1	RH: BADER AND SIERACKI: GRIZZLY DENNING AND CONNECTIVITY
2	GRIZZLY BEAR DENNING HABITAT AND DEMOGRAPHIC CONNECTIVITY IN
3	NORTHERN IDAHO AND WESTERN MONTANA
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10	ABSTRACT—Grizzly Bears (Ursus arctos) are protected in the contiguous United States
11	under the federal Endangered Species Act. The conservation strategy for the species encourages
12	population connectivity between isolated Grizzly Bear Recovery Areas through Demographic
13	Connectivity Areas. Another goal is reestablishment of a breeding population in the Bitterroot
14	ecosystem through natural immigration. Using the locations of 362 verified Grizzly Bear den
15	sites and Maxent as a resource selection function, we predicted 21,091 km^2 of suitable denning
16	habitats. Terrain features, distance to roads and land cover best explained suitable denning
17	habitats in northern Idaho and western Montana. The results support the demographic model for
18	population connectivity and independent of other factors there is suitable denning habitat for
19	hundreds of Grizzly Bears in the Bitterroot analysis area. We suggest additions to the Bitterroot
20	Grizzly Bear Recovery Area and that more effective motorized access management be applied to
21	demographic connectivity areas.

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23	Key words: Bitterroot ecosystem, demographic connectivity, den sites, denning,
24	dispersal, Grizzly Bear, northern Rockies, secure core, selection
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27	The Grizzly Bear (Ursus arctos) was listed in 1975 as a threatened species under the U.S.
28	Endangered Species Act partially due to isolation and populations in the contiguous U.S. remain
29	isolated (USFWS 2021). Linkage of the isolated Grizzly Bear populations into a genetically-
30	diverse metapopulation (as defined by Hanski and Gilpin 1991) would increase the probability of
31	long-term survival (Allendorf and others 2019; Boyce and others 2001; Servheen and others
32	2001; Craighead and Vyse 1996). Two models have been advanced to achieve this. The male-
33	mediated model for genetic interchange (Peck and others 2017) would maintain genetic diversity
34	based on long distance dispersals of male Grizzly Bears. The demographic model is based on
35	maintaining areas of secure suitable habitats occupied by resident female Grizzly Bears that are
36	within known dispersal distances for females (Mattson and others 1996; Proctor and others
37	2015). Due to the much shorter dispersal distances of female Grizzly Bears (McLelland and
38	Hovey 2001; Proctor and others 2004; Graves and others 2014), the demographic model relies on
39	multi-year dispersals. The Conservation Strategy for Grizzly Bear in the Northern Continental
40	Divide Ecosystem (NCDE, USFWS 2018) designated two Demographic Connectivity Areas
41	(DCAs) to provide habitat for resident female Grizzly Bears as shown in Figure 1.
42	Denning behavior in Grizzly Bears is thought to be an evolutionary adaptation to long
43	winter periods where natural foods are unavailable (Craighead and Craighead 1972). By
44	definition, residential occupancy requires availability of suitable habitats in all four seasons so
45	that the demographic model is dependent upon the presence of suitable denning

46	habitats. Denning habitat for Grizzly Bears has not been previously analyzed across the northern
47	Idaho-western Montana region. We compare our results with other large landscape denning
48	studies in the greater Yellowstone ecosystem (Podruzny and others 2002), Alberta (Pigeon and
49	others 2014) and British Columbia (Ciarniello and others 2005). The central purpose of our study
50	was to identify Grizzly Bear denning habitats within the connectivity areas between Recovery
51	Areas and we evaluate and discuss our results within the context of the demographic model.
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54	METHODS
55	Study Area
56	The study area (108,750km ²) includes all or significant portions of four Grizzly Bear
57	Recovery Areas, two Demographic Connectivity Areas and five other potential connectivity
58	areas (USFWS 2000; Proctor and others 2015; Peck and others 2017) as shown in Figure 1. Most
59	of the study area is located within Region 1 of the US Forest Service (USFS) with the exception
60	of the area in northeast Washington within Region 6. It includes the portion of the Bitterroot
61	Recovery Area most likely to receive immigrating Grizzly Bears from the NCDE. Under the
62	influence of the maritime climate pattern this area generally receives greater annual precipitation
63	than areas east of the Continental Divide and south of the Salmon River. A major defining
64	feature is the Bitterroot Mountain Range which runs most of the length of the study area from
65	north to south.
66	Literature Review
67	In addition to the review by Linnell and others (2000) we reviewed 30 published papers

68 and reports on denning in North American Grizzly Bears to identify parameters for modeling.

69	The most frequently reported descriptive statistics were elevation, slope, aspect and landcover as
70	shown in Table 1. Some authors discussed snow for its insulative and security values (Craighead
71	and Craighead 1972), its association with the availability and unavailability of natural food
72	sources including Autumn and Spring (Pigeon and others 2016), as a trigger for final den entry
73	(Craighead and Craighead 1972; Servheen and Klaver 1983) and as part of denning chronologies
74	(Graham and Stenhouse 2014There are no significant differences in den site selection and
75	construction between male and female Grizzly Bears (Aune and Kasworm 1989; Mace and
76	Waller 1997; Pigeon and others 2016) and we did not differentiate between the sexes for our
77	analyses. We derived descriptive information for the verified den sites for slope, elevation,
78	aspect, land cover and remoteness shown in Table 2, Figures 2 and 3 by obtaining values for
79	each den site from ArcGIS Pro and LANDFIRE EVT and calculating minimum and maximum
80	values, the mean, the standard deviation and the range (mean \pm one standard deviation). We
81	assumed that Grizzly Bears in our study area would select den sites in higher terrain with
82	relatively steep slopes, away from close proximity to human habitations and areas with high
83	human activity and away from water bodies.
84	Den Locations
85	Verified Grizzly Bear den site locations ($n = 364$) were provided through data sharing
86	agreements with the USFWS and the Montana Department of Fish, Wildlife and Parks
87	(MDFWP). Due to the status of the Grizzly Bear as a federally protected species we agreed the
88	coordinates of the locations would not be shared or displayed in figures. The locations come
89	from four isolated population areas: the western half of the Northern Continental Divide
90	Ecosystem (NCDE West), the Cabinet Mountains, Yaak River-Purcell Mountains and the Selkirk
91	Mountains and come primarily from bears radio-collared for population trend monitoring from

92	1985-2019 (Mace and Waller 1997; Costello and others 2016; Kasworm and others 2021). Site
93	by site visual analysis using Google Earth Pro revealed two atypical locations that were removed
94	from further evaluation, resulting in study sample $n = 362$.
95	Aspect
96	We found that the distribution of aspect was not uniform. We used the Rayleigh Test of
97	Uniformity in the R circular package (Rao Jammala-Madaka and SenGupta 2001). A test
98	statistic of 0.0965 with P-value of $0.0342 < 0.05$ for a circular mean of 166.5738 degrees
99	disproves the null hypothesis that there is a uniform distribution. We did not assess multimodal
100	distribution.
101	Spatial Autocorrelation of Dens
102	We tested the 362 den sites for spatial autocorrelation using Moran's I test in ArcGIS Pro
103	(ESRI 2020). The resultant z-score of 31.77 indicates that there is $< 1\%$ probability (p = 0.000)
104	that the clustered pattern is the result of random chance. Den sites are often naturally clustered
105	due to use of the same area by the same bear in consecutive years owing to den area fidelity
106	(Aune and Kasworm 1989; Pigeon 2014) and clusters have also been documented from multiple
107	bears contemporaneously. Other factors may be a lack of sufficiently secure and dispersed
108	denning habitat. We developed a model using spatially rarified den locations and compared AUC
109	(area under curve, Jimenez-Valdere 2012) and TSS (True Skill Statistic, Allouche and others
110	2006) values to a six variable model run with the 362 den locations. The rarified model was
111	based on removing spatial autocorrelation from five den clusters after outliers were removed.
112	Autocorrelation distances were developed using the incremental autocorrelation tool in ArcGIS
113	Pro. First peak z-score values of the five ecosystems were averaged ($\bar{x} = 5.6$ km). We used this
114	lag distance in the SDM toolbox for spatial rarefaction. This process reduced the number of

115	points from 362 to 92. The model using all 362 dens had an AUC score of 0.884 and a TSS of
116	0.467 while the spatially rarified dens had a lower AUC (0.85) and a higher TSS (0.54). Warren
117	and others (2019) found that model prediction based on withheld occurrences has questionable
118	reliability for estimation of the interactions between environmental gradients and habitat
119	suitability. Based on this and the test scores we retained all 362 dens in subsequent models. The
120	number of dens that are detected is a small fraction of the total dens as a small percentage of the
121	populations are radio-collared. Significant reduction of the sample size would reduce the amount
122	of variation captured by the data set.
123	Model Development
124	Maxent (Phillips and others 2004) was used to develop a series of models. We used the
125	default 10,000 background sample points and kept them throughout the process for consistency.
126	Low elevation heavily human populated areas were included to show variation across the large
127	landscape and for contrast between suitable and unsuitable denning habitat (Saupe and others
128	2012). Model results were evaluated using AUC, TSS, Percent Contribution of the individual
129	variables and visually.
130	Environmental Variable Creation and Selection
131	We developed and selected a set of 16 rasters with 10m resolution depicting the
132	environmental variables we used in Maxent as shown in Table 3. Continuous variables were re-
133	projected to WGS 84 then converted to an identical extent and cell location using the Project
134	Raster to Template tool from the Marine Geospatial Ecology Toolset (MGET, Roberts and others
135	2010). Categorical variables were resampled to 10m using the "nearest" parameter to preserve
136	values then run through MGET for alignment with the continuous environmental variables.
137	Snow and Trended Elevation

138	The average annual snow accumulation from the years 1981-2010 was extracted from
139	PRISM (Daly and others 2020) raster data. Two 10m downscaled versions were created using
140	ClimateNA (Wang and others 2016) and by inverse distance weighting. We included snow as an
141	environmental variable for initial model testing. However, ideal snow depths have not been
142	documented in relation to Grizzly Bear denning and precipitation and snow are difficult to model
143	with any specificity in mountainous terrain (Larson and others 2013). The snow variable also had
144	high predictive power which led to misleading model values. Daly and others (1994) established
145	a precipitation-elevation relationship and we found that elevation provided essentially the same
146	information with similar model results as snow accumulation. We eliminated both of the snow
147	accumulation variables and adopted a modified (trend surface) elevation raster based on the
148	following rationale. The study area increases in base elevation from the northwest to the
149	southeast with elevations varying from 222m at the confluence of the Snake and Clearwater
150	Rivers to 1950m near Butte, Montana. Known den sites are clustered in the north and eastern
151	portion of the study area where Grizzly Bear research studies are focused. Model runs using an
152	elevation variable resulted in suitable denning habitat being projected to much lower elevations
153	than one would biologically expect in the southeastern portion of the study area. To compensate
154	for elevation differences across the study area we developed a trended elevation variable with
155	base elevations adjusted using points spaced 500m-1km apart on major rivers. The trended
156	elevation model produced better results except along the Snake River where the large elevation
157	difference in the Hells Canyon area caused an anomaly in the trended surface, giving an
158	appearance of relatively high elevations at the top of the canyon. The study area extent was
159	reduced to eliminate this anomaly.

160 Distance from Roads, Downhill Ski Resorts and Water

161	As a proxy for remoteness and disturbance from human activity we created a distance from roads,
162	motorized trails and downhill ski areas 10m raster. Open roads and motorized trail data were
163	extracted from the USFS MUMV data and roads data for state lands in Idaho and Montana. Downhill
164	ski areas were extracted or recreated from ski area parcel polygons (USFS Region 1). Open roads,
165	motorized trails and downhill ski areas were rasterized and a distance surface was created. Initial
166	model runs created a raster surface with a buffer like change in values at \approx 1206m. There was an \approx
167	0.15 drop in probability between the inside of the 1206m distance at similar elevations and outside
168	past the 1206m boundary as shown in Figures 4 and 5. The denning probability decrease past 1206m
169	was likely associated with sampling bias resulting in a small sample size $(n = 4)$ from the interior of
170	the Bob Marshall Wilderness due to Grizzly Bear capture areas being located in more productive and
171	accessible areas (Costello and others 2016; Metzgar and Bader 1992). Denning suitability may
172	decline in interior roadless areas based on factors other than roads and this is accounted for in the
173	other model parameters. Podruzny and others (2002) and Judd and others (1986) concluded that
174	denning habitat is not a limiting factor in the primarily roadless Yellowstone Recovery Area. We
175	assumed that denning habitat is not limiting on the NCDE Grizzly Bear population and that Grizzly
176	Bears have a similar response in the large roadless areas. Distances > 1206m from open roads, the
177	approximate peak in the histogram_of den distances from roads as shown in Figure 6 were changed to
178	1206m as a constant. Fixing distance to road at 1206m effectively removed roads as a significant
179	variable within large Wilderness, National Park or other roadless areas so that the probability of
180	selection in these habitats is primarily based on the other variables, consistent with Podruzny and
181	others (2002), Sorum and others (2019) who did not include roads as a variable. Pigeon and others
182	(2014) used a 1km circular filter to calculate road densities. A zero value would occur in areas \geq
183	1.128km from a road which roughly corresponds to the 1206m distance from roads where our
184	verified den numbers reached their maximum. Without the adjustment, den selection probabilities >

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186	1206m would occur at higher elevations, other factors being equal, than within the 1206m cutoff. For	
187	avoidance of water we used distance from water bodies. Combining rasterized National Wetland	
188	Inventory water bodies (lakes and wetlands) with rivers and streams (USGS 2004), we created a	
189	distance from water raster using the Euclidean Distance tool in ArcGIS Pro.	
190	Land Cover	
191	A 10m or less land cover classification was not available for the study area so we resampled	
192	the LANDFIRE 30m vegetation classification data to 10m using nearest to maintain values to make	
193	the data compatible with Maxent. Using ArcGIS Pro we attached vegetation type attributes from the	
194	LANDFIRE dataset to the 362 den locations. Ninety-five percent of the verified den locations (n =	
195	343) were in the forested classifications and five percent of den locations (n =19) were in the barren	
196	rock and sparsely vegetated classification groups. Rock and sparsely-vegetated classifications mostly	
197	occur at the highest elevations. Adding the forest/non-forest-sparse vegetation variable reduced	
198	overestimation of the relative probability of den selection in rocky and open high elevation habitats	
199	and was more consistent with the literature review and the site by site visual analysis.	
200	Standard Deviation of Curvature	
201	We created a standard deviation of curvature raster with a 500m radius (Ironside and	
202	others 2018) to identify highly variable areas of the landscape. This also allowed for	
203	identification of convex and concave slope complexes.	
204	Correlation Testing	
205	We tested the 16 continuous variables for correlation using a Pearson Correlation Matrix	
206	in R Project as illustrated in Figure 7 and shown in Table 3. Most selected variable pairs lacked	
207	significance at the \leq 0.1 p values. Exceptions included the Slope_25m (standard slope	
208	calculation from ArcGIS) paired with SD_Curvature_1km and Trended Elevation paired with the	
209	Distance from Roads and Ski Area variable. The Slope 25m/SD_Curvature_1km pair was	

210	positively correlated because many areas with steep slopes are rough while areas with low slope
211	values usually occur in relatively flat areas with low topographical roughness. When distance
212	from roads and downhill ski areas increases, trended elevation also increases because most roads
213	are located in valley bottoms or sidehills and are not generally constructed on ridgelines.
214	While the Wetness Accumulation variable showed significant negative correlations with
215	the other variables and would normally be included in a model run, comparing Wetness
216	Accumulation to Distance from Water indicated that there was no contribution of Wetness
217	Accumulation to the model. Distance from water had a contribution of 1.6% and was retained.
218	Model Evaluation
219	Using the raster layers and the verified data set we developed and tested 17 models with
220	differing combinations of variables, reporting statistical scores for the top three. We used AUC
221	and TSS to evaluate model fitness. AUC is the area under the Receiver Operating Characteristic
222	plot. AUC values range from 0 to 1 with 0 indicating all predictions are wrong and 1 indicating
223	all predictions are right. Values of TSS range from -1 to 0 and 0 to 1 with zero being co-
224	equivalent to randomness with values trending towards 1 indicating a better model.
225	Projection of Buffered Polygons (MCP) vs Using the Entire Study Area
226	To assess the value of projecting a localized model to the entire study area, we compared a
227	restricted background model projection to running the model over the entire study area. Minimum
228	Convex Polygons (MCP) were created around verified den sites from the four Grizzly Bear
229	population areas. The MCPs were then buffered 6.3km based on the radius of an average 125km^2
230	female grizzly home range (Mace and Waller 1997) expressed as a circle to encompass the range of
231	environmental variables for females with dens at the edge of the MCP.
232	These areas were sampled with the default 10,000 background points and projected to the
233	entire study area. The projected model had a lower AUC (0.846) than the model that was run over the

234	entire study area (AUC = 0.88). We chose the un-projected model based on a slightly higher AUC
235	and the fact that the selected environmental predictors in the final model are fairly consistent
236	throughout the study area. Comparing similar AUC scores may be misleading (Jimenez-Valdere
237	2012). The higher score of the un-projected model may have been due to the increased variability of
238	environmental predictors in a larger landscape or a function of the random sampling of background
239	data points. Morales and others (2017) cited several papers raising the issue that default
240	parameters may produce over or under fitted results and that Maxent parameters used in research
241	papers were not published. We eliminated parameters used to develop Maxent models to reduce
242	complexity and eliminate issues caused by base elevation difference, snow shadows and lack of
243	den locations in more remote areas due to capture bias. We kept the regularization parameter at
244	1 for consistency after testing a model using a parameter of 0.1 showing little difference. Data
245	was un-projected (WGS 84). A bias file was incorporated to compensate for the change in raster
246	cell area due to latitude.
247	We found a combination of linear and quadratic feature parameters created optimal
248	models. Using hinge features only produced a similar model to our Model13_VEG but with a
249	slightly lower AUC so it was eliminated. We eliminated the Extrapolate, Do Clamping and
250	Fade by Clamping parameters to keep the model simple. We selected Model13_VEG based on
251	acceptable AUC and TSS Scores and the inclusion of the standard deviation of curvature for a
252	1km radius raster. The den sites have a wide ecological amplitude as shown in the histogram of
253	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 four categories: Not Denning Habitat, Low,
Medium and High and the ranges of relative model probabilities for the categories are shown in

257 Table 4.

258	Analysis
259	We used the denning results for the NCDE West as a baseline for a rough comparison
260	with the Bitterroot analysis unit as the NCDE Recovery Area is believed to be at or near K
261	(Costello and others 2016) and there are similarities in habitat security and productivity (Boyce
262	and Waller 2003). The NCDE West analysis unit is 67.4% of the Recovery Area. The current
263	estimated N = 1069 (USFWS 2021) includes a larger Demographic Monitoring Area and
264	assuming $\approx 85\%$ of the population resides within the Recovery Area (n ≈ 900) and assuming
265	equal distribution, ≈ 600 Grizzly Bears reside in the NCDE West. We also reviewed our results
266	in the context of previous Grizzly Bear habitat studies and estimates of K (Merrill and others
267	1999; Carroll and others 2000; Hogg and others 2001; Boyce and Waller 2003; Mowat and
268	others 2013). The NCDE Conservation Strategy habitat management standards define secure
269	core habitat as areas >500m from an open road and at least 10km ² in area. Using these metrics
270	for secure core we evaluated the current habitat situation in the two DCAs and the other
271	identified potential linkage areas.
272	RESULTS
273	We selected Model13_Veg with slope, trended elevation, land cover, distance to roads,
274	downhill ski areas and water and standard deviation of curvature at 1km as our best model and
275	the results are shown in Tables 5, 6 and 7, and Figure 8. The highest quality denning habitats
276	comprise $< 5\%$ of the study area. The results were consistent with those most often reported in
277	the denning literature and this model shows the highest probability denning habitat in areas with
278	suitable slopes (range), position on the landscape and distance from open roads. While having
278 279	suitable slopes (range), position on the landscape and distance from open roads. While having comparable AUC/TSS, we chose Model13_VEG with the curvature variable over aspect because

281	Three Principal Components Model based on a visual inspection which showed it was too
282	generalized and had a lower AUC than Model13_VEG.
283	We found support for the demographic model for population connectivity in that denning
284	and secure core habitats are present to abundant in the potential connectivity areas with the
285	exception of the Salish DCA where there were just a few small secure core areas which are
286	spatially disjunct. The Sapphire Complex, where there have been persistent verified observations
287	of Grizzly Bears and where berry-producing shrubs important to Grizzly Bears are abundant
288	(Hogg and others 2001) has the largest amount of secure core habitat > 500m from an open road
289	(2486km ²) in the largest sizes as shown in Table 7.
290	The Ninemile DCA has contiguous denning habitat likely sufficient to support a small
291	resident population and the presence of female Grizzly Bears with cubs has been verified (Jonkel
292	2021). The area between the CYE and BE along the northern Bitterroot Divide has high public
293	ownership and secure core areas within short distance of each other. The USFS (2020:83)
294	describes the area as containing year-round suitable habitat similar to that within recovery zones and
295	could be used for either short-term movements or for low population densities between recovery
296	zones.
297	Measured against the NCDE West metrics it is reasonable to assume suitable denning
298	habitats in the Bitterroot analysis unit could support over 500 Grizzly Bears, which would satisfy
299	the denning requirements for population estimates of $N = 321-445$ (Boyce and Waller 2003;
300	Mowat and others 2013) calculated for smaller areas than our analysis unit. There is abundant
301	Spring, Summer and Fall Grizzly Bear habitat (Merrill and others 1999; Carroll and others 2001;
302	Boyce and Waller 2003) including broad spatial distribution of key berry-producing plants
303	known to be important to Grizzly Bears (Hogg and others 2001).

304	Our results were consistent with the literature regarding declining selection in the highest,
305	rockiest and most exposed terrain scoured free of soil and snow. Vegetative cover is an important
306	factor due to the stability the roots provide to the structure of the den. Grizzly Bears line the
307	floor of their dens with vegetative matter including boughs and needles from spruce (Picea), fir
308	(Abies) and where available, beargrass (Xerophyllum tenax) (Craighead and Craighead 1972;
309	Jonkel 1987; Servheen and Klaver 1983). Bedding materials consist of what is available at the
310	den site and not on any preference (Judd and others 1986). While Grizzly Bears have long claws
311	that enable digging for food and den excavation, they cannot dig through solid bedrock. These
312	two factors mitigate against denning in areas of rock devoid of nearby vegetative groundcover.
313	The model may slightly overestimate denning suitability in the highest elevations of the Selway-
314	Bitterroot Wilderness and Glacier National Park unless there is a relative abundance of natural
315	cave-like openings. This is because LANDFIRE EVT did not have classifications for alpine fell-
316	fields or alpine bedrock and scree. At the scale of the study area we considered this insignificant.
317	Our results showed den selection away from open roads, consistent with the literature on
318	road impacts on Grizzly Bear den selection, population growth and density as shown in Table 8.
319	DISCUSSION
320	We suggest there is merit to incorporating additional areas in the Bitterroot Recovery
321	Area, particularly north of the Lochsa River and US 12 as we found relatively abundant denning
322	habitat while Carroll and others (2001) and Merrill and others (1999) identified this area as
323	having large concentrations of contiguous high quality Grizzly Bear habitats in Spring, Summer
324	and Fall.
325	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 in

327	regards to slope angle, elevation/snow load and ground cover. We found Grizzly Bear dens at all
328	aspects, as did Aune and Kasworm (1989), Judd and others (1986), Podruzny and others (2002),
329	Libal and others (2011). In terms of study area composition containing both protected areas such
330	as Wilderness and Parks and a high road density component, our study area compares to the
331	Alberta study area defined by Pigeon and others (2014) and the British Columbia study area of
332	Ciarniello and others (2005), with similar results in regards to den selection away from roads and
333	areas with higher human activity. Linnell and others (2000) report that Grizzly and Brown Bears
334	generally select dens 1-2km from open roads and our 362 verified dens had a mean distance of
335	1.96km from open roads and downhill ski areas. By contrast, the Podruzny and others (2002)
336	greater Yellowstone study area, while very similar in size, is primarily remote habitat in roadless
337	Wilderness and National Park and they did not assess the impact of open roads on den site
338	selection. The few roads in their study area are mostly in valley bottoms below denning range
339	and are closed half of the year by snowfall. The greater Yellowstone ecosystem also differs
340	significantly from our study area in climate, elevation, vegetation and primary food sources
341	(Boyce and Waller 2000).
342	Within our study area, data for ungulate winter ranges and Grizzly Bear spring habitat
343	was not seamless and had inconsistent methods and definitions. Future analyses could determine
344	if denning habitats in close proximity to these resources may or may not be more desirable.
345	Our results confirm the presence of significant denning habitat in areas previously
346	identified as potential connectivity areas. The primary difference is that our analysis was based
347	on residential occupancy by female Grizzly Bears rather than transitory males.
348	
349	We suggest these requisites for the demographic model for dispersal.

350	(1) Denning Habitat and Secure Core within Dispersal Distances—. The availability of denning
351	habitats within secure core areas is a fundamental requirement of the demographic model. These
352	are areas where females can survive and raise offspring who become a source of dispersals.
353	We suggest Bear Management Units (BMUs) be identified within key connectivity
354	habitats with standards to maintain all currently secure core habitat. Standards based upon
355	scientific data maintained 68% of a BMU in secure core habitat (USFS 1995). The secure core
356	areas should not shift as this disrupts female Grizzly Bears who learn that areas are secure and
357	pass a significant portion of the maternal home range to their female offspring so that sudden
358	shifts in security conditions would not be conducive to the demographic model.
359	In connectivity habitats, the larger secure areas should be spatially distributed within
360	known dispersal distances for female Grizzly Bears (Mattson and others 1996). From the
361	dispersal information in Graves and others (2014), Proctor and others (2004) and McLellan and
362	Hovey (2001) secure core areas from 0-10km apart might work for 64% and 74% of dispersing
363	females, respectively with 0 representing females who do not disperse from their home ranges,
364	while core from 20-30km apart might work for 22% and 19% of dispersing females,
365	respectively. How Grizzly Bears might best move between and within secure core awaits a future
366	analysis based on habitat quality, least-cost path analysis and circuit theory, as in Proctor and
367	others (2015).
368	(2) Highway Passage Structures—. Highway and rail transportation corridors are zones that
369	fragment Grizzly Bear populations into isolated demographic units (Proctor and others 2002).
370	The two biggest obstacles to female Grizzly Bear dispersal in the study area are the Interstate 90
371	corridor and US Highway 93 from Whitefish to Darby, Montana. While a female grizzly with
372	cubs south of I-90 has been documented (Jonkel 2021) the big issue is the number of dispersing

373	bears and the number that choose to disperse plus the limited number of crossing structures
374	where bears can safely cross highways. These are essential to successful demographic dispersion
375	of Grizzly Bears into historic habitats (Ford and others 2017). Having "multiple shots on goal"
376	would provide a higher likelihood of success.
377	
378	Expansion in the distribution of an established population and dispersals are driven by
379	male bears (Itoh and others 2012; Peck and others 2017; Eriksen and others 2018) and they are
380	the most likely to first use new denning areas. In the connectivity areas and the Bitterroot
381	ecosystem, in the early phase of recolonization competition for prime denning sites should be
382	minimal. However, since Grizzly Bears rarely re-use dens and dens are often clustered in prime
383	areas (Aune and Kasworm 1989), there could be increased competition for denning sites within
384	smaller demographic units.
385	We identified ranges of suitable denning habitats but a few Grizzly Bears may select den
386	sites outside these ranges. There are several factors which can lead to poor den site selection in
387	lower terrain. Both literature (Servheen and Klaver 1983) and anecdotal information show
388	orphaned cubs with no experience have denned in valley bottoms or did not den. Sick or injured
389	bears may be forced to select poor den sites due to an inability to travel or dig. As hunting
390	seasons overlap the denning process, some Grizzly Bears have stayed out late in the Fall feeding
391	on gut piles. By the time they move to den the snow depth at higher elevations may force
392	selection of lower elevation sites.
393	Future Prospects

Recreation activity has the potential to disturb or harm denning Grizzly Bears (Linnelland others 2002). For example, Hilderbrand and others (2000) document a female Grizzly Bear

396	and cubs killed by an avalanche triggered by snowmobiles. Based on the unsupported
397	assumption that bears are largely immune to impacts from both motorized and non-motorized
398	winter recreation the National Forest Plan amendments for NCDE Grizzly Bear habitat
399	management (USFS 2018) have no management standards specific to Grizzly Bears during the
400	denning period. Evidence suggests land managers develop standards that will more adequately
401	protect this resource.
402	
403	Climate change will affect the denning process and den site selection. Evan and
404	Eisenman (2021) predict that interior areas like the Canadian Rockies and the northern Rocky
405	Mountains of the US will see less change in the rate of snowpack melt and the timing of spring
406	runoff than coastal areas while climate models for Montana show that even in areas > 1800m a
407	12% reduction in snow water equivalent is expected (Whitlock and others 2017). Musselman and
408	others (2021) found 34% of snow monitoring stations in western North America exhibit
409	increasing winter snowmelt trends. Pigeon and others (2016) note snow depth is associated with
410	food availability and postulate climate change effects are likely to shorten the denning period for
411	Grizzly Bears. A key factor may be the rate of change and whether plant phenology adapts at the
412	same rate. A possible consequence of earlier den emergence is that natural foods may be largely
413	unavailable, leading some bears to seek out human related foods, which leads to management
414	actions and increased mortality. If dependable snowpack levels increase in elevation, it may pose
415	additional challenges for species dependent on higher elevation remote areas in the Rocky
416	Mountains for denning and hunting, including Grizzly Bears, wolverine (Gulo gulo) and lynx
417	(Lynx canadensis).

418

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