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GRIZZLY BEAR DENNING HABITAT AND DEMOGRAPHIC CONNECTIVITY IN NORTHERN IDAHO AND WESTERN MONTANA

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ABSTRACT—Grizzly Bears (*Ursus arctos*) are protected in the contiguous United States under the federal Endangered Species Act. The conservation strategy for the species encourages population connectivity between isolated Grizzly Bear Recovery Areas through Demographic Connectivity Areas. Another goal is reestablishment of a breeding population in the Bitterroot ecosystem through natural immigration. Using the locations of 362 verified Grizzly Bear den sites and Maxent as a resource selection function, we predicted 21,091 km^2 of suitable denning habitats. Terrain features, distance to roads, and land cover best explained suitable denning habitats in northern Idaho and western Montana. The results support the demographic model for population connectivity, and independent of other factors there is suitable denning habitat for hundreds of Grizzly Bears in the Bitterroot analysis area. We suggest additions to the Bitterroot Grizzly Bear Recovery Area, and that more effective motorized-access management be applied to demographic connectivity areas.

Key words: Bitterroot ecosystem, demographic connectivity, den sites, denning, dispersal, Grizzly Bear, northern Rockies, secure core, selection

The Grizzly Bear (*Ursus arctos*) was listed in 1975 as a threatened species under the US Endangered Species Act partially owing to isolation, and populations in the contiguous US remain isolated (USFWS 2021). Linkage of the isolated Grizzly Bear populations into a genetically diverse metapopulation (as defined by Hanski and Gilpin 1991) would increase the probability of long-term survival (Allendorf and others 2019; Boyce and others 2001; Servheen and others 2001; Craighead and Vyse 1996). Two models have been advanced to achieve this goal. The male-mediated model for genetic interchange (Peck and others 2017) would maintain genetic diversity based on long-distance dispersals of male Grizzly Bears. The demographic model is based on maintaining areas of secure suitable habitats occupied by resident female Grizzly Bears that are within known dispersal distances for females (Mattson and others 1996; Proctor and others 2015). Owing to the much shorter dispersal distances of female Grizzly Bears (McLellan and Hovey 2001; Proctor and others 2004; Graves and others 2014), the demographic model relies on multi-year dispersals. The Conservation Strategy for Grizzly Bear in the Northern Continental Divide Ecosystem (NCDE; USFWS 2018) designated 2 Demographic Connectivity Areas (DCAs) to provide habitat for resident female Grizzly Bears as shown in Figure 1.

Denning behavior in Grizzly Bears is thought to be an evolutionary adaptation to long winter periods where natural foods are unavailable (Craighead and Craighead 1972). By definition, residential occupancy requires availability of suitable habitats in all 4 seasons so that the demographic model is dependent upon the presence of suitable denning habitats. Denning habitat for Grizzly Bears has not been previously analyzed across the northern Idaho-western Montana region. We compare our results with other large landscape denning studies in the greater Yellowstone ecosystem (Podruzny and others 2002), Alberta (Pigeon and others 2014) and British Columbia (Ciarniello and others 2005). The central purpose of our study was to identify Grizzly Bear denning habitats within the connectivity areas between Recovery Areas,

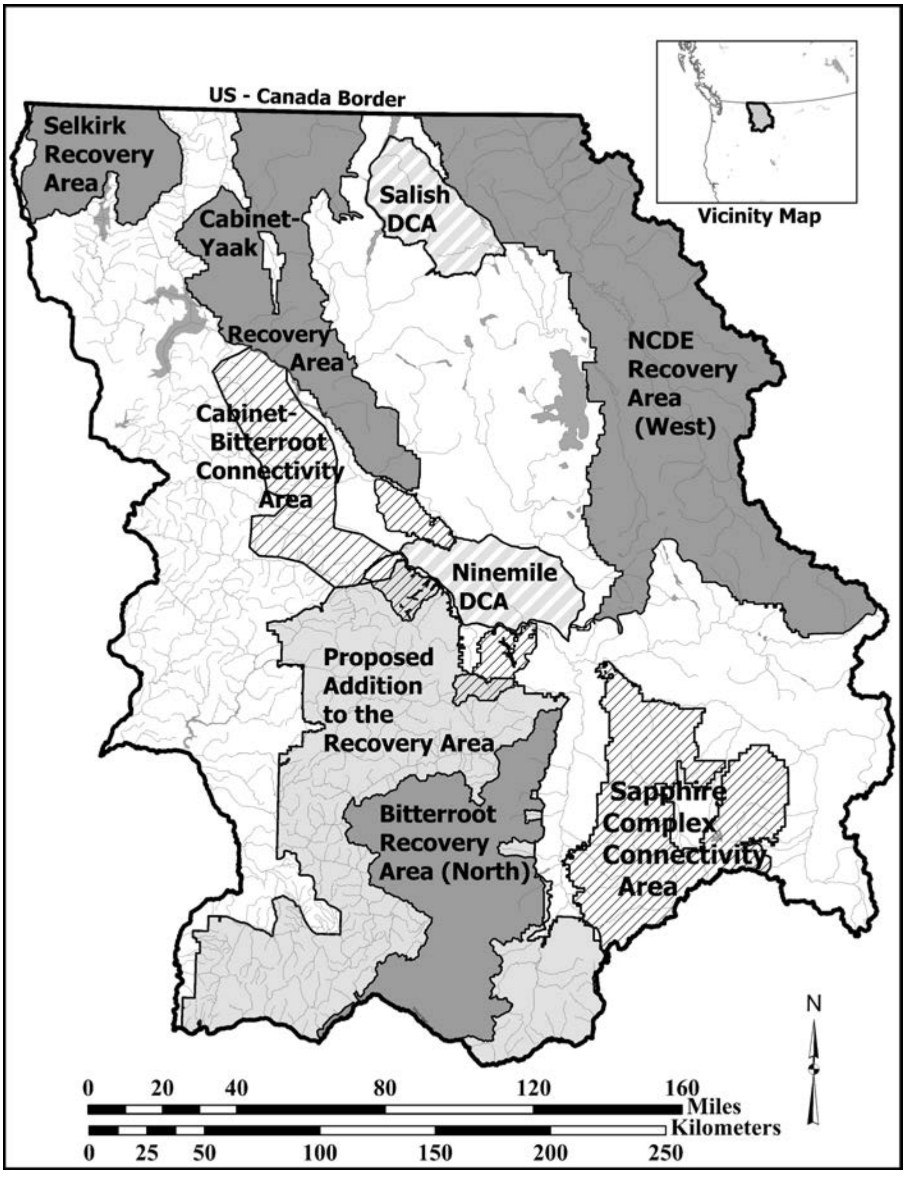

FIGURE 1. The study area in northern Idaho and western Montana showing the locations of Grizzly Bear Recovery Areas and Demographic Connectivity Areas for adult female Grizzly Bears (designated by the U.S. Fish and Wildlife Service), potential connectivity habitats for Grizzly Bears, and areas proposed for addition to the Bitterroot Recovery Area.

and we evaluate and discuss our results in the context of the demographic model.

Methods

Study Area

The study area (108,750 km^2) includes all or significant portions of 4 Grizzly Bear Recovery Areas, 2 Demographic Connectivity Areas and 5 other potential connectivity areas (USFWS 2000; Proctor and others 2015; Peck and others 2017) as shown in Figure 1. Most of the study area is located in Region 1 of the US Forest Service (USFS), with the exception of the area in northeast Washington in Region 6. It includes the portion of the Bitterroot Recovery Area most

TABLE 1. Variables for Grizzly Bear den sites in North American interior populations.

Area	Variables	Source
Yellowstone	elevation, aspect, land cover, remote	Craighead and Craighead (1972)
Yellowstone	elevation, slope, aspect, land cover	Judd and others (1986)
Yellowstone	elevation, slope, aspect, land cover	Podruzny and others (2002)
NCDE-East Front	elevation, slope, aspect, land cover	Aune and Kasworm (1989)
NCDE-Swan Range	elevation, slope, aspect, land cover	Mace and Waller (1997)
NCDE-Mission Range	elevation, slope, aspect, land cover	Servheen and Klaver (1983)
Cabinet-Yaak	elevation, slope, aspect, land cover	Kasworm and others (2021)
Selkirk Range	elevation, slope, aspect, land cover	Kasworm and others (2021)
Alberta-Banff NP	elevation, slope, aspect, land cover, water	Vroom and others (1977)
Alberta-Southwest	elevation, slope, aspect, land cover, remote, water	Pigeon and others (2014)
British Columbia	elevation, land cover, remote	Ciarniello and others (2005)
Alaska-Denali NP	elevation, slope, aspect, land cover, snow, water	Libal and others (2011)
Alaska	elevation, slope, aspect, land cover, snow	Sorum and others (2019)
Alaska-South Central	elevation, slope, land cover	Miller (1990)
Yukon-Southwest	slope, land cover	Libal and others (2012)
Northwest Territories	slope, aspect, land cover	Smereka and others (2017)
Northwest Territories	slope, aspect, land cover	McLoughlin and others (2002)

likely to receive immigrating Grizzly Bears from the NCDE. Under the influence of the maritime climate pattern this area generally receives greater annual precipitation than areas east of the Continental Divide and south of the Salmon River. A major defining feature is the Bitterroot Range, which runs most of the length of the study area from north to south.

Literature Review

In addition to the review by Linnell and others (2000), we reviewed 30 published papers and reports on denning in North American Grizzly Bears to identify parameters for modeling. The most frequently reported descriptive statistics were elevation, slope, aspect, and landcover as shown in Table 1. Some authors discussed snow for its insulative and security values (Craighead and Craighead 1972), its association with the seasonal availability and unavailability of natural food sources across autumn, winter, and spring (Pigeon and others 2016), as a trigger for final den entry (Craighead and Craighead 1972; Servheen and Klaver 1983), and as a factor in denning chronologies (Graham and Stenhouse 2014). There are no significant differences in den-site selection and construction between male and female Grizzly Bears (Aune and Kasworm 1989; Mace and Waller 1997; Pigeon and others 2016) and we did not differentiate between the sexes for our analyses. We derived descriptive information for the verified den sites for slope, elevation, aspect, land cover, and remoteness as shown in Table 2, Figure 2, and Figure 3 by obtaining values for each den site from ArcGIS Pro and LANDFIRE EVT and calculating minimum and maximum values, the mean, the standard deviation, and the range (mean ± 1 standard deviation). We assumed that Grizzly Bears in our study area would select den sites in higher terrain with relatively steep slopes, away from close proximity to human habitations and areas with high human activity, and away from water bodies.

Den Locations

Verified Grizzly Bear den site locations (n = 364) were provided through data sharing agreements with the USFWS and the Montana Department of Fish, Wildlife and Parks

TABLE 2. Descriptive statistics for the verified den sites (n = 362). DISTRSA = distance to roads and ski areas; DISTW = distance to water.

Variable	Min/Max	Mean	SD	Range (± 1SD)
Elevation (m)	1051.3/2426.4	1836.5	221.9	1614.6–2058.4
Slope (°)	3.2/56.0	28.6	8.98	19.6–37.6
DISTRSA (m)	6.2/14595.0	1960.2	1941.0	56.8–3901.2
DISTW (M)	–/2284	721.9	391.7	330.2–1113.6

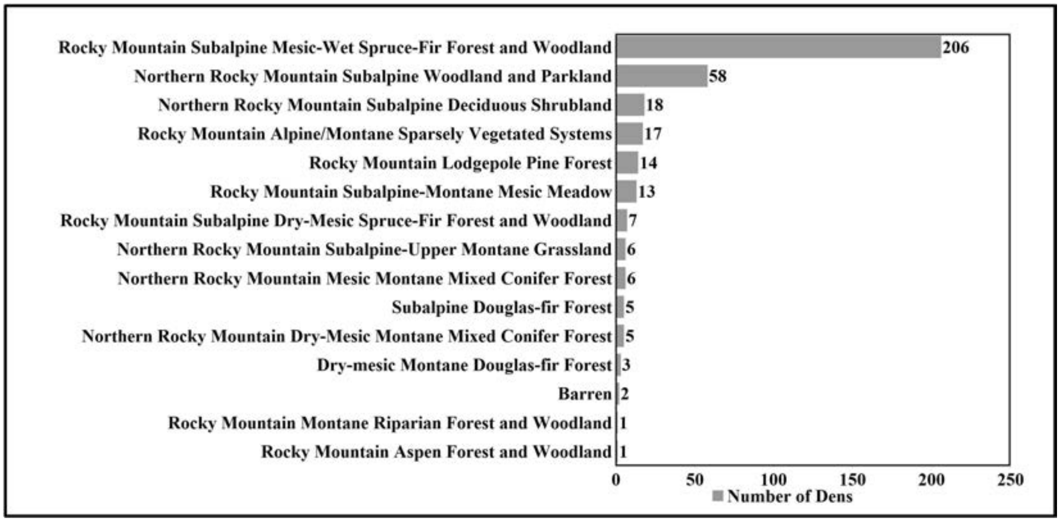

FIGURE 2. Vegetative cover types at verified den sites ($n = 362$) derived from LANDFIRE EVT. Very few dens were located in barren totally open sites. Most den sites were located in forested terrain in subalpine mesic-wet spruce-fir forest and woodland.

(MDFWP). Because the Grizzly Bear is a federally protected species, we agreed the coordinates of the locations would not be shared or displayed in figures. The locations come from 4 isolated population areas: the western half of the Northern Continental Divide Ecosystem (NCDE West), the Cabinet Mountains, Yaak River-Purcell Mountains and the Selkirk Mountains and come primarily from bears radio-collared for population-trend monitoring from 1985–2019 (Mace and Waller 1997; Costello and others 2016; Kasworm and others 2021). Site-by-site visual analysis using Google Earth Pro revealed 2 atypical locations that were removed from further evaluation, resulting in a study sample of $n = 362$.

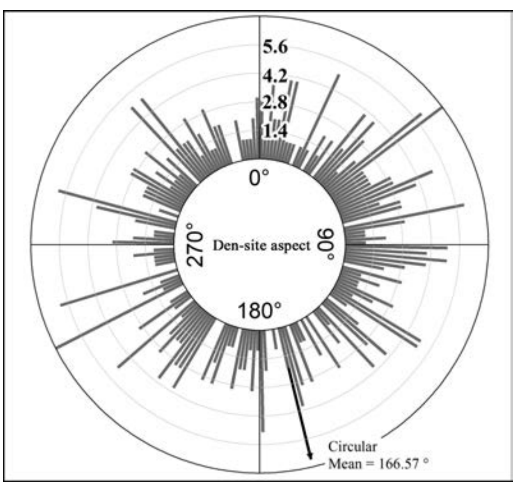

FIGURE 3. Aspect of verified den sites ($n = 362$). Grizzly Bear dens in the study area were located at all aspects, suggesting that topographic roughness and local patterns of snow accumulation play a role, as some southern aspects are shaded by higher surrounding terrain.

Aspect

We found that the distribution of aspect was not uniform. We used the Rayleigh test of uniformity in the R circular package (Rao Jammala-Madaka and SenGupta 2001). A test statistic of 0.0965 with P-value of $0.0342 < 0.05$ for a circular mean of 166.5738 degrees disproves the null hypothesis that there is a uniform distribution. We did not assess multimodal distribution.

Spatial Autocorrelation of Dens

We tested the 362 den sites for spatial autocorrelation using Moran's I test in ArcGIS Pro (ESRI 2020). The resultant z-score of 31.77 indicates that there is <1% probability ($p = 0.000$) that the clustered pattern is the result of random chance. Den sites are often naturally clustered, with use of the same area by the same bear in consecutive years owing to den-area fidelity (Aune and Kasworm 1989; Pigeon 2014), and clusters have also been documented from multiple bears contemporaneously. Other factors may be a lack of sufficiently secure and dispersed denning habitat. We developed a model using spatially rarified den locations and compared AUC (area under curve, Jimenez-Valdere 2012) and TSS (true skill statistic, Allouche and others 2006) values to a 6-variable model run with the 362 den locations. The rarified model was based on removing spatial autocorrelation from 5 den clusters after outliers were removed. We developed autocorrelation distances using the incremental autocorrelation tool in ArcGIS Pro. First peak z-score values of the 5 ecosystems averaged ($\bar{x} = 5.6$ km). We used this lag distance in the SDM toolbox for spatial rarefaction. This process reduced the number of points from 362 to 92. The model using all 362 dens had an AUC score of 0.884 and a TSS of 0.467, whereas the spatially rarified dens had a lower AUC (0.85) and a higher TSS (0.54). Warren and others (2019) found that model prediction based on withheld occurrences has questionable reliability for estimation of the interactions between environmental gradients and habitat suitability. Based on this information and the test scores, we retained all 362 dens in subsequent models. The number of dens that are detected is a small fraction of the total dens, as only a small percentage of the population is radio-collared. Significant reduction of the sample size would reduce the amount of variation captured by the data set.

Model Development

Maxent (Phillips and others 2004) was used to develop a series of models. We used the default 10,000 background sample points and retained them throughout the process for consistency. Low-elevation heavily human-populated areas were included to show variation across the large landscape and for contrast between suitable and unsuitable denning habitat (Saupe and others 2012). Model results were evaluated using AUC, TSS, percent contribution of the individual variables, and visually.

Environmental Variable Creation and Selection

We developed and selected a set of 16 rasters with 10-m resolution depicting the environmental variables we used in Maxent, as shown in Table 3. Continuous variables were re-projected to WGS 84 then converted to an identical extent and cell location using the Project Raster to Template tool from the Marine Geospatial Ecology Toolset (MGET, Roberts and others 2010). We resampled categorical variables to 10 m using the "nearest" parameter to preserve values, then ran them through MGET for alignment with the continuous environmental variables.

Snow and Trended Elevation

The average annual snow accumulation for the years 1981–2010 was extracted from PRISM (Daly and others 2020) raster data. We created two 10-m downscaled versions using ClimateNA (Wang and others 2016) and by inverse distance weighting. We included snow as an environmental variable for initial model testing. However, ideal snow depths have not been documented in relation to Grizzly Bear denning, and precipitation and snow are difficult to model with any specificity in mountainous terrain (Larson and others 2011). The snow variable also had high predictive power, which resulted in misleading model values. Daly and others (1994) established a precipitation-elevation relationship, and we found that elevation provided essentially the same information with similar model results as snow accumulation. We eliminated both of the snow-accumulation variables and adopted a modified (trend surface) elevation raster based on the following rationale. The study area increases in base elevation from the northwest to the southeast, with elevations varying from 222 m at the confluence of the Snake and Clearwater Rivers to 1950 m near Butte, Montana. Known den sites are clustered in the northern and eastern portion of the study area where Grizzly Bear research studies are focused. Model runs using an elevation variable resulted in suitable denning habitat being projected to much lower elevations than one would biologically expect in the southeastern portion of the study area. To compensate for elevation differences across the study area, we developed a trended elevation variable with base elevations adjusted using points spaced 500 m–1 km apart on major rivers. The trended elevation model produced better results except along the Snake River, where the large elevation

TABLE 3. Continuous raster layers used for modeling.

Terrain features	Precipitation	Land cover	Remoteness	Water
Elevation prepared for hydrology (m); Trended elevation	Total annual snow accumulation (800 m)	LANDFIRE EVT	Distance from open roads and downhill ski areas (m)	Distance from lakes, wetlands, running water (m)
Slope (°) 5x5 filter; 11x11 filter (1ha); basic	Total annual snow depth (10 m)	Forest/rock, sparsely vegetated from LANDFIRE		Wetness accumulation
Aspect				
Topographic position index				
Roughness 3x3 filter; 11x11filter (1 ha); 37x37 filter (1 km^2)				

difference in the Hells Canyon area caused an anomaly in the trended surface, giving an appearance of relatively high elevations at the top of the canyon. We reduced the study area extent to eliminate this anomaly.

Distance from Roads, Downhill Ski Resorts, and Water

As a proxy for remoteness and disturbance from human activity, we created a 10-m raster of distance from roads, motorized trails, and downhill ski areas. Open roads and motorized trail data were extracted from the USFS MUMV data and roads data for state lands in Idaho and Montana. Downhill ski areas were extracted or recreated from ski area parcel polygons (USFS Region 1). Open roads, motorized trails, and downhill ski areas were rasterized and a distance surface was created. Initial model runs created a raster surface with a buffer like change in values at $\approx$ 1206 m. There was an $\approx$ 0.15 drop in probability at less than 1206-m distance at similar elevations compared to beyond the 1206-m boundary, as shown in Figure 4 and Figure 5.

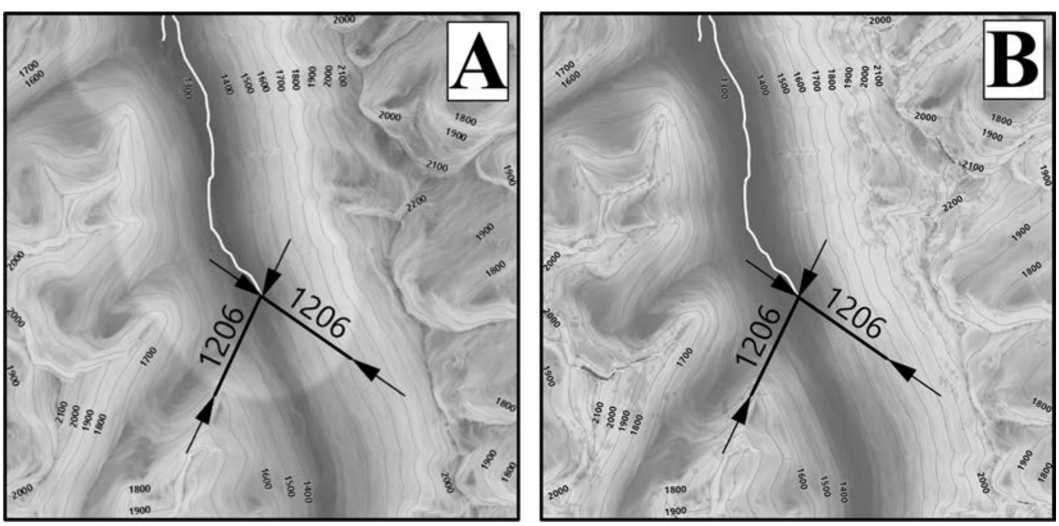

FIGURE 4. Denning probability in relation to roads. As shown in A, distances $\leq$1206m from a road (white line) had a higher denning probability per pixel than the corresponding pixels in the adjusted surface. A slight drop in probability >1206m from roads was assumed due to practically no sampling effort in remote locations. This was compensated for in the final model, and as shown in B there was no significant change.

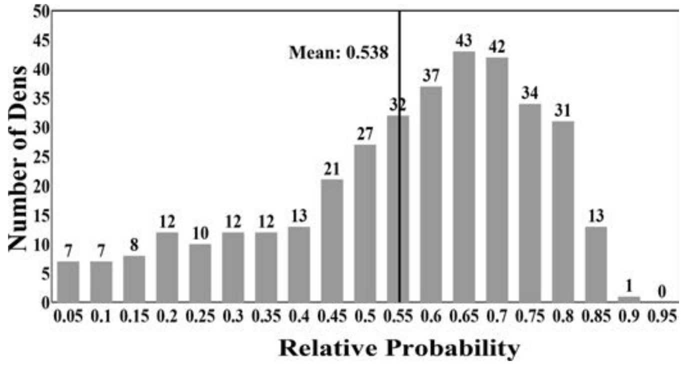

FIGURE 5. Distribution of relative probabilities for Model13_VEG. The majority of dens occur at higher model values with a negative skew, showing fewer dens occurring in the extended left tail in lower-quality habitats.

The denning probability decrease beyond 1206 m was likely associated with sampling bias resulting in a small sample size ($n = 4$) from the interior of the Bob Marshall Wilderness because Grizzly Bear capture areas are located in more productive and accessible areas (Costello and others 2016; Metzgar and Bader 1992). Denning suitability may decline in interior roadless areas based on factors other than roads, and this is accounted for in the other model parameters. Podruzny and others (2002) and Judd and others (1986) concluded that denning habitat is not a limiting factor in the primarily roadless Yellowstone Recovery Area. We assumed that denning habitat is not limiting on the NCDE Grizzly Bear population and that Grizzly Bears have a similar response in the large roadless areas. Distances >1206 m from open roads, the approximate peak in the histogram of den distances from roads as shown in Figure 6, were changed to 1206 m as a constant. Fixing distance to road at 1206 m effectively removed roads as a significant variable within large wilderness, national park, or other roadless areas, so that the probability of selection in these habitats is primarily based on the other variables, consistent with Podruzny and others (2002) and Sorum and others (2019), who did not include roads as a variable. Pigeon and others (2014) used a 1-km circular filter to calculate road densities. A zero value would occur in areas ≥1.128 km from a road, which roughly corresponds to the 1206-m distance from roads where our verified den numbers reached their maximum. Without the adjustment, den selection probabilities >1206 m would occur at higher elevations, other factors

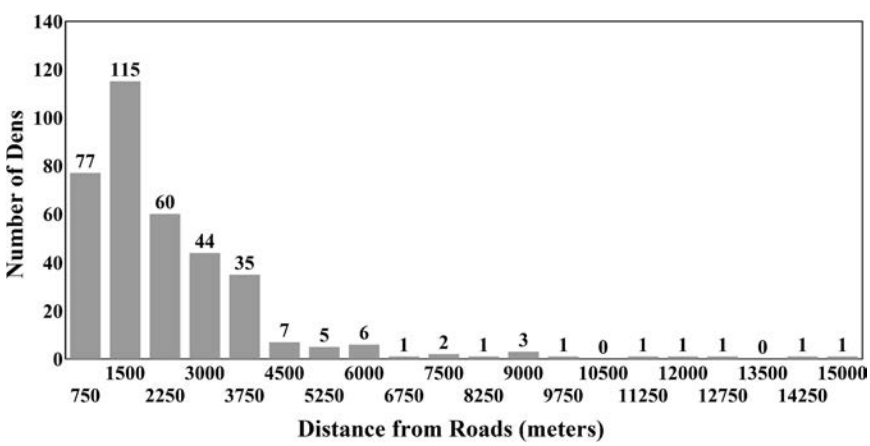

FIGURE 6. Distance from open roads for the verified den sites ($n = 362$). Most den sites were ≥1.5 km from open roads, consistent with the denning literature.

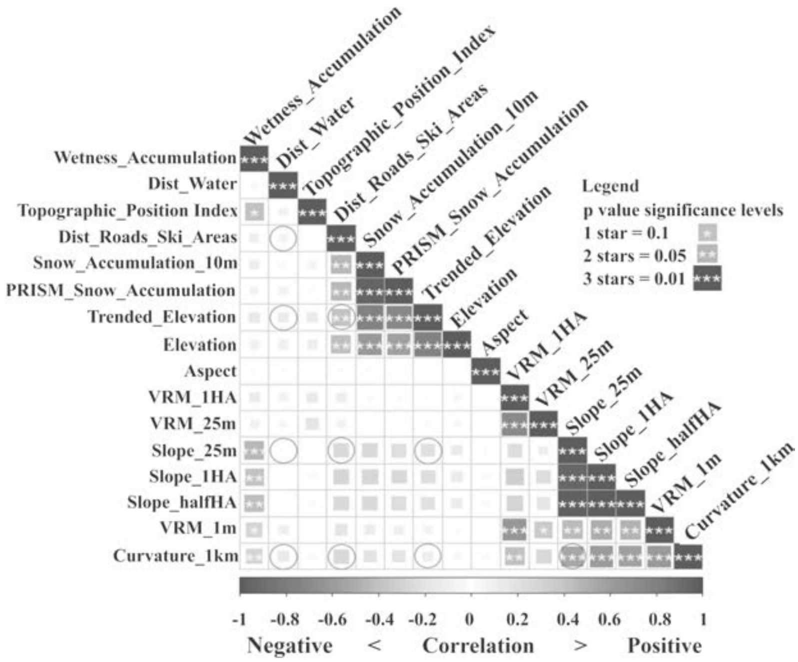

FIGURE 7. Correlation matrix showing the continuous environmental variables used to determine model parameters and significance values.

being equal, than within the 1206-m cutoff. For avoidance of water we used distance from water bodies. Combining rasterized National Wetland Inventory water bodies (lakes and wetlands) with rivers and streams (USGS 2004), we created a distance from water raster using the Euclidean Distance tool in ArcGIS Pro.

Land Cover

A ≤10-m land-cover classification was not available for the study area, so we resampled the LANDFIRE 30-m vegetation classification data to 10 m using 'nearest' to maintain values to make the data compatible with Maxent. Using ArcGIS Pro, we attached vegetation type attributes from the LANDFIRE dataset to the 362 den locations. Ninety-five percent of the verified den locations (n = 343) lay in the forested classifications and 5% of den locations (n =19) fell in the barren rock and sparsely vegetated classification groups. Rock and sparsely vegetated classifications mostly occur at the highest elevations. Adding the forest/non-forest-sparse vegetation variable reduced overestimation of the relative probability of den selection in rocky and open high-elevation habitats and was more consistent with the literature review and the site-by-site visual analysis.

Standard Deviation of Curvature

We created a standard deviation of curvature raster with a 500-m radius (Ironside and others 2018) to identify highly variable areas of the landscape. This also allowed for identification of convex and concave slope complexes.

Correlation Testing

We tested the 16 continuous variables for correlation using a Pearson Correlation Matrix in R Project as illustrated in Figure 7 and shown in Table 3. Most selected variable pairs lacked significance at the ≤ 0.1 P value. Exceptions included the Slope_25 m (standard slope calculation from ArcGIS) paired with SD_Curvature_1 km and Trended Elevation paired with the Distance from Roads and Ski Area variable. The Slope_25 m/SD_Curvature_1 km pair was positively correlated because many areas with steep slopes are rough, whereas areas with low slope values usually occur in relatively flat areas with low topographical roughness. When distance from roads and downhill ski areas increases, trended elevation also increases because most roads are located in valley bottoms or sidehills and are not generally constructed on ridgelines.

Although the Wetness Accumulation variable showed significant negative correlations with the other variables and would normally be included in a model run, comparing Wetness Accumulation to Distance from Water suggested that there was no contribution of Wetness Accumulation to the model. Distance from water had a contribution of 1.6% and was retained.

Model Evaluation

Using the raster layers and the verified dataset, we developed and tested 17 models with differing combinations of variables, reporting statistical scores for the top 3. We used AUC and TSS to evaluate model fitness. AUC is the area under the Receiver Operating Characteristic plot. AUC values range from 0 to 1 with 0 indicating all predictions are wrong and 1 indicating all predictions are right. Values of TSS range from –1 to 0 and 0 to +1 with zero being co-equivalent to randomness with values trending towards 1 indicating a better model.

Projection of Buffered Polygons (MCP) versus Using the Entire Study Area

To assess the value of projecting a localized model to the entire study area, we compared a restricted background model projection to running the model over the entire study area. Minimum Convex Polygons (MCP) were created around verified den sites from the 4 Grizzly Bear population areas. The MCPs were then buffered 6.3 km based on the radius of an average 125-km^2 female grizzly home range (Mace and Waller 1997) expressed as a circle to encompass the range of environmental variables for females with dens at the edge of the MCP.

These areas were sampled with the default 10,000 background points and projected to the entire study area. The projected model had a lower AUC (0.846) than the model that was run over the entire study area (AUC = 0.88). We chose the un-projected model based on a slightly higher AUC and the fact that the selected environmental predictors in the final model are fairly consistent throughout the study area. Comparing similar AUC scores may be misleading (Jimenez-Valdere 2012). The higher score of the un-projected model may have been due to the increased variability of environmental predictors in a larger landscape or a function of the random sampling of background data points. Morales and others (2017) cited several papers raising the issue that default parameters may produce over- or under-fitted results and that Maxent parameters used in research papers were not published. We eliminated parameters used to develop Maxent models to reduce complexity and eliminate issues caused by base elevation difference, snow shadows, and lack of den locations in more remote areas owing to capture bias. We kept the regularization parameter at 1 for consistency after testing a model using a parameter of 0.1 showing little difference. Data was un-projected (WGS 84). A bias file was incorporated to compensate for the change in raster cell area with latitude.

We found a combination of linear and quadratic feature parameters created optimal models. Using hinge features only produced a similar model to our Model13_VEG but with a slightly lower AUC so it was eliminated. We eliminated the Extrapolate, Do Clamping, and Fade by Clamping parameters to keep the model simple. We selected Model13_VEG based on acceptable AUC and TSS Scores and the inclusion of the standard deviation of curvature for a 1-km radius raster. The den sites have a wide ecological amplitude as shown in the histogram of relative probabilities in Figure 7. The majority of dens (82.1%) occur at higher model values with a negative skew showing fewer dens occurring in the extended left tail. Our selected top model was classified by binning by percentile into 4 categories: Not Denning Habitat, Low, Medium, and High, and the ranges of relative model probabilities for the categories are shown in Table 4.

Analysis

We used the denning results for the NCDE West as a baseline for a rough comparison with the Bitterroot analysis unit as the NCDE Recovery Area is believed to be at or near K (Costello and others 2016) and there are similarities in habitat security and productivity (Boyce and Waller 2003). The NCDE West analysis unit is 67.4% of the Recovery Area. The current estimated n = 1069 (USFWS 2021) includes a

TABLE 4. Relative probability classification used for Model13_VEG.

Relative probability	Number of dens	Percent	Category
0–0.17	27	7.5	Not denning
0.17–0.34	38	10.5	Low
0.34–0.6	102	28.2	Medium
0.6–1.0	195	53.9	High

larger Demographic Monitoring Area and assuming ≈ 85% of the population resides within the Recovery Area (*n* ≈ 900) and assuming equal distribution, ≈ 600 Grizzly Bears reside in the NCDE West. We also reviewed our results in the context of previous Grizzly Bear habitat studies and estimates of K (Merrill and others 1999; Carroll and others 2000; Hogg and others 2001; Boyce and Waller 2003; Mowat and others 2013). The NCDE Conservation Strategy habitat management standards define secure core habitat as areas >500 m from an open road and at least 10 km^2 in area. Using these metrics for secure core, we evaluated the current habitat situation in the 2 DCAs and the other identified potential linkage areas.

Results

We selected Model13_Veg with slope, trended elevation, land cover, distance to roads, downhill ski areas and water, and standard deviation of curvature at 1 km as our best model and the results are shown in Tables 5–7, and Figure 8. The highest quality denning habitats comprise <5% of the study area. The results were consistent with those most often reported in the denning literature, and this model shows the highest probability denning habitat in areas with suitable slopes (range), position on the landscape, and distance from open roads. Although they had comparable AUC/TSS, we chose Model13_VEG with the curvature variable over aspect because at a large landscape level bears select den sites on relatively equal aspects. We eliminated the Three Principal Components model based on a visual inspection which showed it was too generalized and had a lower AUC than Model13_VEG.

We found support for the demographic model for population connectivity in that denning and secure core habitats are present to abundant in the potential connectivity areas, with the exception of the Salish DCA where there were just a few small, secure core areas that are spatially disjunct. The Sapphire Complex, where there have been persistent verified observations of Grizzly Bears and where berry-producing shrubs important to Grizzly Bears are abundant (Hogg and others 2001) has the largest amount of secure core habitat >500 m from an open road (2486 km^2) in the largest sizes as shown in Table 7.

The Ninemile DCA has contiguous denning habitat likely sufficient to support a small resident population and the presence of female Grizzly Bears with cubs has been verified (Jonkel 2021). The area between the CYE and BE along the northern Bitterroot Divide has high public ownership and secure core areas within short distance of each other. The USFS (2020:83) describes the area as containing year-round suitable habitat similar to that within recovery zones, which could be used for either short-term movements or for low population densities between recovery zones.

Measured against the NCDE West metrics it is reasonable to assume that suitable denning habitats in the Bitterroot analysis unit could

TABLE 5. AUC and TSS scores for top 3 models.

Model	Variables	AUC	TSS	Comments
Model13_VEG	Trended elevation, slope, DISTRSA, DISTW, standard deviation of curvature	0.885	0.4559	Selected model
Model13_VEG2	Trended elevation, slope, aspect, DISTRA, DISTW	0.884	0.4678	AUC and TSS very similar to selected model, aspect contributed little
Three Principal Components	Principal components created from trended elevation, DISTRA, DISTW, standard deviation of curvature	0.868	0.5294	Very generalized

TABLE 6. Spatial results (km^2) and percentages by analysis unit.

Analysis unit	Total area	No denning	Low	Medium	High
Study Area	108,750	61,039 (56.1)	26,590 (24.5)	15,821 (14.5)	5270 (4.8)
Bitterroot	22,694	7075 (31.2)	8476 (37.3)	5694 (25.1)	1448 (6.4)
NCDE West	15,575	5917 (38.0)	3857 (24.8)	3892 (25.0)	1898 (12.2)
Cabinet-Yaak	6688	2688 (40.2)	1837 (27.5)	1432 (21.4)	729 (10.9)
Sapphire Complex	5801	1773 (30.6)	1960 (33.8)	1602 (27.6)	465 (8.0)
Selkirk	2788	1128 (40.5)	749 (26.9)	627 (22.5)	284 (10.2)
Ninemile DCA	2096	1230 (58.7)	517 (24.7)	263 (12.5)	86 (4.1)
Salish DCA	1902	1548 (81.4)	295 (15.5)	51 (2.7)	8 (0.4)
Ninemile-Bitterroot-2	658	241 (36.7)	241 (36.7)	148 (22.5)	28 (4.3)
Ninemile-Cabinet-Yaak	482	120 (24.8)	176 (36.5)	136 (28.2)	51 (10.5)
Ninemile-Bitterroot-1	482	182 (37.9)	169 (35.1)	97 (20.2)	33 (6.9)
Ninemile-NCDE West	18	7 (39.5)	9 (50.6)	2 (9.4)	0.1 (0.6)

support over 500 Grizzly Bears, which would satisfy the denning requirements for population estimates of $n = 321–445$ (Boyce and Waller 2003; Mowat and others 2013) calculated for smaller areas than our analysis unit. There is abundant spring, summer, and autumn Grizzly Bear habitat (Merrill and others 1999; Carroll and others 2001; Boyce and Waller 2003), including broad spatial distribution of key berry-producing plants known to be important to Grizzly Bears (Hogg and others 2001).

Our results were consistent with the literature regarding declining selection in the highest, rockiest and most exposed terrain scoured free of soil and snow. Vegetative cover is an important factor owing to the stability the roots provide to the structure of the den. Grizzly Bears line the floor of their dens with vegetative matter including boughs and needles from spruce (*Picea*), fir (*Abies*), and where available, Beargrass (*Xerophyllum tenax*) (Craighead and Craighead 1972; Jonkel 1987; Servheen and Klaver 1983). Bedding materials consist of what is available at the den site and not on any preference (Judd and others 1986). Although Grizzly Bears have long claws that enable digging for food and den excavation, they cannot dig through solid bedrock. These 2 factors mitigate against denning in areas of rock devoid of nearby vegetative groundcover. The model may slightly overestimate denning suitability in the highest elevations of the Selway-Bitterroot Wilderness and Glacier National Park unless there is a relative abundance of natural cave-like openings. This is because LANDFIRE EVT did not have classifications for alpine fell-fields or alpine bedrock and scree. At the scale of the study area we considered this insignificant.

TABLE 7. Secure Core Habitat (km^2) in previously identified Connectivity Areas.

Area	Small (10–40 km^2)	Larger (>40 km^2)	All
Sapphire Complex	198	2732	2931
CYE-Bitterroot Connector	469	524	993
Ninemile DCA	115	551	666
Salish DCA	76	0	76

Our results showed den selection away from open roads, consistent with the literature on road impacts on Grizzly Bear den selection, population growth, and density as shown in Table 8.

DISCUSSION

We suggest there is merit to incorporating additional areas in the Bitterroot Recovery Area, particularly north of the Lochsa River and US 12, as we found relatively abundant denning habitat while Carroll and others (2001) and Merrill and others (1999) identified this area as having large concentrations of contiguous high-quality Grizzly Bear habitats in spring, summer, and autumn.

In comparison to other Grizzly Bear denning studies (Vroom and others 1977; Podruzny and others 2002; Pigeon and others 2014; Mace and Waller 1997), our results were consistent with regard to slope angle, elevation/snow load, and ground cover. We found Grizzly Bear dens at all aspects, as did Aune and Kasworm (1989), Judd and others (1986), Podruzny and others (2002), Libal and others (2011). In terms of study area composition containing both protected areas such as designated wilderness and national parks and a high road-density component, our

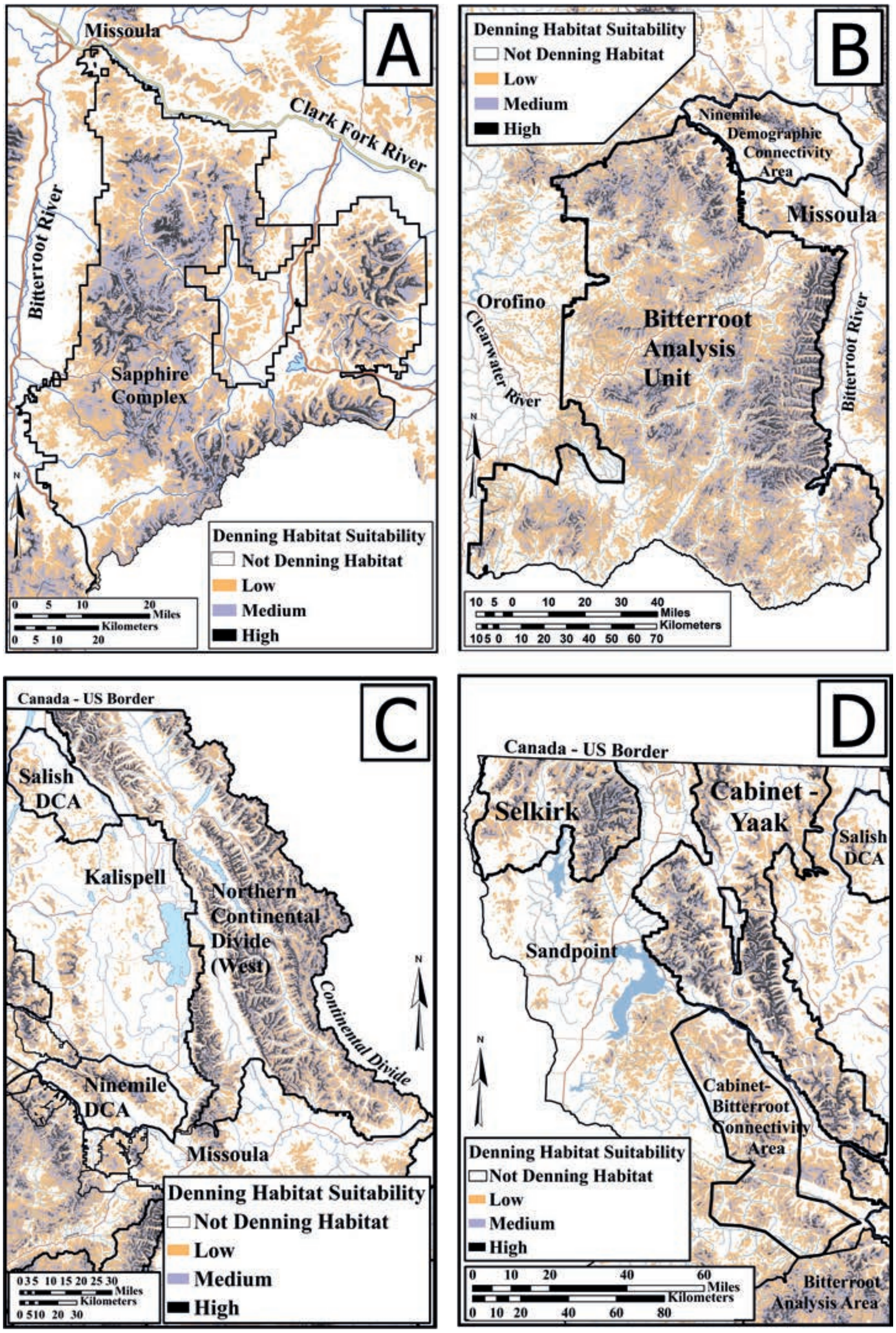

FIGURE 8. Denning suitability results for the analysis units showing the selection for steep slopes, higher elevation, and distance from open roads and water bodies. Medium- and high-suitability habitats are of the most direct importance to demographic connectivity and management.

TABLE 8. Road density impacts on Grizzly Bears. Sources: Boulanger and Stenhouse (2014); Pigeon and others (2014); Proctor and others (2019).

Road density (km/km^2)	Adult female survival rate	Population growth rate	Density bears/1000 km^2	Den selection probability
0	≈100%	Positive	30	N/A
0.6	95%	Static	≈ 30	70%
1.2	85%	Negative	10	30%
1.4	75%	Rapid decline	Lower	N/A
1.6	< 75%	Rapid decline	Lower	N/A
2.0	Lower	Rapid decline	Very low	≈ 0%

study area compares to the Alberta study area defined by Pigeon and others (2014) and the British Columbia study area of Ciarniello and others (2005), with similar results regarding den selection away from roads and areas with higher human activity. Linnell and others (2000) report that Grizzly and Brown Bears generally select dens 1–2 km from open roads and our 362 verified dens had a mean distance of 1.96km from open roads and downhill ski areas. By contrast, the Podruzny and others (2002) greater Yellowstone study area, though very similar in size, is primarily remote habitat in roadless wilderness and national park, and they did not assess the impact of open roads on den-site selection. The few roads in their study area are mostly in valley bottoms below denning range and are closed half of the year by snowfall. The greater Yellowstone ecosystem also differs significantly from our study area in climate, elevation, vegetation, and primary food sources (Boyce and Waller 2000).

In our study area, data for ungulate winter ranges and Grizzly Bear spring habitat were not seamless and had inconsistent methods and definitions. Future analyses could determine if denning habitats in close proximity to these resources may or may not be more desirable.

Our results confirm the presence of significant denning habitat in areas previously identified as potential connectivity areas. The primary difference is that our analysis was based on residential occupancy by female Grizzly Bears rather than transitory males.

Requisites for the Demographic Model of Dispersal

(1) *Denning Habitat and Secure Core within Dispersal Distances.*—The availability of denning habitats within secure core areas is a fundamental requirement of the demographic model. These are areas where females can survive and raise offspring who become a source of dispersals.

We suggest Bear Management Units (BMUs) be identified within key connectivity habitats with standards to maintain all currently secure core habitat. Standards based upon scientific data maintained 68% of a BMU in secure core habitat (USFS 1995). The secure core areas should not shift as this disrupts female Grizzly Bears who learn that areas are secure and pass a significant portion of the maternal home range to their female offspring so that sudden shifts in security conditions would not be conducive to the demographic model.

In connectivity habitats, the larger secure areas should be spatially distributed within known dispersal distances for female Grizzly Bears (Mattson and others 1996). Based on the dispersal information in Graves and others (2014), Proctor and others (2004), and McLellan and Hovey (2001), secure core areas 0–10 km apart might work for 64 and 74% of dispersing females, respectively, with 0 representing females who do not disperse from their home ranges, whereas core areas 20–30 km apart might work for 22 and 19% of dispersing females, respectively. How Grizzly Bears might best move between and within secure core awaits a future analysis based on habitat quality, least-cost path analysis, and circuit theory, as in Proctor and others (2015).

(2) *Highway Passage Structures.*—Highway and rail transportation corridors are features that fragment Grizzly Bear populations into isolated demographic units (Proctor and others 2002). The 2 biggest obstacles to female Grizzly Bear dispersal in the study area are the Interstate 90 corridor and US Highway 93 from Whitefish to Darby, Montana. Although a female grizzly with

cubs has been documented south of I-90 (Jonkel 2021), the big issue is the number of bears that choose to disperse plus the limited number of crossing structures where bears can safely cross highways. These are essential to successful demographic dispersion of Grizzly Bears into historic habitats (Ford and others 2017). Having "multiple shots on goal" would provide a higher likelihood of success.

Expansion in the distribution of an established population and dispersals are driven by male bears (Itoh and others 2012; Peck and others 2017; Eriksen and others 2018), and they are the most likely to first use new denning areas. In the connectivity areas and the Bitterroot ecosystem, in the early phase of recolonization, competition for prime denning sites should be minimal. However, because Grizzly Bears rarely re-use dens and dens are often clustered in prime areas (Aune and Kasworm 1989), there could be increased competition for denning sites within smaller demographic units.

We identified ranges of suitable denning habitats, but a few Grizzly Bears may select den sites outside these ranges. There are several factors that can lead to poor den-site selection in lower terrain. Both literature (Servheen and Klaver 1983) and anecdotal information report that orphaned cubs with no experience have denned in valley bottoms or did not den. Sick or injured bears may be forced to select poor den sites owing to an inability to travel or dig. As hunting seasons overlap the denning process, some Grizzly Bears have stayed out late in the autumn feeding on gut piles. By the time they move to den, the snow depth at higher elevations may force selection of lower-elevation sites.

Future Prospects

Recreation activity has the potential to disturb or harm denning Grizzly Bears (Linnell and others 2002). For example, Hilderbrand and others (2000) document a female Grizzly Bear and cubs killed by an avalanche triggered by snowmobiles. Based on the unsupported assumption that bears are largely immune to impacts from both motorized and non-motorized winter recreation, the National Forest Plan amendments for NCDE Grizzly Bear habitat management (USFS 2018) have no management standards specific to Grizzly Bears during the denning period. Evidence suggests that land managers develop standards to more adequately protect this resource.

Climate change will affect the denning process and den-site selection. Evan and Eisenman (2021) predict that interior areas like the Canadian Rockies and the northern Rocky Mountains of the US will see less change in the rate of snowpack melt and the timing of spring runoff than coastal areas, whereas climate models for Montana show that even in areas >1800 m a 12% reduction in snow water equivalent is expected (Whitlock and others 2017). Musselman and others (2021) found 34% of snow monitoring stations in western North America exhibit increasing winter snowmelt trends. Pigeon and others (2016) note snow depth is associated with food availability and postulate climate change effects are likely to shorten the denning period for Grizzly Bears. A key factor may be the rate of change and whether plant phenology adapts at the same rate. A possible consequence of earlier den emergence is that natural foods may be largely unavailable, leading some bears to seek out human-related foods, which leads to management actions and increased mortality. If dependable snowpack levels rise in elevation, it may pose additional challenges for species dependent on higher-elevation remote areas in the Rocky Mountains for denning and hunting, including Grizzly Bears, Wolverine (*Gulo gulo*), and Lynx (*Lynx canadensis*).

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Literature Cited

*Allendorf FW, Metzgar LH, Horejsi BL, Mattson DJ, Craighead FL. 2019. The status of the Grizzly Bear and conservation of biological diversity in the

* Unpublished

northern Rocky Mountains. Missoula, MT: FLB Citizen Task Force. 21 p. https://www.montanaforestplan.org.

Allouche O, Tsoar A, Kadmon R. 2006. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43:1223–1232.

Aune K, Kasworm W. 1989. Final Report. East Front Grizzly Bear Study. Helena, MT: Montana Department of Fish, Wildlife and Parks. 352 p.

Boyce M, Waller J. 2003. Grizzly Bears for the Bitterroot: Predicting potential distribution and abundance. Wildlife Society Bulletin 31:670–683.

Boyce M, Blanchard BM, Knight RR, Servheen C. 2001. Population viability for Grizzly Bears: A critical review. International Association for Bear Research and Management Monograph Series Number 4. 45 p.

Carroll C, Noss RF, Paquet PC. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecological Applications 11:961–980.

Ciarniello LM, Boyce MS, Heard DC, Seip DR. 2005. Denning behavior and den site selection of Grizzly Bears along the Parsnip River, British Columbia, Canada. Ursus 16:47–58.

Costello CM, Mace RD, Roberts L. 2016. Grizzly Bear demographics in the Northern Continental Divide Ecosystem, Montana: Research results (2004–2014) and suggested techniques for management of mortality. Helena, MT: Montana Department of Fish, Wildlife and Parks. 121 p.

Craighead FC, Craighead JJ. 1972. Grizzly Bear prehibernation and denning activities as determined by radio-tracking. Wildlife Monographs 32. 35p.

Craighead FL, Vyse ER. 1996. Brown/Grizzly Bear metapopulations. In: McCullough DR, editor. Metapopulations and wildlife conservation. Washington, DC: Island Press. p 325–351.

Daly C, National Center for Atmospheric Research Staff (editors). 2020. The Climate Data Guide: PRISM High-Resolution Spatial Climate Data for the United States: Max/min temp, dewpoint, precipitation.

Daly C, Neilson R, Phillips D. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33:140–158.

Eriksen A, Wabakken P, Maartmann E, Zimmermann B. 2018. Den site selection by male Brown Bears at the population's expansion front. PLoS ONE 13(8):e0202653.

[ESRI] Environmental Systems Research Institute. 2020. ArcGIS Pro Version 2.5. ESRI Inc.

Evan A, Eisenman I. 2021. A mechanism for regional variations in snowpack melt under rising temperature. Nature Climate Change. https://doi.org/10.1038/s41558-021-00996-w.

Ford AT, Barrueto M, Clevenger AP. 2017. Road mitigation is a demographic filter for Grizzly Bears. Wildlife Society Bulletin 41:712–719.

Graham K, Stenhouse GB. 2014. Home range, movements and denning chronology of the Grizzly Bear (*Ursus arctos*) in West-Central Alberta. Canadian Field Naturalist 128:223–234.

Graves T, Chandler RB, Royle JA, Beier P, Kendall KC. 2014. Estimating landscape resistance to dispersal. Landscape Ecology 29:1201–1211.

Hanski I, Gilpin M. 1991. Metapopulation dynamics: Brief history and conceptual domain. Biological Journal of the Linnean Society 42:3–16.

Hilderbrand GV, Lewis LL, Larrivee J, Farley SD. 2000. A denning Brown Bear, *Ursus arctos*, sow and two cubs killed in an avalanche on the Kenai Peninsula, Alaska. Canadian Field Naturalist 114:498.

Hogg JT, Weaver NS, Craighead JJ, Steele BM, Pokorny ML, Mahr MH, Redmond RL, Fisher FB. 2001. Vegetation patterns in the Salmon-Selway ecosystem: An improved land cover classification using Landsat TM imagery and wilderness botanical surveys. Missoula, MT: Craighead Wildlife-Wildlands Institute Monograph Number 2. 98 p.

Ironside KE, Mattson DJ, Arundal T, Theimer T, Holton B, Peters M, Edwards TC Jr, Hansen J. 2018. Geomorphometry in landscape ecology: Issues of scale, physiography, and application. Environment and Ecology Research 6:397–412.

Itoh T, Sato Y, Kobayashi K, Mano T, Iwata R. 2012. Effective dispersal of Brown Bears (*Ursus arctos*) in eastern Hokkaido, inferred from analyses of mitochondrial DNA and microsatellites. Mammal Study 37:29–41.

Jammala-Madaka S, SenGupta A. 2001. Circular statistics. In: Topics in circular statistics. CRAN.R-project. Environmental Modelling and Software 25:1197–1207.

Jimenez-Valdere A. 2012. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. Global Ecology and Biogeography 21:498–507.

Jonkel CJ. 1987. Brown Bear. In: Novak M, Baker JA, Obbard ME, Malloch B, editors. Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources. p 457–473.

*Jonkel J. 2021. Verified Grizzly Bear activity FWP R2 outlying areas. Missoula, MT: Montana Department of Fish, Wildlife and Parks, Region 2. 95 p.

Judd SL, Knight RR, Blanchard BM. 1986. Denning of Grizzly Bears in the Yellowstone National Park area. International Conference Bear Management and Research 6:111–117.

Kasworm WF, Radandt TG, Teisberg JE, Welander A, Proctor M, Cooley H. 2021. Cabinet-Yaak Grizzly

Bear Recovery Area 2020 Research and Monitoring Progress Report. Missoula, MT: US Fish and Wildlife Service.

Larson RP, Byrne JM, Johnson DL, Letts MG, Kienzie SW. 2011. Modelling climate change impacts on spring runoff for the Rocky Mountains of Montana and Alberta I: Model development, calibration and historical analysis. Canadian Water Resources Journal 36:17–34.

Libal NS, Belant JL, Leopold BD, Wang G, Owen PA. 2011. Despotism and risk of infanticide influence Grizzly Bear den-site selection. PLoS ONE 6(9):e2.

Libal NS, Belant J, Maraj R, Leopold B. 2012. Microscale den-site selection of Grizzly Bears in southwestern Yukon. Ursus 23:226–230.

Linnell JDC, Swenson JE, Andersen R, Barnes B. 2002. How vulnerable are denning bears to disturbance? Wildlife Society Bulletin 28:400–413.

Mace RD, Waller JS. 1997. Denning ecology of Grizzly Bears in the Swan Mountains, Montana. In: Final Report: Grizzly Bear Ecology in the Swan Mountains, Montana. Helena, MT: Montana Department of Fish, Wildlife and Parks. p 36–41.

Mattson D, Herrero S, Wright RG, Pease CM. 1996. Designing and managing protected areas for Grizzly Bears: how much is enough? In: Wright RG, editor. National Parks and Protected Areas: Their role in environmental protection, Cambridge, MA: Blackwell Science. p 133–164.

McLellan BN, Hovey FW. 2001. Natal dispersal of Grizzly Bears. Canadian Journal of Zoology 79:838–844.

McLoughlin PD, Cluff HD, Messier F. 2002. Denning ecology of barren-ground Grizzly Bears in the central Arctic. Journal of Mammalogy 83:188–198.

Merrill T, Mattson DJ, Wright RG, Quigley HB. 1999. Defining landscapes suitable for restoration of Grizzly Bears *Ursus arctos* in Idaho. Biological Conservation 87:231–248.

Metzgar LH, Bader M. 1992. Large mammal predators in the northern Rockies: Grizzly Bears and their habitat. Northwest Environmental Journal 8:231–233.

Miller SD. 1990. Denning ecology of Brown Bears in southcentral Alaska and comparisons with a sympatric Black Bear population. International Conference on Bear Research and Management 8:279–287.

Morales NS, Fernández IC, Baca-González V. 2017. Maxent's parameter configuration and small samples: Are we paying attention to recommendations? A systematic review. PeerJ, 5, e3093. https://doi.org/10.7717/peerj.3093.

Mowat G, Heard DC, Schwarz CJ. 2013. Predicting Grizzly Bear density in western North America. PLoS One 8(12).

Musselman KN, Addor N, Vano JA, Molotch NP. 2021. Winter melt trends portend widespread declines in snow water resources. Nature Climate Change: DOI:10.1038/ s41558-021-01014-9.

Peck CP, Van Manen FT, Costello CM, Haroldson MA, Landenburger LA, Roberts LL, Bjornlie DD, Mace RD. 2017. Potential paths for male-mediated gene flow to and from an isolated Grizzly Bear population. Ecosphere 8:1–17.

Phillips SJ, Dudik M, Schapire RE. 2004. A maximum entropy approach to species distribution modeling. In: Proceedings of the 21st International Conference on Machine Learning. New York, NY: ACM Press. p 655–662

Pigeon KE, Nielsen SE, Stenhouse GB, Côté SD. 2014. Den selection by Grizzly Bears on a managed landscape. Journal of Mammalogy 95:559–571.

Pigeon KE, Stenhouse G, Côté SD. 2016. Drivers of hibernation: Linking food and weather to denning behaviour of Grizzly Bears. Behavioral Ecology and Sociobiology 70:1745–1754.

Podruzny SR, Cherry S, Schwartz CC, Landenburger LA. 2002. Grizzly Bear denning and potential conflict areas in the greater Yellowstone ecosystem. Ursus 13:19–28.

Proctor MF, McLellan BN, Strobeck C. 2002. Population fragmentation of Grizzly Bears in southeastern British Columbia, Canada. Ursus 13:153–160.

Proctor MF, McLellan BN, Strobeck C, Barclay RMR. 2004. Gender-specific dispersal distances of Grizzly Bears estimated by genetic analysis. Canadian Journal of Zoology 82:1108–1118.

Proctor MF, Nielsen SE, Kasworm WF, Servheen C, Radandt TG, Machutchon AG, Boyce MS. 2015. Grizzly Bear connectivity mapping in the Canada-United States trans-border region. Journal of Wildlife Management 79:544–558.

Proctor M, McLellan BN, Stenhouse GB, Mowat G, Lamb CT, Boyce MS. 2019. Effects of roads and motorized human access on Grizzly Bear populations in British Columbia and Alberta, Canada. Ursus (30e2):16–39.

Roberts JJ, Best BD, Dunn DC, Triml EA, Halpin PN. 2010. Marine Geospatial Ecology Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R, Maching Learning Crash Course. Retrieved from https://developers. google.com/ machine-learning/crash-course/classification/roc-and-auc.

Saupe EE, Barve V, Myers CE, Soberón J, Barve N, Hensz AT, Peterson HL, Owens A, Lira-Noriega A. 2012. Variation in niche and distribution model performance: The need for a priori assessment of key causal factors. Ecological Modelling 237–238:11–22.

Servheen C, Klaver R. 1983. Grizzly Bear dens and denning activity in the Mission and Rattlesnake Mountains, Montana. International Conference on Bear Research and Management 5:201–207.

Servheen C, Waller JS, Sandstrom P. 2001. Identification and management of linkage zones for Grizzly Bears between the large blocks of public land in the Northern Rocky Mountains. ICOET 2001 A Time for Action Proceedings:161–169.

Smereka CA, Edwards M, Pongracz J, Branigan M. 2017. Den selection by barren-ground Grizzly Bears, Mackenzie Delta, Northwest Territories. Polar Biology 40:503–516.

Sorum MS, Joly K, Wells AG, Cameron MD, Hilderbrand GV, Gustine DD. 2019. Den-site characteristics and selection by Brown Bears (*Ursus arctos*) in the central Brooks Range of Alaska. Ecosphere 10:e02822.

[USFS] US Forest Service. 1995. Amendment 19, Flathead National Forest Plan.

[USFS] US Forest Service. 2018. Forest Plan amendments to incorporate habitat management direction for the Northern Continental Divide Ecosystem Grizzly Bear population. Kalispell, MT. 148 p.

[USFS] US Forest Service. 2020. Redd-Bull Environmental Assessment. Lolo National Forest.

[USFWS] US Fish and Wildlife Service 2000. Grizzly Bear recovery in the Bitterroot ecosystem. 292 p.

[USFWS] US Fish and Wildlife Service. 2018. NCDE Subcommittee. Conservation strategy for the Grizzly Bear in the Northern Continental Divide Ecosystem. 170p. + appendices.

[USFWS] US Fish and Wildlife Service. 2021. Biological report for the Grizzly Bear (*Ursus arctos horribilis*) in the Lower-48 States. Version 1.1, 31 January 2021. Missoula, MT. 370 p.

[USGS] US Geological Survey. 2004. National Hydrography Dataset. Reston, VA: USDI, USGS. Reston, VA.

Vroom GW, Herrero S, Ogilvie RT. 1976. The ecology of winter den sites of Grizzly Bears in Banff National Park, Alberta. International Conference on Bear Research and Management 3:321–330.

Wang T, Hamann A, Spittlehouse D, Carroll C. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. PLoS ONE 11(6): e0156720.

Warren DL, Matzke NJ, Iglesias TL. 2019. Evaluating presence-only species distribution models with discrimination accuracy is uninformative for many applications. Journal of Biogeography 47:167–180.

Whitlock C, Cross WF, Maxwell B, Silverman N, Wade AA. 2017. 2017 Montana Climate Assessment. Montana State University and University of Montana, Montana Institute on Ecosystems. 318 p.

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