **19**, 1114–1124.
- Sunquist, M. & Sunquist, F. (2002) *Wild Cats of the World*. University of Chicago Press, Chicago, IL, USA.
- Sweanor, L.L., Logan, K.A. & Hornocker, M.G. (2000) Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology*, **14**, 798–808.
- Vanak, A.T., Fortin, D., Thaker, M., Ogen, M., Owen, C., Greatwood, S. et al. (2013) Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology*, **94**, 2619–2631.
- Wagner, A.P., Frank, L.G. & Creel, S. (2008) Spatial grouping in behaviourally solitary striped hyenas. *Animal Behaviour*, **75**, 1131–1142.
- Wang, J. & Whitlock, M. (2003) Estimating effective population size and migration rates from genetic samples over space and time. *Genetics*, **163**, 429–446.
- Worton, B.J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**, 164–168.

Received 11 October 2014; accepted 5 September 2015
Handling Editor: Anne Loison

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Relatedness (r) for puma dyads. Those included in our analyses of overlap are highlighted.