

1 Towns and Trails Drive Carnivore Connectivity using a Step

2 Selection Approach

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16

17 **Abstract**

18 Global increases in human activity threaten connectivity of animal populations. Protection and

19 restoration of animal movement corridors requires robust models to forecast the effects of human

20 activity on connectivity. Recent advances in the field of animal movement ecology and step

21 selection functions offer new approaches for estimating connectivity. We show how a

22 combination of hidden Markov movement models and step selection functions can be used to
23 simulate realistic movement paths with multiple behavioral states. Simulated paths can be used
24 to generate utilization distributions and estimate changes in connectivity for multiple land use
25 scenarios. We applied movement models to 20 years of grizzly bear (*Ursus arctos*) and gray wolf
26 (*Canis lupus*) data collected in and around Banff National Park, Canada. These carnivores
27 avoided areas near towns in all seasons, avoided areas of high trail density in most seasons, and
28 campgrounds during summer and fall. We simulated movement paths for three landscape
29 scenarios: reference conditions with no anthropogenic development, current conditions, and
30 future conditions with expanded town footprints and trail networks. We counted the number of
31 paths that crossed valley-wide, digital transects through mountain tourist towns of Banff and
32 Canmore, Alberta. We divided current and future crossing rates by the reference crossing rates to
33 estimate connectivity. Current connectivity rates ranged between 7 and 45% of reference values
34 with an average of 21% for grizzly bears and 25% for wolves. Potential town expansion and
35 increased development of trails further decreased connectivity an average of 6% in future
36 scenarios. Anthropogenic developments reduced the amount of available high quality large
37 carnivore habitat in the Bow Valley by an average of 14% under current conditions and 16%
38 under future conditions. Our approach for estimating connectivity provides a robust and flexible
39 method for combining movement models with step selection analyses to estimate connectivity
40 for a variety of species.

41

42 **Key words**

43 connectivity, conservation, corridors, movement ecology, human development, resource
44 selection, step selection, utilization distribution

45 **Introduction**

46 Global increases in human activity threatens wildlife populations and as a result, many
47 conservation programs have increased their focus on ecological connectivity (Hilty et al. 2020).
48 Connectivity analyses of animal movement are frequently used to identify likely dispersal routes
49 between populations (Fattebert et al. 2015, Zeller et al. 2018), seasonal migrations routes (e.g.
50 Fullman et al. 2021), and to highlight natural and anthropogenic pinch points to movement (i.e.
51 wildlife corridors) as priority areas for conservation (Chetkiewicz and Boyce 2009, Suraci et al.
52 2020). Within an animal's home range, wildlife corridors facilitate movements important for
53 reproduction, accessing seasonal resources, and predator-prey processes (Hebblewhite 2005,
54 Panzacchi et al. 2016). At broader scales, connectivity facilitates dispersal (Benz et al. 2016),
55 gene flow, and demographic rescue of subpopulations (Marrotte et al. 2017, Lamb et al. 2020). A
56 wide variety of approaches have been used to estimate connectivity of animal movements, with
57 varying degrees of success (Calabrese and Fagan 2004, Zeller et al. 2018). Emerging techniques
58 in the field of movement ecology offer new opportunities to develop stronger links between
59 movement behavior and estimates of connectivity (e.g. Hooten et al. 2020).

60 Movement models and step selection analyses offer a complementary approach for
61 estimating connectivity either from model predictions (Buderman et al. 2018, Hooten et al. 2020)
62 or from simulated paths (Palmer et al. 2011, Quaglietta and Porto 2019, Zeller et al. 2020). Step
63 selection analyses are a subset of spatial point-process models that are increasingly used to
64 estimate relative selection of resources (Fortin et al. 2005), to understand the effects of human
65 activity on animal movement behaviour (e.g. Suraci et al. 2019), and to create utilization
66 distributions (UDs) that predict spatial variation in intensity of habitat use (Signer et al. 2017).
67 Step selection analyses have become increasingly accessible for practitioners through the

68 development of statistical packages in R (Avgar et al. 2016, Signer et al. 2019, Muff et al. 2020).
69 Several studies have incorporated step selection functions (SSFs) into connectivity analyses by
70 first creating spatial predictions of habitat use and then transforming predictions into resistance
71 layers for cost-distance or circuit theory analyses (Zeller et al. 2018, Brennan et al. 2020, Suraci
72 et al. 2020). Others have used the derived resistance surfaces to simulate animal movements
73 (Quaglietta and Porto 2019, Jayadevan et al. 2020, Zeller et al. 2020). For example, Merkle et al.
74 (2019) simulated movements directly from an SSF to forecast migration routes. Simulated
75 individual-based paths are appealing because they can incorporate sequential, probabilistic
76 movement decisions related to landscape features, speed of travel, and directional persistence
77 (Avgar et al. 2016). Moreover, simulating animal movements is considered the best practice for
78 generate unbiased UD_s from SSFs (Signer et al. 2017). Simulations, while computational
79 intensive, can easily be applied to multiple land use scenarios. Movement simulations from SSFs
80 offer a promising method for assessing the cumulative effects of multiple landscape features on
81 animal movement paths, intensity of use, and connectivity.

82 Realistic simulations need to accommodate the underlying factors that influence animal
83 movement including seasonal (Zeller et al. 2019, Brennan et al. 2020, Zeller et al. 2020) and
84 temporal (Gaynor et al. 2018, Lamb et al. 2020) variability in resource selection and state-
85 specific movement behaviors (Michelot et al. 2016). For example, animals often have low
86 directional persistence and low speed of travel when feeding and resting in slow states and have
87 strong directional persistence and higher speed of travel when travelling in fast states (Fryxell et
88 al. 2008). Such behavioral states are overlooked in classical circuit theory and cost-distance type
89 connectivity models. And failure to incorporate behavioral state into SSFs can lead to biased
90 UD_s, poor estimates of connectivity, and misidentification of wildlife corridors (Abrahms et al.

91 2017). Finally, responses to human activity and estimates of connectivity can vary widely among
92 species (e.g. Rogala et al. 2011, Brennan et al. 2020, Nickel et al. 2020). From a conservation
93 perspective, focussing on the most sensitive species should increase connectivity for most other
94 wildlife (Meurant et al. 2018, Lamb et al. 2020).

95 Large carnivores are an important consideration for landscape-scale measures of
96 connectivity for a number of reasons. First, these iconic and charismatic species are often
97 selected as conservation ‘flagship’ and umbrella species, meaning they hold a particularly deep
98 value for the public and management agencies (Ray et al. 2013). Second, the potential threat of
99 carnivores to human safety requires a detailed understanding of how animals move through
100 human-dominated landscapes (Buchholtz et al. 2020, Lamb et al. 2020). Third, large carnivores
101 have the potential to affect community-level processes through top-down control on prey
102 abundance and thus trophic cascades (Hebblewhite et al. 2005, Hebblewhite and Merrill 2011,
103 Ripple et al. 2014). Consequently, understanding how movements of carnivores are affected by
104 connectivity and corridor design policies (Ford et al. 2020) is an important step towards better
105 management of ecosystem-level process (Terborgh et al. 1999).

106 The novel approaches to quantifying connectivity afforded through SSF-derived
107 simulations may support better land use decision making for carnivore conservation. Here, we
108 focused on assessing carnivore connectivity in a transboundary region of Banff National Park
109 (BNP), AB, Canada where transportation infrastructure, outdoor recreation, and urban areas
110 occupy much of the prime habitat in the valley bottoms of the mountainous landscape. We focus
111 on the movements of grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) because of their
112 management relevance, threatened status, and important ecological roles (e.g. Hebblewhite et al.
113 2005). We used 20 years of grizzly bear and wolf telemetry data to develop seasonal hidden

114 Markov models and SSFs. We simulated animal paths from the movement models and SSFs to
115 assess changes in UDs and connectivity. Based on grizzly bear and wolf responses to human
116 activity in other studies (Whittington et al. 2005, Hebblewhite and Merrill 2008, Lamb et al.
117 2020), we expected grizzly bears and wolves to select linear features as efficient travel routes
118 while avoiding areas near towns and areas with high trail density. We expected avoidance to be
119 most pronounced and connectivity to be lowest during peak tourist visitation in summer. Finally,
120 we expected that connectivity around towns would decrease from current to future conditions
121 due to an expanded town footprint and increased recreational trail density (Gutzwiller et al.
122 2017). Building on the growing field of movement ecology, we provide a flexible approach to
123 generate movement-based estimates of connectivity that can be applied to other taxa and
124 systems.

125

126 **Materials and Methods**

127 **Study area**

128 The study area encompassed 17,450 km² of the Canadian Rockies within and adjacent to BNP
129 (51.2° N, 115.5° W, Appendix S1: Figure S1). We defined the extent of the study area based on
130 movements of radio-collared wolves and grizzly bears monitored from 2000 to 2020. The study
131 area contained rugged topography, short summers and long cold winters. See Whittington et al.
132 (2019) for a description of vegetation and the predator-prey community.

133 The study area contained the tourist towns of Banff and Canmore and several hamlets
134 that occupied the centre of the Bow Valley. Linear features such as the Trans Canada highway, a
135 national railway, and secondary roads bisected the study area. Like many global protected areas
136 (Wittemyer et al. 2008), human activity within the study area increased steadily over the last 20

137 years (Alberta Environment and Parks 2018), with the potential for increasing impacts on
138 wildlife connectivity (Gutzwiller et al. 2017). BNP currently receives over 4 million visitors per
139 year, mostly concentrated in summer. Most anthropogenic developments and recreational
140 activities were concentrated near roads within the Bow Valley. Backcountry areas in the
141 northeastern portion of the study area received minimal human use.

142 **Telemetry data**

143 Researchers fit wolves and grizzly bears with Global Positioning System (GPS) collars to
144 collect data from 2000 to 2020. Researchers captured and collared grizzly bears using a
145 combination of culvert traps and free-range darting and wolves using a net shot from a helicopter
146 under University and Federal government capture and Animal Care permits (see Appendix S1
147 for summary of permits). Researchers programmed most collars to collect GPS locations every
148 two hours. GPS collars had high fix rates with low habitat-induced fix-rate bias (Hebblewhite et
149 al. 2007). We obtained a large sample of locations from both front and backcountry areas (Figure
150 2, Appendix S1: Figures S1 – S3).

151 **Statistical analyses**

152 We used a three stage, individual-based modeling approach to quantify carnivore
153 responses to anthropogenic features and connectivity (Figure 1). Here, we provide an overview
154 of our methods and then provide additional details for each step of the analysis. First, we applied
155 hidden Markov models to animal movement data to predict slow versus fast movement states as
156 well as movement parameters and transition probabilities for both movement states. We
157 associated slow states with feeding or resting behaviour, and fast states with travelling
158 behaviour. Second, we integrated movement states into SSFs, such that each SSF contained
159 interactions between movement state, directional persistence, and movement rates. This enabled

160 us to simulate state-specific movements directly from our SSF. We used results of the SSF to
161 assess responses to anthropogenic features. We also developed home-range scale resource
162 selection function (RSF) models to evaluate scale-dependence of SSF models for connectivity
163 evaluation. Third, we used the combination of hidden Markov models and SSFs with covariates
164 to simulate realistic individual-based movements. We simulated movement paths under three
165 landscape conditions reflecting reference, current, and future levels of anthropogenic
166 development. Reference represented a null model of potential habitat with no anthropogenic
167 development. We compared transect crossing rates and UDs from current and future conditions
168 to reference conditions to estimate connectivity and change in the amount of high-quality habitat
169 for each carnivore.

170 *Movement model*

171 We fit hidden Markov models to grizzly bear and wolf GPS step lengths and turn angles
172 so that we could incorporate movement behaviour into SSFs and to create biologically realistic
173 simulations of animal movement. We used functions from the *moveHMM* package version 1.7 to
174 fit hidden Markov models (Michelot et al. 2016). For each species and season, we fit two-state
175 movement models to reflect slow and fast movements, following previous studies of GPS
176 movement (Fryxell et al. 2008). We used the gamma distribution for step length and the circular
177 von Mises distribution for turn angles (Avgar et al. 2016). We included the cosine of hour as a
178 covariate to allow for diurnal variation in the frequency of slow and fast states. We predicted the
179 probability of being in a fast state for each GPS location, which we then incorporated into the
180 SSF below (Figure 1). We further used parameters from the movement models to simulate
181 movement states, step lengths, and turn angles in the path simulations below.

182

183 *Step and resource selection: responses to development across scales*

184 We developed grizzly bear and wolf SSF and RSF to assess how anthropogenic
185 development, topography, and land cover affected seasonal wolf and grizzly bear movement
186 (Figure 1). One of the challenges of interpreting SSFs is that results can depend on sampling
187 scale, i.e., time between locations (Mahoney et al. 2018). To ensure results of our SSF-based
188 movement models were consistent with third-order within home range processes, we developed
189 complementary RSF models for individual wolf and grizzly bears to evaluate potential scale-
190 dependence in SSF results.

191 The SSF models compared movement and environmental attributes of used steps to
192 matched available locations (Avgar et al. 2016, Signer et al. 2019). We estimated each animal's
193 movement parameters for step length and turn angle. We sampled from these movement
194 parameters to generate random locations around each used location to sample availability. For
195 each animal's step (strata i) we generated $J = 10$ paired random locations. We extracted covariate
196 vectors \mathbf{x}_{ij} for each location and used conditional logistic regression to estimate covariate vector
197 $\boldsymbol{\beta}$.

198 (eq. 1)

199
$$Pr(y_{ij} = 1 | \mathbf{x}_{ij}) = \pi_{ij} = \frac{\exp(\boldsymbol{\beta} \mathbf{x}_{ij})}{\sum_{j=1}^J \exp(\boldsymbol{\beta} \mathbf{x}_{ij})}$$

200 We followed the modelling strategies outlined by Muff et al. (2020) for used-available
201 SSF and RSF designs. We used the Poisson formulation of conditional logistic regression to fit
202 the SSF and included random intercepts for each strata i . We accounted for individual animal
203 variability in selection by including random coefficients for explanatory variables. We set
204 weights for used locations to 1.0 and random locations to 1000, and fixed the variance of the

205 random intercept for strata to 10^4 . We used the R packages amt version 0.0.9 (Signer et al. 2019)
206 to define available locations and glmmTMB version 1.0.1 (Brooks et al. 2017) to estimate the
207 models. We visualized the effects of covariates on the relative probability of selection using
208 relative selection strength (RSS) where $RSS = \exp(\beta x)$ (Avgar et al. 2017).

209 The SSFs included covariates for state-specific speed of travel and directional persistence
210 (Roever et al. 2014, Duchesne et al. 2015). We first predicted the probability of fast state for
211 each used location from the hidden Markov model (section 2.3.1 above, Figure 1). We applied
212 that predicted probability to all paired available locations. Our SSF then included interactions
213 between probability of fast state and the natural logarithm of step length and between probability
214 of fast state and the cosine of turn angle (Avgar et al. 2016). Thus, selection for step lengths
215 (speed) and turn angles (persistence) depended on movement state. The cosine of turn angle
216 reflected a measure of directional persistence with values ranging between -1.0 when animals
217 turned around to 1.0 when they continued in the same direction.

218 We developed RSF models with a ratio of 1:10 used to available locations and sampled
219 available locations within each individual animal's 95% minimum convex polygon. We used
220 logistic regression to fit the RSF and included random intercepts for each animal. We accounted
221 for individual animal variability in selection by including random coefficients for explanatory
222 variables. We set weights for used locations to 1.0 and random locations to 1000, and fixed the
223 variance of the random intercept for strata to 10^4 . We used the R packages amt version 0.0.9
224 (Signer et al. 2019) to define available locations and glmmTMB version 1.0.1 (Brooks et al.
225 2017) to estimate the models. We used the same explanatory variables for both SSF and RSF
226 models. We visually compared parameter estimates for the SSF and RSF models for consistency
227 in responses to anthropogenic development.

228 The SSFs and RSFs included environmental and anthropogenic explanatory variables that
229 were previously found to be important predictors of grizzly bear or wolf resource selection in the
230 Canadian Rockies (Nielsen et al. 2006, Hebblewhite and Merrill 2008, Rogala et al. 2011). To
231 minimize collinearity, we removed explanatory variables that had Pearson correlation
232 coefficients > 0.6 and variance inflation factors > 2.0 . When two variables were highly
233 correlated, we selected the covariate based on biological relevance and predictive power that we
234 assessed with univariate plots. All models contained the same 17 environmental and
235 anthropogenic covariates. Environmental covariates included five land cover classes, elevation
236 (m), the negative cosine of aspect such that south = 1.0 and north = -1.0, slope (degrees),
237 proximity to forest edge (km), proximity to large patch of vegetated habitat greater than 9 km²
238 (Proctor et al. 2015), and an indicator variable for whether the area had burned since 1960. See
239 Appendix S1: Table S2 for details.

240 Covariates for anthropogenic development included proximity to towns (km), proximity
241 to campgrounds (km), density of formal trails (km/km², 500 m radius), and indicator variables
242 for whether the animal was on or off trails and the railway. We classified distance to town based
243 on a digitized aerial photograph of buildings and developed areas within towns. We excluded
244 green spaces and golf courses from the town footprint. We predicted that carnivores would select
245 for trails and the railway as travel routes. We predicted that carnivores would avoid areas near
246 towns, campgrounds, and areas of high trail density, especially in summer during peak visitation
247 (Rogala et al. 2011). We lacked direct measures of human activity so we included an interaction
248 between trail density and the natural logarithm of distance to paved road (km). We assumed that
249 trail use would be highest near trail heads along paved roads (Rogala et al. 2011, Zhai et al.
250 2018). We included an interaction between proximity to town and time of day (cosine of hour)

251 because we expected stronger avoidance of towns during the day compared to the night
252 (Hebblewhite and Merrill 2008). We applied a decay term ($1 - \exp^{-10 * \text{distance}}$) to the distance
253 covariates so that the influence of these features had an asymptote near 500 m (Shepherd and
254 Whittington 2006, Rogala et al. 2011). We scaled all other continuous covariates by their mean
255 and standard deviation to improve model convergence.

256 Animal resource selection and responses to anthropogenic development can vary
257 seasonally. Thus, we defined four seasons and created separate SSF models for each species and
258 season. We defined seasons based on animal movement, plant phenology, and human visitation
259 rates to BNP. We classified *Spring* as May and June which included plant emergence, ungulate
260 parturition, grizzly bear mating, wolf denning, and moderate levels of human activity; *Summer* as
261 July and August during the height of berry season and peak visitation; and *Fall* as September and
262 October when plants have senesced and the study area received moderate levels of visitation, and
263 *Winter* as November through April for wolves with lower levels of visitation in backcountry
264 areas and high levels of visitation near ski hills and towns.

265 *Connectivity and habitat degradation*

266 We simulated individual-based carnivore movements from our SSFs across three
267 landscape scenarios, from which we estimated connectivity and changes in the amount of high
268 quality habitat (Figure 1). We used a combination of the hidden Markov models and SSFs to
269 simulate carnivore movements throughout the study area (Figure 1, Appendix S1: Figure 1). We
270 simulated 200,000 paths within the 17,000 km² study area for each species, season, and landscape
271 scenario. We selected random start locations and initial directions of travel. For each path, we
272 sampled $s = 720$ movement states (steps, s) with two-hour fix interval across $t = 60$ days from the
273 hidden Markov models. We chose 60 days to match the duration of spring, summer, and fall

274 seasons used in the step selection analyses. For each step, we sampled $n = 20$ step lengths and
275 turn angles from the state-specific movement parameters. We extracted environmental attributes
276 of the proposed locations and used the combination of environmental attributes and movement
277 parameters to calculate probability of use conditional on the 20 sample locations (equation 1).
278 We probabilistically selected one of the proposed locations and continued to the next step. We
279 repeated this process for all steps in the path.

280 The study occurred in a rugged environment where steep, rocky mountain ranges can
281 influence animal movements. We therefore defined unavailable habitat as barren landscapes with
282 slopes ≥ 35 degrees, which were used by grizzly bears and wolves 1.9 and 0.2% of the time,
283 respectively. We also classified towns and developed areas as unavailable habitat. To create
284 realistic movement paths, we reduced the probability of simulated steps jumping across
285 mountain ranges and towns by sampling four equidistant locations along proposed steps. We
286 rejected steps if any of those locations occurred in the unavailable habitat. We minimized
287 boundary effects on spatial predictions of use by terminating paths when $> 40\%$ of the proposed
288 steps occurred outside the study area and by setting the study area boundary > 30 km from the
289 towns of Banff and Canmore. Finally, start locations could occur in poor quality habitat, so we
290 removed the first twelve ($t = 1$ day) steps from each path while paths oriented to higher quality
291 habitat.

292 We simulated animal movements for three scenarios with varying levels of anthropogenic
293 development: reference, current, and future. First, we removed the effect of towns, roads, and the
294 railway from SSFs when simulating paths under reference conditions, which we used as a null
295 model of movement (Heinemeyer et al. 2019, Brennan et al. 2020). In reality, First Nations have
296 occupied the study area for over 11,000 years (Langemann 2011) and the reference condition

297 underestimated the historical effects of human activity. Second, we simulated animal movements
298 under current conditions from which we developed our SSFs. Finally, we simulated animal
299 movements under one future scenario with expanded development and trail density. We
300 modified the town of Canmore's developed footprint to reflect residential and business
301 development proposals in the 2020 Smith Creek and Three Sisters area structure plans
302 (QuantumPlace Developments Ltd. 2020b, a). We excluded green spaces and golf courses from
303 the developed footprint given that carnivores can use these areas for movement. The developed
304 footprint for the town of Banff is legally fixed under the National Parks Act and is not expected
305 to increase. However, like many mountain towns, the creation and intensity of use on informal
306 trails has increased near Banff and Canmore over the last ten years. We, thus added an inventory
307 of informal trails to the existing formal trail network and updated metrics of trail density.
308 Increased use of existing and new recreational trails has the potential to reduce wildlife
309 connectivity (Gutzwiller et al. 2017). We simulated animal movements with the updated town
310 and trail layers to estimate future connectivity.

311 To calculate connectivity, we created digital, cross-valley transects through the towns of
312 Banff and Canmore (Figure 2, Figure 3). We aligned transects so that they crossed the narrowest
313 movement corridors under current condition, where the combination of rugged topography and
314 development created pinch points to movement. We counted both the number of simulated paths
315 and individual steps that crossed transects on the north and south sides of the valley. We used
316 number of unique paths that crossed the transects as our metric of connectivity to reflect the
317 population level value of corridors. We calculated connectivity as $100 * n_{cross} / n_{reference}$, where
318 n_{cross} was the number of unique paths that crossed in current or future conditions and $n_{reference}$ was

319 the number of unique paths that crossed under reference conditions with no anthropogenic
320 development. We evaluated how connectivity changed with species, seasons, and time period.
321 Finally, we examined the effects of anthropogenic development on the amount of high
322 quality habitat available to carnivores. We calculated UDs as the number of simulated locations
323 that occurred within each 210 x 210 m² grid cell and then divided the tallies by the number of
324 total simulated locations (Signer et al. 2017). We classified reference UDs into three equal area
325 bins representing low, medium, and high quality habitat. We applied the same break points and
326 habitat classifications to UDs from the current and future scenarios. We then calculated changes
327 in the amount of high quality habitat. We focussed our analysis within a five km radius of the
328 Trans Canada Highway between Banff and Canmore (366 km²). The five km radius represented
329 the 0.99 and 0.95 quantiles of grizzly bear and wolf step lengths, respectively, and the focal
330 study approximately covered the peak to peak width of the Bow Valley. We calculated the
331 proportion of high quality habitat degraded due to anthropogenic development relative to
332 reference conditions (Heinemeyer et al. 2019). For example, our calculation of habitat
333 degradation under current conditions was $(AreaHigh_{Reference} - AreaHigh_{Current})/TotalArea$,
334 whereby *AreaHigh* represented the area of high quality habitat and *TotalArea*, represented the
335 total area of the focal study. Our metric of habitat degradation thus accounted for both decreased
336 UDs near anthropogenic developments and concurrent increased UDs as simulated animals spent
337 more time in less developed portions of the landscape. We visually evaluated how habitat
338 degradation varied with species, seasons, and time period.
339

340 **Results**

341 **Movement state**

342 We analysed GPS data from 34 grizzly bears (19 females, 15 males, 72,217 locations) and 33
343 wolves (13 females, 20 males, 84,434 locations; Appendix S1: Figure S1 – S3). Hidden Markov
344 models revealed that grizzly bears and wolves spent a similar proportion of time in their fast state
345 ($p = 0.64$ and 0.60 respectively). Grizzly bears and wolves had the same median step lengths for
346 slow steps (16 m) (Appendix S2: Table S1). Wolf fast steps (median = 1270 m) were on average
347 2.5 times longer than grizzly bear fast steps (median = 496 m). Grizzly bears had a much
348 stronger diurnal cycle of movement states than wolves (Figure 4). Grizzly bears increased their
349 proportion of time in slow states at night. Wolves had a weaker and sometimes opposite diurnal
350 cycle. Wolves increased the proportion of time in slow states at night during fall and winter only.
351 Wolves increased the proportion of time in fast states at night during spring and summer, which
352 coincided with the longest days of the year.

353 **Step and resource selection: responses to development across scales**

354 As expected, we found that wolves and grizzly bears generally avoided areas with high
355 levels of human activity in all seasons (Figure 5, Figure 6, Supplementary Table S2). Both
356 species strongly avoided areas near towns (median $\beta = 1.11$, range from 0.44 to 2.08) and 95%
357 CI's excluded zero on 6 of the 7 models (Figure 4). Grizzly bear and wolf responses to areas near
358 town changed slightly at night, though the effect size was small compared to avoidance of towns
359 in general. Parameter estimates for distance to town were >10 times larger than parameter
360 estimates for the distance to town by night time interaction (Figure 5, Figure 6). Grizzly bear
361 avoidance of towns diminished at night in all seasons (e.g., summer $\beta = -0.05$, SE = 0.01). Wolf
362 response to towns diminished at night during winter ($\beta = -0.05$, SE = 0.01), but strengthened

363 during summer ($\beta = -0.05$, SE = 0.01), and fall ($\beta = -0.05$, SE = 0.01). Grizzly bears and wolves
364 avoided areas with high trail density near paved roads (median $\beta = -0.93$, range from -1.92 to
365 0.151) with all but one estimate being less than zero and five out of seven models with 95% CI's
366 that excluded zero. Carnivore responses to trail density tapered with distance to paved roads
367 (Figure 6). Wolves avoided areas near vehicle accessible campgrounds during summer when
368 campgrounds were most active (e.g., summer $\beta = 1.00$, SE = 0.41). Grizzly bears avoided areas
369 near campgrounds during the fall but not during the summer berry season nor in the spring.
370 Grizzly bears and wolves weakly selected trails during all seasons with the strongest selection for
371 grizzly bears in summer and for wolves in winter. Grizzly bears selected the railway during the
372 spring and fall and avoided the railway during the summer berry season. Wolves strongly
373 selected the railway during winter and weakly selected the railway at other times of the year.

374 RSF models had similar parameter estimates compared to SSF models confirming
375 minimal scale-dependence of our SSF results (Figure 5, Appendix S2: Table S3, Table S4). Most
376 (84%) of the SSF and RSF anthropogenic parameters had the same positive or negative sign.
377 Most sign differences occurred for parameters with 95% CI's that overlapped zero. From a
378 management perspective, the biggest difference in parameter estimates was that the grizzly bear
379 fall SSF suggested weak avoidance of areas near town ($\beta = 0.44$, SE = 0.26), whereas the RSF
380 suggested grizzly bears selected areas near town ($\beta = -0.81$, SE = 0.13). Otherwise, all other
381 parameter estimates for distance to town were positive. Overall, the RSF results supported the
382 scale-independence of our SSF results regarding carnivore avoidance of areas near towns and
383 areas with high trail density.

384 **Connectivity and habitat degradation**

385 Simulated paths under reference, current, and future land use scenarios had similar
386 movement attributes compared observed paths (e.g., Figure 2, Figure 3). Both simulated and
387 observed paths contained series of short steps with high turn angles interspersed with long
388 distance movements with strong directional persistence. Under reference conditions, simulated
389 paths were concentrated in the valley bottoms and used areas within the current footprint of
390 towns. The combination of towns and rugged topography constrained the movements of both
391 observed and simulated paths under current and future scenarios. This resulted in UDs with low
392 frequencies of occurrence near towns and areas of high trail density and high UDs in more
393 remote areas of the Bow Valley (Appendix S1: Figures S4 - S5).

394 Grizzly bear and wolf connectivity across digital transects on the north and south sides of
395 Banff and Canmore ranged between 7 and 45% under current conditions with mean values of
396 21% for grizzly bears and 25% for wolves (Figure 7). Grizzly bear and wolf connectivity further
397 decreased from current to future conditions an average of 6% and 5% respectively (range = 0 to
398 13%). Connectivity for grizzly bears and wolves was highest in the spring. Grizzly bear
399 connectivity was lowest in the summer, whereas wolf connectivity was lowest in the fall and
400 winter. Grizzly bear connectivity was on average higher along the northern transects compared to
401 the southern transects. Wolf connectivity was highest on the northern side of Banff and lowest on
402 the southern side of Canmore.

403 Grizzly bears and wolves UDs showed high intensity of use through the valley bottoms
404 including areas near Banff and Canmore under reference conditions (Figure 2, Figure 3,
405 Supplementary Figures S4 and S5). UDs under current and future conditions showed a
406 cumulative decrease in use in and around the towns. The decrease in use near towns was offset

407 by increased use in more remote areas of the valley. The proportion of high quality habitat
408 degraded due to anthropogenic development increased from current (mean = 0.145, range =
409 0.088 to 0.183) to future conditions (mean = 0.164, range = 0.126 to 0.198; Figure 8). Habitat
410 degradation was highest in summer and lowest in the spring and fall for grizzly bears. Habitat
411 degradation was high for wolves in the summer, fall, and winter, and lowest in the spring.

412

413 **Discussion**

414 Our study used a combination of hidden Markov models and SSFs to estimate utilizations,
415 connectivity, and changes in the amount of high quality due to current and future estimates of
416 anthropogenic development. Our approach assessed the cumulative effects of multiple
417 anthropogenic features on carnivore movements and connectivity around the towns of Banff and
418 Canmore, Alberta, which averaged 23% relative to reference conditions. A scenario of future
419 development and trail expansion would further reduce connectivity by an average of 5 to 6%. By
420 using empirically-derived parameters in an individual-based simulation, our approach offers a
421 tangible response variable for scientists to convey to land use decision makers. For example,
422 rather than translating how ‘current density’ may change under different scenarios, we are able to
423 estimate a percent change in the number of animals moving through a corridor under predicted
424 land use scenarios.

425 The main advantages of our approach are as follows: 1) simulated movements directly
426 from an SSF with multiple behavioural states helped create realistic movement paths where
427 movement decisions were based on resource selection parameters; 2) our approach avoided
428 transforming SSFs into resistance surfaces used for circuit-theory and cost-distance analyses,
429 which have an weak theoretical link to movement ecology; and 3) estimates for changes in UDs

430 and connectivity have a simpler interpretation and a tighter link to movement probabilities
431 compared to least-cost and circuit theory based estimates of connectivity. We chose to estimate
432 connectivity by comparing transect crossing rates of simulated paths through narrow movement
433 corridors, which in our study area are of conservation concern. Our approach could easily be
434 expanded to examine the frequency with which paths travel between habitat patches (e.g. Suraci
435 et al. 2020), between summer and winter ranges (Merkle et al. 2019), across highways with
436 increased mortality risk (e.g. Quaglietta et al. 2019), or through other areas of conservation
437 concern.

438 Our study supports the growing body of research showing that wildlife avoid some forms
439 of human activity (e.g. Gaynor et al. 2018, Tucker et al. 2018, Nickel et al. 2020), which can lead
440 to habitat fragmentation and reductions in connectivity (e.g. Bischof et al. 2017, Hilty et al.
441 2020, Suraci et al. 2020). Given the global growth in human activity adjacent to protected areas
442 (Wittemyer et al. 2008), and concurrent impacts of growing recreation in these landscapes
443 (Gutzwiller et al. 2017), our approach and results emphasize the importance of cumulative
444 effects assessment in regions surrounding parks and protected areas.

445 Numerous studies have found that grizzly bears (Chetkiewicz and Boyce 2009, Morales-
446 González et al. 2020) and wolves (Hebblewhite and Merrill 2008, Rogala et al. 2011, Anton et
447 al. 2020) avoid human activity, which can contribute to the fragmentation of populations
448 (Proctor et al. 2012, Bischof et al. 2017). However, few studies have compared the behaviour of
449 the two species. Wolves in our study exhibited stronger avoidance of towns, similar responses to
450 trails, and weaker selection for the railway compared to grizzly bears. Grizzly bears and wolves
451 had higher connectivity estimates in spring, which coincided with lower levels of human activity
452 and a concentration of food resources and wolf movements to and from den sites in valley

453 bottoms. Interestingly, wolf connectivity estimates were slightly higher than grizzly bear
454 connectivity estimates. One reason for this disconnect could be that wolves had faster speeds of
455 travel, fewer steps were required to traverse corridors, and perhaps simulated steps could more
456 easily jump across towns. Parameterizing models using path selection functions or collecting
457 finer resolution GPS data could help reduce the probability of paths crossing inhospitable
458 features. For instance, path selection functions can sometimes produced stronger regression
459 coefficients and better connectivity models compared to SSFs (Zeller et al. 2015, Zeller et al.
460 2018). Further, we did not assess how individual variability in animal responses to anthropogenic
461 development affected connectivity (Muff et al. 2020). Simulating movements from random
462 coefficients could highlight estimates of connectivity for both wary and habituated animals and
463 could help identify areas likely to have high levels of human wildlife conflict (Buchholtz et al.
464 2020, Lamb et al. 2020).

465 Two limitations of our study bear further consideration for similar work in the future.
466 First, we lacked direct measurements of human activity on trail networks (Alberta Environment
467 and Parks 2018). Because carnivores typically avoid encounters with people rather than linear
468 features, our lack of high resolution trail use data likely reduced the effect size and precision of
469 parameter estimates for trail density. Estimates of recreational activity could be improved by
470 directly tracking individual movements (Heinemeyer et al. 2019), inferring activity from mobile
471 device data (Corradini et al. 2021), or modelling spatial and temporal trends in trail use (Ladle et
472 al. 2019). Better estimates of recreational activity would improve our understanding of how
473 recreational activity affects wildlife movement and our ability to manage human-wildlife
474 coexistence (Rogala et al. 2011, Naidoo and Burton 2020). Second, our data consisted of animal
475 movements within established home ranges rather than dispersal or nomadic movements that are

476 important for landscape-scale connectivity (Fattebert et al. 2015). Other studies suggest animals
477 select different resources and may have increased tolerance for human activity when dispersing
478 when compared to movement within the home range. For instance, resistance models for Iberian
479 lynx under-estimated connectivity when they were developed using GPS data from within home
480 range movements (Blazquez-Cabrera et al. 2016). Further development and evaluation of
481 connectivity models using dispersal data would be important when evaluating connectivity
482 between isolated populations (Zeller et al. 2018).

483 Restoration actions, such as removal of human footprint, managing or consolidating
484 recreational activity, and trail closures have potential to improve habitat quality and connectivity.
485 Wildlife increased their use of corridors and degraded habitat following reductions in human
486 activity, both in our ecosystem (Duke et al. 2001, Shepherd and Whittington 2006, Whittington
487 et al. 2019) and around the world (Ngoprasert et al. 2017). For example, early work in our study
488 area demonstrated positive wildlife connectivity consequences of removing recreational footprint
489 in the Cascade wildlife corridor on the north side of the Banff town site (Duke et al. 2001), and
490 positive effects of a temporal road closure on wildlife habitat quality (Whittington et al. 2019).
491 Our approach for simulating animal movements and assessing connectivity could be applied to
492 assess the effects of potential restoration actions on fine-scale connectivity (Wang et al. 2014,
493 Mariela et al. 2020, Suraci et al. 2020). Simulations and restoration actions could focus on
494 highway mitigations (Quaglietta et al. 2019), reductions in trail density, permanent closures,
495 seasonal closures, or temporal closures (Whittington et al. 2019). In the face of global increases
496 in human activity, especially surrounding parks and protected areas (Wittemyer et al. 2008),
497 proactive habitat protection and restoration actions will be required to maintain habitat quality
498 and connectivity for wide ranging wildlife (Hilty et al. 2020).

499

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506

507 **Supporting Information**

508 Appendix S1. Maps of study area, observed GPS locations, and predicted utilization distributions
509 from step selection function models.

510 Appendix S2: Tables of parameter estimates from movement models, step selection functions,
511 and resource selection functions.

512

513 **Data availability**

514 We will submit GPS movement data, scripts to fit hidden Markov models, step selection
515 functions, and simulations under current conditions to Data Dryad.

516

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744 urban forest park? An examination integrating GPS data and space syntax theory. *Urban*
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746

747 **List of Figures**

748 Figure 1. Workflow to assess connectivity and change in habitat quality using hidden Markov
749 models, SSFs, and RSFs. We classified movement behaviors into slow and fast states and then
750 used those states in SSF models and in path simulations. Simulated points can be used to
751 estimate UDs and changes in habitat quality. Connectivity can be measured by comparing
752 movement rates through corridors, across transects, or between patches relative to a reference
753 model of movement with no anthropogenic development.

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755 Figure 2. Illustration of our connectivity modeling approach in Figure 1 for one species (wolf)
756 and one season (summer) showing the distribution of observed wolf paths around the town of
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758 utilization distribution. We used hidden Markov models and SSFs to simulate 200,000
759 movement paths across a two-month window. We tallied the number of paths that crossed the
760 valley wide transect and calculated connectivity as the ratio of current to reference and future to
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769 Figure 4. Grizzly bear and wolf movement state probabilities (slow versus fast movements) and
770 95% CI's depended on time of day. Movement states were predicted from hidden Markov
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772 resting and travel behaviours, respectively.

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774 Figure 5. Human use related parameter estimates and 95% CI's from grizzly bear and wolf SSF
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776 selection for high values of the covariate.

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778 Figure 6. Grizzly bear and wolf relative selection strength and 95% CI's as a function of distance
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780 predictions from SSFs while holding all variables constant at their mean except for distance to
781 town, trail density, time of day (Day = 1200 hours, Night = 2400 hours), and distance to paved
782 road (Near = 0 km and Far = 20 km).

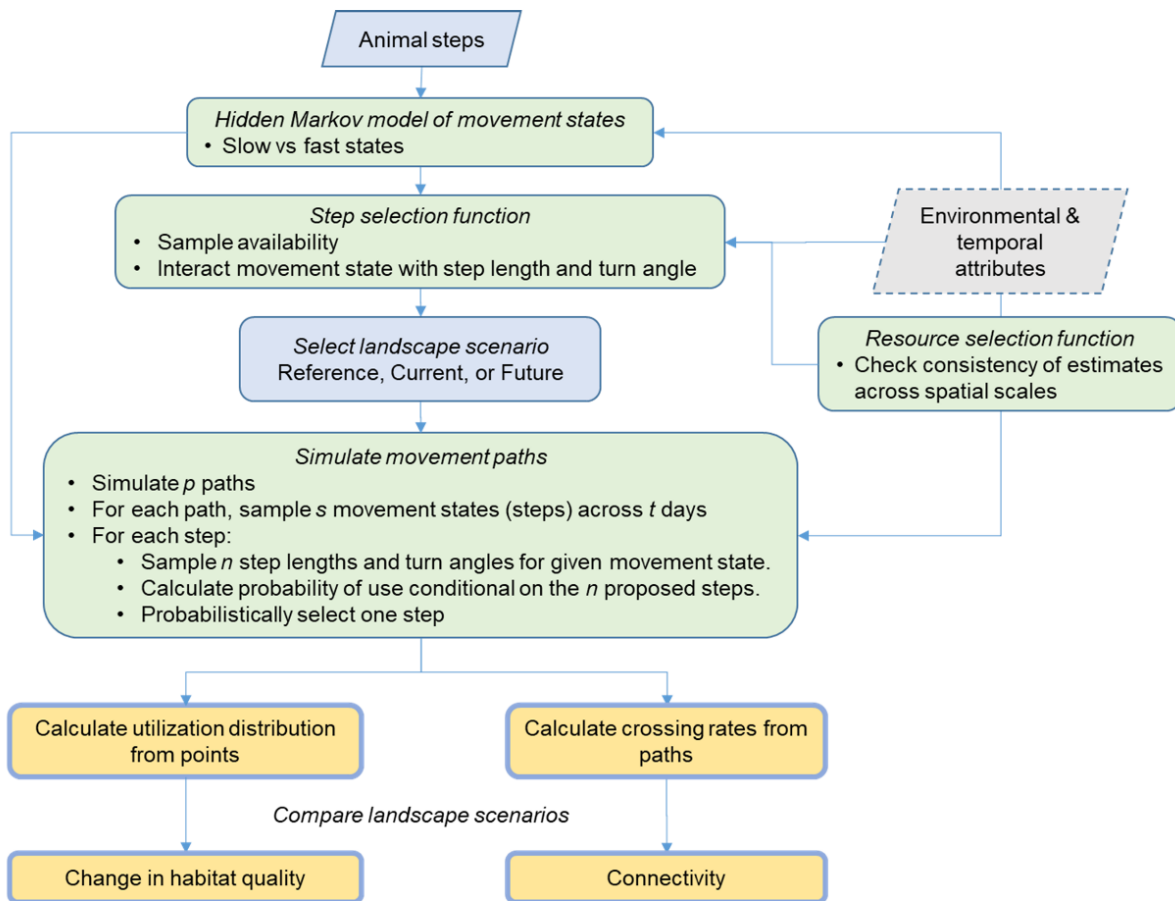
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784 Figure 7. Connectivity estimates for grizzly bears and wolves around the towns of Banff and
785 Canmore under current and future footprints of anthropogenic development. We estimated
786 connectivity by comparing the number of simulated paths that crossed transects under current
787 and future conditions to crossing rates from reference conditions. We simulated 200,000 paths
788 for each species, season, and time period. On average, connectivity decreased from Current to
789 Future for grizzly bears by 6.5%, and, wolves by 5.1%. Grizzly bears have no connectivity
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793 reference to current and future time periods. We estimated habitat degradation for the Bow
794 Valley between Banff and Canmore, Alberta, Canada
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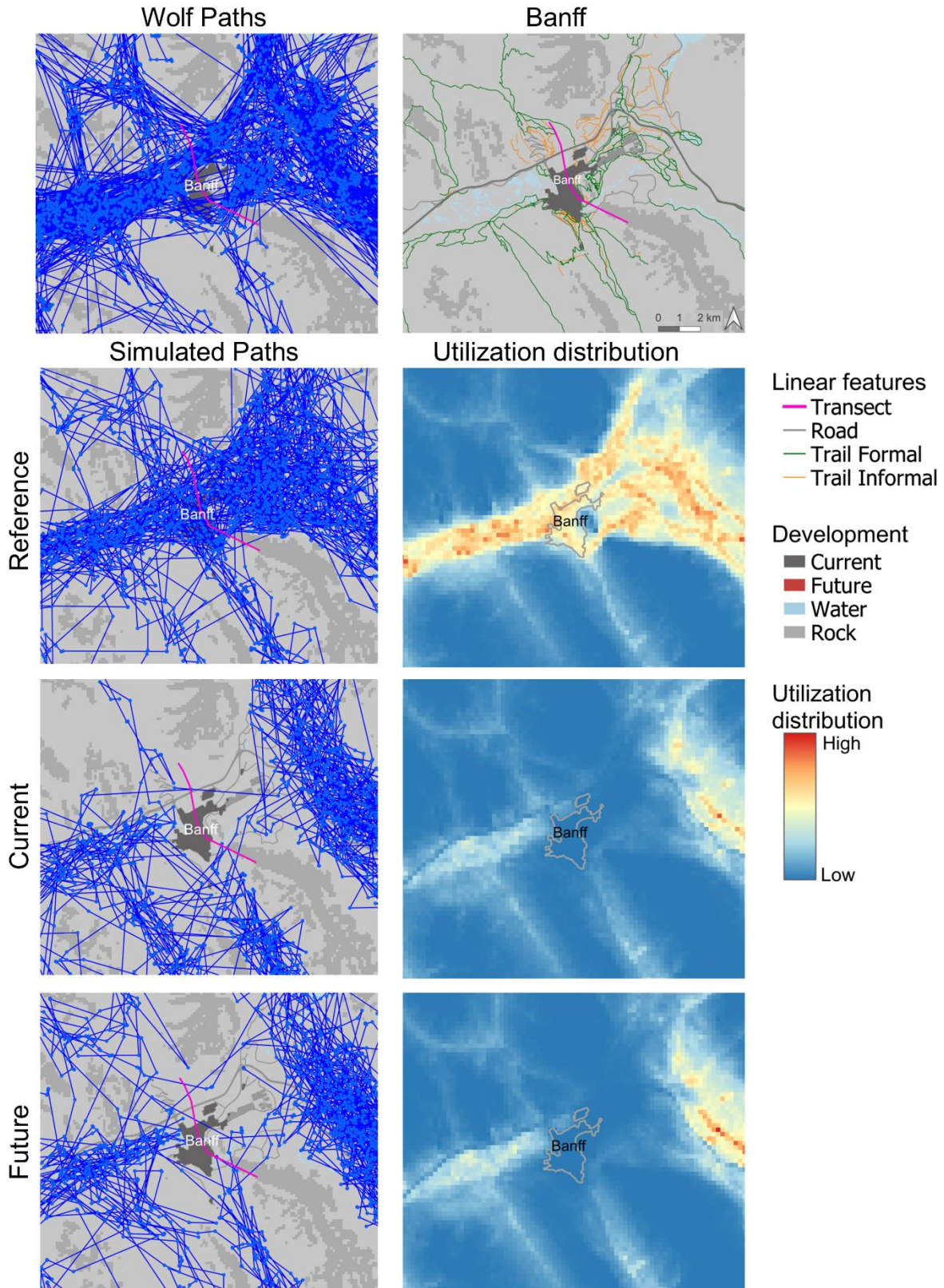
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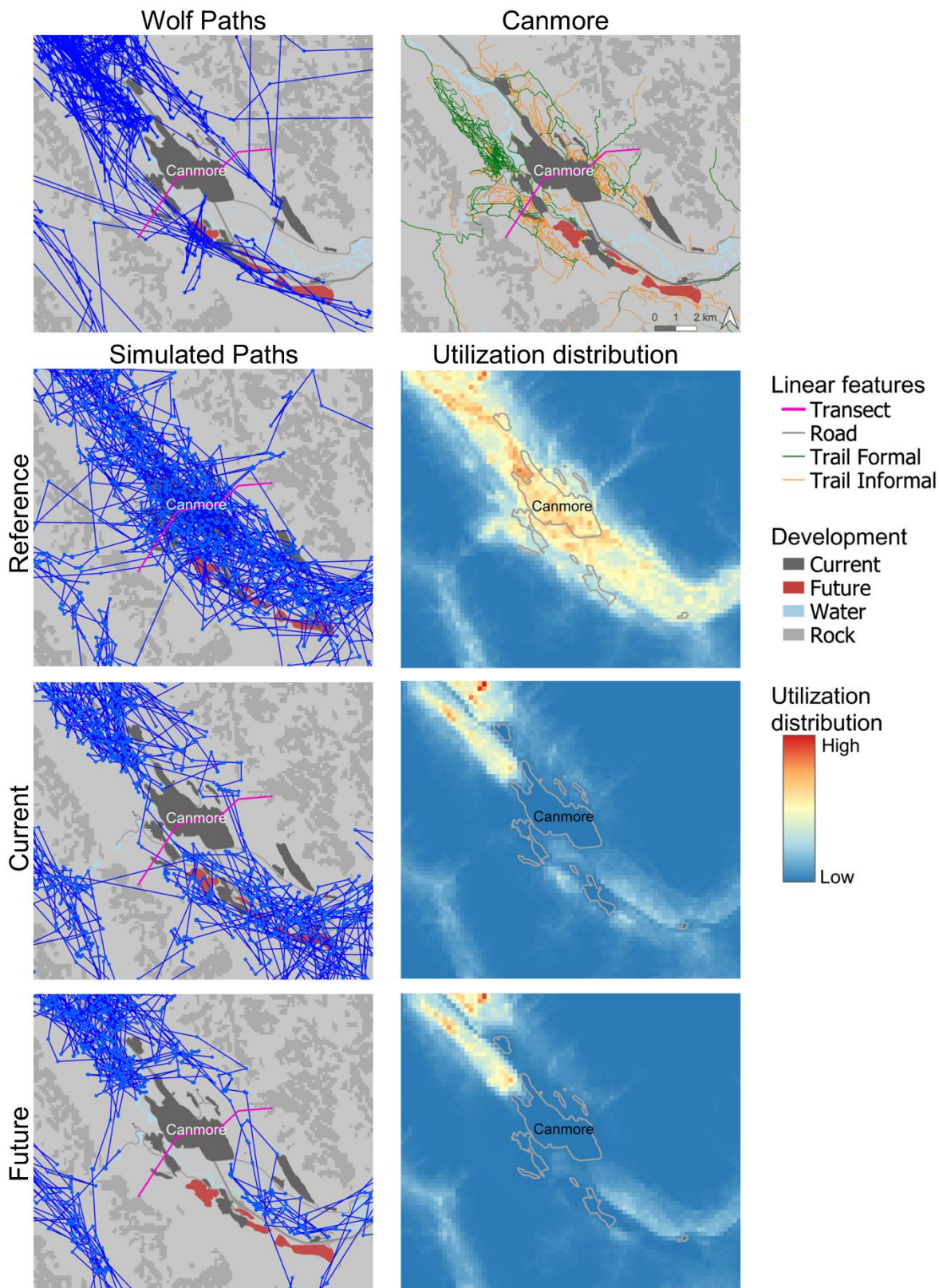
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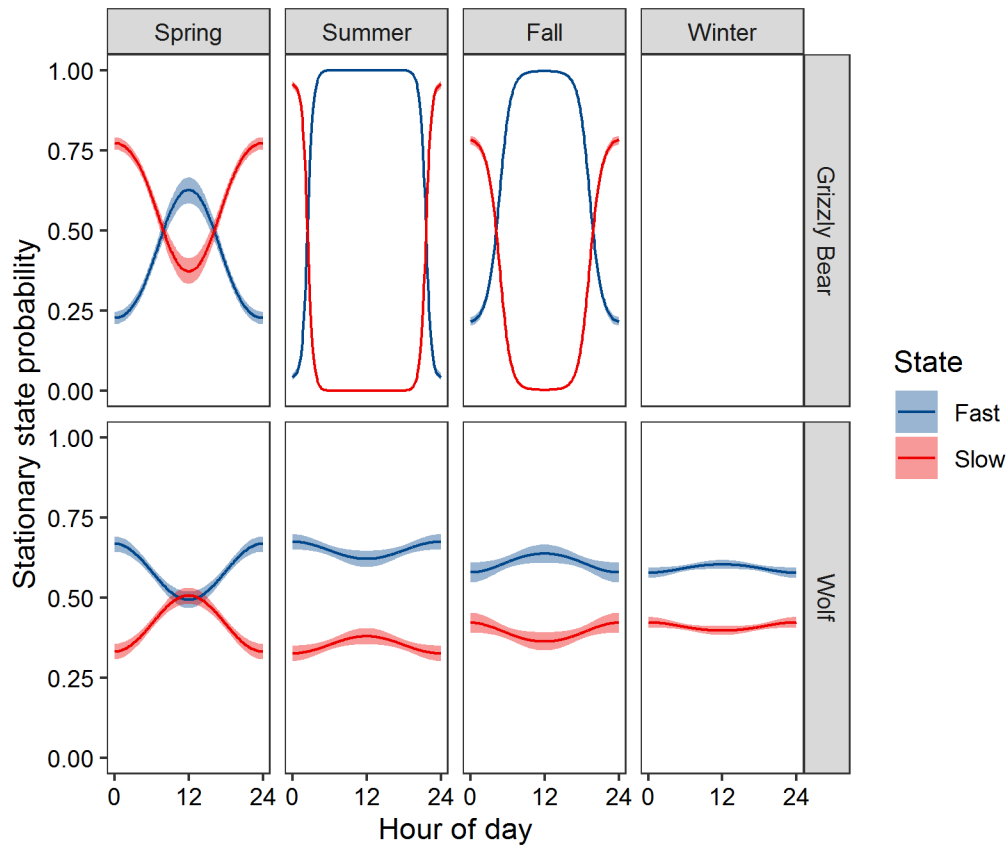
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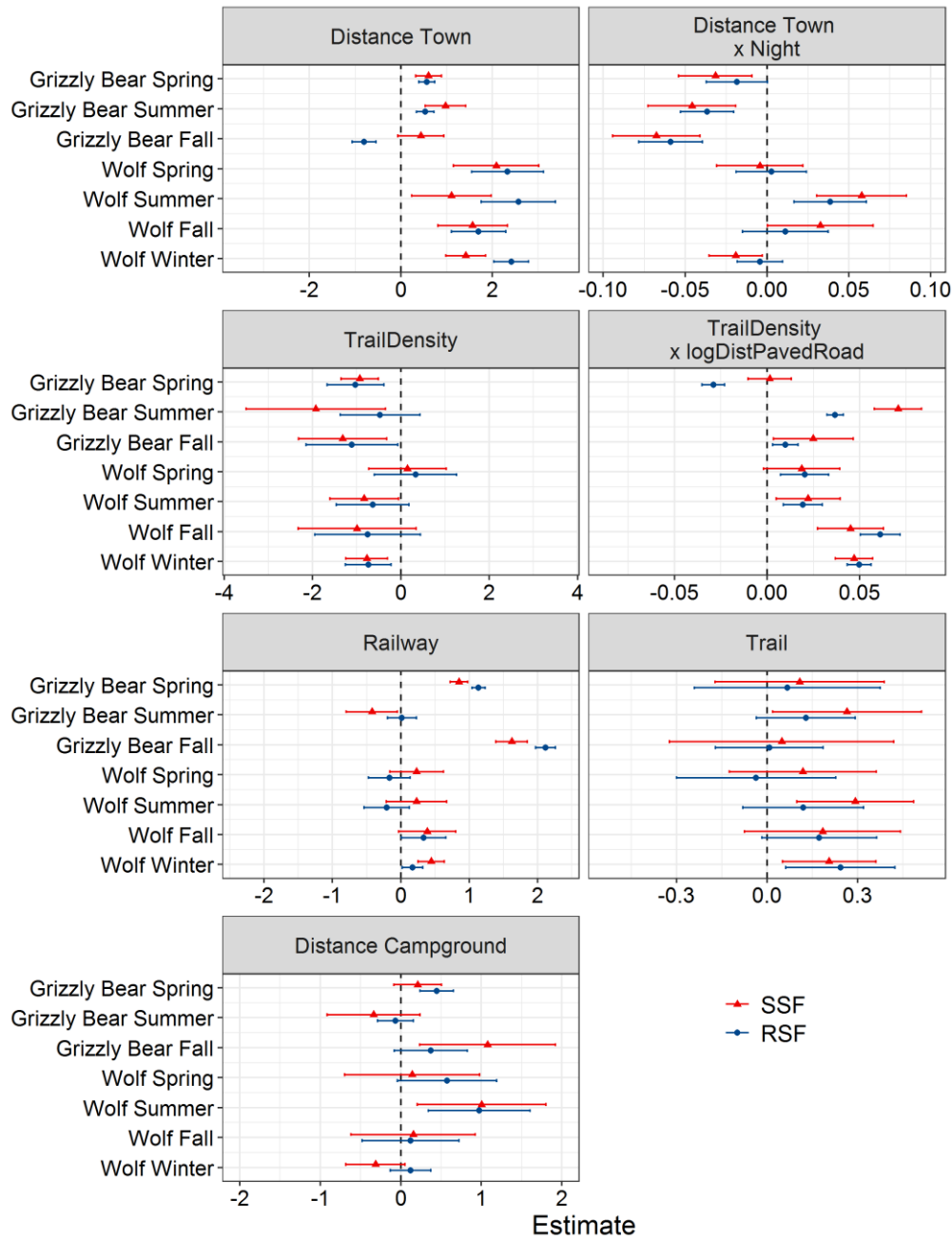
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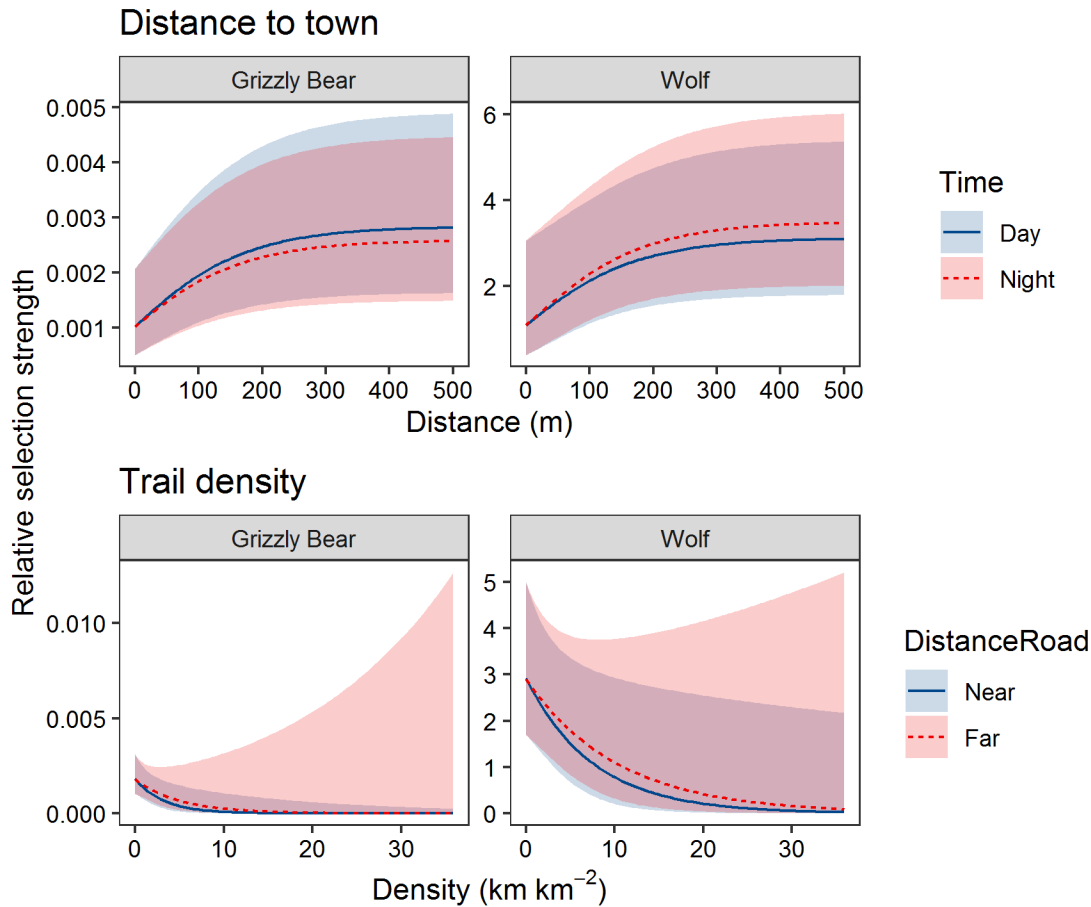
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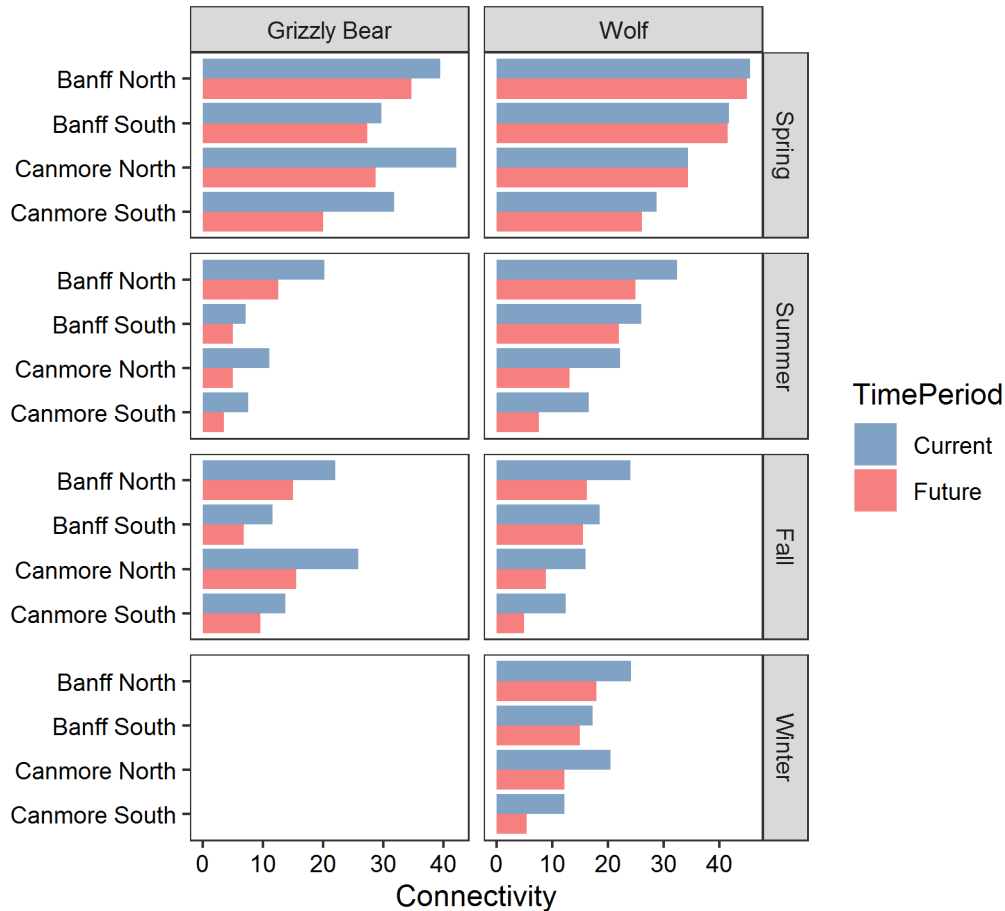
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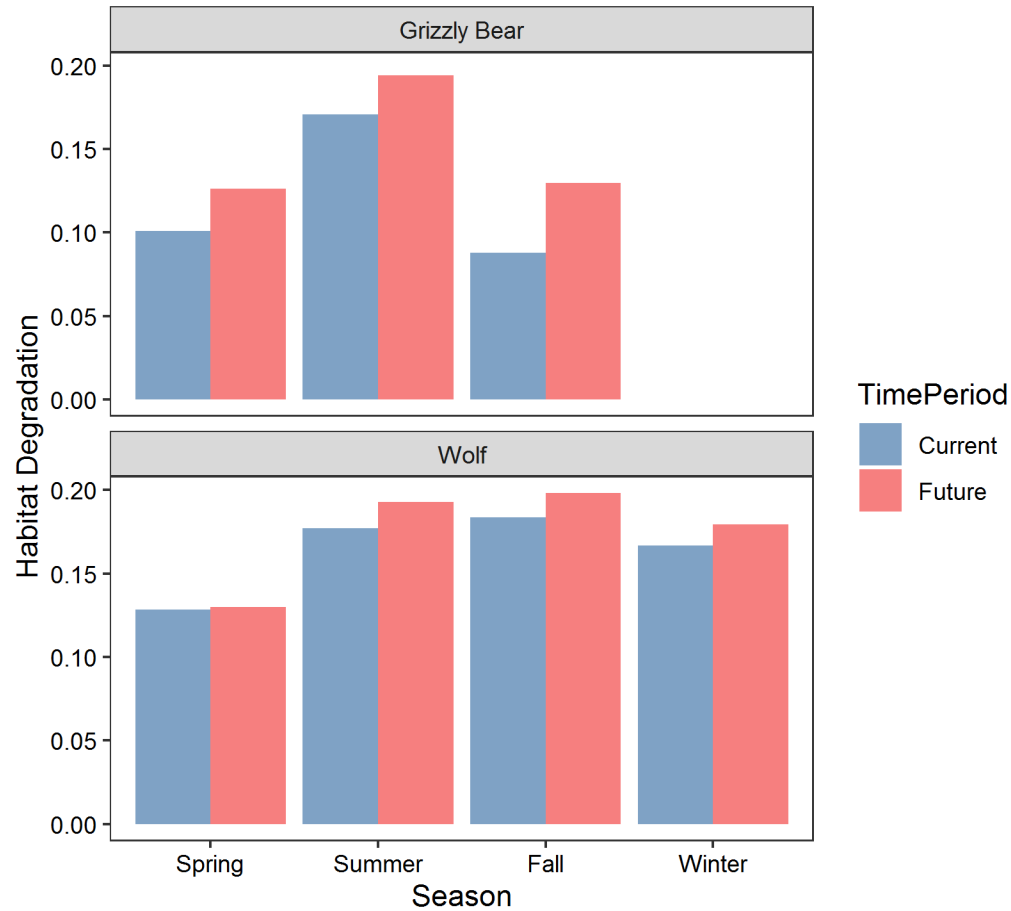
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