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Spatiotemporal Railway Use by Grizzly Bears in Canada's Rocky Mountains

SONYA Z. POLLOCK,¹ *University of Alberta, Department of Biological Sciences, Edmonton, AB T6G 2E9, Canada*

JESSE WHITTINGTON, *Parks Canada Agency, Banff, AB T1L 1K2, Canada*

SCOTT E. NIELSEN, *University of Alberta, Department of Renewable Resources, Edmonton, AB T6G 2H1, Canada*

COLLEEN C. ST. CLAIR, *University of Alberta, Department of Biological Sciences, Edmonton, AB T6G 2E9, Canada*

ABSTRACT Railway networks contribute to the direct mortality of wildlife through collisions with trains, which can threaten vulnerable wildlife populations even in protected areas, including grizzly bears (*Ursus arctos*) in Banff and Yoho National Parks, Canada. Mitigation to reduce bear-train collisions requires information about how grizzly bears use the railway spatially and temporally and how particular types of use might increase collision vulnerability. We used data from 27 grizzly bears fitted with global positioning system (GPS) collars between 2000 and 2016 to relate railway use by bears via resource selection functions to variables that described land cover, human use, and topography. We used the same suite of explanatory variables to distinguish pairs of 4 types of steps, in which 3 successive GPS points (with 2-hr fix rates) included ≥ 1 within 30 m of the rail (hereafter on) and 2 others that defined locations where bears effectively entered the railway (first fix off rail, next 2 on), crossed it (only the middle fix on the rail), continued along the railway (all 3 fixes on), or exited the railway corridor (first 2 on, last off). We compared both sites of higher use and each of these 4 step types to the relative frequency of bear-train collisions, predicting a positive correlation for continue step types. Relative to available locations, bears were more likely to use the railway close to railroad sidings (sections of twinned track where trains sometimes stop), at intermediate distances from human-use features (e.g., town sites, highways, trails), in areas with lower values of the compound topographic index (a proxy for wetness; within 500 m), and within 90 m of rugged terrain. Seasonally, bears made greater use of the railway in spring and fall. Among 1,515 sequences of 3 steps, crossing locations comprised $>50\%$ and were most distinct from continue locations (about 20%), which occurred in areas with more rugged terrain (within 300 m), closer to railway sidings, in spring and fall, and with steps that were 60% shorter. Contrary to our prediction, past reports of bear-train collisions were negatively correlated with continue locations and unrelated to overall use or any other movement type. Our results suggest that railway use by bears increased where it provided increased forage or easier travel, particularly in spring and fall, but more work will be needed to determine the mechanistic basis of bear-train collisions. Meanwhile, mitigation efforts such as habitat alteration or warning systems might target locations where past strikes are concentrated for grizzly bears or other sensitive populations. © 2019 The Wildlife Society.

KEY WORDS Banff National Park, grizzly bear, habitat selection, movement, railway, step discrimination function, *Ursus arctos*, wildlife-train collisions.

Collisions with vehicles are a major source of mortality for wildlife with the potential for population declines (Fahrig and Rytwinski 2009, Benito-Lopez et al. 2010). Although the implications of road mortality are documented, there is a comparative lack of railway-associated research, despite high rates of wildlife-train collisions (Santos et al. 2017, St. Clair et al. 2017), including for species that attract conservation concern, such as Asian elephants (*Elephas maximus*; Joshi and Singh 2007, Dasgupta and Ghosh 2015, Roy and

Sukumar 2017) and grizzly bears (*Ursus arctos*; Waller and Servheen 2005, Hopkins et al. 2014, Murray et al. 2017). Population viability of large, wide-ranging mammals may be reduced by train strikes because large home ranges increase encounter rates with railways, and low reproductive rates limit recovery from anthropogenic mortality (Carr and Fahrig 2001, Laurance et al. 2009). Reducing the likelihood of collisions is of particular importance for threatened species in protected areas, especially as railway networks and traffic volume continue to grow (Dulac 2013, Laurance et al. 2015, Olson and van der Ree 2015).

If strike risk increases with railway use by animals, mitigating vulnerability to train collisions logically requires information on the spatial and temporal factors that are

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¹E-mail: spollock@ualberta.ca

associated with railway use. Similar to roads, railway tracks can intersect important habitat, such as areas associated with forage, cover, or movement routes (Gunson et al. 2011). These intersections can result in species-specific, spatial aggregations of wildlife, resulting in high-risk collision locations or mortality hotspots (Malo et al. 2004, Langen et al. 2009, Gunson et al. 2012). Habitat selection and risk of mortality may also change temporally. Railway use may be more pronounced during certain times of day (e.g., nocturnal periods when animals avoid human activity; Hebblewhite and Merrill 2008, Schwartz et al. 2010a, Steiner et al. 2014), or in particular seasons when rail-associated movements may be related to forage availability (Nielsen et al. 2003, Mkanda and Chansa 2011), breeding (Seo et al. 2015), or migration (Gundersen et al. 1998).

In addition to obtaining food resources, wildlife may exploit railways as energy-efficient travel corridors. Similar linear features increased the movement rates or hunting efficiency for red foxes (*Vulpes vulpes*) and wolves (*Canis lupus*; Adkins and Stott 1998, Latham et al. 2011, Dickie et al. 2017). This advantage may be especially pronounced in mountainous regions where rugged topography influences animal movement (Noss et al. 1996, Whittington et al. 2004). Relative to roads, railways may be more attractive as travel routes because they are narrower, potentially speeding access to hiding cover, and contain little human activity (Jalkotzy et al. 1997, Tremblay and St. Clair 2009, Dorsey et al. 2015), features that may increase the permeability of railways for animal movement (Whittington et al. 2005, Jasinska et al. 2014).

In addition to identifying population-level, spatiotemporal patterns of railway use, individual-level information about animal movement can reveal differences in behavioral states (Nathan et al. 2008) that might also contribute to collision vulnerability. Animals that regularly use railways to travel along tracks may be more vulnerable to strikes than animals with briefer encounter durations (e.g., via crossings). Conversely, animals that make less frequent use of a railway may be less experienced with trains and more likely to be surprised by them. Vulnerability may also be associated with adjacent attractants, where bears may be more likely to enter or exit the railway corridor. Previous research has correlated the crossing of linear features to particular landscape characteristics (Sunga et al. 2017), habitat quality (Laurian et al. 2008), and human use (Fahrig 2007). Recognizing where animals concentrate their movements has been effective at reducing mortality along highways (Dussault et al. 2007, Lewis et al. 2011, Baigas et al. 2017), as demonstrated by highway crossing structures (Clevenger et al. 2002, Schuster et al. 2013, Loraamm and Downs 2016) and the placement of other suggested mitigations (e.g., speed reductions; Baigas et al. 2017) and warning systems (Huijser and McGowan 2003, Backs et al. 2017, Seiler and Olsson 2017). Such mitigation may be enhanced by identifying locations with particular movement types (Barnum 2003, Gomes et al. 2009).

Mitigating railway mortality has become increasingly important for a vulnerable population of grizzly bears in Canada's Rocky Mountain Parks, where train collisions have

become the leading source of human-caused mortality (Bertch and Gibeau 2010). Collision risk might be high for grizzly bears, partly because they are especially wide-ranging (Nielsen et al. 2004b, Munro et al. 2006, Schwartz et al. 2010b), but the bears in this population also exhibit unusually low reproductive rates (Garshelis et al. 2005), which appear to stem from food limitation in this mountainous, heavily forested landscape with a short growing season (Gibeau et al. 2002, Chruszcz et al. 2003, Nielsen et al. 2013). The population may be particularly limited by the absence of animal-based protein sources such as salmon (*Oncorhynchus* spp.; McLellan 2011, Lopez-Alfaro et al. 2015, Nielsen et al. 2017). These factors may increase the attraction to, or necessity of, forage opportunities associated with railways, which, similar to roadsides, enhance growth and productivity of many plant species (Hansen and Clevenger 2005, Roeber et al. 2008a, Pollock et al. 2017). In addition, the railway produces energy-rich attractants that include spilled agricultural products (Dorsey et al. 2017, Gangadharan et al. 2017, Popp 2017) and rail-killed ungulates (Wells et al. 1999, Hopkins et al. 2014, Murray et al. 2017).

Our objectives were to determine which factors predict bear use of railways, how particular movement types compare to associated habitat, and if greater use predicts increased strike risk. For our first objective, we hypothesized that railway use by bears increases in areas with higher forage quality, security, or travel efficiency, predicting that it would be higher in areas of greater vegetation cover, more distant from human use features, and in areas with more rugged topography. For our second objective, we identified locations where 3 successive fixes from global positioning system (GPS)-collared bears depicted locations where they entered, crossed, continued along, or exited the railway corridor (defined below). We hypothesized that the more sustained railway use caused by continuing along the railway with 3 successive GPS fixes and slower movement rates would correlate with foraging habitat relative to crossing locations or faster movement. For our third objective, we hypothesized that if greater railway use conveys a greater risk of mortality, locations with greater overall use and continue movement types would exhibit higher rates of past mortality.

STUDY AREA

We used location data from 27 GPS-collared grizzly bears that were collared between 2000 and 2016 (days monitored $\bar{x} = 259 \pm 151$ [SD], range = 35–665) in Banff and Yoho National Parks, Canada (Fig. 1; 6,641 km² and 1,313 km², respectively). Over 4 million people visit these parks each year (Parks Canada 2018), challenging coexistence between grizzly bears and humans. Banff and Yoho are bisected by the 4-lane Trans-Canada Highway (i.e., highway), which has an estimated traffic volume of >8 million vehicles/year, and the Canadian Pacific Railway (i.e., railway), which carries 25–35 trains/day (Wells et al. 1999). The railway parallels the highway at an average distance of 416 m \pm 325 m (Dorsey 2011), and passes through montane and subalpine

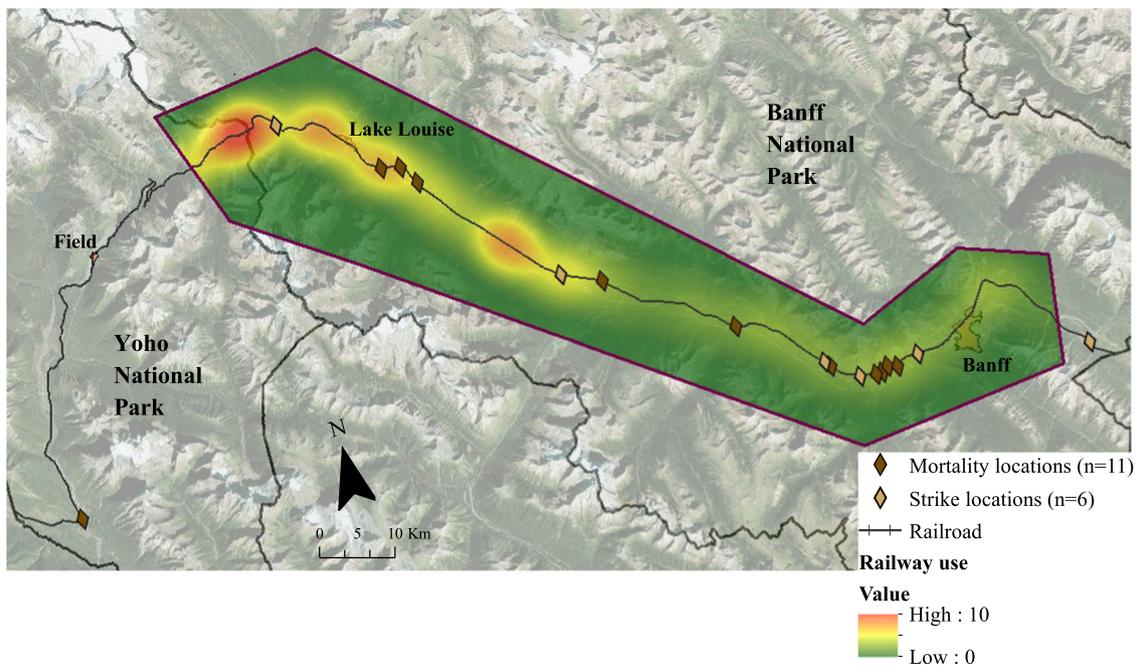


Figure 1. Railway use and associated movement by grizzly bears in Banff and Yoho National Parks, Canada, 2000–2016. A subsection of the Canadian Pacific Railway through Banff National Park is provided in color to illustrate the kernel density values of railway use by grizzly bears (red areas = highest use). Confirmed grizzly bear mortality locations ($n = 11$) are denoted by dark brown diamonds. Reported grizzly bear strike locations ($n = 6$) are denoted by light brown diamonds.

ecoregions, with elevations ranging from 1,100 m to 1,600 m. The majority of Banff and Yoho Parks occur above treeline in the alpine ecoregion, with some mountain ranges reaching 3,500 m (Holland and Coen 1983). The parks experience long, cold winters (between fall and spring equinoxes) with an average low of -15°C and short, mild summers (between spring and fall equinoxes) with an average high of 21°C . Several areas in the parks are snow-covered for approximately 10 months a year, with some lower elevation locations snow-free for approximately 6 months a year (annual snowfall $\bar{x} = 240\text{--}480$ cm; Janz and Storr 1977). The cool climate, along with the rugged and mountainous terrain limits vegetation productivity, which causes bears to select for habitat at lower elevations where the railway and major roads also occur (Gibeau et al. 2002). Further, historical fire suppression has resulted in predominantly dense forest cover from Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and Engelmann spruce (*P. engelmannii*), which decreases grizzly bear foraging habitat on a broad scale (Hamer and Herrero 1987b, Luckman and Kavanagh 2000). Primary foods for grizzly bears in the region include sweetvetch roots (*Hedysarum* spp.), graminoids (grasses, sedges, and rushes), horsetail (*Equisetum arvense*), and various fruits, such as buffaloberries (*Shepherdia canadensis*) and bearberries (*Arctostaphylos uva-ursi*). Mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus canadensis*), and moose (*Alces alces*) inhabit the parks with cougars (*Puma concolor*), wolves (*Canis lupus*), coyotes (*C. latrans*), and black bears (*U. americanus*). Fencing and wildlife crossing structures along the highway have reduced wildlife-vehicle collisions by up to 80% (Clevenger et al. 2001), but no similar mitigation

exists for the railroad where collision rates have increased over the past few decades for several species, including bears (*Ursus* spp.; Gilhooly et al. 2019). The study area includes 3 townsites (Banff, Lake Louise, and Field), a network of roads and hiking trails, 3 ski resorts, several campgrounds, and numerous day-use areas.

METHODS

We obtained research ethics approval from the University of Alberta Animal Care and Use Committee (AUP00000438). Parks Canada staff captured and collared grizzly bears in Banff and Yoho National Parks via culvert traps and free-range darting, following protocols approved by the Parks Canada Animal Care Committee (Parks Canada Research Collection Permit LL-2012-10975). We fitted GPS collars to 34 individual bears (Vectronic Iridium GPS Plus, Berlin, Germany; Followit Iridium GPS, Lindesberg, Sweden), which recorded GPS locations every 2 hours from the time of emergence from dens (Mar–Apr) or collaring (May–Jun) each year until collars dropped (variable timing) or den entry (Oct–Nov). Our dataset included 26 bears collared from 2012–2016 and 8 bears collared previously for other purposes (2000–2004, 2009, 2010). We ran our analyses using bears that had ≥ 1 GPS location on the railway (27 of 34 bears).

We used ArcMap (version 10.3; Environmental Systems Research Institute [ESRI], Redlands, CA, USA) and Geospatial Modelling Environment software (version 0.7.4.0, www.spatial ecology.com, accessed 1 Dec 2017) to measure land cover, human-use, and topographical data that we created or received from Parks Canada and hypothesized would influence railway use and movement by grizzly bears

Table 1. Variables predicted to influence habitat selection and movement by grizzly bears ($n = 27$) on a railway in Banff and Yoho National Parks, Canada, 2000-2016.

Category	Variable	Variable range	Variable description
Land cover	Canopy cover ^a	0.00–90.00	Percentage of forest cover ^b
	Terrain wetness ^a	3.55–26.03	Compound topographic index (CTI); increases with wetter sites ^b
	Land cover	0 or 1 and 0–100	Presence or percentage of land cover in 7 categories ^{b,c}
Human use	Distance to edge ^a	0.06–0.80	Euclidean distance (km) to nearest forest edge
	Distance to stream ^a	0.00–0.81	Euclidean distance (km) to nearest stream
	Distance to water bodies ^a	0.00–1.00	Euclidean distance (km) to nearest water body
	Distance to towns ^a	0.25–1.00	Euclidean distance (km) to nearest town
	Distance to roads ^a	0.00–1.00	Euclidean distance (km) to nearest road
	Distance to highways ^a	0.00–0.96	Euclidean distance (km) to nearest highway
	Distance to railroad sidings ^a	0.00–1.00	Euclidean distance (km) to nearest railroad siding
	Distance to trails ^a	0.00–1.00	Euclidean distance (km) to nearest human use trail
	Distance to landfills ^a	0.12–1.00	Euclidean distance (km) to nearest landfill
	Distance to gravel pits ^a	0.25–1.00	Euclidean distance (km) to nearest gravel pit
Topography	Distance to wildlife crossing structures ^a	0.31–1.00	Euclidean distance (km) to nearest wildlife crossing
	Terrain ruggedness ^a	0.00–0.18	Terrain ruggedness index (TRI) ^d
Movement	Step length	2–8,289	Distance to successive GPS location (m/2-hr period); log transformed
Temporal	Season		Spring (den emergence to 14 Jun); summer (15 Jun–7 Aug); fall (8 Aug to den entry)
	Time of day		Day (sunrise to sunset); night (civil twilight end to civil twilight start); crepuscular (civil twilight start to sunrise and sunset to civil twilight end)

^a Indicates variables for which we tested a quadratic term.

^b Indicates variables for which we tested multiple scales (100 m, 200 m, 500 m).

^c Land cover categories and definitions: upland tree = >5% tree cover by crown closure, mesic or dry moisture regime; wetland tree = >5% tree cover by crown closure, wet or aquatic moisture regime; upland herb = >5% herbaceous cover, mesic or dry moisture regime; wetland herb = >5% herbaceous cover, wet or aquatic moisture regime; shrub = >5% shrub cover, any moisture regime; water = <5% vegetated, aquatic moisture regime; barren land = <5% vegetated, mesic or dry moisture regime.

^d indicates where we tested multiple scales (90 m and 300 m).

in the study area (Table 1). We defined a railway-associated GPS location as one that fell within 30 m on either side of the railway corridor. We dummy coded land cover variables that consisted of a land cover layer with 7 classifications: upland tree, wetland tree, upland herbaceous, wetland herbaceous, shrub, water, and barren land (Table 1; McDermid 2005). We used a digital elevation model and calculated a compound topographic index, $\ln(\text{upstream contributing area in m}^2 / \tan[\text{slope}])$, a proxy for terrain wetness (Sorensen et al. 2006) that others have demonstrated to be correlated with the presence of bear foods (Nielsen et al. 2004c). We obtained a layer depicting the percentage of forest canopy cover in the study area and, along with the aforementioned land cover variables, calculated values at 4 scales: within 30 m of the railway and the average proportion within 100-m, 200-m, and 500-m radii. We calculated the Euclidean distance from each rail-associated GPS location to the nearest forest edge, stream, and water body, and to 7 human-use features: roads, highways, towns, human-use trails, railway sidings, gravel pits, and former landfill sites. Railway sidings are places where the track was twinned to permit one train to slow or stop while another passes on the main line. In our study area, slower trains are associated with higher rates of grain spillage (Gangadharan et al. 2017) and we occasionally witnessed piles of grain at sidings where we presumed a leaky car had stopped (S. Z. Pollock, University of Alberta, personal observation). We included gravel pits and former landfills because bears are generally attracted to these sites for their photophilic and disturbance-tolerant vegetation

(e.g., alfalfa, clover, dandelion; Nielsen et al. 2004c, Roever et al. 2008a). We transformed each distance measurement (m) using a decay function, which predicts the decreasing influence of a feature as the distance between the feature and the animal increases. The exponential decay function, $1 - \exp(-0.002 \times \text{distance})$, was inversely related to distance such that values of zero occurred at the feature and approached 1 at distances >1,000 m (Nielsen et al. 2009). Lastly, for topography, we measured terrain ruggedness at 90 m and 300 m using circular moving windows (ArcMap Vector Ruggedness tool) and calculated the decay distance to wildlife crossing structures because of the similar way they could constrain movement. We used these values because of their correspondence to the resolution of our geographic information system (GIS) layers (30 m) and similarity to other studies of grizzly bears (Nielsen et al. 2004b, Roever et al. 2008a).

Temporal variables consisted of season and time of day. We defined seasons based on regional grizzly bear foraging habits (Nielsen et al. 2004a); spring correlated with the hypophagic period (den emergence to 14 Jun), summer with early hyperphagia (15 Jun–7 Aug), and fall with late hyperphagia (8 Aug to den entry). For each date, we divided time of day into day, night, and crepuscular periods using the National Research Council of Canada's sunrise and sunset calendar and definition of civil twilight, when the center of the sun's disk is 6° below the horizon. We defined day as the time between sunrise and sunset, night as civil twilight end to civil twilight start, and, crepuscular periods spanned civil twilight start to sunrise and sunset to civil

twilight end. We examined movement patterns using step length, which we calculated as the Euclidean distance between sequential GPS locations and then log-transformed length to normalize the distribution.

We used resource selection functions (Boyce et al. 2002, Manly et al. 2002) to assess which variables (above) were indicative of railway use by grizzly bears. We first analyzed the data at the home range scale by comparing used and available locations along the railway within individual 100% minimum convex polygons (third-order selection; Johnson 1980). We divided the railway into 30-m segments and classified each segment as used by the animal (a GPS location was recorded), or available (if the railway segment was within the bear's home range but no GPS location was recorded).

With the same suite of explanatory variables, we compared 4 types of movements, which we defined for each GPS point that occurred within 30 m of the railway by considering the position of the fixes immediately preceding and following it. Within these sequences, the middle position described, over a 6-hour period, locations where bears entered the railway, crossed it, continued along it, or exited the railway (Fig. 2). These assignments to movement types lacked high spatial precision but still distinguished movements in relation to the rail with only 1 fix (cross), versus 2 (enter or exit) or 3 (continue). We included only points that were obtained within 5 minutes of the targeted 2-hour fix rate. We used logistic regression to contrast all 6 pairwise comparisons of these 4 movement types, which we termed step discrimination functions. We intended this analysis to identify differences among our explanatory

variables in the patterns of successive fixes relative to the railway corridor, without assuming knowledge of animal motivation or that this temporal scale is most correlated with movement decisions. Our hypothesis that greater railway use would occur in areas with greater benefits emphasized the contrast between steps that continued along versus crossed the railway.

For all models, we used generalized linear mixed models with a binomial distribution and individual bear as the random effect (lme4 version 1.1-12; R version 3.2.1, <https://cran.r-project.org>, accessed 15 Jan 2018). We standardized all non-categorical variables to have a mean of zero and a standard deviation of 1. We assessed bivariate multicollinearity using Pearson's correlation coefficient ($|r| > 0.6$) and retained the variable with the lowest univariate Akaike's Information Criterion score (AIC; Burnham and Anderson 2002). Similarly, we assessed linear and quadratic terms and retained land cover variables at the appropriate scale via AIC. Because we considered each of 12 land cover and 7 human-use covariates to have potential biological importance, we constructed models with all subsets of variables and selected the top model (as indicated by the lowest AIC for small sample sizes [AIC_c] value) for each category using an information-theoretic approach (Burnham and Anderson 2002; MuMIn version 1.15.1; R version 3.2.1, <https://cran.r-project.org>, accessed 15 Jan 2018). We then compared models with combinations of top model variables for land cover, human use, and topography, plus their 2-way interactions, using the AIC_c (Burnham and Anderson 2002). For the step discrimination functions, we included 2-way interactions with temporal variables (season

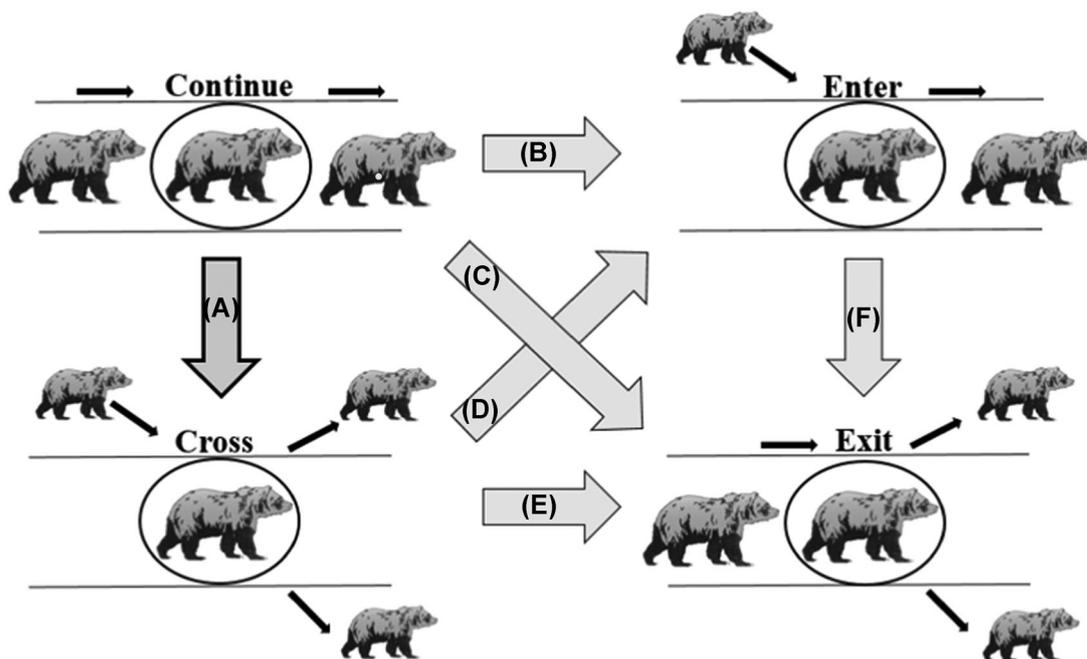


Figure 2. Schematic for step discrimination functions contrasting locations along the Canadian Pacific Railway in Banff and Yoho National Parks, Canada, collected between 2000 and 2016, where grizzly bears exhibited 3 successive global positioning system locations. For each contrast, the second point (depicted with circles) defined 4 types of rail use: continue, cross, enter, and exit. Paired contrasts compared (A) continued versus crossed movements, (B) continued versus entered, (C) continued versus exited, (D) crossed versus entered, (E) crossed versus exited, and (F) entered versus exited.

and time of day) and step length (the Euclidian distance between successive steps). We assessed the predictive ability of fitted models using the area under the receiver operating characteristic curve (ROCR version 1.0-7; R version 3.2.1, <https://cran.r-project.org>, accessed 15 Jan 2018).

To test for correlations between locations with bear mortality and those with concentrated railway use, we conducted decile analyses (Boyce et al. 2002). To do this, we first calculated kernel density estimates for overall railway use and each of the 4 movement types (i.e., enter, cross, continue, exit) along the railway throughout the study site. Then, we generated an available point every 100 m along the railway and attributed to each of these points their associated kernel density value from each of the 5 analyses described above. Next, and separately for each analysis, we ordered the kernel density values from low to high and separated them into decile bins. Then we compared the decile values to the proportion of grizzly bear mortalities that could be attributed to each of the 10 bins for each of the 5 types of use or steps. We calculated the proportion of mortalities in 2 ways: once from the 11 locations where 14 grizzly bears have been killed by train strikes and confirmed with the presence of a carcass (Government of Canada Open Data) and again by adding 6 additional locations where a strike (involving 7 bears) was reported, but no carcass was found (Fig. 1). Finally, we obtained a correlation coefficient between the proportion of mortalities in each decile bin and the decile rank of the bin. A positive correlation would demonstrate increasing numbers of mortalities with increased railway use overall, or any one of the movement types we defined.

RESULTS

We fitted 34 grizzly bears (19 female, 15 male) with GPS-collars intermittently between 2000 and 2016 with an approximately 2-hour fix rate, but only 27 bears (14 female, 13 male) had ≥ 1 railway-associated GPS location (within 30 m of the railway; Table S1, available online in Supporting Information), resulting in 1,515 unique railway GPS locations ($\bar{x} = 56.2 \pm 91.6$ [SD], range = 1–401). Seasonally, 47% of the

total railway GPS locations occurred in spring, 20% in summer, and 33% in fall (Table S2, available online in Supporting Information). As for diel patterns, 70% occurred during the day, 23% at night, and 7% at crepuscular time periods (Table S2). Three bears used the railway more extensively than others: a large male, a young adult male, and a sub-adult male who had 10%, 20%, and 26% of the total railway GPS locations, respectively. Bears crossed the railway 3 times more often than they continued along it, which were 24% less prevalent than enter and exit movements. Our criteria for defining steps identified 675 railway crossings by 27 grizzly bears (\bar{x} /individual = 25 ± 28.1 , range = 1–117), 304 enter locations for 24 bears ($\bar{x} = 12.6 \pm 21.3$, range = 1–84), 231 continue locations for 14 bears ($\bar{x} = 16.5 \pm 35.7$, range = 1–133), and 305 exit locations for 24 bears ($\bar{x} = 12.7 \pm 21.1$, range = 1–83).

Based on a third-order resource selection function, overall grizzly bear use of the railway was most strongly influenced by human-use features followed by land cover and topographical characteristics. The best-fitting form of distance to some human-use features was quadratic, revealing that bears selected the railway at intermediate distances from towns, highways, and trails, but the linear term fit best for railway sidings, showing that bears selected for these areas (Table 2). Among the land cover-related variables, bear use of the railway was negatively associated with the compound topographical index (terrain wetness), at a 500-m scale. Relative to available points, grizzly bears selected areas along the railway that had higher shrub cover and that were located closer to water bodies (Table 2). Topography was also an important determinant, with bears more likely to use the railway at intermediate distances from wildlife crossings and in areas that were more rugged at a local scale (90 m). The most supported model included an interaction in which railway use by bears increased farther from towns when the compound topographical index (terrain wetness) was higher at a 500-m scale (Table 2).

The most predictive model distinguishing movement pairs occurred, as we predicted, for movements that continued along versus crossed the railway (Table S3a, available online

Table 2. Top model results for the resource selection function describing characteristics of locations where grizzly bears selected for the railway (relative to available points) in Banff and Yoho National Parks, Canada, 2000–2016. We present standardized parameter estimates, standard error, odds ratios, and 95% confidence intervals. The area under the receiver operating characteristic curve for the model was 0.75.

Parameter	Estimate	SE	Odds ratio	95% CI
Intercept	−3.70	0.16		
Terrain wetness 500 m	−0.25	0.04	0.78	0.72 to 0.85
Shrub	0.28	0.07	1.32	1.15 to 1.51
Distance to water bodies	−0.10	0.03	0.91	0.85 to 0.96
Distance to railroad sidings	−0.14	0.03	0.87	0.82 to 0.91
Distance to trails	−0.17	0.04	0.84	0.78 to 0.91
Distance to trails (quadratic)	−0.11	0.04	0.90	0.83 to 0.96
Distance to towns	−0.17	0.08	0.84	0.73 to 0.98
Distance to towns (quadratic)	−0.45	0.09	0.64	0.53 to 0.77
Distance to highways	−0.01	0.04	0.99	0.91 to 1.06
Distance to highways (quadratic)	−0.16	0.04	0.85	0.79 to 0.92
Distance to wildlife crossings	0.18	0.06	1.20	1.06 to 1.36
Distance to wildlife crossings (quadratic)	0.23	0.05	1.26	1.14 to 1.39
Terrain ruggedness 90 m	0.17	0.03	1.19	1.13 to 1.25
Terrain wetness 500 m × distance to towns	0.64	0.10	1.90	1.55 to 2.32

in Supporting Information; area under the curve of the receiver operating characteristic [AUROC] = 0.88). The tendency for bears to continue along the railway was best predicted by topography, via a positive association with terrain ruggedness (300 m), which was a covariate in all 3 models that contrasted continue with the other movement types (Tables S3a-c). A model including the quadratic term was better supported, which reflected rapidly increasing selection for the railway as surrounding topography became more rugged. The largest effect sizes for continued use of the railway occurred for a human-use variable (railroad sidings) and season, with bears demonstrating prolonged use of the railway near sidings especially in fall (Table S3a). Bears also took smaller steps with continued use of the railway compared to all other movement types (Tables S3a-c, Table S4). Step lengths increased in rugged areas and with distance from railroad sidings and human-use trails (Tables S3a-c). Compared to crossings, continued use of the railway tended to occur at night ($\beta = 1.04$, 95% CI = 0.61–1.47).

Railway crossings were influenced by 4 main effects that were associated with land cover, human-use, and topographical variables. Crossing locations had a negative association with herbaceous cover (200-m scale) and occurred farther from railroad sidings compared to locations where bears entered or exited the railway (Table S3d,e). Crossings were characterized by less rugged terrain at a local 90-m scale (vs. entries) and occurred farther from wildlife crossings (vs. exits; Table S3d,e). Our analysis of temporal variables revealed that bears were more likely to cross the railway in summer, relative to spring (vs. entries: $\beta = 0.62$, 95% CI = 0.21–1.03; vs. exits: $\beta = 0.59$, 95% CI = 0.18–0.99) and fall (vs. entries: $\beta = 0.83$, 95% CI = 0.35–1.32; vs. exits: $\beta = 0.78$, 95% CI = 0.30–1.26). Bears also traveled more quickly (i.e., longer steps on a log scale) when they crossed the railway (vs. entries: $\beta = 0.14$, 95% CI = 0.003–0.29; vs. exits: $\beta = 0.32$, 95% CI = 0.16–0.48; Table S4, available online in Supporting Information).

Enter and exit locations were spatially similar with no land cover, human-use, or topographical variable performing better than the null model, resulting in our least predictive analysis. The variable with the strongest association was time of day. Bears were more likely to enter the railway during the day and at crepuscular periods and to exit it at night (Table S3f).

Based on our decile analysis, there were no strong linear associations between locations of confirmed bear mortality ($n = 11$) and areas of concentrated railway use (Fig. 1; $r = 0.11$, $P = 0.77$), or among movements that entered ($r = -0.38$, $P = 0.27$), crossed ($r = 0.40$, $P = 0.26$), continued along the railway ($r = -0.36$, $P = 0.30$), or exited it ($r = -0.32$, $P = 0.36$; Table S5, available online in Supporting Information). However, this analysis was based on only 11 confirmed mortality sites which, after conversion to proportions that were compared to the deciles for each use and movement type, resulted in regressions of just 10 points and low statistical power (range = 0.06–0.23). In a second analysis, we added reported strike sites ($n = 6$ for 17 locations that included the 11 confirmed mortalities) to determine how their

inclusion affected the strength of correlations. Results were similar, with no significant associations between collision locations and areas of concentrated railway use (Fig. 1; $r = 0.04$, $P = 0.89$), and movements that entered ($r = -0.54$, $P = 0.11$), crossed ($r = 0.30$, $P = 0.40$), or exited the railway ($r = -0.41$, $P = 0.24$; Table S5). There was a significant negative relationship between locations of more frequent collisions (confirmed mortalities and reported strikes) and continued use of the railway ($r = -0.63$, $P = 0.04$). Crossing and overall use sites (which were composed mostly of crossing sites) were unusual in generating a positive (but non-significant) correlation coefficient with the sites of greater bear mortality or strikes, whereas the other 3 coefficients were negative in both analyses.

DISCUSSION

Wildlife mortality occurs on railways around the world, but only a few recent studies have assessed where wildlife use and die along railways (Kušta et al. 2014, Dorsey et al. 2017, Roy and Sukumar 2017). We sought to determine the spatiotemporal factors associated with land cover, human use, and topography that influence railway use and movement by grizzly bears in the Canadian Rocky Mountains. Our results indicated that bears made greater use of the railway (as continue steps and overall use) where local forage, which could include both natural vegetation and spilled grain, was likely more abundant. Railway use also increased with adjacent rugged topography and in areas with lower values for the compound topographic index, which we considered to be a proxy for wetness (Sorensen et al. 2006). When we contrasted the rail-associated movements defined by 3 successive locations as enter, cross, continue, and exit, the greatest step discrimination was between continue and cross movements. Railway segments containing higher proportions of confirmed mortalities plus reported strikes (17 events) were negatively correlated with continue movements, but were not significantly associated with any of the other movement types or use overall.

Overall railway selection by bears was consistent with the hypotheses that their use would reflect advantages in foraging opportunities, travel efficiency, or avoidance of people. Forage-based opportunities were evident in the variables contributing to overall use, with greater shrub cover, and enter locations, with greater herbaceous cover within 200 m. These variables could indicate the presence of several bear-attracting plants that are enhanced along roads (Nielsen et al. 2004c, Roever et al. 2008a) and railways (Pollock et al. 2017) and are important to bears, such as horsetail, dandelions, and berry-producing shrubs. The availability of forage along transportation corridors generally promotes higher frequencies of road crossings (Chruszcz et al. 2003, Gagnon et al. 2007, Meisingset et al. 2013) and wildlife-vehicle collisions (Ramp et al. 2005, Ng et al. 2008, Grosman et al. 2009). Railway crossings tended to occur in areas where there was less herbaceous cover (200 m), which may reflect reduced foraging opportunity, and therefore a lessened attraction to the railway. Grizzly bears selected areas with lower values for the compound topographical

index; however, others working in similar landscapes reported that it is correlated with bear foods (Nielsen et al. 2004c). One reason for this discrepancy is that the index does not perform well in flat areas, which occurred adjacent to the railway through much of our study area. Alternatively, the terrain wetness that is often correlated with growth in herbaceous plants consumed by bears (Turney and Roberts 2004, Chetkiewicz and Boyce 2009) may have been subsumed by greater relative attraction in dry areas for railway-associated attractants, such as disturbance-tolerant plants (Pollock et al. 2017), spilled grain (Gangadharan et al. 2017), and rail-killed ungulates (Murray et al. 2017).

We found some evidence to support the hypothesis that bears use the railway in ways that minimize their encounter rate with people. Bears exhibited consistent attraction to railway sidings but a quadratic relationship to towns, roads, and trails. Attraction to sidings is consistent with forage-based benefits, which were further supported by the shorter step lengths that generally signal better habitat for bears (McLoughlin et al. 2000). Slower trains appear to deposit more grain (Gangadharan et al. 2017), which makes sidings among the locations where spilled grain has the most potential to accumulate (Dorsey 2011). Sidings also contain other types of human activity that could attract bears, including disturbance-tolerant plants (Hansen and Clevenger 2005, Rutkowska et al. 2013, Wrzesien et al. 2016), infrastructure and opportunity to accumulate refuse (Raman 2011, Joshi 2013), and petrochemical scents (Derocher and Stirling 1991), whereas the likelihood of encountering people, limited mainly to railway personnel, is relatively low. Attraction to human-use features with minimal human activity may be optimal for bears in the region because much of the most productive montane habitat is associated with high densities of people (Gibeau et al. 2002) and use of high human use areas increases risk of bear mortality (Chruszcz et al. 2003, Nielsen et al. 2006, Lamb et al. 2016). Consistent with this trade-off between risk and reward, bears were more likely to use the railway closer to people when surrounding habitat was drier (500 m), which may have signalled a greater need for anthropogenic resources in areas with potentially less natural food availability (Frid and Dill 2002, Rode et al. 2006). Even the attraction by bears to shrub cover may have stemmed partly from its importance as hiding cover next to the railway (Gibeau et al. 2002, Switalski and Nelson 2011).

Also consistent with the benefits we hypothesized, bears appeared to increase use of the railway where it enhanced travel efficiency. Overall railway use and locations where bears entered the railway were positively and linearly associated with local (90 m) ruggedness. Bears were more likely to continue along the railway when terrain was rugged at a broader scale (300 m). Topography is among the landscape characteristics that can impede movement for animals (Belisle 2005) and travel costs are typically higher in structurally complex landscapes (Shepard et al. 2013), particularly for wide-ranging animals (Crete and Lariviere 2003, Dickie et al. 2017). Our analyses of step lengths reinforced this interpretation of travel efficiency.

Bears demonstrated shorter step lengths on the railway during continue movements and close to railroad sidings, consistent with foraging behavior generally (Turchin 1998) and in other studies of grizzly bears (Roever et al. 2010, Graham and Stenhouse 2014, Kite et al. 2016). Bears demonstrated longer steps where they crossed the railway and in areas with rugged topography, indicative of travel (vs. foraging behavior). Others have reported similar increases in travel speed when animals cross transportation corridors, potentially partly as a behavioral response to fear (Dussault et al. 2007, Roever et al. 2010, Leblond et al. 2013).

Temporal predictors of railway use included season and time of day. Increased railway use during spring and fall may have resulted from the combination of high energy demands of bears post- and pre-hibernation and the scarcity of high caloric food resources on the broader landscape (Lopez-Alfaro et al. 2013). Similar seasonal peaks of selection by bears have been demonstrated for roads and towns (Roever et al. 2008b, Graham et al. 2010, Cristescu et al. 2016). In the mountain parks, bears typically make greater use of low elevation habitat with the emergent foods in the spring, and then follow the phenology of plants to higher elevations in the summer (Hamer and Herrero 1987a, Mace et al. 1999). Spring selection of the railway may therefore reflect early herbaceous feeding opportunities, particularly in forested or mountainous regions, where comparatively higher temperatures along the railway advances snowmelt and vegetative growth (Munro 2000, Roever et al. 2008a, Pollock et al. 2017). Fall railway selection may be associated with fruit availability along railway edges (Pollock et al. 2017) or the higher deposition of train-spilled grains due to an increase in fall exports (Gangadharan et al. 2017). Easy accessibility to high energy fruits and grains along the railway would be highly beneficial for grizzly bears because they need to rapidly gain fat for winter hibernation (Hertel et al. 2016).

In contrast to the predictable increase of railway use in spring and fall, we were surprised by the prevalence of railway use during the day (~70%) because it corresponds to the period of greater probability for encountering humans. In other landscapes with high densities of people, grizzly bears typically avoid people by increasing nocturnal or crepuscular activity (Schwartz et al. 2010a, Coleman et al. 2013, Fortin et al. 2016). Some avoidance of people may be reflected in our results by the greater tendency for bears to cross (relative to continue along) the railway during the day, increased railway use in spring and fall (periods of lesser tourism), and use of the railway farther from trails and townsites, where human density was higher. High human density in the valley bottom may generally limit the potential for bears to avoid people in this study area (Chruszcz et al. 2003).

The ultimate purpose of our analyses of railway use and our discrimination of step types was to determine whether these sites could predict past mortality locations. We found some limited evidence for such associations despite the constraint of small sample sizes that limited statistical power, but the direction of these relationships was

unexpected. In contrast to our initial prediction that strike risk would increase at continue locations where bears spent more time on the railway, these were negatively correlated with the locations that included confirmed mortalities and unconfirmed strikes. This pattern might have occurred because continue locations were predicted by features, such as sidings and rugged terrain, that cause trains to travel more slowly. Faster trains likely reduce the time with which wildlife can detect approaching trains and increase the likelihood of a panic-stricken and maladaptive response to them (Backs et al. 2017). The possibility that surprise or inexperience increases mortality risk, is consistent with the fact that the correlation coefficients with mortality and strikes were positive, albeit non-significantly, only for crossing and overall use sites (which were comprised by ~45% crossing locations). Crossing sites occurred in areas with lower terrain ruggedness, which may promote cross-valley movement. Particularly in these areas, factors that reduce the ability for bears to detect trains, such as track curvature, limited sight lines, or foul weather may increase strike risk (Burley 2015, Backs et al. 2017, Dorsey et al. 2017). Better information about these effects could be used to identify optimal locations for attractant removal (Gangadharan et al. 2017, Murray et al. 2017), provision of alternative travel routes (I. R. Pengelly and J. D. Hamer, unpublished report), use of deterrents (Babinska-Werka et al. 2015), or installation of train-triggered warning devices (Backs et al. 2017).

Our study had limitations that may have reduced our ability to determine how grizzly bear railway use or movement decisions affected their risk of collisions with trains. The primary limitation is sample size in the number of confirmed mortality events (11) and the number of bears (3) that frequently used the rail, causing high interpretive reliance on a few individuals. We increased our power to detect association with sites of past mortality by including the 6 locations where strikes were reported, but no carcass was found. Even if bears were not struck, those locations of near misses provide interpretive information to suggest that sites of higher use does not readily translate to sites of greater collision risk. A second limitation stems from the 2-hour fix rates of the GPS collars, which may have been too coarse to maximize biological relevance of the movement types we defined. For grizzly bears, the behavioral states that might signal movement decisions likely require fix rates more frequent than 1-hour intervals (Cristescu et al. 2015). Lower fix rates also make it harder to identify actual movement paths (Swain et al. 2008, Brown et al. 2013) and this problem would be exacerbated in areas with steeper topography and denser canopy cover where fix success declines further (Frair et al. 2004, Heard et al. 2008). A third limitation is that we measured railway selection intermittently from 2000–2016 in which several environmental changes likely affected railway use by bears. For example, bears may have selected habitats near humans more often in years of poor food availability (Mattson et al. 1992, Baruch-Mordo et al. 2014, Obbard et al. 2014) and our GIS-derived land cover measures would have

underestimated fluctuations of plant productivity (Boyce et al. 2002, Nielsen et al. 2010).

Despite these limitations, our study demonstrated spatial and temporal patterns of railway use and movement by grizzly bears that support some suggestions for mitigation. The strongest of these was the striking seasonality in railway use by bears, which reasonably prioritizes mitigation to spring and fall months when trains are most likely to encounter bears. We found that foraging is the most consistent explanatory variable for heightened use of the railway by bears, which recommends removal of attractants that include vegetation, train-spilled grain, and rail-killed ungulates. These efforts should be focused where collision risk appears to be heightened, such as 2 known hotspots of mortality or areas with high railway use by bears. Such hotspots may be associated with specific attractants near the rail (St. Clair et al. 2019) or with landscape-scale topographical features (A. Gangadharan, University of Alberta, unpublished data) that are necessarily part of the large home ranges and associated travel routes of bears. Thus, railway mitigation might logically extend to these larger scales to include habitat enhancement, such as forest thinning or prescribed burns, to increase natural forage productivity and potentially lessen bear attraction to the railway (Nielsen et al. 2004c, 2006; Pengelly and Hamer 2006). Use of larger spatial scales in the analysis of bear movements will also identify the topographical pinch points that funnel movement for bears and other wildlife (Whittington et al. 2004, 2005), which may encourage additional mitigation via warning devices (Backs et al. 2017), exclusion (e.g., via partial fencing, Ascensão et al. 2013), or alternative travel routes (e.g., via clearing of trails adjacent to the rail; I. R. Pengelly and J. D. Hamer, unpublished report). We encourage others to analyze and interpret wildlife use and movement in relation to railways as an important part of understanding, and ultimately, improving mitigation of rail-associated wildlife mortality.

MANAGEMENT IMPLICATIONS

Seasonal patterns of railway use by grizzly bears indicate that mitigation efforts should be emphasized in spring and fall. We could not predict locations of mortality from overall use or any of the 4 step types, but a larger sample size may have amplified the tendency for crossing locations to correlate with mortality sites. Until more information is available, managers might target site-specific mitigation in 2 areas we identified where past mortality of grizzly bears has been concentrated.

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LITERATURE CITED

- Adkins, C. A., and P. Stott. 1998. Home ranges, movements and habitat associations of red foxes *Vulpes vulpes* in suburban Toronto, Ontario, Canada. *Journal of Zoology* 244:335–346.
- Ascensão, F., A. P. Clevenger, M. Santos-Reis, P. Urbano, and N. Jackson. 2013. Wildlife–vehicle collision mitigation: Is partial fencing the answer? An agent-based model approach. *Ecological Modelling* 257:36–43.
- Babinska-Werka, J., D. Krauze-Gryz, M. Wasilewski, and K. Jasinska. 2015. Effectiveness of an acoustic wildlife warning device using natural calls to reduce the risk of train collisions with animals. *Transportation Research Part D: Transport and Environment* 38:6–14.
- Backs, J. A. J., J. A. Nychka, and C. C. St. Clair. 2017. Warning systems triggered by trains could reduce collisions with wildlife. *Ecological Engineering* 106A:563–569.
- Baigas, P. E., J. R. Squires, L. E. Olson, J. S. Ivan, and E. Roberts. 2017. Using environmental features to model highway crossing behavior of Canada lynx in the Southern Rocky Mountains. *Landscape and Urban Planning* 157:200–213.
- Barnum, S. A. 2003. Identifying the best locations along highways to provide safe crossing opportunities for wildlife. Pages 246–252 in *International Conference on Ecology and Transportation*, 24–29 August 2003, Lake Placid, New York, USA.
- Baruch-Mordo, S., K. R. Wilson, D. L. Lewis, J. Broderick, J. S. Mao, and S. W. Breck. 2014. Stochasticity in natural forage production affects use of urban areas by black bears: implications to management of human–bear conflicts. *PLoS ONE* 9(1):e85122.
- Belisle, M. 2005. Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology* 86:1988–1995.
- Benito-Lopez, A., R. Alkemade, and P. Verweij. 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biological Conservation* 143:1307–1316.
- Bertch, B., and M. L. Gibeau. 2010. Grizzly bear monitoring in and around the Mountain National Parks: mortalities and bear/human encounters 1980–2009. Parks Canada Report, Lake Louise, Alberta, Canada.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Brown, D. D., R. Kays, M. Wikelski, R. Wilson, and A. P. Klimley. 2013. Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry* 1:20.
- Burley, B. 2015. Determinants of risk in bear–train interactions. Thesis, University of Calgary, Calgary, Alberta, Canada.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.
- Carr, L. W., and L. Fahrig. 2001. Effect of road traffic on two amphibian species of differing vagility. *Conservation Biology* 15:1071–1078.
- Chetkiewicz, C.-L. B., and M. S. Boyce. 2009. Use of resource selection functions to identify conservation corridors. *Journal of Applied Ecology* 46:1036–1047.
- Chruszcz, B., A. P. Clevenger, K. E. Gunson, and M. L. Gibeau. 2003. Relationships among grizzly bears, highways and habitat in the Banff-Bow Valley, Alberta, Canada. *Canadian Journal of Zoology* 81:1378–1391.
- Clevenger, A. P., B. Chruszcz, and K. E. Gunson. 2001. Highway mitigation fencing reduces wildlife–vehicle collisions. *Wildlife Society Bulletin* 29:646–653.
- Clevenger, A. P., P. J. Wierzchowski, B. Chruszcz, and K. E. Gunson. 2002. GIS-generated expert based models for identifying wildlife habitat linkages and mitigation passage planning. *Conservation Biology* 16:503–514.
- Coleman, T. H., C. C. Schwartz, K. A. Gunther, and S. Creel. 2013. Grizzly bear and human interaction in Yellowstone National Park: an evaluation of bear management areas. *Journal of Wildlife Management* 77:1311–1320.
- Crete, M., and S. Larivière. 2003. Estimating the costs of locomotion in snow for coyotes. *Canadian Journal of Zoology* 81:1808–1814.
- Cristescu, B., G. B. Stenhouse, and M. S. Boyce. 2015. Predicting multiple behaviors from GPS radio collar cluster data. *Behavioral Ecology* 26:452–464.
- Cristescu, B., G. B. Stenhouse, and M. S. Boyce. 2016. Grizzly bear space use, survival, and persistence in relation to human habituation and access. *Human-Wildlife Interactions* 10:240–257.
- Dasgupta, S., and A. K. Ghosh. 2015. Elephant–railway conflict in a biodiversity hotspot: determinants and perceptions of the conflict in Northern West Bengal, India. *Human Dimensions of Wildlife* 20:81–94.
- Derocher, A., and I. Stirling. 1991. Oil contamination of polar bears. *Polar Record* 27(160):56–57.
- Dickie, M., R. Serrouya, and S. A. Boutin. 2017. Faster and farther: wolf movement on linear features and implications for hunting behavior. *Journal of Applied Ecology* 54:253–263.
- Dorsey, B. P. 2011. Factors affecting bear and ungulate mortalities along the Canadian Pacific Railroad through Banff and Yoho National Parks. Thesis, Montana State University, Bozeman, USA.
- Dorsey, B. P., A. P. Clevenger, and L. J. Rew. 2017. Relative risk and variables associated with bear and ungulate mortalities along a railroad in the Canadian Rocky Mountains. Pages 135–155 in L. Borda-de-Agua, R. Barrientos, P. Beja, and H. M. Pereira, editors. *Railway ecology*. Springer, New York, New York, USA.
- Dorsey, B. P., M. Olsson, and L. J. Rew. 2015. Ecological effects of railways on wildlife. Pages 219–227 in R. van der Ree, D. J. Smith, and C. Grilo, editors. *Handbook of road ecology*. John Wiley & Sons, Chichester, West Sussex, United Kingdom.
- Dulac, J. 2013. Global land transport infrastructure requirements: Estimating road and railway infrastructure capacity and costs to 2050. International Energy Agency, Paris, France.
- Dussault, C., J.-P. Ouellet, C. Laurian, R. Courtois, M. Poulin, and L. Breton. 2007. Moose movement rates along highways and crossing probability models. *Journal of Wildlife Management* 71:2338–2345.
- Fahrig, L. 2007. Non-optimal movement in human-altered landscapes. *Functional Ecology* 21:1003–1015.
- Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society* 14(1):21.
- Fortin, J. K., K. D. Roade, G. V. Hilderbrand, J. Wilder, S. Farley, C. Jorgensen, and B. G. Marcot. 2016. Impacts of human recreation on brown bears (*Ursus arctos*): a review and new management tool. *PLoS ONE* 11(1):e0141983.
- Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* 41:201–211.
- Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6(1):11.
- Gagnon, J. W., T. C. Theimer, N. L. Dodd, S. Boe, and R. E. Schweinsburg. 2007. Traffic volume alters elk distribution and highway crossings in Arizona. *Journal of Wildlife Management* 71:2318–2323.
- Gangadharan, A., S. Z. Pollock, P. S. Gilhooly, A. J. Friesen, B. P. Dorsey, and C. C. St. Clair. 2017. Grain spilled from moving trains create a substantial wildlife attractant in protected areas. *Animal Conservation* 20:391–400.
- Garshelis, D. L., M. L. Gibeau, and S. Herrero. 2005. Grizzly bear demographics in and around Banff National Park and Kananaskis country, Alberta. *Journal of Wildlife Management* 69:277–297.
- Gibeau, M. L., A. P. Clevenger, S. Herrero, and J. Wierzchowski. 2002. Grizzly bear response to human development and activities in the Bow River watershed, Alberta. *Biological Conservation* 103:227–236.
- Gilhooly, P. S., S. E. Nielsen, J. Whittington, and C. C. St. Clair. 2019. Wildlife mortalities on roads and railways following highway mitigation. *Ecosphere* 10(2):e02597.
- Gomes, L., C. Grilo, C. Silva, and A. Mira. 2009. Identification methods and deterministic factors of owl roadkill hotspot locations in Mediterranean landscapes. *Ecological Research* 24:355–370.
- Graham, K., J. Boulanger, J. Duval, and G. B. Stenhouse. 2010. Spatial and temporal use of roads by grizzly bears in West-Central Alberta. *Ursus* 21:43–56.
- Graham, K., and G. B. Stenhouse. 2014. Home range, movements, and denning chronology of the grizzly bear (*Ursus arctos*) in west-central Alberta. *Canadian Field-Naturalist* 128:223–234.
- Grosman, P. D., J. A. G. Jaeger, P. M. Biron, C. Dussault, and J.-P. Ouellet. 2009. Reducing moose–vehicle collisions through salt pool removal and displacement: an agent-based modeling approach. *Ecology and Society* 14(2):17.
- Gundersen, H., H. P. Andeassen, and T. Storaas. 1998. Spatial and temporal correlates to Norwegian moose–train collisions. *Alces* 34:385–394.

- Gunson, K. E., D. Ireland, and F. Schueler. 2012. A tool to prioritize high-risk road mortality locations for wetland-forest herpetofauna in southern Ontario, Canada. *North-Western Journal of Zoology* 8:409–413.
- Gunson, K. E., G. Mountrakis, and L. J. Quackenbush. 2011. Spatial wildlife-vehicle collision models: a review of current work and its application to transportation mitigation projects. *Journal of Environmental Management* 92:1074–1082.
- Hamer, D., and S. Herrero. 1987a. Grizzly bear food and habitat in the front ranges of Banff National Park, Alberta. *International Conference on Bear Research and Management* 7:199–213.
- Hamer, D., and S. Herrero. 1987b. Wildlife's influence on grizzly bear feeding ecology in Banff National Park, Alberta. *International Conference on Bear Research and Management* 7:179–186.
- Hansen, M. J., and A. P. Clevenger. 2005. The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. *Biological Conservation* 125:249–259.
- Heard, D. C., L. M. Ciarniello, and D. R. Seip. 2008. Grizzly bear behavior and global positioning system collar fix rates. *Journal of Wildlife Management* 72:596–602.
- Hebblewhite, M., and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology* 45:834–844.
- Hertel, A. G., S. M. J. G. Steyaert, A. Zedrosser, A. Mysterud, H. K. Lodberg-Holm, H. W. Gelink, J. Kindberg, and J. E. Swenson. 2016. Bears and berries: species-specific selective foraging on a patchily distributed food resource in a human-altered landscape. *Behavioral Ecology and Sociobiology* 70:831–842.
- Holland, W. D., and G. M. Coen. 1983. Ecological land classification of Banff and Jasper National Parks. Canadian Forestry Service Publication M-83-2, Edmonton, Alberta, Canada.
- Hopkins, J. B., III, J. Whittington, A. P. Clevenger, M. A. Sawaya, and C. C. St. Clair. 2014. Stable isotopes reveal rail-associated behavior in a threatened carnivore. *Isotopes in Environmental and Health Studies* 50:322–331.
- Huijser, M. P., and P. T. McGowan. 2003. Overview of animal detection and animal warning systems in North America and Europe. Pages 1–16 in *International Conference on Ecology and Transportation*, 24–29 August 2003, Lake Placid, New York, USA.
- Jalkotzy, M. G., P. I. Ross, and M. D. Nasserden. 1997. The effects of linear developments on wildlife: a review of the selected scientific literature. Canadian Petroleum Producers, Calgary, Alberta, Canada.
- Janz, B., and D. Storr. 1977. The climate of the contiguous mountain parks. Parks Canada Department of Indian and Northern Affairs Project Report No. 30, Edmonton, Alberta, Canada.
- Jasinska, K., J. Werka, D. Krauze-Gryz, and M. Wasilewski. 2014. Sonic deterring devices UOZ-1 as a tool to limit collisions with animals along the railways. *Sylvan* 158(2):143–150.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Joshi, R. 2013. Evaluating the impact of human activities during the Maha-Kumbh 2010 fair on elephants in the Shivalik Elephant Reserve. *Tropical Natural History* 13:107–129.
- Joshi, R., and R. Singh. 2007. Asian elephants are losing their seasonal traditional movement tracks: a decade of study in and around the Rajaji National Park, India. *Gajah* 27:15–26.
- Kite, R., T. Nelson, G. B. Stenhouse, and C. Darimont. 2016. A movement-driven approach to quantifying grizzly bear (*Ursus arctos*) near-road movement patterns in west-central Alberta, Canada. *Biological Conservation* 195:24–32.
- Kušta, T., M. Hola, Z. Keken, M. Ježek, T. Zika, and V. Hart. 2014. Deer on the railway line: spatiotemporal trends in mortality patterns of roe deer. *Turkish Journal of Zoology* 38:479–485.
- Lamb, C. T., G. Mowat, B. N. McLellan, S. E. Nielsen, and S. Boutin. 2016. Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore. *Journal of Animal Ecology* 86:55–65.
- Langen, T. A., K. Ogden, and L. Schwarding. 2009. Predicting hotspots of herpetofauna road mortality along highway road networks: model creation and experimental validation. *Journal of Wildlife Management* 73:104–114.
- Latham, A. D. M., M. C. Latham, M. S. Boyce, and S. Boutin. 2011. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications* 21:2854–2865.
- Laurance, W. F., M. Goosem, and S. G. W. Laurance. 2009. Impacts of roads and linear clearings on tropical forests. *Trends in Ecology and Evolution* 24:659–669.
- Laurance, W. F., S. Sloan, L. Weng, and J. A. Sayer. 2015. Estimating the environmental costs of Africa's massive "developmental corridors". *Current Biology* 25:3202–3208.
- Laurian, C., C. Dussault, J.-P. Ouellet, R. Courtois, M. Poulin, and L. Breton. 2008. Behavior of moose relative to a road network. *Journal of Wildlife Management* 72:1550–1557.
- Leblond, M., C. Dussault, and J.-P. Ouellet. 2013. Avoidance of roads by large herbivores and its relation to disturbance intensity. *Journal of Zoology* 289:32–40.
- Lewis, J. S., J. L. Rachlow, J. S. Horne, E. O. Garton, W. L. Wakkinen, J. Hayden, and P. Zager. 2011. Identifying habitat characteristics to predict highway crossing areas by black bears within a human-dominated landscape. *Landscape and Urban Planning* 101:99–107.
- Lopez-Alfaro, C., S. P. Coogan, C. T. Robbins, J. K. Fortin, and S. E. Nielsen. 2015. Assessing nutritional parameters of brown bear diets among ecosystems gives insight into differences among populations. *PLoS ONE* 10(6):e0128088.
- Lopez-Alfaro, C., C. T. Robbins, A. Zedrosser, and S. E. Nielsen. 2013. Energetics of hibernation and reproductive trade-offs in brown bears. *Ecological Modelling* 270:1–10.
- Loraamm, R. W., and J. A. Downs. 2016. A wildlife movement approach to optimally locate wildlife crossing structures. *International Journal of Geographical Information Science* 30(1):74–88.
- Luckman, B., and T. Kavanagh. 2000. Impact of climate fluctuations on mountain environments in the Canadian Rockies. *AMBIO: A Journal of the Human Environment* 29(7):371–380.
- Mace, R. D., J. S. Waller, T. L. Manley, K. Ake, and W. T. Wittinger. 1999. Landscape evaluation of grizzly bear habitat in western Montana. *Conservation Biology* 13:367–377.
- Malo, J. E., F. Suarez, and A. Diez. 2004. Can we mitigate animal-vehicle accidents using predictive models? *Journal of Applied Ecology* 41: 701–710.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies. Second edition. Kluwer, Dordrecht, The Netherlands.
- Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *Journal of Wildlife Management* 56:432–442.
- McDermid, G. J. 2005. Remote sensing for large-area, multi-jurisdictional habitat mapping. Dissertation, Department of Geography, University of Waterloo, Ontario, Canada.
- McLellan, B. N. 2011. Implication of a high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. *Canadian Journal of Zoology* 89:546–558.
- McLoughlin, P. D., S. H. Ferguson, and F. Messier. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evolutionary Ecology* 14:39–60.
- Meisingset, E. L., L. E. Loe, O. Brekkum, and A. Mysterud. 2013. Red deer habitat selection and movements in relation to roads. *Journal of Wildlife Management* 77:181–191.
- Mkanda, F. X., and W. Chansa. 2011. Changes in temporal and spatial pattern of road kills along the Lusaka-Mongu (M9) highway, Kafue National Park, Zambia. *South African Journal of Wildlife Research* 41: 68–78.
- Munro, R. H. 2000. The impacts of transportation corridors on grizzly and black bear habitat use patterns near Golden, Thesis, University of Victoria, Victoria, British Columbia, Canada.
- Munro, R. H., S. E. Nielsen, M. H. Price, G. B. Stenhouse, and M. S. Boyce. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. *Journal of Mammalogy* 87:1112–1121.
- Murray, M. H., S. Fassina, J. B. Hopkins, III, J. Whittington, and C. C. St. Clair. 2017. Seasonal and individual variation in the use of rail-associated food attractants by grizzly bears (*Ursus arctos*) in a national park. *PLoS ONE* 12(5):e0175658.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the USA* 105:19052–19059.

- Ng, J. W., C. Nielson, and C. C. St. Clair. 2008. Landscape and traffic factors influencing deer-vehicle collisions in an urban environment. *Human-Wildlife Interactions* 2(1):34-47.
- Nielsen, S. E., M. S. Boyce, and G. B. Stenhouse. 2004a. Grizzly bears and forestry. I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. *Forest Ecology and Management* 199(1):51-65.
- Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2003. Development and testing of phenologically driven grizzly bear habitat models. *Ecoscience* 10(1):1-10.
- Nielsen, S. E., M. R. L. Cattet, J. Boulanger, J. Cranston, G. J. McDermid, A. B. A. Shafer, and G. B. Stenhouse. 2013. Environmental, biological and anthropogenic effects on grizzly bear body size: temporal and spatial considerations. *BMC Ecology* 13:31.
- Nielsen, S. E., G. Cranston, and G. B. Stenhouse. 2009. Identification of priority areas for grizzly bear conservation and recovery in Alberta, Canada. *Journal of Conservation Planning* 5:38-60.
- Nielsen, S. E., S. Herrero, M. S. Boyce, B. Benn, R. D. Mace, M. L. Gibeau, and S. Jevons. 2004b. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies Ecosystem of Canada. *Biological Conservation* 120:101-113.
- Nielsen, S. E., T. A. Larsen, G. B. Stenhouse, and S. C. P. Coogan. 2017. Complementary food resources of carnivory and frugivory affect local abundance of an omnivorous carnivore. *Oikos* 126:369-380.
- Nielsen, S. E., G. McDermid, G. B. Stenhouse, and M. S. Boyce. 2010. Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. *Biological Conservation* 143:1623-1643.
- Nielsen, S. E., R. H. Munro, E. L. Bainbridge, G. B. Stenhouse, and M. S. Boyce. 2004c. Grizzly bears and forestry II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. *Forest Ecology and Management* 199(1):67-82.
- Nielsen, S. E., G. B. Stenhouse, and M. S. Boyce. 2006. A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation* 130:217-229.
- Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* 10:949-963.
- Obbard, M. E., E. J. Howe, L. L. Wall, B. Allison, R. Black, P. Davis, L. Dix-Gibson, M. Gatt, and M. N. Hall. 2014. Relationships among food availability, harvest, and human-bear conflict at landscape scales in Ontario, Canada. *Ursus* 25:98-110.
- Olson, K. A., and R. van der Ree. 2015. Railways, roads and fences across Kazakhstan and Mongolia threaten the survival of wide-ranging wildlife. Pages 472-478 in R. van der Ree, D. J. Smith, and C. Grilo, editors. *Handbook of road ecology*. John Wiley & Sons, Chichester, West Sussex, United Kingdom.
- Parks Canada Agency. 2018. Parks Canada Attendance 2017-2018. <<https://www.pc.gc.ca/en/docs/pc/attend>>. Accessed 1 Mar 2018.
- Pengelly, I., and D. Hamer. 2006. Grizzly bear use of pink hedysarum roots following shrubland fire in Banff National Park, Alberta. *Ursus* 17:124-131.
- Pollock, S. Z., S. E. Nielsen, and C. C. St. Clair. 2017. A railway increases the abundance and accelerates the phenology of bear-attracting plants in a forested, mountain park. *Ecosphere* 8(10):e01985.
- Popp, J. N. 2017. Railways offer grain on a silver platter to wildlife, but at what cost? *Animal Conservation* 20:403-404.
- Raman, T. R. S. 2011. Framing ecologically sound policy on linear intrusions affecting wildlife habitats. Nature Conservation Foundation, Mysuru, India.
- Ramp, D. J., J. Caldwell, K. A. Edwards, D. Warton, and D. B. Croft. 2005. Modelling of wildlife fatality hotspots along the snowy mountain highway in New South Wales, Australia. *Biological Conservation* 126:474-490.
- Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. *Biological Conservation* 133:70-80.
- Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2008a. Grizzly bears and forestry I: road vegetation and placement as an attractant to grizzly bears. *Forest Ecology and Management* 256:1253-1261.
- Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2008b. Grizzly bears and forestry II: grizzly bear habitat selection and conflicts with road placement. *Forest Ecology and Management* 256:1262-1269.
- Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2010. Grizzly bear movements relative to roads: application of step selection functions. *Ecography* 33:1113-1122.
- Roy, M., and R. Sukumar. 2017. Railways and wildlife: a case study of train-elephant collisions in Northern West Bengal, India. Pages 157-177 in L. Borda-de-Agua, R. Barrientos, P. Beja, and H. M. Pereira, editors. *Railway ecology*. Springer, New York, New York, USA.
- Rutkovska, S., I. Pucka, P. Everts-Bunders, and J. Paidere. 2013. The role of railway lines in the distribution of alien plants species in the territory of Daugavpils City (Latvia). *Estonian Journal of Ecology* 62(3):212-225.
- Santos, S. M., F. Carvalho, and A. Mira. 2017. Current knowledge on wildlife mortalities in railways. Pages 11-22 in L. Borda-de-Agua, R. Barrientos, P. Beja, and H. M. Pereira, editors. *Railway ecology*. Springer, New York, New York, USA.
- Schuster, R., H. Romer, and R. R. Germain. 2013. Using multi-scale distribution and movement effects along a montane highway to identify optimal crossing locations for a large-bodied mammal community. *PeerJ* 1:e189.
- Schwartz, C. C., S. L. Cain, S. Podruzny, S. Cherry, and L. Frattaroli. 2010a. Contrasting activity patterns of sympatric and allopatric black and grizzly bears. *Journal of Wildlife Management* 74:1628-1638.
- Schwartz, C. C., M. A. Haroldson, and G. C. White. 2010b. Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. *Journal of Wildlife Management* 74:654-667.
- Seiler, A., and M. Olsson. 2017. Wildlife deterrent methods for railways - an experimental study. Pages 277-291 in L. Borda-de-Agua, R. Barrientos, P. Beja, and H. M. Pereira, editors. *Railway ecology*. Springer, New York, New York, USA.
- Seo, C., J. Thorne, T. Choi, H. Kwon, and C. H. Park. 2015. Disentangling roadkill: the influence of landscape and season on cumulative vertebrate mortality in South Korea. *Landscape and Ecological Engineering* 11:87-99.
- Shepard, E. L. C., R. P. Wilson, W. G. Rees, E. Grundy, S. A. Lambertucci, and S. B. Vosper. 2013. Energy landscapes shape animal movement ecology. *American Naturalist* 182:298-312.
- Sorensen, R., U. Zinko, and J. Seibert. 2006. On the calculation of the topographic wetness index: evaluation of different methods based on field observations. *Hydrology and Earth System Sciences* 10:101-112.
- St. Clair, C. C., J. A. J. Backs, A. J. Friesen, A. Gangadharan, P. S. Gilhooly, M. H. Murray, and S. Z. Pollock. 2019. Animal learning may contribute to both problems and solutions for wildlife-train collisions. *Philosophical Transactions of the Royal Society B* 374:20180050.
- St. Clair, C. C., A. Gangadharan, S. Z. Pollock, P. S. Gilhooly, A. Friesen, and B. Dorsey. 2017. Gaining momentum on awareness of the ecological effects of railways. *Animal Conservation* 20:407-408.
- Steiner, W., F. Leisch, and K. Hacklander. 2014. A review on the temporal pattern of deer-vehicle accidents: impact of seasonal, diurnal and lunar effects in cervids. *Accident Analysis and Prevention* 66:168-81.
- Sunga, J., J. Sayers, K. Cottenie, C. Kyle, and D. M. Ethier. 2017. The effects of roads on habitat selection and movement patterns of the American badger subspecies *Taxidea taxus jacksoni* in Ontario, Canada. *Canadian Journal of Zoology* 95:821-828.
- Swain, D. L., T. Wark, and G. J. Bishop-Hurley. 2008. Using high fix rate GPS data to determine the relationships between fix rate, prediction errors and patch selection. *Ecological Modelling* 212:273-279.
- Switalski, T. A., and C. R. Nelson. 2011. Efficacy of road removal for restoring wildlife habitat: black bear in the Northern Rocky Mountains. *Biological Conservation* 144:2666-2673.
- Tremblay, M. A., and C. C. St. Clair. 2009. Factors affecting the permeability of transportation and riparian corridors to the movements of songbirds in an urban landscape. *Journal of Applied Ecology* 46:1314-1322.
- Turchin, P. 1998. *Quantitative analysis of movement*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Turney, L., and A.-M. Roberts. 2004. Grizzly bear spring, summer, and fall - habitat suitability model. Morice Lakes Innovative Forest Practices Agreement, Smithers, British Columbia, Canada.
- Waller, J. S., and C. Servheen. 2005. Effects of transportation infrastructure on grizzly bears in Northwestern Montana. *Journal of Wildlife Management* 69:985-1000.

- Wells, P., J. G. Woods, G. Bridgewater, and H. Morrison. 1999. Wildlife mortalities in railways: monitoring methods & mitigation strategies. Pages 1–11 *in* International Conference on Ecology and Transportation, 13–16 September 1999, Missoula, Montana, USA.
- Whittington, J., C. C. St. Clair, and G. Mercer. 2004. Path tortuosity and the permeability of roads and trails to wolf movement. *Ecology and Society* 9(1):4.
- Whittington, J., C. C. St. Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications* 15:543–553.

- Wrzesien, M., B. Denisow, Z. Mamchur, M. Chuba, and I. Resler. 2016. Composition and structure of the flora in inter-urban railway areas. *Acta Agrobotanica* 69(3):1666.

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