Modeling multi-scale resource selection for bear rubs in northwestern Montana

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Abstract: Both black (*Ursus americanus*) and grizzly bears (*U. arctos*) are known to rub on trees and other objects, producing a network of repeatedly used and identifiable rub sites. In 2012, we used a resource selection function to evaluate hypothesized relationships between locations of 887 bear rubs in northwestern Montana, USA, and elevation, slope angle, density of open roads and distance from areas of heightened plant-productivity likely containing forage for bears. Slope and density of open roads were negatively correlated with rub presence. No other covariates were supported as explanatory variables. We also hypothesized that bear rubs would be more strongly associated with closed roads and developed trails than with game trails. The frequencies of bear rubs on 30 paired segments of developed tracks and game trails were not different. Our results suggest bear rubs may be associated with bear travel routes, and support their use as ''random'' sampling devices for non-invasive spatial capture–recapture population monitoring.

Key words: bear rub, non-invasive genetic sampling, Resource Selection Function, *Ursus americanus, Ursus arctos*

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Both black (*Ursus americanus*) and grizzly bears (*U. arctos*) are known to rub on trees and occasionally on other objects such as power poles, bridge pilings, and rocks (Burst and Pelton 1983; Green and Mattson 2003; Kendall et al. 2008, 2009; Karamanlidis et al. 2012; Sawaya et al. 2012). Although the exact reasons for bear rubbing behavior are uncertain, rubbing is thought to facilitate intra- and inter-sexual olfactory or other sensory (e.g., foot pads) communication between individuals (Burst and Pelton 1983, Green and Mattson 2003). This behavior produces a network of repeatedly used and identifiable trees (or other objects), which ostensibly promotes intraspecific communication. Incidental to the rubbing behavior is the deposition of hair, which makes bear rubs useful in non-invasive DNA-based studies of bear populations.

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Capture–recapture demographic studies requiring the live capture of bears are often limited by small sample sizes, making it difficult to infer vital rates, abundance or trends of bear populations, particularly for large study areas (Kendall et al. 2008, Stetz et al. 2010, Sawaya et al. 2012). Because collecting hair and other sources of DNA can sample far more individuals than live capture, non-invasive genetic sampling methods are increasingly used to study bears and other uncommon or cryptic species (e.g., Waits and Paetkau 2005). Baited hair traps combined with hair collected from bear rubs have been used to produce statistically robust abundance estimates for grizzly bears in large study areas such as the 32,000-km^2 Northern Continental Divide Ecosystem (Kendall et al. 2009). In Banff National Park, Canada, estimates of grizzly bear abundance and population growth-rate models were found to be similar when using data collected from bear rubs alone or when using hair traps and bear rubs combined (Sawaya et al. 2012). Bear rubs therefore could be an important component of studies to generate valuable data for the conservation of bears (Kendall et al. 2009; Stetz et al. 2010, 2014; Karamanlidis et al. 2012, 2014; Sawaya et al. 2012).

Knowing the features of the landscape most commonly associated with bear rubs may help researchers improve study design by targeting searches for bear rubs in the areas most likely to contain them. Green and Mattson (2003) found that bear rub locations in Yellowstone National Park, USA, tended to be associated with micro-sites of decreased slope, decreased distance to forest edge, and decreased amount of deadfall, and on slopes oriented away from north when compared with sites of bear activity without bear rubs. Bear rubs in northern Japan were also associated with sites of low slope near trails and game trails (Sato et al. 2014), and Burst and Pelton (1983) noted that bear rubs used by black bears in Great Smoky Mountains National Park, USA, tended to be on trails infrequently used by people and on ridge tops. These studies suggest that bear rub locations may be associated with potential bear travel routes such as ridge tops, trails, and areas with decreased amounts of deadfall. These studies further indicate that bear rub locations may not be random, and instead, may be concentrated in areas frequently used by bears and may be selected to maximize intraspecific communication. Given the recent surge of interest in using DNA samples obtained from bear rubs for population monitoring, understanding bear rub-site selection may have important implications for the design of spatial capture–recapture monitoring. Therefore, to further understand selection of bear rub sites, we quantitatively assessed both the landscape-scale and trail-level associations of bear rub locations with features reported to be associated with selection by bears.

Habitat selection and the timing of rubbing behaviors may influence the selection of bear rub locations. Rubbing behavior of male grizzly bears (Kendall et al. 2009) and grizzly bears in general (Green and Mattson 2003, Sato et al. 2014), has been reported to peak in the spring and early summer, though female grizzly bears have also been shown to increase the frequency of rubbing later in the summer (Kendall et al. 2009). Stetz et al. (2014) found no seasonal patterns of bear rub use by black bears in Glacier National Park, USA. Both black and grizzly bears have been shown to select for mid- and low-elevation habitat throughout much of their active season (Raine and Kansas 1990, Mace et al. 1996, Belant et al. 2010). Bear use of low- and mid-elevation habitat and the findings of Green and Mattson (2003) led us to predict bear rubs would be associated with low slope at low to middle elevations.

Food availability may be an important driver of habitat selection for bears (Neilsen et al. 2010). Previous habitat studies found bears selected for open-canopy areas with available forage, such as avalanche chutes, meadows, shrub lands, burns, and cutting units in all seasons (Kasworm and Manley 1988; Mace et al. 1996, 1999; Waller et al. 1998; Lyons et al. 2003; Ciarniello et al. 2007). Increasing levels of greenness (a remotely sensed index of leaf area based on the Normalized Difference Vegetation Index [NDVI]) has also been shown to have a strong correlation to habitat selection by grizzly bears (Mace et al. 1999). Greenness is not commonly used to model black bear habitat. The grasses, forbs, and berries frequently eaten by black bears, however, are associated with meadows, avalanche chutes, and shrub lands (Grenfell and Brody 1986, Raine and Kansas 1990) that have increased leaf area (Clevenger et al. 2002). We predicted that bear rubs would be found near habitat patches that had potential forage for bears.

In addition to the above landscape variables, human development can also affect bear resource selection, and hence, possibly the location of bear rubs. Given the potentially negative effect of open roads on habitat selection by bears (Kasworm and Manley 1988; Mace et al. 1996, 1999; Wielgus et al. 2002; Gaines et al. 2005; Ciarniello et al. 2007), we predicted that bear rub density would be negatively correlated to the density of open roads. We defined open roads as those that were not gated during the spring, summer, and autumn when bears are active. Bear rubs may also be associated with travel corridors for bears (Burst and Pelton 1983, Green and Mattson 2003). Although bears may avoid open roads, developed trails and closed roads (developed tracks) have few obstructions, usually have low gradients, and may be used to facilitate travel and access to food sources for bears (Roever et al. 2008). Bears also travel on natural game trails; however, because game trails are often discontinuous and have numerous obstructions such as thick vegetation and deadfall, bears may prefer to use developed tracks in some areas. We therefore hypothesized that bear rubs would be found more frequently along developed tracks than along game trails. We tested the trail-level associations of bear rubs by comparing the frequency of bear rubs along segments of developed tracks and game trails in areas of similar habitat.

This study seeks to better understand the selection of bear rub sites in regard to bear habitat and provide information that may aid in the design of capture–recapture studies that use bear rubs as sampling devices. At the landscape level, we hypothesized that bear rubs would be found (1) in areas with decreased slope, (2) in areas with decreased densities of open roads, (3) near potential foraging sites represented by areas of open canopy and increased NDVI values, and (4) at middle to low elevations. At the trail scale level, we hypothesized that rubs would be more frequent along developed tracks than along game trails.

Study area

We collected data in the Cabinet–Yaak Ecosystem (CYE) in northwestern Montana, USA (Fig. 1). The study area boundary roughly follows the portion of the Cabinet–Yaak grizzly bear recovery zone in Montana and small areas of peripheral habitat, which together represent important habitat for the conservation of bears in this region. Areas with insufficient or poorly defined road data were removed. The majority of lands in the study area were publicly owned and administered by the Kootenai, and Lolo, National Forests; the remaining lands belonged to private timber companies or were small private holdings in valley bottoms. Road densities ranged from 0 km/km^2 in the 381-km^2 Cabinet Mountain Wilderness to 4.14 km/km^2 in the northeastern portion of the study area. Average open-road density for our study area was 0.93 km/km^2. Elevations in the Cabinet Mountains ranged from 610 m to 2,644 m and from 550 m to 2,348 m in the Yaak region. Weather in the CYE was subject to a Pacific maritime regime, with 100–150 cm of precipitation annually. The CYE is in the Inland maritime region of the Northern Rocky Mountains described by Habeck (1997). Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) dominated the driest, low-elevation areas (Habeck 1997). Grand fir (*Abies grandis*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) dominated in wetter valleys and drainages of the area (Habeck 1997). Lodgepole pine (*Pinus contorta*) is a primary post-fire species in the region and was common at low- and middle-elevation sites with some stands found at higher elevations (Habeck 1997). Subalpine fir (*A. lasiocarpa*), Engelmann spruce (*Picea engelmannii*), western hemlock, western larch (*Larix occidentalis*), and mountain hemlock (*Tsuga mertensiana*) were found at mid- to high elevations (Habeck 1997). The black bear was the most abundant bear species in the region (Kasworm et al. 2006), with an estimated population of 1,513 individuals within bear management units 100 and 104, which were closely aligned with our study area (Mace and Chilton-Radandt 2011). The CYE harbored only a small population of grizzly bears, estimated at 30–40 individuals (Kasworm et al. 2006).

Methods

To test our hypotheses at the landscape and trail-level scales, we identified bear rubs based on signs of bark discoloration and smoothness, a bear trail or compacted area at the base of the tree or post, or when bear hair was present. Bear rubs may also have had scratches or bite marks, which indicated their use by bears. To test the relationship of bear rub locations and landscape-scale features, we used 887 bear rubs identified in 2011 and 2012 by crews trained to identify bear rubs along recreational trails, and open and closed roads (Kendall et al. 2014). Of the rubs used in the analysis, 364 were along trails, 206 were along closed roads, and 392 were along open roads. Known bear rubs were considered "used" during both scales of analysis (landscape- and trail-level). At the landscape-scale, we compared bear "used" sites with a control group of 10,000 random points placed along the roads and trails within the study area. We did not visit the sites of randomly assigned points; therefore, we considered them as "available" and not "unused" (Manly et al. 2002). To test the hypothesis that bear rubs are more strongly associated with developed tracks than with game trails, in 2012 we surveyed 30 sites for rubs along trails and game trails. Each site consisted of a 1-km section of developed track and a 1-km section of corresponding game trails. To control for potential differences in habitat between game trails and developed trail locations, surveyed game trail segments were located within 1 km of the developed tracks we sampled. We selected survey sites across the study area, in a variety of vegetation communities, including low-elevation ponderosa pine stands, riparian areas, mid-elevation stands of Douglas fir and Engelmann spruce, and areas dominated by subalpine

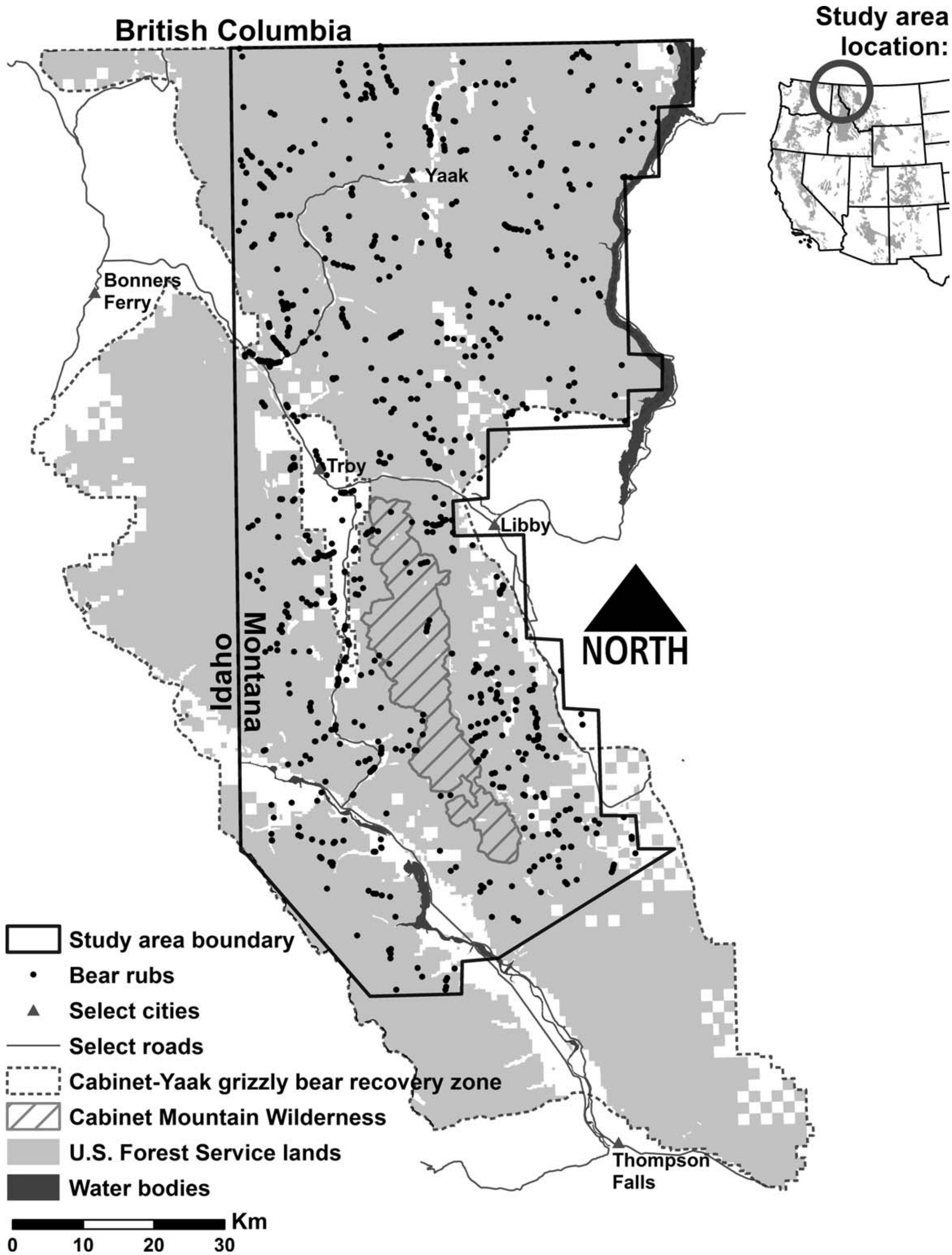

Fig. 1. Location of the study area and 887 bear rub locations identified in 2011 and 2012 in the Cabinet–Yaak region of northwestern Montana, USA.

fir. Bear rubs located along the paired 1-km segments of trails and game trails were not used in the landscape-scale analysis.

Landscape covariates

We assigned elevation and slope angle to all bear rubs and random points based on the Arc Second National Elevation Dataset digital elevation model. To model the effect of areas of open canopy with high greenness values on the likelihood of a mapped point being a bear rub and not a random point, we selected cells that had both an open-canopy cover type and an NDVI value above the mean for the study area. We selected open-canopy cover types using the National Land Cover Database (Fry et al. 2006). Using the Western United States 250-m eMODIS Remote Sensing Phenology Data (http://phenology.cr.usgs.gov/), we defined "high greenness" as cells with a maximum NDVI value above the mean greenness for the study area. This delineation included areas of high productivity and excluded open areas of low productivity such as bare rock, bare soil, and open water.

To map the 30-m^2 cover-type layer with the 250-m^2 NDVI layer, we resampled the 250-m^2 cells of the eMODIS data to create 30-m^2 cells each with the same NDVI values as the parent cells. We then selected all cells, which met both the cover type and greenness conditions. To assess the proximity of bear rubs to these cells, we calculated the shortest distance from each bear rub and each random point to the center of the nearest cell meeting the qualifying conditions. We predicted that the probability of a selected point being a bear rub would decrease as distance from a qualifying cell increased. We derived density of open roads from U.S. Forest Service Geographic Information System (GIS) layers for the Kootenai and Lolo National Forests, which included an inventory of U.S. Forest Service and private roads. We calculated densities for roads open to the public during the spring, summer, and autumn, when bears are active, because bears may not select against closed and re-contoured roads (Mace et al. 1996, 1999). All spatial analyses were done using ArcGIS 10.2.2 (ESRI, Redlands, California, USA).

Analyses

Landscape-scale bear-rub RSF model. To estimate the effects of landscape variables on bear rub occurrence within the study area (landscape-scale), we used a resource selection function (RSF) framework in a used–available design (Boyce and McDonald 1999, Manly et al. 2002). As we note above, the used–available design provides a relative probability of the occurrence of bear rubs. We conducted univariate logistic regression for individual covariates (slope, elevation, density of open roads, and distance from greenness). We screened for collinearity among all covariates by excluding covariates that had pairwise correlation coefficients of $|r| > 0.7$ in the same multiple logistic regression (Dormann et al. 2013). We generated RSFs using generalized linear models (GLM) with a binomial distribution and logit-link function using the R statistical computing package (R Development Core Team 2008). Owing to the small number of variables tested and the support in the literature for the inclusion of each covariate, we estimated a binomial GLM for all 16 possible combinations of covariates. We selected the top model using Akaike's Information Criterion (AIC) and used AIC weights to rank variable importance (Burnham and Anderson 2001). To assess model fit, we applied the Hosmer and Lemeshow (1980) χ^2 goodness-of-fit test with groups of 5, 10, and 15. If a model fails to predict the data used to develop the model, the resultant H–L test statistic for the P-value is <0.05. We also used k-folds cross-validation (Boyce et al. 2002) to determine the predictive capacity of our top model(s). The k-folds cross-validation randomly divides the data set into 5 folds, and then uses 80% of the data iteratively to fit the model, and the withheld 20% to validate it. Predictions are evaluated based on the frequency of occurrence of observed locations in predicted ranked bins of habitat quality from 1 to 10, and a high positive Spearman rank correlation is used to assess goodness-of-fit (Boyce et al. 2002). To understand the effects of covariates on the relative probability of bear rub occurrence, we plotted the coefficients estimated by the GLMs to make probability functions for all top covariates (Keating and Cherry 2004).

Paired developed track and game trail segments. To test the hypothesis that bear rubs are more strongly associated with developed tracks than with game trails, we used a paired t-test to test for a difference between the frequencies of bear rubs on paired segments of developed tracks and game trails.

Results

Landscape covariates

Elevation, distance from areas of open canopy, and distance to areas of high greenness had large

Table 1. Descriptive statistics for landscape variables associated with bear rubs located by the Cabinet–Yaak Grizzly Bear DNA Project (*n* = 887) during 2011 and 2012, and points (*n* = 10,000) randomly generated along roads and trails using ArcGIS 10.2.2. Both bear rubs and random points were within or on the periphery of the Cabinet–Yaak grizzly bear recovery zone in northwestern Montana, USA.

Landscape variable	Type	Units	Mean	Range	SD	*n*
Elevation	Bear rub	m	1,197	570–2,030	331	887
	Random	m	1,191	560–2,330	322	10,000
Open-road density	Bear rub	km/km^2	0.85	0.00–3.30	0.71	887
	Random	km/km^2	0.95	0.00–4.10	0.77	10,000
Slope	Bear rub	degrees	13	0.39–46.00	8.20	887
	Random	degrees	14	0.00–53.00	8.70	10,000
Distance to greenness	Bear rub	m	264	1–1,829	258	887
	Random	m	267	4–1,838	257	10,000

variances, which were similar for both bear rubs and random points (Table 1). The mean and variance for slope and density of open roads was smaller for bear rubs than for random points (Table 1). None of the landscape variables were excluded from model testing because they all had pairwise correlation coefficients of $|r| \leq 0.53$.

RSF model for bear rub locations

Of the 16 models tested, the model including only slope angle ($P < 0.01$) and density of open roads ($P < 0.01$) was the top-ranked model, with approximately half of the AIC weight ($w_i = 0.483$; Table 2). The probability of a bear rub being present was negatively correlated with increasing slope (Table 2; Fig. 2a). The probability of a bear rub being present was also negatively correlated with increased densities of open roads (Table 2; Fig. 2b). Elevation and distance from greenness were not supported in any model (Table 2). Though the addition of the distance to greenness variable had a ΔAIC of <2, both the univariate and multivariate analysis suggest that this is a nested model and that distance to greenness is an uninformative parameter as per Arnold (2010). When using 5, 10, or 15 groups ($g = 5, 10, 15$) the Hosmer and Lemeshow (1980) goodness-of-fit test showed adequate fit for all of the top models and consistently showed evidence of poorer fit for models with high ΔAIC values. The *P*-values resulting from the test using $g = 10$ are reported (Table 2). The *k*-folds cross-validation revealed adequate model predictive capacity, with Spearman rank correlations ranging from 0.65 to 0.79 for the top 4 models considered (Table 2).

Paired developed track and game trail segments

The frequency of bear rubs on developed trails and roads (1.00/km; SD = 1.05/km; $n = 30$) did not differ ($P = 0.59$) from their frequency on game trails (0.83/km; SD = 1.05/km; $n = 30$).

Discussion

We found that bear rubs were common both along developed trails and roads and along game trails, suggesting that bear rubs are located along a variety of linear features and can be found in places where developed trails and roads may not exist. Other studies of bear rubs have found them on game trails (Burst and Pelton 1983, Green and Mattson 2003, Sato et al. 2014), but did not quantify how common bear rubs were along game trails. By controlling for habitat differences between searches for bear rubs along developed tracks and game trails, we were able to demonstrate that, in regard to use of bear rubs, bears do not seem to differentiate between game trails and developed tracks. This interpretation is consistent with the hypothesis that bear rub locations may be related to bear travel routes, as was suggested previously (Burst and Pelton 1983, Green and Mattson 2003).

Because the distribution of roads and trails is not random, their exclusive use to survey for bear rubs to use as sampling devices may introduce bias into spatial capture–recapture models. So although sampling along roads and trails is an efficient method for collecting samples from rub trees, certain habitats may be underrepresented. Researchers may consider placing rub poles with a non-food attractant to sample areas without trees or where there is insufficient coverage from existing bear rubs (e.g., Dumond et al. 2015). The use of game trails in areas with inadequate road and trail coverage may help make using DNA obtained from bear rubs a cost-effective way to increase sample size while not

Table 2. Results for the top 4 models describing 887 bear rub locations collected during 2011 and 2012 in the Cabinet–Yaak region of northwestern Montana, USA, including β-coefficients with 95% confidence intervals, standard error (SE), Wald statistic, *P*-values, Akaike's Information Criterion (AIC) weights, ΔAIC, Hosmer and Lemeshow (1980) *P*-values (H–L *P*-Value), and *k*-folds cross-validation Spearman rank correlation and SE across 5 partitions of the data. Statistics generated using a generalized linear model. Model components: slope, density of open roads (km/km^2), elevation, distance to an area of high greenness, and open-canopy cover type.

Model	Name	β-coeff.	SE	95% CI	−95% CI	Wald statistic	*P*-value	AIC wt	ΔAIC	H–L *P*-value	*k*-folds Spearman rank correlation	SE
1	Slope	−0.023	0.004	−0.014	−0.031	−5.17	<0.005	0.483	0	0.427	0.654	0.085
	Open_Road	−0.226	0.049	−0.13	−0.322	−4.623	<0.005					
2	Slope	−0.023	0.004	−0.013	−0.031	−5.163	<0.005	0.248	1.3	0.388	0.717	0.072
	Open_Road	−0.232	0.049	−0.14	−0.329	−4.692	<0.005					
	Dist_Green	−<0.001	−<0.001	−<0.001	−<0.001	−0.815	0.415					
3	Slope	−0.022	0.009	−0.014	−0.031	−5.061	<0.005	0.178	2.0	0.544	0.716	0.087
	Open_Road	−0.227	0.056	−0.117	−0.337	−4.037	<0.005					
	Elevation	<0.001	<0.001	<0.001	<0.001	−0.028	0.978					
4	Slope	−0.022	0.004	−0.014	−0.031	−5.057	<0.005	0.091	3.3	0.388	0.786	0.049
	Open_Road	−0.232	0.056	−0.121	−0.343	−4.102	<0.005					
	Elevation	−<0.001	<0.001	−<0.001	−<0.001	−0.001	0.999					
	Dist_Green	−<0.001	<0.001	−<0.001	−<0.001	−0.815	0.416					

adding a substantial spatial bias to population estimates obtained from spatial capture–recapture models (e.g., Sawaya et al. 2012, Stetz et al. 2014). Future research may examine what the potential effects of foot and vehicle traffic are on the spatial relationships of bear rubs

There were also few strong relationships between landscape-scale factors affecting bear rub occurrence and previous studies of resource selection by both bear species in the region. For example, we found that bear rubs were not strongly associated with the 1,000–2,000-m elevations most strongly tied to habitat selection by grizzly and black bears in the region (Kasworm and Manley 1988, Mace et al. 1996). Though grizzly bear use of bear rubs varies with sex and season, Stetz et al. (2014) did not find any temporal trends in black bear detection rates at bear rubs in Glacier National Park. Though black and grizzly bears commonly select mid-elevation habitat, they are known to use both high- and low-elevation areas when food sources are abundant there (Raine and Kansas 1990, Belant et al. 2010). Black bears are likely the primary users of bear rubs in the region, based on their higher densities in general in northwestern Montana; therefore, our result is consistent with the findings of Stetz et al. (2014) in suggesting that black bears may use bear rubs throughout their active season. Late summer and early autumn use of bear rubs by female grizzly bears (Kendall et al. 2009) may have led to the establishment of some bear rubs at higher elevations.

Areas with abundant forage plants for bears have been shown to be an important component of habitat for bears in all seasons (Grenfell and Brody 1986; Raine and Kansas 1990; Mace et al. 1996, 1999; Waller and Servheen 2005; Ciarniello et al. 2007). Additionally, Green and Mattson (2003) found decreased distance to forest edge to be a good predictor of bear rub location. Our work, however, found that increasing distance from open areas of high greenness did not affect the probability of a bear rub being present. The poorly defined relationship between bear rubs and greenness in open areas suggests that bear rubs may not be located near this type of habitat component, or that greenness in open areas, as measured here, is not an important habitat component for bears in this region. Therefore, our assumption that this type of habitat component may be valuable throughout the active season and related to bear rub location does not appear valid. So, although greenness has been

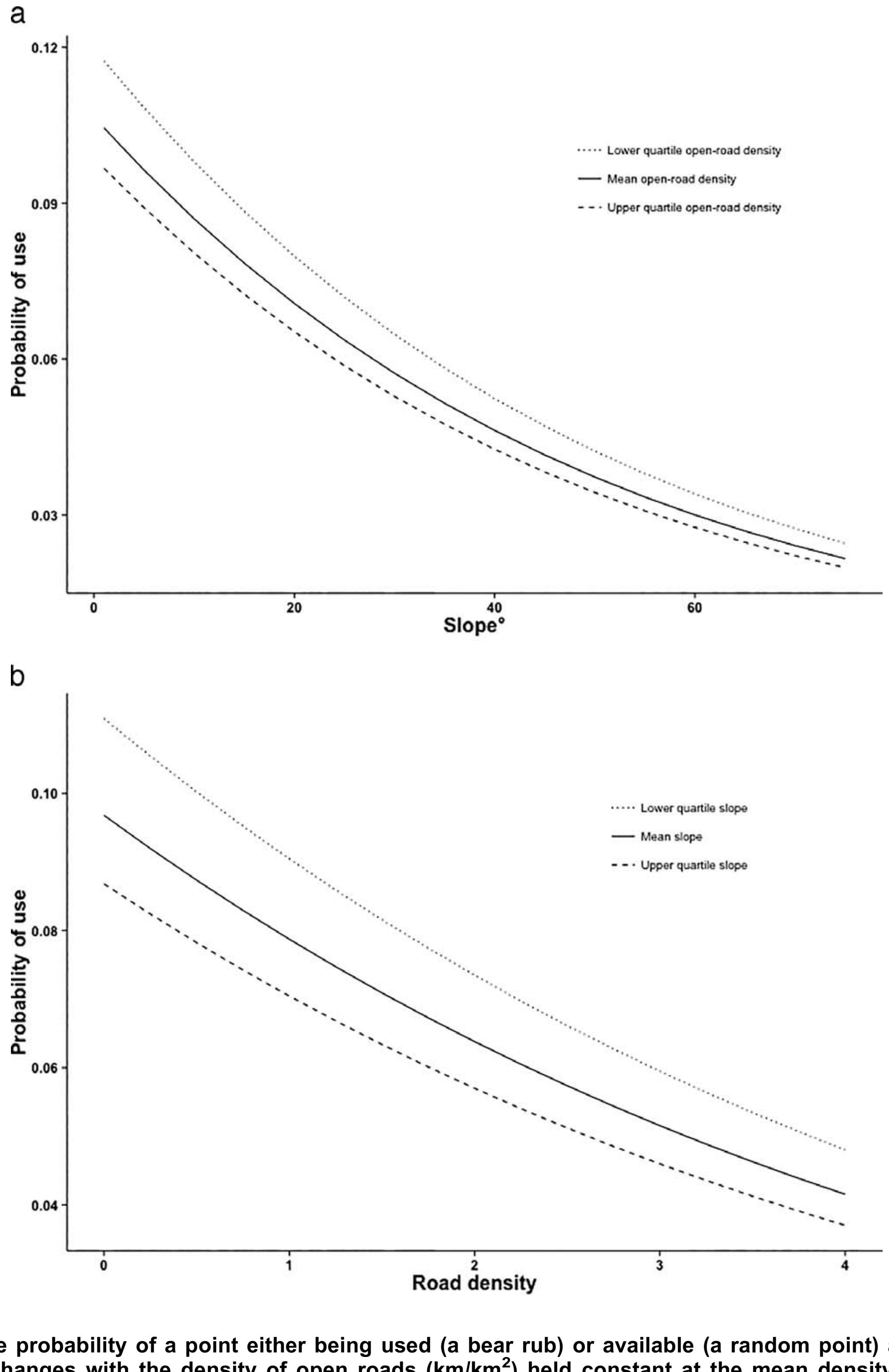

Fig. 2. The probability of a point either being used (a bear rub) or available (a random point) as (a) slope (degrees) changes with the density of open roads (km/km^2) held constant at the mean density, the upper quartile, and the lower quartile; and (b) as density of open roads (km/km^2) changes with slope (degrees) held constant at the mean, the lower quartile, and the upper quartile. Model based on the locations of 887 bear rubs found in the Cabinet–Yaak region of northwestern Montana, USA, during 2011 and 2012.

linked to selection of habitat by grizzly bears, it is a measure of plant productivity, and not a direct measure of food availability or habitat quality for bears in all regions (Mace et al. 1996, Clevenger et al. 2002); it may vary throughout the season. If bear rubs are clustered near habitat with increased importance for bears, a measurement of distance from bear rubs to a variety of recurring food resources that reflect seasonal shifts in use by bears may better represent the relationship between bear rubs and important components of habitat for grizzly and black bears. Bear rubs may also be most associated with bear travel routes, which also could be considered a habitat component. It is unknown how bears use the habitat surrounding bear rub sites. However, if bear rubs are most common along travel routes, bears rubs may be more associated with the behaviors related to traveling rather than the behavior of foraging. Future studies could address differences between bear species in the distribution of bear rubs to further understand the potential for interspecific spatial separation; for example, are there differences between black or grizzly bear resource selection overall, and selection for the locations of bear rubs specifically? Other studies appear to show that black and grizzly bears use the same bear rubs across a range of habitat conditions (Stetz et al. 2014), which suggests that there may be little difference in rub site selection between the 2 species in this region.

Locations of bear rubs may be more associated with travel routes used by bears (such as developed trails, closed roads, game trails, or ridge tops [Burst and Pelton 1983]) than by the presence of other resources such as food. We found that increases in slope angle had a negative relationship with bear rub density. Low slope angle is most commonly associated with valley bottoms and ridge tops, which may be used as bear travel routes (Burst and Pelton 1983). The consistent relationship between low slope and presence of bear rubs indicates that it may be an important component to models of location of bear rubs and supports the idea that bear rubs may be associated with potential travel routes for bears. If open roads have a negative influence on habitat selection by bears (Kasworm and Manley 1988; Mace et al. 1996, 1999; Wielgus et al. 2002; Gaines et al. 2005; Ciarniello et al. 2007), then the negative association between open roads and bear rub locations may be a reflection of habitat selection. The relationship we found between bear rub locations and densities of open roads was not strong and the nature of the interaction between bears and roads was quite complex. The resolution of the results presented is, therefore, insufficient to make a detailed interpretation of the potentially convoluted relationship between roads and behavior of bears.

Our results suggesting a negative association with open roads and bear rubs could be in part due to a potential sampling bias. To access trails and closed roads, crews sometimes drove along open roads and walked along trails and closed roads, which may have biased the distribution of identified bear rubs. However, the distribution of bear rubs along open roads, closed roads, and trails shows that a substantial number of the bear rubs we identified were found along open roads, so the effect of this potential bias may be minimal. Moreover, the used–available design we used may also be biased if the "available" sample contained a large number of unknown "used" sites (Keating and Cherry 2004, Johnson et al. 2006). Given the relative rarity of bear rubs on the landscape, we believe this bias is unlikely and our analyses yielded useful insights into the probability that slope angle, open road density, elevation, and distance to greenness have an effect on the occurrence of bear rubs (Johnson et al. 2006, Keating and Cherry 2006, Beyer et al. 2010).

Despite the potential for non-random differences in the distribution of bear rubs at several scales, our study showed few substantial differences in where bear rubs occurred. The variables slope angle and density of open roads, where we did find a weak relationship to rub location, are common across the landscape. So, although rub locations are not truly random, their limited association with common features and lack of relationships to others indicates that their placement along roads and trails may be somewhat random. This finding is important in helping to justify the use of bear rubs as "random" sampling devices for spatial capture–recapture population monitoring using non-invasive genetic sampling techniques. Given the non-random distribution of roads and trails, care must be taken when designing spatial capture–recapture studies to survey for rubs in all available habitats and as evenly as possible across the study area. To decrease potential spatial bias arising from sampling along roads and trails, researchers may consider searching for rubs along game trails or using erected rubbing poles with a non-food attractant (Dumond et al. 2015). Though detection probabilities at bear rubs for male and female grizzly bears are similar in some areas (Sawaya et al. 2012), their use varies by sex and season (Kendall et al. 2008, Sawaya et al. 2012). Thus, in addition to ensuring a thorough spatial sampling effort, bear rubs used for sampling should be checked throughout the bear's active season. Black bears may use bear rubs throughout their active season, but capture probabilities using bear rubs may be lower than at hair-trap sites for black bears (Stetz et al. 2014). Also, the association of bear rubs with trails, game trails, and areas of low slope suggests that bears may be selecting locations of bear rubs along bear travel routes. Potential bear travel routes such as ridge tops, valley bottoms, trails, roads, and game trails are common and widespread; therefore, the association between bear rub location and bear travel routes does not seem to conflict with their use as "random" sampling devices if care is taken to ensure adequate sampling coverage. Lastly, despite the increasingly common use of bear rubs in the West (e.g., Kendall et al. 2009, Stetz et al. 2014) and research demonstrating their prevalence in the eastern United States (e.g., Burst and Pelton 1983), we are not aware of any studies using rubs to collect bear hair for genetic analysis in this region. We agree with Sawaya et al. (2013, who called for more research into using bear rubs for genetic sampling studies in eastern North America).

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