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Assessing wolves and cougars as conservation surrogates

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Abstract

Large carnivores have been posited as potential conservation surrogates to inform the design and prioritization of conservation planning. We show that wolves *Canis lupus* and cougars *Puma concolor* may have potential to serve as a surrogate suite for conserving landscape heterogeneity, hypothesized to be a determinant of biodiversity in some landscapes. We examined habitat and landscape features associated with the spatial distribution of wolf- and cougar-killed prey in the basin of the North Fork of the Flathead River in Montana. The spatial distribution of wolf-killed prey was driven largely by cover type, whereas physiographic characteristics were the primary driver of the distribution of cougar-killed prey. Spatial templates, generated using >0.66 probability quantiles from spatially explicit models of kill site distribution, estimated over three times as much high-quality habitat for wolves (1005 km²) than for cougars (381 km²). While there were only minor differences in the proportional representation of land cover types between the wolf and cougar templates, 40% of the cougar template fell outside the wolf template, and the former contained over three times more rugged terrain than the latter. The use of a combined wolf–cougar spatial template resulted in a 15% increase in total area and 91% increase in the amount of rugged terrain identified. Based on our models, the advantage of using both wolves and cougars as a focal suite in north-west Montana is the ability to identify a greater area of high-quality habitat, and capture landscape heterogeneity that may be important to conserving biodiversity.

Introduction

Conservation professionals continue to search for species that can be used to direct the design and prioritization of planning efforts. These species, often referred to as conservation surrogates, can potentially be employed to locate areas of high species richness (Ricketts *et al.*, 1999; Niemi & McDonald, 2004; Woodroffe & Ginsberg, 2005), track changes in population distribution and abundance (McKenzie, Hyatt & McDonald, 1992) or, in the case of protected animals with large spatial requirements, act as ‘umbrellas’ by providing protected space for smaller sympatric species (Wilcox, 1984). One approach to selecting surrogates has been to identify keystone species (Power *et al.*, 1996) whose impacts on the ecosystem are large relative to their abundance. Some large carnivores can be classified as keystone species (McLaren & Peterson, 1994; Kunkel, 2003; Ripple & Beschta, 2004) and may be ideal to employ as focal species when identifying areas to conserve spatial heterogeneity (e.g. environmental gradients) and thus biodiversity (Huston, 1994).

Wolves *Canis lupus* and cougars *Puma concolor* have the potential to be keystone species through reciprocal

predator–prey effects that reduce prey abundance and thereby release plants from excessive herbivory (Beschta & Ripple, 2009). These carnivores are also hypothesized to serve as focal species for conservation planning primarily because of their large area requirements (Terborgh *et al.*, 1999; Carroll, Noss & Paquet, 2001). However, beyond their potential to initiate trophic cascades and use large areas, little evidence exist for their value as conservation surrogates (Noss *et al.*, 1996; Caro & O’Doherty, 1999; but see McLaren & Peterson, 1994). Indeed, recent work on wolves indicates that their potential to serve as a surrogate may be limited because they are capable of persisting in functionally degraded (e.g. fragmented) landscapes as long as human-caused mortality is low and ample prey exists (Whittington, St. Clair & Mercer, 2005; Hebblewhite & Merrill, 2008).

To overcome habitat-based discrepancies between surrogates and species of conservation concern, Carroll *et al.* (2001) recommended the selection of multiple focal species based upon differences along axes of habitat association and topographic tolerance (i.e. ruggedness). In effect, these axes represent a way to describe how sympatric species may partition space, and provide a useful construct for assessing the suitability of potential surrogates for conserving landscape

heterogeneity. For example, Kunkel & Pletscher (2001) found that wolves focused their activity in areas where resources for prey were greatest and prey were most abundant. By contrast, Hopcraft *et al.* (2005) observed that African lions *Panthera leo* were often located in areas where prey were easiest to catch (i.e. where landscape attributes facilitated ambushing prey). These differences suggest that processes mediating the spatial distribution of kills from coursing and ambush predators can be dependent on the resolution of scale. Both may have similar area and cover type requirements, but ambush predators may select hunting habitat at a finer grain than coursing predators, where increased structural complexity or ruggedness facilitates ambush (Atwood, Gese & Kunkel, 2009; Cresswell, Lind & Quinn, 2010). A species suite that displays divergence in how landscape attributes affect the spatial distribution of kills may have the potential to function as a conservation surrogate by maximizing spatial heterogeneity in prospective protected areas.

We hypothesized that wolves and cougars may be good candidates for a focal suite by expanding the breadth of surrogate value in terms of divergence in habitat associations or topographic tolerance. We examined the spatial distribution of wolf- and cougar-killed prey in and near Glacier National Park, Montana, USA, from 1985 through 1996, to assess the potential for using the two species as surrogates for identifying and conserving landscape heterogeneity. Based on the framework of Carroll *et al.* (2001), we examined whether the use of two, rather than one species resulted in a measurable increase in potential protected area and landscape heterogeneity. Accordingly, we evaluated landscape-scale (e.g. cover type, aspect, ruggedness) habitat attributes to determine how they were associated with the distribution of predator kills. Next, we developed spatially explicit models of kill site locations to quantify and compare landscape attributes and composition of potential suitable areas. Our work may help provide valuable information for decisions regarding conservation planning at a regional scale.

Materials and methods

Study area

The 3000-km² study area was a mosaic of public (including Glacier National Park) and private property in the basin of the North Fork of the Flathead River, Montana, USA. Climate was transitional between northern Pacific coastal and continental types. Temperatures ranged from -9°C in January to 16°C in July (Singer, 1979). Snow normally covered the area from mid-November to mid-April, and averaged 65 cm (Singer, 1979). Lodgepole pine *Pinus contorta* dominated most of the valley, but sub-alpine fir *Abies lasiocarpa*, spruce *Picea* spp., western larch *Larix occidentalis* and Douglas-fir *Pseudotsuga menziesii* were present, as were meadow and riparian areas. Wolf and cougar (winter density of adult cougars) densities were estimated at 12 wolves per 1000 km² and 17 cougars per 1000 km², respec-

tively (Pletscher *et al.*, 1997). White-tailed deer *Odocoileus virginianus* and elk *Cervus elaphus* were the predominant prey species for wolves; white-tailed deer were the primary prey species for cougars (e.g. Bureau, 1992; Rachael, 1992; Pletscher *et al.*, 1997; Kunkel & Pletscher, 1999). Moose *Alces alces* and mule deer *O. hemionus* were also preyed on by wolves and cougars, but historically have comprised < 7% of kills detected (e.g. Boyd *et al.*, 1994; Kunkel *et al.*, 1999), since wolf colonization.

Capture and handling

From 1985 to 1996, we captured wolves using foothold traps, immobilized them with 4 mg kg⁻¹ of tiletamine HCl and zolazepam HCl, and placed very high-frequency (VHF) radio collars on adults (Ream *et al.*, 1991). We captured cougars using hounds, immobilized treed individuals with 8.4 mg kg⁻¹ of ketamine hydrochloride and 0.47 mg kg⁻¹ xylazine hydrochloride, and placed VHF radio collars on adults (Hornocker & Wiles, 1972). From 1993 to 1995, we captured white-tailed deer *O. virginianus* using Clover traps (Clover, 1956) and fitted adult females with VHF radiocollars containing mortality sensors. We located radiocollared predators from the ground or air > 4 times per week during winter (November to April), and located kill sites by snow-tracking. We monitored radio-collared deer for mortalities two to three times per week during fall and winter. When mortalities occurred, we investigated the site and the remains to determine cause of death (Kunkel, 1997). Animal capture and handling protocols were approved by the University of Montana's Animal Care and Use Committee: IACUC #A3327-01.

Resource selection modeling

We used a Geographic Information System (GIS) with a 30-m grid cell resolution (USGS Seamless Server national elevation and land cover data) to determine slope, aspect, elevation, land cover type, and distance from road and water features for predator kill and random locations. We used Landsat 5 thematic mapper and Landsat 7 enhanced thematic mapper (Landsat.org, Global Observatory for Ecosystem Services, Lansing, MI, USA) imagery from the end of each winter (April) to create normalized difference vegetation index (NDVI) surfaces for 1990–1996. For each kill, we chose 20 random locations, selected from circular buffers centered on kill sites with radii (i.e. 1.12 km) equal to the 95% movement distance between consecutive daily locations (Johnson *et al.*, 2006), to represent resource availability. Kill site location and availability were related to nine categorical cover and aspect variables, and six continuous variables [i.e. distance from road, water, and anthropogenic features (m), elevation (m), ruggedness and NDVI]. Ruggedness was calculated at the scale of 90 × 90 m (3 × 3 30-m² grid cells), and ranged from zero to one as ruggedness increased (Sappington, Longshore & Thompson, 2007).

We developed resource selection function (RSF; Manly *et al.*, 2002) models to test for differences in effects of cover

(wetland as the reference category), topography and vegetation structure (based on NDVI) on wolf and cougar kill locations. We used conditional logistic regression (Compton, Rhymer & McCollough, 2002), with strata consisting of kill locations paired to 20 random locations, to estimate the RSF (e.g. Kauffman *et al.*, 2007). For each predator species, we created sets of hypothesized models of kill site attributes and then fit RSF models. We controlled for multicollinearity by eliminating any one of a pair of variables with $r^2 \geq 0.50$, and checked continuous variables for linearity using the quartile method (Hosmer & Lemeshow, 2000). We used Akaike's information criterion with a small sample size correction (AIC_c) to aid in determining top models for each predator, and considered models with ΔAIC_c values > 2.0 to measurably differ in information content (Burnham & Anderson, 2002). Following the determination of top kill site models, we used a constrained model selection approach to select a consistent set of parameters to compare the intensity of selection (via coefficient and odds ratio values) between species-specific models (Hosmer & Lemeshow, 2000). We used AIC_c to rank model candidates based on Akaike weights, and then used the sum of all w_i for each variable to rank them in order of relative importance (w_i ; Burnham & Anderson, 2002). We used the summed w_i to select the most important variables to build comparative models of kill site distribution relative to landscape attributes.

In matched case-control logistic regression, goodness-of-fit statistics for overall model performance are difficult to compute (Zhang, 1999). Therefore, we calculated log-likelihood χ^2 statistics to assess overall model fit, and the Hosmer & Lemeshow (2000) $\Delta\chi^2$ statistic to identify cases and clusters that had a large influence on the parameters of the models (e.g. Johnson, Seip & Boyce, 2004). We evaluated predictive performance using k -fold cross-validation for case-control design (Fortin *et al.*, 2009), using a test-to-training ratio of 20% (i.e. five subsets). Following Fortin *et al.* (2009), we built RSF models using 80% of randomly selected strata and then estimated scores for the observed and random locations of the 20% withheld strata. We used RSF scores to rank the observed location of each stratum against its associated random locations from 1 to 21 (i.e. each stratum contained 1 observed and 20 random locations, resulting in 21 potential ranks), where 1 was the lowest and 21 was the highest rank. We summed ranks of observed locations for the 21 potential bins and performed Spearman rank correlations (r_s) between bin ranking (i.e. 1–21) and its associated frequency. We repeated this process 100 times, and reported the mean and range of expected r_s values. Finally, to determine whether multiple predator species, as opposed to a single predator species, were more effective in capturing spatial heterogeneity within potential protected areas, we used the most suitable quantile (i.e. predicted values > 0.66) from the constrained (i.e. comparative) RSF models as spatial templates to assess potential area, landscape elements and ruggedness conserved. We used a GIS to overlay land cover types and physiographic characteristics on the species-specific quantile templates, and recorded the degree to which they fell within template boundaries.

Results

The number of wolf packs present in the study area ranged from one to three from 1985 to 1988, and two to four from 1989 to 1996 (see Pletscher *et al.*, 1997 for details). During that time, we radio-collared and followed 52 adult wolves (1985–1991: 22 wolves; 1992–1996: 30 wolves) distributed throughout all available packs. From 1992 through 1996, we radiocollared 40 (31 adults and nine juveniles) cougars and 67 female white-tailed deer. Over the duration of the study, we detected 491 wolf- and 229 cougar-killed ungulates (i.e. white-tailed deer, elk *C. elaphus*, moose *A. alces*, and mule deer *O. hemionus*). White-tailed deer (wolves: 68%; cougars: 83%) and elk (wolves: 22%; cougars: 11%) represented the most common prey species for both predators, followed by moose (8%) and mule deer (1%) for wolves, and mule deer (5%) and moose (1%) for cougars. Because of the relative paucity of moose and mule deer kills, we restricted our analyses to white-tailed deer and elk kills for wolves and white-tailed deer kills for cougars.

Landscape attributes of predator kill sites

Based on RSF model coefficients, relative probability of a wolf kill was positively related to grassland ($\beta = 3.208$), pasture (2.441), deciduous ($\beta = 2.233$), shrub ($\beta = 1.693$) and evergreen ($\beta = 1.678$) cover, frozen lakes ($\beta = 1.984$), and south aspects ($\beta = 0.666$), and decreased with increasing ruggedness ($\beta = -0.123$) and elevation ($\beta = -0.002$). The relative probability of a cougar kill increased on south aspects ($\beta = 0.826$), on or along frozen lakes ($\beta = 2.297$), and with increasing ruggedness ($\beta = 0.072$) and NDVI value ($\beta = 0.067$), and decreased with increasing distance from water ($\beta = -0.003$) and elevation ($\beta = -0.003$). Substantial differences existed in the constrained models (i.e. constant sets of parameters across species-specific predation models) of landscape attributes of wolf and cougar kill sites (Table 1). Based on odds ratios, and in comparison with the reference category (i.e. wetland), wolves were over five times more likely to kill prey in pasture cover, nearly four times more likely to kill prey in grassland cover, over 2.5 times more likely to kill prey in deciduous cover, and approximately 1.7 and 1.5 times more likely to kill prey in shrub and evergreen cover, respectively (Table 1). Cougars were over two times more likely to kill prey at more rugged sites and in areas with greater NDVI values, and approximately 1.5 times more likely to kill prey on or along open water than were wolves (Table 1). There were no pronounced differences in the odds of wolf and cougar kills relative to elevation, south aspect and distance from water (Table 1).

In all models, a strong majority of predictor variables were selected for and models containing the top 10 variables were consistently ranked either first or second. All final models displayed adequate fit (wolf-best: $\chi^2_{(13)} = 931$, $P < 0.001$; cougar-best: $\chi^2_{(14)} = 406$, $P < 0.001$; wolf-constrained: $\chi^2_{(14)} = 932$, $P < 0.001$; cougar-constrained: $\chi^2_{(14)} = 405$, $P < 0.001$). Spearman rank correlations from the k -fold cross-

Table 1 Odds ratios for independent variables in top-ranked (best) and consistent-set (constrained) resource selection function models predicting wolf and cougar hunting success in the North Fork of the Flathead River Basin, Montana, 1985–1996

Model	<i>n</i>	Deciduous	Evergreen	Grass evergreen	Pasture	Shrub	Water	South	Ruggedness	NDVI	Distance from water
Wolf-best	10 080	9.332	5.537	24.729	11.488	5.434	7.273	1.946	0.885	0.583	
SE		0.756	0.731	0.754	0.774	0.763	0.769	0.207	0.011	0.339	
<i>P</i> value		0.003	0.021	< 0.0001	0.002	0.026	0.009	0.040	< 0.0001	0.112	
Cougar-best	4 662						9.942	2.285	1.931	1.271	0.997
SE							1.045	0.378	0.012	0.426	0.0004
<i>P</i> value							0.028	0.029	< 0.0001	0.032	< 0.0001
Wolf-constrained	10 080	9.240	5.311	24.458	11.367	5.382	7.134	1.921	0.885	0.581	1.000
SE		0.759	0.731	0.754	0.774	0.763	0.770	0.325	0.011	0.337	0.0001
<i>P</i> value		0.003	0.022	< 0.0001	0.001	0.027	0.011	0.044	< 0.0001	0.063	0.572
Cougar-constrained	4 662	3.517	3.561	6.468	2.152	3.049	9.942	2.285	1.931	1.270	0.997
SE		1.083	1.023	1.086	1.187	1.072	1.045	0.378	0.012	0.424	0.0004
<i>P</i> value		0.246	0.214	0.085	0.519	0.297	0.028	0.029	< 0.0001	0.027	< 0.0001

SE, standard error; NDVI, normalized difference vegetation index.

validations indicated a strong relationship between the training and test data (wolf-best: $r_s = 0.91 \pm 0.03$; cougar-best: $r_s = 0.76 \pm 0.04$; wolf-constrained: $r_s = 0.80 \pm 0.03$; cougar-constrained: $r_s = 0.76 \pm 0.05$).

Comparison of potential protected areas

The most suitable wolf RSF quantile contained over three times the area (1005 km²) of the most suitable cougar quantile (381 km²) (Fig. 1); 60% of the latter was subsumed by the former (Fig. 2). However, despite the difference in area of high-quality hunting habitats, there were only minor differences in the proportional representation of land cover types between the quantile templates. For example, proportions of deciduous forest and frozen water cover types were similar between templates, whereas the wolf template contained greater proportions of grassland and pasture cover (wolf: 14%; cougar: 3%) and the cougar template contained greater proportions of evergreen forest (cougar: 65%; wolf: 53%) and shrub/scrub (cougar: 18%; wolf: 12%) cover types. The greatest difference between templates related to the proportions of rugged terrain (i.e. ruggedness index > 0.3; 41% for the cougar template and 12% for the wolf template).

Discussion

We investigated the concept that wolves and cougars may have value as surrogates for use in identifying, and ultimately conserving, landscape heterogeneity. Implicit to our methodological approach was the notion that the spatial distribution of killed prey could be used to capture landscape heterogeneity (Sergio *et al.*, 2008), hypothesized as one of the major drivers of biological diversity at a landscape scale (Huston, 1994). There are life-history characteristics of some top predators that support those notions, including having large spatial requirements, a tendency to select habitats characterized by topographical and structural complexity (e.g. Carroll *et al.*, 2001), and having diets comprised of multiple secondary prey items (e.g. Kunkel *et al.*, 1999). By using wolves and cougars together, we were able to take advantage of divergence in a life-history characteristic (i.e. selection for topographical complexity) and thereby improve our ability to identify landscape heterogeneity over using a single species alone. The results of this work indicate that wolves and cougars may have use as a surrogate suite, but that use is not without limitations.

Our use of predator kills proved to be an effective method for evaluating the efficacy of using wolves and cougars as a surrogate suite. The spatial distribution of wolf kills was driven largely by cover type, whereas the spatial distribution of cougar kills was driven primarily by physiographic characteristics. Comparison of spatially explicit models of kill site distribution revealed a 15% increase in highly suitable area (i.e. areal extent of combined 'most suitable' RSF templates) when wolf and cougar suitability templates were combined. While the increase in suitable area resulting from using both species may be negligible, inclusion of the cougar

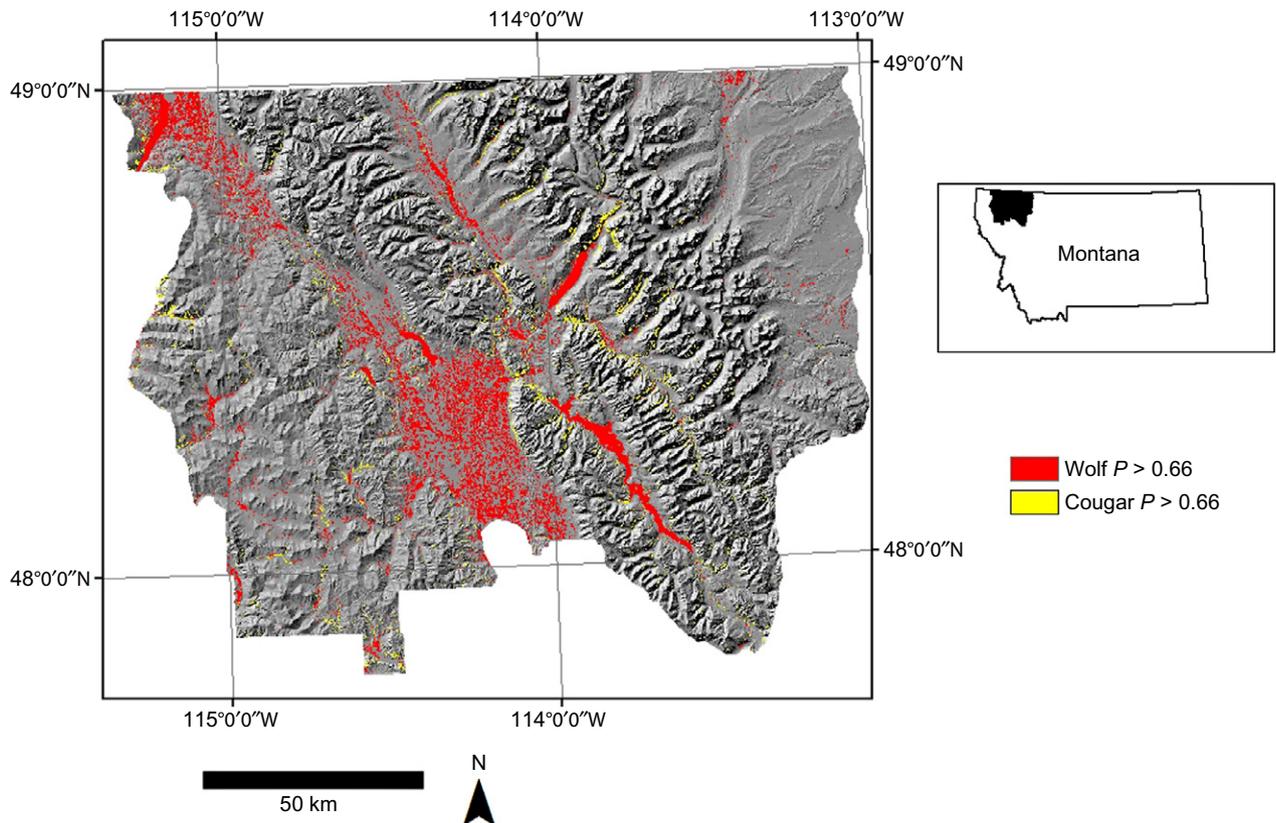


Figure 1 Most suitable quantile [i.e. resource selection function (RSF) value > 0.66] probability surfaces from RSF models for the spatial distribution of wolf- and cougar-killed prey in the North Fork of the Flathead River Basin, Montana.

template substantially increased the amount of rugged terrain. The latter finding suggests that a wolf–cougar suite may be an effective approach to conservation planning if the goal is to conserve spatial heterogeneity. However, it is important to consider limitations of our approach. First, our analyses are based on data collected during winter (April–November), rather than the entire year, and therefore do not account for seasonal variability in prey space use (e.g. Leach & Edge, 1994). Second, by using data only from kill site locations, we were likely missing important spatial information on where predators search for and encounter prey (Hebblewhite, Merrill & McDonald, 2005; Atwood *et al.*, 2009). As a result of these limitations, our estimates of the area of highly suitable winter hunting habitat may underestimate the area of both winter and annual suitable habitat.

In order for a suite of conservation surrogates to have optimal value, there must be a discrepancy between individual surrogate species either along an axis of habitat or landscape attributes selected (Carroll *et al.*, 2001). For a wolf–cougar suite, the primary discrepancy occurs along the landscape attribute axis. Our constrained model comparison provides a useful framework for drawing inferences about how species–landscape relationships contribute to the partitioning of spatial heterogeneity in the distribution of

kill sites. Models indicated cougar-killed prey were more often distributed in areas with greater structural and topographical complexity than were wolf-killed prey. For example, cougar-killed prey were more likely to be found in areas characterized by greater ruggedness, and less likely to be found in areas characterized by structurally simple cover types such as grassland and pasture. Landscape physiography can influence the spatial patterns of where wolves and cougars encounter and kill their prey (e.g. Kunkel *et al.*, 1999; Hebblewhite *et al.*, 2005; Kauffman *et al.*, 2007; Atwood *et al.*, 2009). For example, for wolves, structurally simple cover types may facilitate prey detection and cursorial hunting behavior (Creel & Winnie, 2005), whereas rugged, structurally complex habitats may better enable the ambush hunting behavior of cougars. Our work suggests that, relative to the Carroll *et al.* (2001) axes of habitat association, these two generalist predators diverge primarily along the axis of topographical tolerance. That divergence, in turn, provides support for the notion of using wolves and cougars as conservation surrogates.

Large-bodied habitat generalists, such as wolves and cougars, have wide niche breadths, move over large spatial scales, exploit multiple habitat types that differ in productivity, and often subsume a mosaic of patches critical to smaller-bodied habitat specialists (Terborgh *et al.*, 1999).

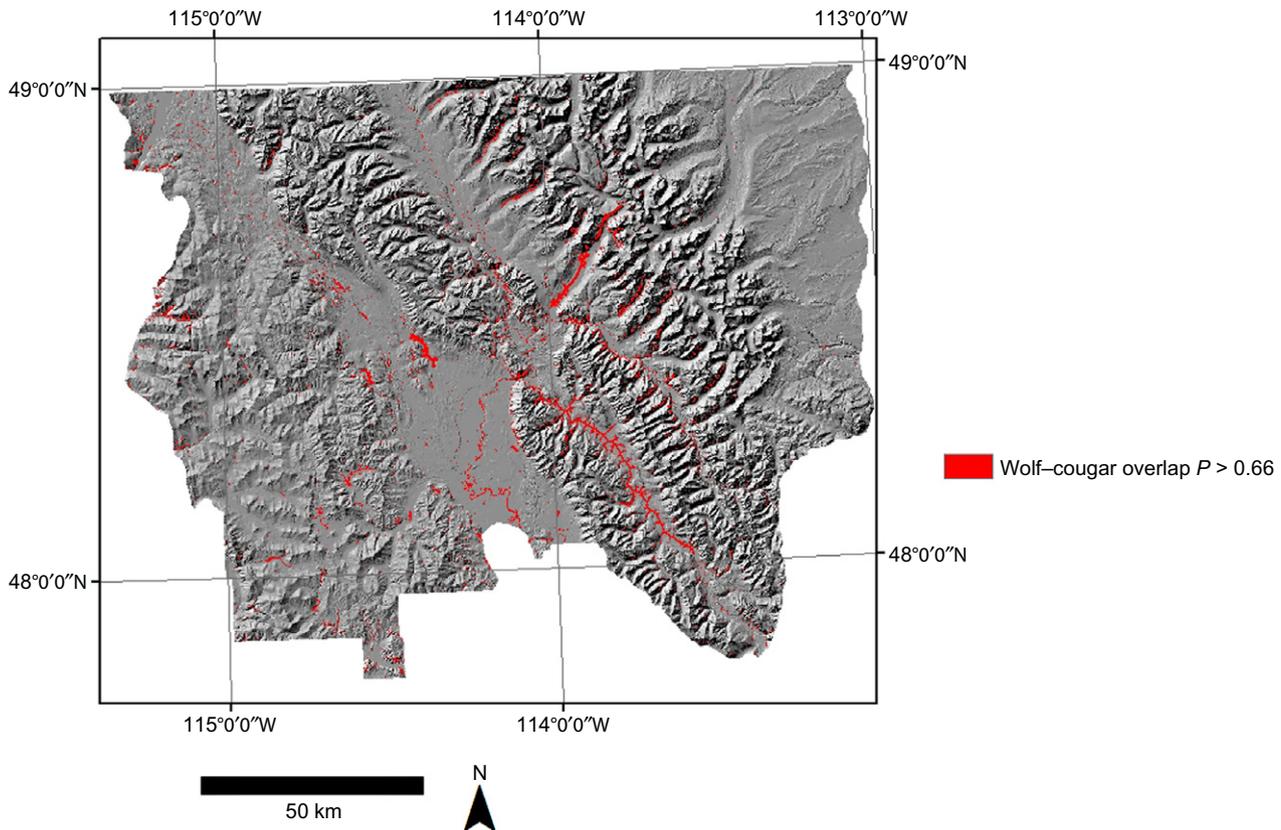


Figure 2 Overlap area of wolf and cougar most suitable quantile (i.e. resource selection function value > 0.66) probability surfaces from resource selection function models.

The divergence in topographical tolerance we observed likely incorporates a component of spatial scale that may be important to smaller-bodied species that are the target of conservation efforts (e.g. Sergio, Marchesi & Pedrini, 2004). Our findings, and those of others (e.g. Husseman *et al.*, 2004; Atwood, Gese & Kunkel, 2007), suggest that cougars may select hunting habitat at a finer scale than wolves, where vegetation and topographical complexity facilitate the ambush of prey. It is important to note that such fine-scale information may not be readily available from remotely sensed datasets. Thus, if a goal in using large-bodied surrogates is to conserve finer-scale landscape attributes, then modeling should either be based on field data or include site inspections (e.g. Johnson *et al.*, 2004) when using only remotely sensed data. A salient point can be made that a large proportion of cougar-attributed topographical complexity was captured within the wolf suitability template, thereby rendering the contribution of the cougar suitability template and, perhaps, site inspections marginal. That may be the case for our study area, but not always so for others: area-specific considerations are warranted.

Our concept of using the distribution of kill site locations is predicated on the notion that by using carnivore species with discrepant hunting styles, we are more likely to detect

effects of spatial heterogeneity and scale that influence the distribution of prey. Implicit in this notion is the assumption that prey may be vulnerable to different predators based on their association with open (e.g. grassland) or structured (e.g. conifer forest) habitats (Atwood *et al.*, 2009). Our data support that notion: cougars killed prey in areas of greater vegetation structure, as indexed by NDVI, than wolves. However, wolves killed prey where prey were most abundant, whereas cougars killed prey where fine-scale complexity facilitated ambush, suggesting that wolf-mediated risk effects may be responsible for prey spending time away from areas of low structural complexity (i.e. low NDVI). It is worth noting that in a similar system in south-central Alberta, Alexander, Logan & Paquet (2006) had a slightly different finding in that the occurrence of cougars and wolves were, at times, positively related to NDVI values at different sampling intervals during winter. Our assessment pooled observations over the entire winter period and may obscure finer-scale temporal associations with NDVI values.

Conclusions

Because managing for multiple species makes conservation more complicated and expensive, conservationists have

searched for individual species that may serve as surrogates for simplifying approaches and reducing costs. While prioritizing conservation work is necessary in a world of limited resources, trying to limit or simplify approaches too greatly may severely reduce the conservation benefits. Using single species as surrogates for conservation may significantly underestimate the size, types and attributes of landscapes necessary to ensure significant or comprehensive conservation benefit. A more appropriate approach may be one that uses a small number of species that greatly contrast in their habitat requirements (maximizing umbrella potential), serve > 1 type of surrogate role, and combined have synergistic ecosystem impacts (Carroll *et al.*, 2001).

A logical question to ask is whether our work represents an improvement over simply using a GIS to identify and delineate large areas of high heterogeneity within a landscape. An approach based solely on landscape metrics fails to completely account for how wolves and cougars are responding to their environment, competitors and their prey. Such responses are important to include in modeling efforts because researchers have identified a link between the presence of top predators and increased biodiversity (e.g. Sergio *et al.*, 2004, 2008). For example, Wilmers *et al.* (2003) found that wolves can facilitate resources essential to other species that are otherwise scarcely available or temporally ephemeral, such as carrion subsidies. Moreover, declines in wolves and cougars have been shown to cause trophic cascades with effects on both terrestrial and aquatic ecosystems (Ripple & Beschta, 2006; Beschta & Ripple, 2009). Last, it is worth acknowledging that charismatic species such as wolves and cougars can function as flagship species to anchor conservation efforts in strategic terms such as fundraising and publicity (Dalerum *et al.*, 2008). Given what has been mentioned earlier, we believe we have identified two species that when used together provide an efficient approach to comprehensive conservation of many western North American landscapes.

We used the spatial distribution of predator kills to generate a probability surface that then served as a template (Fig. 1) to identify landscape heterogeneity. Our work suggests that wolves and cougars might have value for use as a surrogate suite to capture landscape heterogeneity. However, it is important to acknowledge that our work represents an initial step, rather than an endpoint, in conservation planning. Important additional steps should include developing movement-based RSF models for predator and prey species to aid in identifying habitats important to other life-history needs, characterizing landscape permeability, and identifying opportunities to maintain functional connectivity between core habitats (*sensu* Chetkiewicz & Boyce, 2009). The additional steps proposed take time to yield actionable results, and the fundamental challenge will be integrating research with regional planning in a way that ensures the latter can be informed by the former.

Finally, we caution that further work in other landscapes is needed to test the efficacy of selecting cougars and wolves as paired surrogate species because wolves and cougars are relatively adaptive in habitat use. Further research directed

at components of habitat needs beyond foraging may elucidate further contrasts and value. Most importantly, work is needed to directly quantify the umbrella benefit. We need to know how many other species are captured under the umbrella of managing for landscapes required by wolves and cougars. Last, we recommend that modeling approaches, such as ours, be integrated into an adaptive framework to ultimately inform conservation planning decisions.

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