

# A railway increases the abundance and accelerates the phenology of bear-attracting plants in a forested, mountain park

SONYA Z. POLLOCK,<sup>1,†</sup> SCOTT E. NIELSEN,<sup>2</sup> AND COLLEEN C. ST. CLAIR<sup>1</sup>

<sup>1</sup>Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9 Canada

<sup>2</sup>Department of Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2H1 Canada

**Citation:** 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. 10.1002/ecs2.1985

**Abstract.** Vegetation enhancement along railways has not been well studied, despite high rates of mortality from train strikes across numerous species, including sensitive populations in protected areas. This situation describes grizzly bears (*Ursus arctos*) in the mountain parks of Canada, where train strikes have become the leading source of known mortality. We hypothesized that attraction by bears to railways occurs partly because of increases in the richness, diversity, cover, and maturation rate of plants consumed by bears relative to adjacent forest and that this effect may increase with elevation. We quantified and compared responses in plants used by bears to the railway (ballast), forest edge, and within adjacent forest for two growing seasons (May–October) at 19 locations spanning an elevational gradient in Banff and Yoho National Parks in the Canadian Rocky Mountains. Overall, richness, diversity, and total cover of plants consumed by bears were greatest at the forest edge. On the forest edge or ballast, flowering rates of some species were over three times higher and fruit occurrence was up to five times higher than 50 m into the adjacent forest. Enhancement of berry productivity along rail edges increased with elevation. Buffaloberry (*Shepherdia canadensis*), an important regional pre-hibernation resource, had more fruit, faster ripening, and higher sugar content for shrubs located within 15 m of the rail than within surrounding interior forest. Our results demonstrate that railway edges can increase the quantity and quality of palatable vegetation resources of both native and introduced species, potentially increasing strike risk for bears and other wildlife. Potential mitigation of this risk could include removal of attractants along the rail, particularly at locations where other factors increase the risk of collisions, and creation of forest openings, either through natural processes or through forest modification that would provide forage in less risky habitats.

**Key words:** berry productivity; ecological trap; edge; elevation; grizzly bears; invasive species; phenology; railway; Rocky Mountain Parks; *Ursus arctos*; vegetation; wildlife–train collisions.

**Received** 2 February 2017; revised 18 July 2017; accepted 25 August 2017; final version received 21 September 2017.  
Corresponding Editor: James W. Cain III.

**Copyright:** © 2017 Pollock et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** spollock@ualberta.ca

## INTRODUCTION

Transportation networks pose a major threat to the persistence of wildlife species through the loss, fragmentation, and degradation of habitat (Spellerberg 1998, Bennett et al. 2011). Transportation infrastructure also affects wildlife species directly through vehicle-caused mortality, which can compromise population viability for species with low

reproductive rates, large home ranges, and small population sizes (Alexander and Waters 2000, Trombulak and Frissell 2000). As the impact of roads on wildlife has become more recognized, mitigation practices, such as fencing and crossing structures, have successfully reduced wildlife–vehicle collisions (Beckman et al. 2010). Advances in road ecology have, however, generally ignored the effects of railways on wildlife, despite a global

footprint of over 1 million kilometers of track (UIC 2014, Popp and Boyle 2017). Like roads, railways cause collisions with wildlife (van der Grift 1999); however, the significance of this mortality is poorly described in the literature, with estimates of railway mortality available for only a few species of conservation concern in India (Joshi 2010, Palei et al. 2013), Europe (Boscagli 1987, Huber et al. 1998, Kaczensky et al. 2003) and North America (Gibeau and Herrero 1998, Benn and Herrero 2002, Waller and Servheen 2005, Hopkins et al. 2014). Attention to both direct and indirect effects of railways on wildlife is needed because the prevalence of railways is increasing around the world (Alexander 2012, Prater et al. 2013, Tolliver et al. 2013).

A fundamental ecological consequence of railways, as with many other kinds of linear features, is the suite of changes that occur in adjacent vegetation. This effect has been extensively studied along forest edges (reviewed by Suárez-Esteban et al. 2016), powerline rights-of-way (Eldegard et al. 2015, Lampinen et al. 2015), seismic lines (van Rensen et al. 2015), trails (reviewed by Ballantyne and Pickering 2015), and road verges (Gelbard and Belnap 2003, Roever et al. 2008), with a few studies addressing railways (Hansen and Clevenger 2005, Wang et al. 2015). In general, edges increase light and temperature to enhance vegetative growth (Harper et al. 2005, Delgado et al. 2007) for both native species (Mallik and Karim 2008) and non-native species (Hansen and Clevenger 2005) that readily colonize disturbed sites. Such changes to vegetation may be especially prevalent at higher altitudes and latitudes and for forested habitats, where light, temperature, and moisture are often more limited (McClellan and Hovey 2001). Examples of photophilic, invasive, and disturbance-tolerant plants include dandelion (*Taraxacum officinale*) and clover (*Trifolium* spp.), which thrive along roadsides and, in some cases, are intentionally seeded for the purposes of rapid colonization, growth, and erosion control (Rentch et al. 2005, Roever et al. 2008). For these species, edges typically increase plant abundance (reviewed by Vilà and Ibáñez 2011) and speed phenological development (Marrriott et al. 1997), further increasing the attraction of wildlife to these productive and palatable species (reviewed by Bennett 1991).

Strong attraction to forest edges caused by transportation infrastructure can produce ecological

traps for wildlife populations (sensu Gates and Gysel 1978) if mortalities increase from wildlife–vehicle collisions (Meisingset et al. 2014, van der Ree et al. 2015) or hunting (Brashares et al. 2001, Laurance et al. 2009). For these reasons, and to increase human safety, roadside vegetation is sometimes removed or mowed to reduce attractants (Rea 2003, Milton et al. 2015). Such mitigation often targets areas with increased animal density, which may be associated with a water source (Glista et al. 2007), a movement route (Whittington et al. 2005), or high-quality habitat (Gibeau et al. 2002, Nielsen et al. 2006). In addition to vegetation enhancement, wildlife can be attracted to railways from spilled agricultural products (Waller and Servheen 2005, Dorsey 2011, Hopkins et al. 2014, Gangadharan et al. 2017, Murray et al. 2017) and carcasses from train collisions (Wells et al. 1999, Murray et al. 2017). Mitigating transportation corridors in relation to these sources of attraction (Gunson et al. 2010), and enhancing surrounding habitats away from high-risk locations, can provide a cost-effective alternative to mitigation that targets entire regions, such as fences and crossing structures (reviewed by Glista et al. 2009). Such solutions are particularly helpful in protected areas and other locations that require high permeability of habitats and minimal human infrastructure.

The challenge of understanding and mitigating railway edges is most pressing when it involves threatened species and protected areas. This situation occurs in the Canadian mountain parks where rail-associated mortality is high for several wide-ranging mammals (Wells et al. 1999), including the local population of grizzly bears, whose leading source of known mortality is collisions with trains (Bertch and Gibeau 2009). This population of grizzly bears has one of the lowest reproductive rates in North America (Garshelis et al. 2005), which may be related to a comparatively high reliance on plant matter and a lack of concentrated animal-based protein (e.g., salmon; Hilderbrand et al. 1999, López-Alfaro et al. 2015, Nielsen et al. 2017). Bear habitat selection is generally determined by the availability, quantity, and quality of food resources, which in turn are influenced by both temporal (e.g., seasonal) and spatial (e.g., elevation) factors (Nielsen et al. 2010). In the spring, grizzly bears in the mountain parks select habitat at lower elevations to exploit the early

phenological stages of vegetation such as forbs, e.g., horsetail (*Equisetum* spp.), and graminoids that have a higher plant digestibility and nutritional value (Hamer and Herrero 1987a). Early availability of vegetation is critical to grizzly bears (Munro 2000) and could be further enhanced by roads or railways due to snow plowing and greater albedo resulting in earlier melting of snow and ice. Furthermore, some berry-producing plants are more prevalent at lower elevations and in areas of higher local solar radiation, e.g., buffaloberry (*Shepherdia Canadensis*; Nielsen et al. 2004b, 2010). Fruit maturation also occurs earlier when in areas of high light availability, e.g., strawberry (*Fragaria* spp.; Palencia et al. 2013). The characteristics of railways therefore have the potential to accelerate maturation and increase the abundance of berry-producing plants, which in turn may attract foraging bears and other wildlife.

The impetus for this study stemmed from an increase in bear–train collisions in the last two decades. We hypothesized that various effects of the railway opening, that is, light, heat, and disturbance, would enhance vegetation growth, productivity, and phenology, as well as the diversity of plants consumed by bears (hereafter bear forage plants), especially in locations where heat or light is limiting such as mountainous environments. We predicted that these effects would be apparent in comparisons of vegetation measured adjacent to the rail vs. in the adjacent forest and that greater effects would occur in spring and at higher elevations.

## METHODS

### Study area

The study was conducted along the Canadian Pacific Railway (hereafter railway) that bisects both Banff National Park in southwestern Alberta and Yoho National Park in southeastern British Columbia. Here, the railway runs approximately parallel to the four-lane Trans-Canada highway and traverses over 130 km of montane and subalpine ecosystems. Historical fire management in the mountain parks has led to a dense forest canopy and a lack of open areas and vegetation in early seral stages, ultimately decreasing the availability of grizzly bear foraging habitat (Hamer and Herrero 1987b, Herrero 1994, Luckman and Kavanagh 2000). A cool

climate imposes a short growing season and the rocky terrain confines the majority of high-quality habitat to low elevations where the railway and most roads occur. Grizzly bears in the region are known to rely heavily on vegetation, which includes graminoids (grasses, sedges, and rushes), horsetails, sweetvetch roots (*Hedysarum* spp.), and a variety of fruits, such as bearberries (*Arctostaphylos uva-ursi*), buffaloberries, and strawberries (Hamer and Herrero 1987a, Munro et al. 2006). Grizzly bears in the study area appear to select the railway more strongly in the spring and fall (Friesen 2016, Murray et al. 2017), which may reflect the seasonal availability of these plant types relative to surrounding areas. Many other mammals are also susceptible to rail mortality, including moose (*Alces alces*), elk (*Cervus canadensis*), deer (*Odocoileus hemionus*; *Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*), wolves (*Canis lupus*), cougars (*Puma concolor*), coyotes (*Canis latrans*), and black bears (*Ursus americanus*) (Gilhooly 2016).

### Sampling locations and data collection

We established 19 sampling sites along the railway: 15 in Banff National Park and 4 in Yoho National Park (Fig. 1). Locations were chosen in relation to documented train strikes of grizzly bears, concentrated grizzly bear activity assessed previously via observations or GPS collars, and to ensure a representative spread of the study area over an elevational gradient (1100–1600 m). At each sample site, three 50-m transects were established parallel to the railway and, whenever possible, on the north side of the tracks ( $n = 14$  north;  $n = 5$  south). The first ballast transect was placed where the ballast rock from the railway met the vegetation line which typically occurred within 5 m of the rail ( $\bar{x} = 4.0 \text{ m} \pm 2.03$ ;  $n = 19$ ). The second edge transect was placed along the forest edge, typically occurring 15 m from the rail ( $\bar{x} = 14.0 \text{ m} \pm 7.5$ ;  $n = 13$ ). The third forest transect was placed in the adjacent forest, approximately 45 m from the edge ( $\bar{x} = 45.7 \text{ m} \pm 12.44$ ;  $n = 18$ ). Along each transect, large nails were hammered into the ground at distances of 6.25, 18.75, 31.25, and 43.75 m, to establish semi-permanent central points for four sampling plots.

Vegetation measurements were collected every two weeks from May through October, 2013–2014, to quantify the abundance and phenology

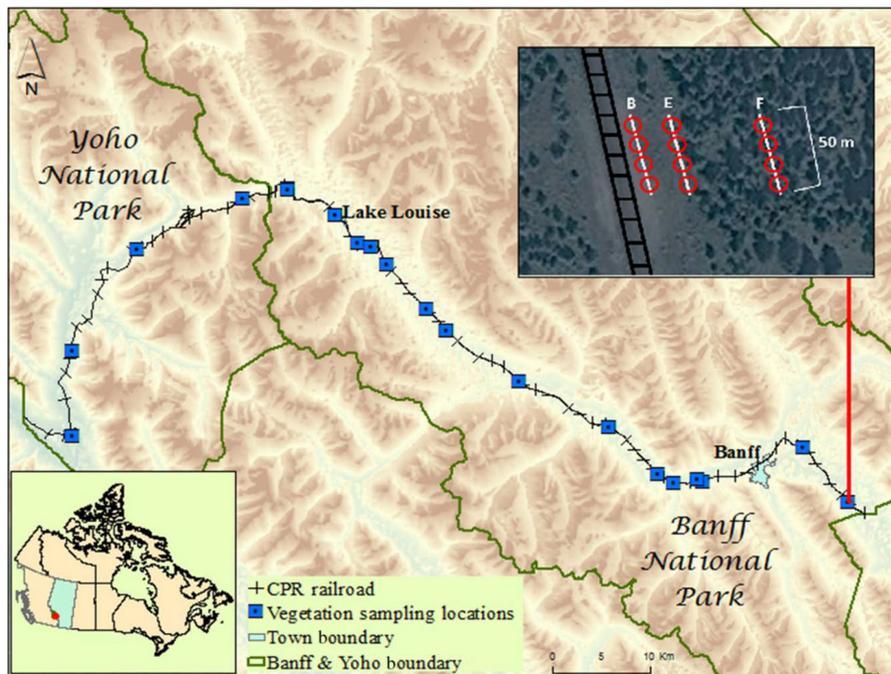


Fig. 1. Locations of vegetation sampling ( $n = 19$  blue squares) along the Canadian Pacific Railway running through Banff and Yoho National Parks (left inset). The sampling design included three transects parallel to the railway (right inset) with the first (“B”) positioned where the ballast meets the vegetation line, the second (“E”) along the forest edge, and the third (“F”) approximately 50 m into the forest. We placed four 1-m<sup>2</sup> circular plots (red circles) along each 50-m transect and recorded plant responses every two weeks within each plot between May and October in 2013 and 2014.

of grizzly bear forage plants along ballast, edge, and forest transects. We placed a 1-m<sup>2</sup> circular plot at each of the four set distances (using the nail as the center point), estimated the abundance of each forage species using percent cover, and assigned a numerical code describing the most mature stage of vegetative and reproductive phenology within the plot for each species (adapted from Dierschke 1972 and Bater et al. 2011, Table 1; Appendix S1: Table S1). Additionally, during a sampling visit in late July of both years, we counted berries on the closest three shrubs of each berry-producing species (usually buffaloberry) that occurred within 1 m of either side of each transect. We picked the ripest-looking berry from each of the three shrubs and combined their juices to measure sugar content via % Brix by squeezing the juice onto a refractometer (after Nielsen and Nielsen 2010). During the same visit, we measured canopy cover at the central point of each plot using a handheld

densiometer and later averaged the values for each transect.

We collected additional vegetation measurements on buffaloberries (*S. canadensis*) during 2013–2015 at 2–6 sites (depending on year). Buffaloberries are a dominant late-summer food resource for grizzly bears in the region (Hamer 1996, Munro et al. 2006). Our goal was to contrast productivity and ripening rate of railside shrubs located within 15 m of the railway ( $\bar{x} = 10.1 \pm 3.5$  m) to forest shrubs located approximately 50 m from the edge in the adjacent forest ( $\bar{x} = 57.6 \pm 23.4$  m). We established focal shrubs associated with the edge and forest transects at each site, by selecting the 3–4 closest shrubs that bore fruit on at least three branches. At each focal shrub, we identified the three branches containing the highest number of berries, secured a piece of flagging tape 30 cm from its tip, and counted the number of berries within this span (following Noble 1985, Johnson and Nielsen 2014). During each visit, we also

Table 1. Common and Latin names of grizzly bear forage plants identified in one or more transects adjacent to a railway in Banff and Yoho National Parks.

Common name	Bear forage plants	Type	May	Jun	Jul	Aug	Sep	Oct	Ballast	Edge	Forest
Alfalfa	<i>Medicago</i> spp.	Shoot	×	×	×				1	3	0
Clover	<i>Trifolium</i> spp.	Shoot	×	×	×	×			11	5	2
Cow parsnip	<i>Heracleum lanatum</i>	Shoot			×	×			0	0	2
Dandelion	<i>Taraxacum officinale</i>	Shoot	×	×	×	×			18	10	9
Field horsetail	<i>Equisetum arvense</i>	Shoot	×	×					10	5	4
Fireweed	<i>Epilobium angustifolium</i>	Shoot			×	×			4	6	8
Grass and sedges	<i>Poa</i> spp. and <i>Carex</i> spp.	Shoot	×	×	×				19	13	18
Rushes	<i>Juncus</i> spp.	Shoot	×	×	×				4	5	2
Milkvetch	<i>Astragalus</i> spp.	Root	×	×			×	×	4	7	2
Sweetvetch	<i>Hedysarum</i> spp.	Root	×	×			×	×	5	8	8
Bearberry	<i>Arctostaphylos uva-ursi</i>	Fruit	×	×			×	×	9	11	16
Bilberry	<i>Vaccinium myrtillus</i>	Fruit			×	×	×		0	2	5
Black gooseberry	<i>Ribes lacustre</i>	Fruit			×	×	×		0	2	1
Blackcurrant	<i>Ribes nigrum</i>	Fruit			×	×	×		0	2	5
Blueberry	<i>Vaccinium myrtilloides</i>	Fruit			×	×	×		0	0	5
Buffaloberry	<i>Shepherdia canadensis</i>	Fruit			×	×	×		4	9	14
Crowberry	<i>Empetrum nigrum</i>	Fruit			×	×	×		0	0	1
Dwarf bilberry	<i>Vaccinium caespitosum</i>	Fruit			×	×	×		1	2	6
Dwarf blackberry	<i>Rubus pubescens</i>	Fruit			×	×	×		2	0	1
Gooseberry	<i>Ribes oxycanthoides</i>	Fruit			×	×	×		0	2	1
Grouseberry	<i>Vaccinium scoparium</i>	Fruit			×	×	×		0	3	7
Huckleberry	<i>Vaccinium membranaceum</i>	Fruit			×	×	×		1	0	2
Lingonberry	<i>Vaccinium vitis-idaea</i>	Fruit			×	×	×		1	1	2
Lowbush cranberry	<i>Viburnum edule</i>	Fruit			×	×	×		2	1	3
Raspberry	<i>Rubus idaeus</i>	Fruit			×	×	×		4	0	2
Saskatoonberry	<i>Amelanchier alnifolia</i>	Fruit			×	×	×		1	2	4
Strawberry	<i>Fragaria virginiana</i>	Fruit			×	×	×		15	13	17
Twinberry	<i>Lonicera involucreta</i>	Fruit			×	×	×		2	1	6

Notes: Plants are arranged by forage type (shoots, roots, and fruit), and crosses indicate the months of availability. The final three columns describe the number of transects on which each species was recorded.

collected one or two berries (from non-labeled branches or a neighboring shrub) to measure sugar content. If berries were changing color, and therefore varied within the shrub, one berry from each color variant was used. We also installed time-lapse cameras (Wingscapes TimelapseCam; Wingscapes, Birmingham, Alabama, USA) to record fine-scale berry maturation at two shrubs per transect and site and when possible always positioned them facing north (303°–56°). Cameras were programmed to take a picture every half hour between the hours of 10:00 and 16:00 to minimize glare from solar movement (Nijland et al. 2013).

#### Data analysis

We identified all plant species known to be consumed by grizzly bears in the region (Hamer and Herrero 1987a, Raine and Kansas 1989, Raine and Riddell 1991). Using data from these species,

we estimated various responses associated with food abundance and phenology and used individual transects as our unit of replication, sampling site and year as random effects, and forest as the reference category in comparisons. For each transect, we tallied the number of species present (species richness), summed total proportional cover of each species, and calculated the Shannon species diversity index ( $H'$ ; Shannon 1948) based on proportional cover. We also modeled the summed, proportionate, horizontal cover of available bear foods in each plot (percentage available) by combining plant species by forage type (shoot, root, fruit) and included all phenological stages that are consumed by bears as follows: shoot available (vegetative codes 3–6); root available (reproductive codes 0–3 and 8–13); and fruit available (reproductive codes 10–12; Table 1; Appendix S1: Table S1).

We tested for the effects of transect type (ballast, edge, or forest), season, elevation, and their interaction on species richness and diversity using linear mixed-effects models (R package “lme4”) and on total proportional cover of bear foods and available forage types using mixed-model beta regression with a logit link (R package “glmmADMB”). Using beta regression, we also examined the percent cover of eight common species that occurred in over 50% of our sampling sites as a function of transect type only. Seasons were defined according to regional bear feeding habits: spring = hypophagia (start of sampling season to 14 June); summer = early hyperphagia (15 June–7 August); and fall = late hyperphagia (8 August–end of sampling season; Nielsen et al. 2004a).

To further investigate the effect of the rail on vegetation phenology and berry productivity, we derived binomial response variables for all fruiting species (1 for reproductive codes 10–12, 0 for codes  $\leq 9$  and 13) and for seven species with conspicuous flowers (1 for reproductive codes 4–8, 0 for codes  $\leq 3$  and  $\geq 9$ ; alfalfa, clover, cow parsnip, dandelion, fireweed, milkvetch, sweetvetch) and compared the occurrence of fruiting and flowering among transect types using logistic mixed-model regression. We also compared the summed berry count and average sugar content of berries among transect types (and separately, as a function of canopy cover) from the single annual sampling protocol (above) using negative binomial and linear mixed-effects models, respectively. We included week as a covariate for sugar content models to account for temporal trends. And lastly, we modeled repeated buffaloberry counts and ripening rates (via sugar content) of railside to forest shrubs as a function of transect type, season, elevation, and their interaction (and separately, as a function of canopy cover) using negative binomial and linear mixed-effects models, respectively. Julian dates associated with buffaloberry ripening from the time-lapse cameras were also linearly modeled.

In all analyses, we avoided use of correlated variables within models (Pearson correlation coefficient;  $r > |0.6|$ ), scaled numerical predictors, and selected final models based on the Akaike information criterion corrected for small sample sizes (AIC<sub>c</sub>; Burnham and Anderson 2002). We created nine a priori candidate models to test how vegetation responded to spatial (transect type and elevation) and temporal (seasonal) factors, which

included quadratic fits and two-way interactions. We averaged parameter estimates across models that were within 4 AIC<sub>c</sub> scores of the top model (Burnham and Anderson 2002). All analyses and graphics were conducted using RStudio (Version 0.99.465; RStudio, Inc., Boston, Massachusetts, USA).

## RESULTS

In total, we identified 28 grizzly bear forage plants within one or more of our transects (Table 1). Of these, 18 species were berry-producers, eight species were classified as shoots, and two species were classified as roots according to the portion of the plant targeted by grizzly bears (Table 1). The eight most common species included three berry-producing plants (bearberry, buffaloberry, and strawberry), three invasive forbs (clover, dandelion, and horsetail), one non-invasive forb used for its root (sweetvetch), and graminoids (*Poa* and *Carex* spp.). Among these species, five exhibited higher cover along the ballast than in the forest and seven species had higher cover on edges than in the forest (Fig. 2). Only clover was similar among the three transect types and only horsetail exhibited higher cover along the ballast when compared to both edge and forest transects (Fig. 2).

Total cover from all forage plants was, on average, twice as high on edges as it was on either of ballast or forest transects across seasons (Fig. 3), but with large differences in the magnitude and direction of effects among species (Fig. 2). Total plant cover was also higher in summer and fall relative to spring (Fig. 3a). Species richness and diversity were highest along edges, but lowest on ballast transects relative to the adjacent forest. As with total cover, richness and diversity metrics were best described by the interaction between transect type and season (Table 2), with higher values in the summer and fall relative to spring (Appendix S1: Tables S2–S4). There was no significant effect of elevation on diversity, richness, or total cover (all  $P \geq 0.59$ ). However, a significant interaction between elevation and transect type revealed that vegetation enhancement at the edge, relative to the forest, declined with elevation ( $P < 0.001$ ; Fig. 3b), opposite to the elevational pattern we predicted.

Plant reproduction was advanced, relative to the forest, with an average of threefold greater

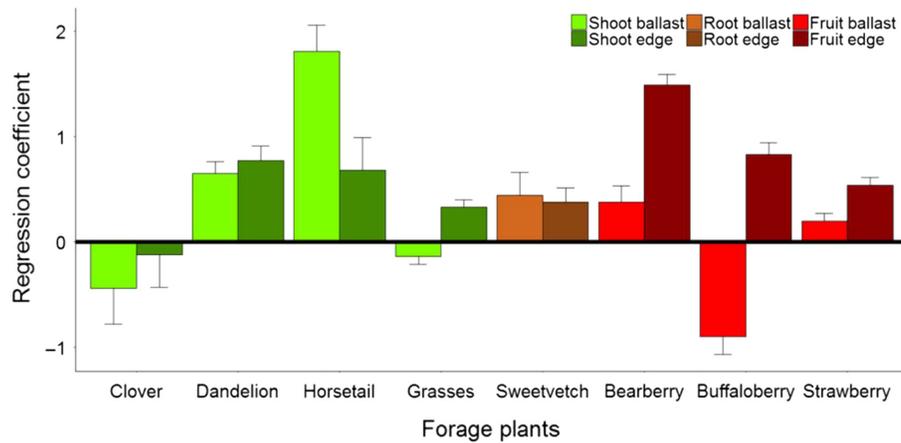


Fig. 2. Standardized coefficients with standard error from a beta regression mixed-effects model describing the percent cover of eight common grizzly bear forage plants. Shoot species are represented by green, root species by brown, and fruit species by red, along ballast transects (lighter colors) and edge transects (darker colors) relative to an adjacent forest (black line).

odds of flowering along the ballast (odds ratio = 3.64 [1.75–7.57],  $P < 0.001$ ) and edge transects (odds ratio = 3.60 [1.69–7.68],  $P < 0.001$ ). Fruiting was similarly increased along the ballast, again relative to forest (odds ratio = 2.99 [1.93–4.63],  $P < 0.001$ ), and fruiting was even more enhanced along the edge with a fivefold greater odds (odds ratio = 5.27 [3.52–7.89],  $P < 0.001$ ). Although fruiting was more frequent along the ballast compared to the forest, its

interaction with plant cover reduced the overall percent of cover available to bears, for which values were highest along the edge, then in the forest, particularly in the fall (Appendix S1: Table S5). Elevation was an important variable describing the cover of available shoots and roots (Table 2), with greater cover at low elevations along ballast and edge transects, relative to the forest, and a higher overall availability in the summer (Appendix S1: Tables S6, S7).

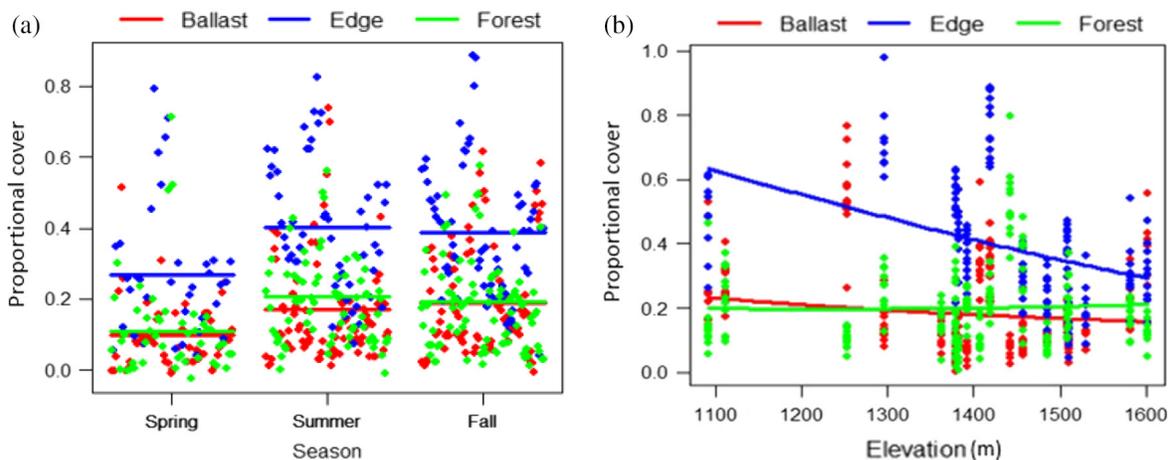


Fig. 3. Modeled means (lines) and measured values (symbols) for total proportional cover of forage plants averaged across four 1-m<sup>2</sup> circular plots by (a) season (spring, summer, and fall) and transect type (ballast, edge, and forest) holding elevation constant at its median value and (b) elevation (quadratic) and transect type (ballast, edge, and forest) holding the most common season constant (fall).

Table 2. Top model selection results ( $<4 \Delta AIC_c$ ), degrees of freedom (df), and Akaike weights for various plant responses.

Dependent variable	Top models ( $<4 \Delta AIC_c$ )	df	Weights
Plant richness	Transect type $\times$ season	11	1.000
Plant diversity	Transect type	5	0.686
	Transect type $\times$ season	11	0.314
Total plant cover	Transect type $\times$ season	11	1.000
Cover fruiting shrubs	Transect type $\times$ season	9	0.996
Cover available shoots	Season $\times$ elevation + elevation <sup>2</sup>	10	0.416
	Season $\times$ elevation	9	0.358
	Transect type $\times$ elevation + elevation <sup>2</sup>	10	0.112
Cover available roots	Transect type $\times$ elevation	9	0.701
	Transect type $\times$ elevation + elevation <sup>2</sup>	10	0.280
Summed berry count (single visit)	Transect type $\times$ elevation + elevation <sup>2</sup>	10	0.600
	Transect type	6	0.176
	Transect type $\times$ elevation	9	0.161
Average sugar content (single visit)	Transect type $\times$ elevation + week	10	0.500
	Transect type $\times$ elevation + elevation <sup>2</sup> + week	11	0.393
	Transect type + week	7	0.095
Buffaloberry count	Transect type $\times$ season + week	8	1.000
Buffaloberry sugar content	Transect type $\times$ elevation + elevation <sup>2</sup> + week	9	0.820

Note: Models were selected using the Akaike information criterion adjusted for small sample sizes ( $AIC_c$ ; model output tables are located in Appendix S1).

Somewhat paradoxically, summed berry counts and average brix measures were higher on the ballast, despite the higher occurrence of fruiting and abundance of fruiting cover at edges (Appendix S1: Tables S8, S9). Elevation was included in the top model for both metrics (Table 2), with berry counts and sugar content positively associated with elevation, particularly on edge transects (Appendix S1: Tables S8, S9). These responses likely reflect light levels because forest edge transects at higher elevations had lower canopy cover when compared to low-elevation sites ( $t = 1.38$ ,  $df = 22$ ,  $P = 0.09$ ). Both berry count and sugar content declined with increasing canopy cover, whether measured by single visits ( $\beta > -2.38$ ,  $P < 0.006$ ) or repeat visits to buffaloberry plants ( $\beta > -1.24$ ,  $P < 0.001$ ).

Our buffaloberry-specific models revealed complex effects of the rail on berry ripening. Railside buffaloberry shrubs were more productive, relative to the forest, but matured and also senesced, sooner, lessening the duration over which berries were available (Appendix S1: Table S10). Across transects, ripening rates were highest at intermediate elevations (Appendix S1: Table S11). Time-lapse cameras indicated that rail-associated berries ripened an average of  $8.58 \pm 4.36$  d earlier than forest-associated shrubs ( $t = -5.46$ ,  $df = 32.7$ ,

$P < 0.001$ ) and, as expected, ripening dates were delayed where canopy cover was higher ( $t = 5.59$ ,  $df = 33$ ,  $P < 0.001$ ).

## DISCUSSION

Railways around the world potentially threaten wildlife by attracting them via enhanced vegetation diversity, growth rates, and productivity, but these effects have generally not been quantified. Our results show that the forest edge along a railway in a mountainous region had higher species richness, diversity, and cover for seven of the eight most commonly-occurring species that are consumed by grizzly bears. Similarly, the forest edge had higher availability of palatable fruits, shoots (stem/leaf/flower), and roots compared to adjacent forest plots. Fruiting species produced more berries near the rail, especially early in the season and at higher elevations when and where ambient temperatures are generally lower. Our focal fruiting shrub, buffaloberry, also exhibited earlier ripening and higher sugar content near the rail. Together these results demonstrate that the railway significantly increases vegetation growth and productivity, but that this relationship varies among seasons and with elevation.

Plant phenology generally influences availability of foods to bears (Blanchard and Knight 1991, Nielsen et al. 2003, Bater et al. 2011, Coogan et al. 2012, Nijland et al. 2013), but these effects may be especially important in spring and fall. In spring, the railway is one of the first snow-free locations where new growth occurs (Munro 2000) and favors dandelion, which is both highly palatable and among the earliest species available (Keane et al. 2001, DeJaco and Batzli 2013). Later in the spring, horsetail may be particularly important when its protein content can exceed 30% (Hamer and Herrero 1987a, Munro et al. 2006).

In late summer and fall, berry-producing plants are important to bears, but dense tree cover in much of the study area minimizes fruit availability (Hamer 1996). Light limitation undoubtedly explains why berry-producing shrubs in the ballast were highly productive, although poor soil there was likely the reason for lower cover. The independence of fruit productivity and shrub abundance has been documented for several species, including buffaloberry, where optimal fruit production occurs under low canopy cover, yet shrub prevalence is greatest under intermediate canopy conditions (Noyce and Coy 1990, Hamer 1996, Nielsen et al. 2004b). Canopy density in areas adjacent to transportation corridors may therefore be a good indicator of the quantity and quality of vegetation and help to predict the occurrence of foraging bears (e.g., Denny and Nielsen 2017). Increasing availability of high-resolution imagery has made it possible to measure canopy structure, and hence fruit production, in similar, forested habitat (Barber et al. 2016).

The effects of the rail on the phenology of buffaloberry are particularly interesting because it is a staple late-summer food of grizzly bears in the area (Hamer and Herrero 1987a). Despite the positive effects of light on fruit production, the earlier maturation of berries along the rail may combine with their more rapid senescence there to generate a net reduction in berry availability as forage. Bears generally target high densities of berries to maximize intake rate (Welch et al. 1997) and the immediate railway right-of-way likely shortens the window of availability when berries are both abundant and ripe. At lower elevations, better conditions for berry production appear to occur at the forest edge where fruit availability extends across summer and fall seasons. At higher elevations,

optimal conditions for berry ripening may be closer to the rail in our study area because cooler temperatures there extend food availability at ideal phenological stages (Hamer and Herrero 1987a, Waller and Mace 1997, Munro et al. 2006).

Our study had several characteristics that limit the inferences we can draw in relation to the effects of rail-associated vegetation changes on related ecological phenomena, including risk of train strikes on wildlife. First, we did not measure several variables that are important to plant growth and community structure, such as soil conditions (Molina-Venegas et al. 2016) or climatic variables (Smith-Ramirez and Armesto 1994, Schroder et al. 2014). Future work that includes other location-based covariates would help to identify the fine-scale mechanisms behind railway plant communities and allow for more predictive models. Another limitation to our study was our inability to determine how much of the reduction in berries was due to rapid maturation and desiccation vs. other factors, for example, harvesting from animals or disturbance from wind. We observed large volumes of desiccated berries at the base of shrubs and attempted to quantify them using nets, but these measures were confounded with effects of weather, especially wind. More work is warranted to describe the complex relationships among berry productivity, senescence, and availability in relation to railways and other transportation infrastructure.

Despite these limitations, our results provide new information for estimating temporal and spatial factors that increase risk of train strikes on grizzly bears and other wildlife attracted to rail-side vegetation. Perhaps the most important of our results is the illustration that the temporal effects of the rail on plant phenology are intertwined with the spatial effect of elevation, which further interacts with the seasonal availability of bear forage plants. Whereas dandelion and horsetail are important spring forage for bears, the enhancing effect of the rail was greater at lower elevations. By contrast, the phenological effects of the rail on buffaloberry appeared to create a net increase in berry abundance only at high elevations where berries were protected from desiccation. These effects may combine to help explain the results of a concurrent study, which demonstrated that bear use of the rail was also highest in the spring and fall (Murray et al. 2017).

If vegetation enhancement increases bear use of the rail and strike risk increases with relative use, it should follow that the frequency of bear strikes is greater in the spring at low elevations and higher in fall at higher elevations. The available data do not support this prediction; bear strikes over the past 17 yr peaked in spring and fall, but did so independently of elevation (Fig. 4;  $\beta = -0.11$ ,  $P = 0.28$ ). Even in the wetter and more productive montane area west of our study area, 70% of bear–train collisions occurred during the spring green-up period (Wells et al. 1999). For bears, spring coincides with a period in which both fat reserves and food intake are very low (Nelson et al. 1983), which suggests that strike risk is not likely to be explained by slight increases in the volume of vegetation.

A more subtle potential interpretation might be found in the kind of food bears target in spring, which is known to be protein-rich resources including young plants, sharply contrasting the high-energy foods (e.g., fruit) that are targeted in preparation for winter dormancy (Hellgren et al. 1988, Gibeau and Herrero 1998, López-Alfaro et al. 2013). If railside vegetation enhances the growth of critical foods at critical times, it may exacerbate the attraction and increase collision risk for bears. The most important of these spring herbaceous forage plants, in our study area and elsewhere, is likely dandelion and field horsetail. Both are highly

nutritious, but also thrive in poor, disturbed soils with ample light (Solbrig and Simpson 1974, Husby 2013), and would benefit from the additional moisture afforded by rail maintenance (snow plowing through late winter) and drainage from the elevated, porous ballast. Other sources of protein may also be associated with the rail to attract bears in spring (e.g., ungulate calves or scavenging opportunities; Wells et al. 1999, Hopkins et al. 2014, Murray et al. 2017), in addition to other rail-based attractants (e.g., increased movement associated with the mating season; Sawaya et al. 2013).

Similar effects could also occur in fall if, for example, railways attract bears with enhanced berry production. That season may also involve additional or interacting causes of vulnerability to train strikes. For example, bear use of berries in fall generally increases overlap between people and bears, which contributes to several forms of human-caused mortality (Benn and Herrero 2002, Lamb et al. 2016), some of which may be reduced on the private lands controlled by railways. In our study area, a peak in fall of grizzly bear–train collisions could be associated with enhanced fruit along the railway edge, but it may stem from other attractants, such as train-spilled grain, which has higher transport rates than (Gangadharan et al. 2017).

Our work supports some tentative suggestions for mitigation, particularly when combined with

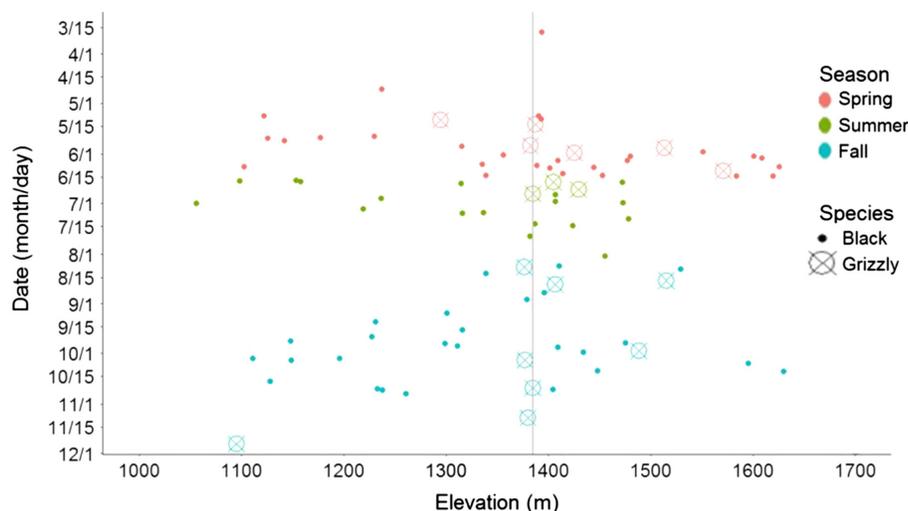


Fig. 4. Train collision events (symbols) with grizzly and black bears in Banff and Yoho National Parks from 2000 to 2016 by date (month/day), elevation, and season (spring, summer, and fall). The gray vertical line represents the median elevation for all strikes.

other kinds of information. First, the variable and species-specific responses of vegetation make location-based mitigation suggestions difficult. Nonetheless, it may be wise to remove or limit the growth of bear forage plants in locations where multiple collisions have occurred, particularly if topography impedes escape from approaching trains and track curvature combines with vegetation to limit sightlines and sound transmission (sensu Burley 2015, Backs et al. 2017). Strike risk may be further reduced by improving wildlife habitat away from the railway, such as by creation of other forest gaps, forest thinning, or prescribed fire to imitate similar edge effects in safer locations (Hamer 1999, Wender et al. 2004, Neill and Puettmann 2013, Braid et al. 2016). Encouraging the growth of non-palatable vegetation along the rail may also minimize the attraction to these high-risk, rai-side locations via effects on both bears and the ungulate species they may target as fawns or scavenging opportunities.

In sum, our results show that a railway increases the diversity, richness, and cover of forage plants consumed by bears, relative to adjacent forested habitat, which could increase attraction by bears and other wildlife, making them vulnerable to train collisions. This result is consistent with several other studies that demonstrated attraction by bears to vegetation enhancement at forest edges (Nielsen et al. 2004a, Theberge et al. 2005, Northrup et al. 2012, Stewart et al. 2013), where many forms of human-caused mortality are concentrated (Nielsen et al. 2004a, 2006, Manning and Baltzer 2011, Takahata et al. 2014, Gilhooly 2016). Given the prevalence of wildlife–train collisions worldwide (Seiler and Helldin 2006), and the profound effects that railways potentially have on adjacent vegetation, more work is needed to know how, when, and where rai-side vegetation increases risk of strikes. This information may be most important in areas with limited forage availability such as in mountainous or forested regions (Nielsen et al. 2004b), or where fire suppression has diminished natural fire cycles (Stewart et al. 2012). For grizzly bears, there is a critical need to understand how enhanced vegetation, and other railway attractants, can create ecological traps. Mitigating collision vulnerability will contribute to the conservation and sustainability of future populations, for grizzly bears in North America, and many other threatened or

endangered species worldwide, while increasing the sustainability of rail-based transportation.

## ACKNOWLEDGMENTS

We are grateful for extensive logistical support and funding to conduct this project from the Joint Initiative for Grizzly Bear Conservation by Parks Canada and Canadian Pacific Railway with matching funds from the Collaborative Research and Development Program of the Natural Science and Engineering Council (File CRDPJ 441928-12). For their invaluable assistance, we thank many individuals at Parks Canada (B. Burley, A. Forshner, B. Fyten, D. Garrow, D. Gorrie, D. Gummer, B. Hunt, T. Hurd, R. Kubian, K. McCleary, S. Michel, S. Norris, J. Park, and J. Whittington); Canadian Pacific Railway (C. Bunce, P. Busse, K. Roberge, L. Hoffman, J. Pemberton, and J. Van Humbeck); and NSERC (T. Anderson). We are thankful for manuscript suggestions from A. Gangadharan and for field assistance by K. Cave, S. Fassina, A. Friesen, P. Gilhooly, L. Harrap, B. Jackson, J. Put, M. Kinley, C. Lord-May, B. Moriarty, N. de Nijs, G. Pachman, L. Put, M. Raymond, and J. Tress. There are no competing interests for the authors of this manuscript.

## LITERATURE CITED

- Alexander, P. E. 2012. Rail transportation energy efficiency-oriented technologies. Pages 787–791 in *Proceedings of the 2012 Joint Rail Conference*, Philadelphia, Pennsylvania, USA. Amer Soc Mechanical Engineers, New York, New York, USA.
- Alexander, S. M., and N. M. Waters. 2000. The effects of highway transportation corridors on wildlife: a case study of Banff National Park. *Transportation Research* 8:307–320.
- 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* 106:563–569.
- Ballantyne, M., and C. M. Pickering. 2015. The impacts of trail infrastructure on vegetation and soils: current literature and future directions. *Journal of Environmental Management* 164:53–64.
- Barber, Q. E., C. W. Bater, A. C. R. Braid, N. C. Coops, P. Tompalski, and S. E. Nielsen. 2016. Airborne laser scanning for modelling understory shrub abundance and productivity. *Forest Ecology and Management* 377:46–54.
- Bater, C. W., N. C. Coops, M. A. Wulder, T. Hilker, S. E. Nielsen, G. McDermid, and G. B. Stenhouse. 2011. Using digital time-lapse cameras to monitor species-specific understory phenology in support of wildlife habitat assessment. *Environmental Monitoring and Assessment* 180:1–13.

- Beckman, J. P., A. P. Clevenger, M. P. Huijser, and J. A. Hilty. 2010. Safe passages: highways, wildlife, and habitat connectivity. Island Press, Washington, D.C., USA.
- Benn, B., and S. Herrero. 2002. Grizzly bear mortality and human access in Banff and Yoho National Parks, 1971–1998. *Ursus* 13:213–221.
- Bennett, A. F. 1991. Roads, roadsides and wildlife conservation: a review. Pages 99–117 in D. A. Saunders and R. J. Hobbs, editors. *Nature conservation 2: the role of corridors*. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.
- Bennett, V. J., W. P. Smith, and M. G. Betts. 2011. Toward understanding the ecological impact of transportation corridors. General Technical Report PNW-GTR-846. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Berth, B., and M. L. Gibeau. 2009. Grizzly bear monitoring in and around the Mountain National Parks: mortalities and bear/human encounters 1990–2007. Report, Parks Canada, Lake Louise, Alberta, Canada.
- Blanchard, M. B., and R. R. Knight. 1991. Movements of Yellowstone grizzly bears. *Biological Conservation* 58:41–67.
- Boscagli, G. 1987. Brown bear mortality in Central Italy from 1970 to 1984. Pages 97–98 in P. Zager, J. Beecham, G. Matula Jr., and H. Reynolds III, editors. *Bears: their biology and management. A Selection of Papers from the 7th International Conference on Bear Research and Management*, Williamsburg, Virginia, USA, and Plitvice Lakes, Yugoslavia. International Association for Bear Research and Management.
- Braid, A. C. R., D. Manzer, and S. E. Nielsen. 2016. Wildlife habitat enhancements for grizzly bears: survival rates of planted fruiting shrubs in forest harvests. *Forest Ecology and Management* 369:144–154.
- Brashares, J. S., P. Arcese, and M. K. Sam. 2001. Human demography and reserve size predict wildlife extinction in West Africa. *Proceedings of the Royal Society of London B: Biological Sciences* 268:2473–2478.
- 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-Verlag, New York, New York, USA.
- Coogan, S. C. P., S. E. Nielsen, and G. B. Stenhouse. 2012. Spatial and temporal heterogeneity creates a “brown tide” in root phenology and nutrition. *ISRN Ecology*. <https://doi.org/10.5402/2012/618257>
- DeJaco, C. E., and G. O. Batzli. 2013. Palatability of plants to small mammals in non-native grasslands of east-central Illinois. *Journal of Mammalogy* 94:427–435.
- Delgado, J. D., N. L. Arroyo, J. R. Arévalo, and J. M. Fernández-Palacios. 2007. Edge effects of roads on temperature, light, canopy cover, and canopy height in laurel and pine forests (Tenerife, Canary Islands). *Landscape and Urban Planning* 81:328–340.
- Denny, C. K., and S. E. Nielsen. 2017. Spatial heterogeneity of the forest canopy scales with the heterogeneity of an understory shrub based on fractal analysis. *Forests*. <https://doi.org/10.3390/f8050146>
- Dierschke, H. 1972. On the recording and presentation of phenological phenomena in plant communities. English translation of: *Zur Aufnahme und Darstellung phänologischer Erscheinungen in Pflanzengesellschaften*. Forest Management Institute, Ottawa, Ontario, Canada.
- 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, Montana, USA.
- Eldegard, K., Ø. Totland, and S. R. Moe. 2015. Edge effects on plant communities along power line clearings. *Journal of Applied Ecology* 52:871–880.
- Friesen, A. J. 2016. Individual and seasonal variation in grizzly bear selection for the railway and other linear features in Banff National Park, Canada. Thesis. University of Alberta, Edmonton, Alberta, Canada.
- Gangadharan, A., S. Pollock, P. Gilhooly, A. Friesen, B. Dorsey, and C. C. St. Clair. 2017. Grain spilled from moving trains create a substantial wildlife attractant in protected areas. *Animal Conservation*. <https://doi.org/10.1111/acv.12336>
- 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.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871–883.
- Gelbard, J. L., and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology* 17:420–432.
- 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, Canada. *Biological Conservation* 103:227–236.
- Gibeau, M. L., and S. Herrero. 1998. Roads, rails and grizzly bears in the Bow River Valley, Alberta. Pages 104–108 in G. L. Evink, editor. *Proceedings of the International Conference on Wildlife Ecology and Transportation (ICOWET)*, Fort Myers,

- Florida, USA. U.S. Dept. of Transportation, Federal Highway Administration, Washington, D.C., USA.
- Gilhooly, P. S. 2016. Evaluation of highway mitigation on the frequency of wildlife-vehicle collisions on the highway and an adjacent railway in a montane ecosystem. Thesis. University of Alberta, Edmonton, Alberta, Canada.
- Glista, D. L., T. L. DeVault, and J. A. DeWoody. 2007. Vertebrate road mortality predominantly impacts amphibians. *Herpetological Conservation and Biology* 3:77–87.
- Glista, D. L., T. L. DeVault, and J. A. DeWoody. 2009. A review of mitigation measures for reducing wildlife mortality on roadways. *Landscape and Urban Planning* 91:1–7.
- Gunson, K. E., G. Mountrakis, and L. J. Quackenbush. 2010. 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. 1996. Buffaloberry [*Shepherdia canadensis* (L.) Nutt.] fruit production in fire-successional bear feeding sites. *Journal of Range Management* 49:520–529.
- Hamer, D. 1999. Forest fire's influence on yellow hedsarum habitat and its use by grizzly bears in Banff National Park, Alberta. *Canadian Journal of Zoology* 77:1513–1520.
- Hamer, D., and S. Herrero. 1987a. Grizzly bear food and habitat in the front ranges of Banff National Park, Alberta. Pages 199–213 in P. Zager, J. Beecham, G. Matula Jr., and H. Reynolds III, editors. *Bears: their biology and management. A Selection of Papers from the 7th International Conference on Bear Research and Management*, Williamsburg, Virginia, USA, and Plitvice Lakes, Yugoslavia. International Association for Bear Research and Management.
- Hamer, D., and S. Herrero. 1987b. Wildfire's influence on grizzly bear feeding ecology in Banff National Park, Alberta. Pages 179–186 in P. Zager, J. Beecham, G. Matula Jr., and H. Reynolds III, editors. *Bears: their biology and management. A Selection of Papers from the 7th International Conference on Bear Research and Management*, Williamsburg, Virginia, USA, and Plitvice Lakes, Yugoslavia. International Association for Bear Research and Management.
- 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.
- Harper, K. A., S. E. MacDonald, P. J. Burton, J. Chen, K. D. Brososfske, S. C. Saunders, E. S. Euskirchen, R. Roberts, M. S. Jaiteth, and P.-A. Esseen. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19:768–782.
- Hellgren, E. C., M. R. Vaughan, and R. L. Kirkpatrick. 1988. Seasonal patterns in physiology and nutrition of black bears in Great Dismal Swamp, Virginia-North Carolina. *Canadian Journal of Zoology* 67:1837–1850.
- Herrero, S. 1994. The Canadian National Parks and grizzly bear ecosystems: the need for interagency management. Pages 7–21 in J. J. Claar, P. Schullery, L. J. Lyon, M. R. Johnson, C. Servheen, and S. E. Broadbent, editors. *Bears: their biology and management. A Selection of Papers from the 9th International Conference on Bear Research and Management*, Missoula, Montana, USA. International Association for Bear Research and Management.
- Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77:132–138.
- Hopkins III, J. B., J. Whittington, A. P. Clevenger, M. A. Sawaya, and C. C. St. Clair. 2014. Stable isotopes reveal rail-associated behaviour in a threatened carnivore. *Isotopes in Environmental and Health Studies* 50:322–331.
- Huber, D., J. Kusak, and A. Frkovic. 1998. Traffic kills of brown bears in Gorski Kotar, Croatia. *Ursus* 10:167–171.
- Husby, C. 2013. Biology and functional ecology of *Equisetum* with emphasis on the giant horsetails. *Botanical Review* 79:147–177.
- Johnson, K. M., and S. E. Nielsen. 2014. Demographic effects on fruit set in the dioecious shrub Canada buffaloberry (*Shepherdia canadensis*). *PeerJ* 2:e526.
- Joshi, R. 2010. Train accidental deaths of leopards *Panthera pardus* in Rajaji National Park: a population in threat. *World Journal of Zoology* 5:156–161.
- Kaczensky, P., F. Knauer, B. Krze, M. Jonozovic, M. Adamic, and H. Gossow. 2003. The impact of high speed, high volume traffic axes on brown bears in Slovenia. *Biological Conservation* 111:191–204.
- Keane, B., M. H. Collier, J. R. Shann, and S. H. Rogstad. 2001. Metal content of dandelion (*Taraxacum officinale*) leaves in relation to soil contamination and airborne particulate matter. *Science of the Total Environment* 281:63–78.
- 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.

- Lampinen, J., K. Ruokolainen, and A.-P. Huhta. 2015. Urban power line corridors as novel habitats for grassland and alien plant species in South-Western Finland. *PLoS ONE* 10:e0142236.
- 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.
- López-Alfaro, C., S. C. P. Coogan, C. T. Robbins, J. J. Fortin, and S. E. Nielsen. 2015. Assessing nutritional parameters of brown bear diets among ecosystems gives insight into differences among populations. *PLoS ONE* 10:e0128088.
- López-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.
- Luckman, B., and T. Kavanagh. 2000. Impact of climate fluctuations on mountain environments in the Canadian Rockies. *Ambio* 29:371–380.
- Mallik, A. U., and M. N. Karim. 2008. Roadside revegetation with native plants: experimental seeding and transplanting of stem cuttings. *Applied Vegetation Science* 11:547–554.
- Manning, J. L., and J. L. Baltzer. 2011. Impacts of black bear baiting on Acadian forest dynamics: An indirect edge effect? *Forest Ecology and Management* 262:838–844.
- Marriott, C. A., G. R. Bolton, and E. I. Duff. 1997. Factors affecting the stolon growth of white clover in ryegrass/clover patches. *Grass and Forage Science* 52:147–155.
- McClellan, B. N., and F. W. Hovey. 2001. Habitats selected by grizzly bears in a multiple use landscape. *Journal of Wildlife Management* 65:92–99.
- Meisingset, E. L., L. E. Loe, Ø. Brekkum, and A. Mysterud. 2014. Targeting mitigation efforts: the role of speed limit and road edge clearance for deer-vehicle collisions. *Journal of Wildlife Management* 78:679–688.
- Milton, S. J., W. R. J. Dean, L. E. Sielecki, and R. van der Ree. 2015. The function and management of roadside vegetation. Pages 373–381 in R. van der Ree, J. Smith, and C. Grilo, editors. *Handbook of road ecology*. John Wiley and Sons, Chichester, UK.
- Molina-Venegas, R., A. Aparicio, S. Lavergne, and J. Arroyo. 2016. How soil and elevation shape local plant diversity in a Mediterranean hotspot. *Biodiversity Conservation* 25:1133–1149.
- Munro, R. H. 2000. The impacts of transportation corridors on grizzly and black bear habitat use patterns near Golden, B.C. Thesis. University of Victoria, Victoria, British Columbia, Canada.
- Munro, R. H. M., 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:e0175658.
- Neill, A. R., and K. J. Puettmann. 2013. Managing for adaptive capacity: Thinning improves food availability for wildlife and insect pollinators under climate change conditions. *Canadian Journal of Forest Research* 43:428–449.
- Nelson, R. A., G. E. Folk, E. W. Pfeiffer, J. J. Craighead, C. J. Jonkel, and D. L. Steiger. 1983. Behavior, biochemistry and hibernation in black, grizzly, and polar bears. Pages 284–290 in E. C. Meslow, editor. *Bears: their biology and management. A Selection of Papers from the 5th International Conference on Bear Research and Management*, Madison, Wisconsin, USA. International Association for Bear Research and Management.
- 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* 199:51–65.
- Nielsen, S. E., R. H. M. Munro, E. L. Bainbridge, G. B. Stenhouse, and M. S. Boyce. 2004b. Grizzly bears and forestry II. Distribution of grizzly bear foods in clear-cuts of west-central Alberta, Canada. *Forest Ecology and Management* 199:67–82.
- 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* 10:1–10.
- 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* 143:1623–1634.
- Nielsen, S. E., and C. Nielsen. 2010. A landscape analysis of huckleberry in southeast British Columbia, spatial-temporal patterns of forest fires, and protocols for long-term monitoring of inter-annual variation in fruit production for huckleberry and buffaloberry. Final Report for Habitat Conservation Trust Foundation, University of Alberta, Edmonton, Alberta, Canada.
- 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.

- Nijland, W., N. C. Coops, S. C. P. Coogan, C. W. Bater, M. A. Mulder, S. E. Nielsen, G. McDermid, and G. B. Stenhouse. 2013. Vegetation phenology can be captured with digital repeat photography and linked to variability of root nutrition in *Hedysarum alpinum*. *Applied Vegetation Science* 16: 317–324.
- Noble, W. 1985. *Shepherdia canadensis*: its ecology, distribution, and utilization by the grizzly bear. Department of Agriculture, Forest Service, Intermountain Research Station, Fire Sciences Laboratory, Missoula, Montana, USA.
- Northrup, J. M., G. B. Stenhouse, and M. S. Boyce. 2012. Agricultural lands as ecological traps for grizzly bears. *Animal Conservation* 15:369–377.
- Noyce, K. V., and P. L. Coy. 1990. Abundance and productivity of bear food species in different forest types of Northcentral Minnesota. Pages 169–181 in L. M. Darling, et al., editors. *Bears: their biology and management*. A Selection of Papers from the 8th International Conference on Bear Research and Management, Victoria, British Columbia, Canada. International Association for Bear Research and Management.
- Palei, N. C., B. P. Rath, and C. S. Kar. 2013. Death of elephants due to railway accidents in Odisha, India. *Gajah* 38:39–41.
- Palencia, P., F. Martinez, J. J. Medina, and J. López-Medina. 2013. Strawberry yield efficiency and its correlation with temperature and solar radiation. *Horticultura Brasileira* 31:93–100.
- Popp, J. N., and S. P. Boyle. 2017. Railway ecology: Underrepresented in science? *Basic and Applied Ecology* 19:84–93.
- Prater, M. E., A. Sparger, P. Bahizi, and D. O'Neil Jr. 2013. Rail market share of grain and oilseed transportation. *Journal of the Transportation Research Forum* 52:127–150.
- Raine, M. R., J. L. Kansas. 1989. Black bear seasonal food habits and distribution by elevation in Banff National Park. Pages 297–304 in L. M. Darling, et al., editors. *Bears: their biology and management*. A Selection of Papers from the 8th International Conference on Bear Research and Management, Victoria, British Columbia, Canada. International Association for Bear Research and Management.
- Raine, M. R., and R. N. Riddell. 1991. Grizzly bear research in Yoho and Kootenay National Parks 1988–1990. Final Report for Canadian Parks Service Western Region, Beak Associates Consulting, Calgary, Alberta, Canada.
- Rea, R. V. 2003. Modifying roadside vegetation management practices to reduce vehicular collisions with moose *Alces alces*. *Wildlife Biology* 9:81–91.
- Rentch, J. S., R. H. Fortney, S. L. Stephenson, H. S. Adams, W. N. Grafton, and J. T. Anderson. 2005. Vegetation-site relationships of roadside plant communities in West Virginia, USA. *Journal of Applied Ecology* 42:129–138.
- Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2008. Grizzly bears and forestry I: road vegetation and placement as an attractant to grizzly bears. *Forest Ecology and Management* 256:1253–1261.
- Sawaya, M. A., A. P. Clevenger, and S. T. Kalinowski. 2013. Demographic connectivity for ursid populations at wildlife crossing structures in Banff National Park. *Conservation Biology* 27:721–730.
- Schroder, W., G. Schmidt, and S. Schonrock. 2014. Modelling and mapping of plant phenological stages as bio-meteorological indicators for climate change. *Environmental Sciences Europe*. <https://doi.org/10.1186/2190-4715-26-5>
- Seiler, A., and J. O. Helldin. 2006. Mortality in wildlife due to transportation. Pages 165–189 in J. Davenport and J. L. Davenport, editors. *The ecology of transportation: managing mobility for the environment*. Springer, Dordrecht, The Netherlands.
- Shannon, C. A. 1948. A mathematical theory of communication. *Bell System Technical Journal* 27: 379–423.
- Smith-Ramirez, C., and J. J. Armesto. 1994. Flowering and fruiting patterns in the temperate rainforest of Chiloe, Chile: ecologies and climatic constraints. *Journal of Ecology* 82:353–365.
- Solbrig, O. T., and B. B. Simpson. 1974. Components of regulation of a population of dandelions in Michigan. *Journal of Ecology* 62:473–486.
- Spellerberg, I. F. 1998. Ecological effects of roads and traffic: a review. *Global Ecology and Biogeography Letters* 7:317–333.
- Stewart, B. P., T. A. Nelson, and K. Laberee. 2013. Quantifying grizzly bear selection of natural and anthropogenic edges. *Journal of Wildlife Management* 77:957–964.
- Stewart, B. P., T. A. Nelson, M. A. Wulder, S. E. Nielsen, and G. B. Stenhouse. 2012. Impact of disturbance characteristics and age on grizzly bear habitat selection. *Applied Geography* 34:614–625.
- Suárez-Esteban, A., L. Fahrig, M. Delibes, and M. Fedriani. 2016. Can anthropogenic linear gaps increase plant abundance and diversity? *Landscape Ecology* 31:721–729.
- Takahata, C., S. E. Nielsen, A. Takii, and S. Izumiyama. 2014. Habitat selection of a large carnivore along human-wildlife boundaries in a highly modified landscape. *PLoS ONE* 9:e86181.
- Theberge, J., S. Herrero, and S. Jevons. 2005. Resource selection by female grizzly bears. Pages 153–178 in S. Herrero, editor. *Biology, Demography, Ecology*

- and Management of Grizzly Bears In and Around Banff National Park and Kananaskis Country: The Final Report of the Eastern Slopes Grizzly Bear Project. Faculty of Environmental Design, University of Calgary, Calgary, Alberta, Canada.
- Tolliver, D., P. Lu, and D. Benson. 2013. Comparing rail fuel efficiency with truck and waterway. *Transportation Research* 24:69–75.
- Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18–30.
- UIC. 2014. International Union of Railways: railway statistics 2014 synopsis. Paris, France. [http://uic.org/IMG/pdf/synopsis\\_2014.pdf](http://uic.org/IMG/pdf/synopsis_2014.pdf)
- van der Grift, E. A. 1999. Mammals and railroads: impacts and management implications. *Lutra* 42: 77–98.
- van der Ree, R., D. J. Smith, and C. Grilo. 2015. The ecological effects of linear infrastructure and traffic. Pages 1–9 *in* R. van der Ree, J. Smith, and C. Grilo, editors. *Handbook of road ecology*. John Wiley and Sons, Chichester, UK.
- van Rensen, C. K., S. E. Nielsen, B. White, T. Vinge, and V. J. Lieffers. 2015. Natural regeneration of forest vegetation on legacy seismic lines in boreal habitats in Alberta's oil sands region. *Biological Conservation* 184:127–135.
- Vilà, M., and I. Ibáñez. 2011. Plant invasions in the landscape. *Landscape Ecology* 26:461–472.
- Waller, J. S., and R. D. Mace. 1997. Grizzly bear habitat selection in the Swan Mountains, Montana. *Journal of Wildlife Management* 61:1032–1039.
- Waller, J. S., and C. Servheen. 2005. Effects of transportation infrastructure on grizzly bears in Northwestern Montana. *Journal of Wildlife Management* 69:985–1000.
- Wang, G., A. R. Gillespie, S. Liang, A. Mushkin, and Q. Wu. 2015. Effect of the Qinghai–Tibet Railway on vegetation abundance. *International Journal of Remote Sensing* 36:5222–5238.
- Welch, C. A., J. Keay, K. C. Kendall, and C. T. Robbins. 1997. Constraints on frugivory by bears. *Ecology* 78:1105–1119.
- Wells, P., J. G. Woods, G. Bridgewater, and H. Morrison. 1999. Wildlife mortalities on railways: monitoring methods and mitigation strategies. Pages 85–88 *in* G. L. Evink, P. Garrett, and D. Zeigler, editors. *Proceedings of the Third International Conference on Wildlife Ecology and Transportation (ICOWET)*, Missoula, Montana, USA. Florida Department of Transportation, Tallahassee, Florida, USA.
- Wender, B. W., C. A. Harrington, and J. C. Tappeiner. 2004. Flower and fruit production of understory shrubs in western Washington and Oregon. *Northwest Science* 78:124–140.
- 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.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1985/full>