The Influence of a Railway on Grizzly Bears (*Ursus arctos*) in Canada's Rocky Mountain Parks

by

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Abstract

Human-modified landscapes can threaten the persistence of wildlife populations through the loss, fragmentation and degradation of habitat. Linear features such as roads and railways are a common cause of habitat alteration which can also threaten wildlife directly through collisions with vehicles. Although the adverse effects of roads on wildlife have been extensively studied and have resulted in widespread mitigation measures (e.g. fencing and highway crossing structures), far less attention has been paid to railways. This is unfortunate because the reliance on railway transport continues to grow in many regions of the world, along with the density of railway networks, the volume of goods transported, and the speeds with which trains travel. In addition, railways can have high rates of wildlife-train collisions, which can lessen population viability, particularly for wildlife species that have low reproductive rates, large home ranges, or small and declining populations. This situation has occurred for a population of grizzly bears (*Ursus arctos*) in Canada's Rocky Mountain Parks, for which the leading cause of recorded mortality is collisions with trains. To mitigate collision vulnerability for bears in the area, and potentially for other species and regions, one must understand the factors that contribute to bear-train collisions to identify the types of mitigation and locations where it could achieve the greatest benefits.

I examine causes of bear vulnerability to rail-associated mortality in three ways. First, I examined vegetation enhancement along the Canadian Pacific Railway that bisects Banff and Yoho National Parks. Specifically, I measured and compared the diversity, richness, abundance, productivity, and phenology of bear-attracting plants at the railway ballast, at the forest edge, and within the adjacent forest spanning an elevational gradient. Second, I investigated the spatiotemporal factors associated with railway selection by grizzly bears using GPS data from 27 collared bears. Specifically, I tested the influence of habitat, human-use, and topographical variables on locations where grizzly bears used the railway and where particular movement types occurred. Further, I determined whether locations of concentrated use and movement were correlated with locations of past bear-train strikes. In a third chapter, I investigated the potential for bears to be exposed to railway-based contaminants. Specifically, I measured the concentrations of metals and PAHs in two railway-associated foods that are known to attract bears; rail-side dandelion (*Taraxacum officinale*) and train-spilled grain. I analyzed hair samples to determine whether bears that used the railway, and four other anthropogenic features, had comparatively higher concentrations of heavy metals in their fur.

For vegetation enhancement, I found that the railway had higher species diversity, richness, total cover, and accelerated phenology of vegetation when compared to the adjacent forest. In addition, fruiting species at the railway had higher productivity, earlier ripening, and higher sugar content. Based on information from GPS collars, I found that bears demonstrated strong seasonality in railway use (spring and fall), which may correlate with the seasonal availability of bear-attracting plants that grow along the railway. Bears tended to use the railway in areas with lower landscape-scale habitat quality, where terrain was locally rugged, close to railway sidings (low-speed sections of track), and at intermediate distances from towns, highways, and trails. Among movement types, bears entered the railway where habitat productivity was higher, close to railway sidings, and in locations constrained by local rugged terrain. Bears demonstrated prolonged use of the railway (via continue movements) in areas where landscape-scale terrain was rugged. Step lengths were consistently shorter when bears were on versus off the railway. No aspect of use or movement predicted sites of higher mortality, but prolonged use of the railway (via continue movements) occurred in areas with lower rates of mortality. My analyses of contaminants revealed that railway-associated forage contained elevated levels of 10 heavy metals and 16 PAHs when compared to reference samples, with much higher contamination in train-spilled grain. However, mycotoxin contamination of grain occurred at very low levels. I found that male bears had higher metal concentrations in hair samples than females, but higher metal concentrations did not correlate with greater frequency of rail use. However, metal concentrations near the hair root were correlated with bear use of ski hills in the fall.

My results showed that the railway enhances vegetation that may attract bears and other wildlife; that bears use the railway both for foraging opportunities (natural or anthropogenic) and for travel through rugged terrain; and, that railway-associated foods (dandelion and train-spilled grain) contained elevated levels of metals and PAHs. Risk of strike associated with rail use by bears and other wildlife may be reduced by removing attractants, particularly in areas with high rates of past mortality or where rugged terrain constrains movement, and especially in spring and fall. Managers might compensate for attractant removal near the rail by enhancing the productivity of critical bear foods such as berry-producing shrubs, in safe areas via forest thinning or prescribed burns. Removal of attractants, especially grain, and regular maintenance and cleaning of areas of heightened contamination (e g. railway sidings and lubricating stations), may reduce contaminant exposure to wildlife who forage along railways. Wildlife-train collisions will likely increase as railway networks continue to grow. Understanding how railways influence bears and other wildlife, including causes of and mitigation for train strikes, will contribute to the conservation of grizzly bears in North America, and many other sensitive populations worldwide.

Preface

This dissertation is an original work by Sonya Zoey Pollock. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Animal Care and Use Committee, Project Name "University of Alberta Grizzly Bear Mitigation Project", AUP00000438. GPS collar data and bear hair samples used for this project were collected by the Parks Canada Agency (Banff, Alberta).

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I would like to dedicate this dissertation to the memory of my father, Darrel Coleman Pollock. You showed me the beauty of nature, the awe of wildlife, and respect for the wonderful world we live in. I know that you would be very proud of me, dad. I will love you forever and I miss you every day.

"Every atom you possess has almost certainly passed through several stars and been part of millions of organisms on its way to becoming you"

– Bill Bryson

Table of Contents

List of Tables

List of Figures

Chapter 1: General Introduction

The growth of the human population and rapid economic development has led to an increased dependency on, and expansion of, transportation networks such as roads and railways (Dulac 2013, Laurance et al. 2014, Ibisch et al. 2016). It has been projected that between 2010 and 2050, the length of roads and railway tracks will increase by 60% globally (Dulac 2013). Transportation networks can adversely affect wildlife abundance and distribution through both indirect and direct effects such as habitat loss and fragmentation, habitat degradation through chemical and noise pollution, restriction of wildlife movement, increased hunting vulnerability via human access, and mortality through collisions with vehicles, to name a few (reviewed by Trombulak and Frissell 2000, Fahrig and Rytwinski 2009, Benito-Lopez et al. 2010). Despite substantial progress in identifying, evaluating, and mitigating the effects of roads on wildlife, far less attention has been paid to railways, even though they occupy over a million kilometers of track worldwide (Dulac 2013) and have similar negative ecological effects (Dorsey et al. 2015, Popp and Boyle 2017). Mitigating the adverse effects of railways is becoming increasingly important as the reliance on rail transport continues to grow in some regions.

Compared to roads, railways have several attractive advantages. Environmental benefits include energy efficiency, a reduction in pollution emissions, and a lower land use requirement (Tolliver et al. 2013, Borda-de-Agua et al. 2017). Economic benefits include high travel speeds and the capacity to transport large volumes of goods and people (Facanha and Horvath 2006, Uherek et al. 2010, Dulac 2013). And safety benefits include lower fatality risk for passengers (Savage 2013, Borda-de-Agua et al. 2017). Even though railways offer many socio-economic benefits, they can be highly detrimental to wildlife, primarily via collisions with trains (van der Grift 1999, Dorsey 2011, Dasgupta and Ghosh 2015), which can surpass mortality rates on nearby roads or highways (e.g., Huber et al. 1998, Waller & Servheen 2005). Particularly susceptible to the direct negative effects of railways are large, wide-ranging animals because they are more likely to encounter rail networks (Carr and Fahrig 2001, Rytwinski and Fahrig 2011, Torres et al. 2016) and have lower reproductive rates and population densities, making mortality from train collisions a potential limiting factor for population viability (Rytwinski and Fahrig 2012, Grilo et al. 2015).

Transportation networks may pose a threat when they intersect protected areas like reserves, wildlife sanctuaries, and national parks, where the conservation of wildlife and ecosystems are prioritized. Highways and railways pass through several nature reserves throughout Africa, with high rates of mortality for wildlife across species (Collinson et al. 2015, Epps et al. 2015, Kioko et al. 2015), including the endangered African elephant (*Loxodonta africana*) and the African hunting dog (*Lycaon pictus*; Drews 1995, Whittington-Jones and Davies-Mostart 2015). In India, large animals of conservation concern like the Indian rhinoceros (*Rhinoceros unicornis*), tiger (*Panthera tigris*), and the Asiatic elephant (*Elephas maximus*) are struck by trains annually in protected areas (Singh et al. 2002, Joshi and Singh 2007, Palei et al. 2013). In India, more than 200 endangered Asiatic elephants have been killed by trains between 1987 and 2013, with the mortality rate rising as the number and speed of trains increase (Dasgupta and Ghosh 2015). A significant increase in railway traffic is predicted for Africa and India as many of their railway lines convert from the narrow, meter-gauge lines to the larger standard or broad-gauge lines, thus allowing for greater speeds and carrying capacity (Nagendra et al. 2009, Rail working group 2009).

Another region with high rates of mortality from train strikes across species, including sensitive populations in protected areas, occurs in the Canadian Rocky Mountain Parks in

Western Canada. Train collisions are the leading cause of human-caused mortality for grizzly bears in the region (Bertch and Gibeau 2010). There have been 17 collision events (confirmed mortalities and reported strikes) with 21 individual bears since the millennium in Banff and Yoho National Parks (Parks Canada, personal communication). There are approximately 80 grizzly bears in these two parks (Parks Canada 2017a) and the population has some of the lowest densities and reproductive rates in North America (Garshelis et al. 2005, Whittington and Sawaya 2015), making a reduction in railway mortality a priority. Due to particularly low densities and reproductive rates and sensitivity to human disturbance, grizzly bears in the province of Alberta (of which Banff National Park is a part) were designated as a threatened species in 2010 (Clark and Slocombe 2011). Similarly, due to small and fragmented populations in the neighbouring province of British Columbia (of which Yoho National Park is a part), 9 of 56 population units of grizzly bears are considered threatened with several historic populations completely extirpated (Boyce et al. 2016). High human-use in the mountain parks continues to challenge the coexistence between grizzly bears and humans (Gibeau et al. 2002, Chruszcz et al. 2003, Bertch and Gibeau 2010). Collectively, these parks are visited by over 4 million tourists a year (Parks Canada 2017b), have three townsites (Banff, Lake Louise, and Field), three large ski hills, numerous human-use trails, and are bisected by a major transportation corridor which consists of the busy four-lane TransCanada highway and the parallel Canadian Pacific Railway (hereafter railway). Fencing along the highway has greatly reduced road-associated mortality, by as much as 80% for ungulates (Clevenger et al. 2001, Gilhooly 2016). However, wildlife-train collisions remain high along the unmitigated railway for several species in addition to the grizzly bear, including black bears (*Ursus americanus*), wolves (*Canis lupus*), elk (*Cervus canadensis),* and deer (*Odocoileus hemionus*; *O. virginianus)* (Wells et al. 1999, Dorsey 2011, Gilhooly 2016).

Attraction to the railway by bears and other wildlife could be due to several factors, including the availability and abundance of palatable forage and the use of the railway as an energy efficient travel corridor. Like roadsides, railways and their verges can increase heat, light, and disturbance which enhances vegetative growth for bear-attracting plants like dandelion (*Taraxacum officinale*) and clover (*Trifolium* spp.) in the spring, grasses and horsetail (*Equisetum arvense*) in the summer, and berry-producing plants in the fall (Hansen and Clevenger 2005, Roever et al. 2008, Pollock et al. 2017). In addition to vegetation growing along railways, bears can be attracted to deposits of train-spilled agricultural grains (e.g., wheat) that can accumulate on the tracks over time (Dorsey 2011, Waller and Servheen 2005, Gangadharan et al. 2017). A concurrent study quantifying grain deposition in Banff and Yoho National Parks estimated that 110 tons were spilled along the railway line each year, enough to meet the caloric needs of the regional population of grizzly bears (Gangadharan et al. 2017). Further, railways can provide bears with scavenging opportunities from carcasses of animals that have been struck and killed by trains (Wells et al. 1999, Murray et al. 2017). For bears in the mountain parks, forage opportunities along railways may be especially attractive because the population is considered comparatively reliant on vegetation and thus protein-limited (Hilderbrand et al. 1999, Lopez-Alfaro et al. 2015; Nielsen et al. 2016). Further, vegetation can be limited in the study area due to a short growing season, rocky terrain, and historic fire suppression, all of which restrict the growth and distribution of plant species that bears depend on for survival (Hamer and Herrero 1987b, Herrero 1994, Luckman and Kavanagh 2000).

In addition to forage availability, the use of the railway as a relatively flat, energy-efficient travel route could be particularly beneficial in the mountain parks where the surrounding topography is rugged, and movement is concentrated to the valley bottom where the railway and most roads also occur (Noss et al. 1996, Whittington et al. 2004). Certain sections of railway may be used to navigate this human-dominated landscape whilst avoiding people on nearby trails and roads, or potentially to avoid other conspecifics. Travel along railways and their verges may be favoured to nearby roadsides due to a lower traffic volume and narrower width which increases proximity to hiding cover (Jalkotzy et al. 1997, Dorsey et al. 2015). Other wide-ranging animals, particularly wolves, have been shown to use linear features like railways to move greater distances more quickly, efficiently travelling between habitat patches and to increase hunting opportunity (Whittington et al. 2005, Latham et al. 2011, Dickie et al. 2016).

Although the problem of wildlife-train collisions and the ecological effects of railways is beginning to be recognized as demonstrated by the emerging field of railway ecology (e.g. Borda-de-Agua et al. 2017, Popp and Boyle 2017), few studies have addressed the environmental contaminants that could jeopardize the health of animals who forage on railway-associated foods (Levengood et al. 2015, Wierzbicka et al. 2015). Railway transportation, although generally less polluting than road transport, is an acknowledged emitter of polycyclic aromatic hydrocarbons (hereafter, PAHs) and heavy metals (Metrak et al. 2015). Sources of PAHs from the railway largely stems from machine grease and oils, as well as creosote, a preservative used for wooden railway ties (Wilkomirski et al. 2011, Kohler et al. 2000). PAHs are highly toxic, accumulate in the environment, and have carcinogenic and mutagenic effects on organisms (Abdel-Shafy and Mansour 2016). Heavy metals from railway emissions mainly originate from material abrasion and fuel combustion (Liu et al. 2009) and are of concern due to a broad range of toxic effects like carcinogenesis, organ damage, negative reproductive effects, and disruption to the nervous system (Jan et al. 2015). Vegetation growing along railways, and potentially train-spilled grain, may act as sinks for PAHs and metal contamination, providing an exposure pathway to foraging wildlife, which is especially concerning in protected areas with vulnerable or rare populations.

This research is a part of the broader Grizzly Bear Conservation Initiative, a 5-year project in collaboration with Parks Canada and the Canadian Pacific Railway, which aims to identify the causes of, and mitigation for, grizzly bear-train collisions in Canada's Rocky Mountain Parks. Generally, my dissertation objectives were to increase understanding on how railways influence grizzly bears in Banff and Yoho National Parks and to provide recommendations to reduce railway-associated mortality. Specifically, I studied the abundance and phenology of bear-attracting plants along the Canadian Pacific Railway in Banff and Yoho National Parks, as well as grizzly bear habitat selection and toxicant exposure in relation to the railway, and secondarily to other human-use areas, in these two parks. Conserving this iconic species in an area that comprises a UNESCO World Heritage Site is a priority for both ecological integrity and to demonstrate Canadian stewardship practices on a global level.

Summary of Dissertation Objectives, Hypotheses, and Methodologies

Bears are known to forage along railways and are attracted to the various food sources there. This attraction is thought to contribute to train collision vulnerability of bears and other wildlife (Huber et al. 1998, Dorsey 2011). In chapter 2, entitled A Railway Increases the Abundance and Accelerates the Phenology of Bear-Attracting Plants in a Forested, Mountain Park, my objective was to determine if the railway enhances vegetation that has the potential to attract bears. To do so, I quantified and compared responses in plants to the railway (ballast), forest edge, and adjacent forest for two growing seasons (May to October) at 19 locations spanning an elevational gradient in Banff and Yoho National Parks. I hypothesized that the various effects of the railway (i.e., light, heat, and disturbance) would enhance vegetation diversity, growth, productivity, and phenology of plants consumed by bears.

Mitigating train collision vulnerability for bears requires knowledge on the spatial and temporal characteristics associated with their railway use, which has received limited study to date (Popp and Boyle 2017). In chapter 3, entitled Spatiotemporal Railway Use by Grizzly Bears in the Canadian Rocky Mountains, my objectives were two-fold. My first objective was to determine the spatiotemporal factors that contributed to grizzly bear use of the railway and fine-scale movement types where grizzly bears entered, crossed, continued to travel along, or exited the railway. To do so, I conducted resource selection and step discrimination functions using GPS data from 27 bears collected intermittently between 2000 and 2016 in Banff and Yoho National Parks. For each analysis, we estimated the contribution of habitat, human-use, and topography on railway use and movement. My second objective was to determine how railway use and the four movement types (above) correlated with locations where bears were historically struck by trains. To do so, I compared the prevalence of railway use and the four movement types to the relative frequency of bear-train collisions using kernel density and deciles analyses. I hypothesized that habitat and human-use factors would be most influential in determining where bears used the railway, both generally, and where they entered the railway corridor because of foraging opportunity and/or to avoid human activity. Secondly, I hypothesized that topography would be most influential in determining where bears continued to move along the railway because the railway could be an energy efficient travel route in the mountainous study area. Lastly, I hypothesized that bear-train strikes are more likely to occur in high-use areas and/or where bears spend prolonged time on the railway due to a higher likelihood of encountering a train.

A consequence of railways that has not been thoroughly addressed is if wildlife who forage along railways are exposed to railway-associated toxicants, especially in protected areas with sensitive species. Exposure could occur in at least two ways; via consumption of rail-side vegetation and train-spilled agricultural grains. In chapter 4, entitled Railway-Associated Attractants as Potential Toxicants for Wildlife, my objectives were two-fold. My first objective was to determine if forage in the form of rail-associated vegetation and train-spilled grain potentially exposes bears and other wildlife to toxicants consisting of one of more of heavy metals, PAHs, and mycotoxins. To test this, I collected dandelion and grain samples along the railway and compared toxicant concentrations to respective references and/or government standards. My second objective was to test if metal concentrations measured in the hair of individual grizzly bears were correlated with their frequency of railway use or the use of other anthropogenic features. To do this, I analyzed metal contents in hair samples from 20 GPS-collared grizzly bears in Banff and Yoho National Parks and used principal components analysis to evaluate if metal contents varied in relation to the use of five anthropogenic features. I predicted that toxicants associated with railway operation (metals and PAHs) or decomposing grain (mycotoxins) would occur in higher concentration in samples collected from the railway relative to reference samples. Secondly, I predicted that bears that used the railway, or other human-use areas, more frequently would have higher metal concentrations in their fur.

I conclude my dissertation by summarizing and interpreting the results from chapters 2-4 and then integrating these results with mitigation suggestions that aim to both reduce railway-associated mortality and lessen the negative effects of railways on grizzly bears in Canada’s Rocky Mountain Parks.

Chapter 2: A Railway Increases the Abundance and Accelerates the Phenology of Bear-Attracting Plants in a Forested, Mountain Park

Sonya Z. Pollock, Scott E. Nielsen, and Colleen C. St. Clair

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 to 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 forest modification that would provide forage in less risky habitats.

Keywords: Berry productivity; Ecological trap; Edge; Elevation; Grizzly bears; Invasive species; Phenology; Railway; Rocky Mountain Parks; *Ursus arctos*; Vegetation; Wildlife-train collisions.

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 have 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 (e.g., Eldegard et al. 2015, Lampinen et al. 2015), seismic lines (e.g., van Rensen et al. 2015), trails (reviewed by Ballantyne and Pickering 2015) and road verges (e.g., Gelbard and Belnap 2003, Roever et al. 2008), with a few studies addressing railways (e.g., 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 (e.g., Mallik and Karim 2008) and non-native species (e.g., 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 (e.g., Marriott 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 (e.g., Meisingset et al. 2014, van der Ree et al. 2015) or hunting (e.g., 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 (e.g., Rea

2003, Milton et al. 2015). Such mitigation often targets areas with increased animal density, which may be associated with a water source (e.g., Glista et al. 2007), a movement route (e.g., Whittington et al. 2005), or high-quality habitat (e.g., Gibeau et al. 2002, Nielsen et al. 2006). In addition to vegetation enhancement, wildlife can be attracted to railways from spilled agricultural products (Dorsey 2011, Waller and Servheen 2005, 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 (e.g., Gunson et al. 2011), 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 are collisions with trains (Bertch and Gibeau 2010). 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. 2016). 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 like forbs, horsetails (*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 ploughing 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 and 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, i.e. 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 are 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 (CPR, 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*; *O. 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. 2.1). 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 to 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 m +/- 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 m +/- 7.5; n = 13). The third 'forest' transect was placed in the adjacent forest, approximately 45 m from the edge ($\bar{x}$ = 45.7 m +/- 12.44; n = 18). Along each transect, large nails were hammered into the ground at distances of 6.25 m, 18.75 m, 31.25 m 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 of grizzly bear forage plants along ballast, edge and forest transects. We placed a 1-m^2 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 2.1, Table 2.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 hand-held densiometer and later averaged the values for each transect.

We collected additional vegetation measurements on buffaloberries (*Shepherdia 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 m +/- 3.5 m) to forest shrubs located approximately 50 m from the edge in the adjacent forest ($\bar{x}$ = 57.6 m, +/- 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 collected one or two berries (from non-labelled branches or a neighboring shrub) to measure sugar content. If berries were changing colour, and therefore varied within the shrub, one berry from each colour variant was used. We also installed time lapse cameras (Wingscapes TimelapseCams™) to record fine-scale berry maturation at two shrubs per transect and site and when possible always positioned them facing north (303° to 56°). Cameras were programmed to take a picture every half hour between the hours of 10 am and 4 pm 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 used 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 modelled the summed, proportionate, horizontal cover of available bear foods in each plot ('% 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 2.1, Table 2.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 8 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 June 14), summer = early hyperphagia (June 15 to August 7), and fall = late hyperphagia (August 8 – 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 <=9 and 13) and for 7 species with conspicuous flowers (1 for reproductive codes 4–8, 0 for codes <=3 and >=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 effect models, respectively. We included week as a covariate for sugar content models to account for temporal trends. And lastly, we modelled 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 modelled.

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 (AICc; Burnham and Anderson 2002). We created 9 *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 AICc scores of the top model (Burnham and Anderson, 2002). All analyses and graphics were conducted using R Studio 3.2.1.

Results

In total, we identified 28 grizzly bear forage plants within one or more of our transects (Table 2.1). Of these, 18 species were berry-producers, 8 species were classified as shoots and 2 species as roots according to the portion of the plant targeted by grizzly bears (Table 2.1). The eight most common species included three berry-producing plants (bearberry, buffaloberry and strawberry), three invasive forbs (clover, dandelion, 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. 2.2). 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. 2.2).

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. 2.3), but with large differences in the magnitude and direction of effects among species (Fig. 2.2). Total plant cover was also higher in summer and fall relative to spring (Fig. 2.3a). 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 2.2), with higher values in the summer and fall relative to spring (Tables 2.S2-2.S4). There was no significant effect of elevation on diversity, richness, or total cover (all p's >= 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. 2.3b), opposite to the elevational pattern we predicted.

Plant reproduction was advanced, relative to the forest, with an average of three-fold greater 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 five-fold 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, followed by the forest, particularly in the fall (Table 2.S5). Elevation was an important variable describing the cover of available shoots and roots (Table

2.2), with greater cover at low elevations along ballast and edge transects, relative to the forest, and a higher overall availability in the summer (Tables 2.S6 and 2.S7).

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 (Table 2.S8 and 2.S9). Elevation was included in the top model for both metrics (Table 2.2), with berry counts and sugar content positively associated with elevation, particularly on edge transects (Table 2.S8 and 2.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 (Table 2.S10). Across transects, ripening rates were highest at intermediate elevations (Table 2.S11). Time-lapse cameras indicated that rail-associated berries ripened an average of 8.58 +/- 4.36 days 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 in a mountainous region has higher species richness, diversity and cover for seven of the eight most common species consumed by grizzly bears. Similarly, the forest edge along a railway 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 favours 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 is particularly interesting because it is a staple late-summer food of grizzly bears in the area (Hamer and Hererro 1987). 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 versus other factors, e.g. 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 railside 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 dandelions 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 years peaked in spring and fall, but did so independently of elevation (Fig. 2.4; $\beta = -0.11$, $p = 0.28$). 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 ploughing 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 then (see Gangadharan et al. 2017).

Our work supports some tentative suggestions for mitigation, particularly when combined with 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, railside 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 (e.g., Nielsen et al. 2004a, Nielsen et al. 2006, Manning and Balzer 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 railside 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 depleted 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.

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There are no competing interests for the authors of this manuscript.

Tables

Table 2.1 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. 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.

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

Table 2.2 Top model selection results (< 4 ∆AICc), degrees of freedom (*df*) and Akaike weights for various plant responses. Models were selected using the Akaike Information Criterion adjusted for small sample sizes (AICc; model output tables are located in the appendix).

Dependent variable	**Top models (< 4∆AICc)**	***df***	**Weights**
Plant richness	Transect type * Season	11	1.000
Plant diversity	Transect type	5	0.686
	Transect type * Season	11	0.314
Total plant cover	Transect type * Season	11	1.000
Cover fruiting shrubs	Transect type * Season	9	0.996
Cover available shoots	Season * Elevation + Elevation^2	10	0.416
	Season * Elevation	9	0.358
	Transect type * Elevation + Elevation^2	10	0.112
Cover available roots	Transect type * Elevation	9	0.701
	Transect type * Elevation + Elevation^2	10	0.280
Summed berry count (single visit)	Transect type * Elevation + Elevation^2	10	0.600
	Transect type	6	0.176
	Transect type * Elevation	9	0.161
Average sugar content (single visit)	Transect type * Elevation + Week	10	0.500
	Transect type * Elevation + Elevation^2 + Week	11	0.393
	Transect type + Week	7	0.095
Buffaloberry count	Transect type * Season + Week	8	1.000
Buffaloberry sugar content	Transect type * Elevation + Elevation^2 + Week	9	0.820

Table 2.S1 (a) Vegetative and (b) reproductive phenology codes for shrubs and herbs (adapted from Dierschke 1972 and Bater et al. 2011). We assigned a numerical code describing the most mature stage of vegetative and reproductive phenology for each species within each 1-m^2 circular plot every two weeks from May-October in 2013 and 2014.

(a)

Vegetative phenology codes			
Shrub Code	Description	Herb Code	Description
0	Closed bud	0	Without shoots above ground
1	Buds with green tips	1	Shoots without folded leaves
2	Green leaf out, not unfolded	2	first leaves unfolded
3	Leaf unfolding up to 25%	3	2 or 3 leaves unfolded
4	Leaf unfolding up to 50%	4	Several leaves unfolded
5	Leaf unfolding up to 75%	5	Almost all leaves unfolded
6	Full leaf unfolding	6	Plant fully developed
7	First leaves turned yellow	7	Stem and/or first leaves fading
8	Leaf yellowing up to 50%	8	Yellowing up to 50%
9	Leaf yellowing over 50%	9	Yellowing over 50%
10	Bare	10	Dead

(b)

Reproductive phenology codes	
Shrub & Herb Code	Description
0	Without blossom buds
1	Blossom buds recognizable
2	Blossom buds strongly swollen
3	Shortly before flowering
4	Beginning flowering
5	In bloom up to 25%
6	In bloom up to 50%
7	Full bloom
8	Fading
9	Completely faded
10	Bearing green fruit
11	Bearing ripe fruit
12	Bearing overripe fruit
13	Post fruiting

Table 2.S2 (a) Model selection results from linear mixed models assessing richness of forage plants as a function of 9 *a priori* candidate models. Models were selected using the Akaike Information Criterion adjusted for small sample sizes (AICc). The top model (in bold) regression estimates and standard errors are displayed in the lower table (b). For transect type, forest was used as the reference category and for season, fall was used as the reference category.

(a)

Model #	Model	*Df*	logLik	AICc	∆AICc	Weights
5	**Transect type * Season**	**11**	**-1063.77**	**2150.01**	**0.00**	**1.000**
6	Transect type * Elevation	8	-1099.51	2215.27	65.25	0.000
1	Transect type	5	-1103.22	2216.54	66.52	0.000
8	Transect type * Elevation + Elevation^2	9	-1099.19	2216.71	66.69	0.000
2	Season	5	-1124.60	2259.30	109.29	0.000
7	Season * Elevation	8	-1125.79	2267.82	117.81	0.000
9	Season * Elevation + Elevation^2	9	-1124.94	2268.19	118.18	0.000
3	Elevation	4	-1153.65	2315.36	165.35	0.000
4	Elevation + Elevation^2	5	-1152.71	2315.53	165.52	0.000

(b)

Final model	B	S.E
Intercept	4.82	0.25
Transect: Ballast	-0.71	0.22
Transect: Edge	1.26	0.25
Season: Spring	-1.43	0.26
Season: Summer	0.44	0.23
Transect: Ballast * Season: Spring	0.56	0.37
Transect: Edge * Season: Spring	-0.14	0.41
Transect: Ballast * Season: Summer	-0.63	0.33
Transect: Edge * Season: Summer	-0.49	0.36

Table 2.S3 (a) Model selection results from linear mixed models assessing diversity of forage plants as a function of 9 *a priori* candidate models. Models were selected using the Akaike Information Criterion adjusted for small sample sizes (AICc). Top models that fell within < 4 AICc (in bold) were averaged and the final model regression estimates and standard errors are displayed in the lower table (b). For transect type, forest was used as the reference category and for season, fall was used as the reference category.

(a)

Model #	Model	*Df*	logLik	AICc	ΔAICc	Weights
1	**Transect type**	**5**	**-378.55**	**767.21**	**0.00**	**0.686**
5	**Transect type * Season**	**11**	**-373.15**	**768.77**	**1.56**	**0.314**
6	Transect type * Elevation	8	-384.35	784.94	17.74	0.000
8	Transect type * Elevation + Elevation^2	9	-385.88	790.08	22.87	0.000
2	Season	5	-399.84	809.78	42.57	0.000
7	Season * Elevation	8	-404.03	824.32	57.11	0.000
3	Elevation	4	-408.88	825.82	58.61	0.000
9	Season * Elevation + Elevation^2	9	-405.41	829.14	61.93	0.000
4	Elevation + Elevation^2	5	-410.20	830.51	63.30	0.000

(b)

Final averaged model	B	S.E
Intercept	1.06	0.07
Transect: Ballast	-0.20	0.05
Transect: Edge	0.21	0.06
Season: Spring	-0.06	0.11
Season: Summer	0.03	0.06
Transect: Ballast * Season: Spring	0.02	0.07
Transect: Edge * Season: Spring	-0.03	0.08
Transect: Ballast * Season: Summer	-0.04	0.08
Transect: Edge * Season: Summer	-0.03	0.07

Table 2.S4 (a) Model selection results from beta regression mixed models assessing total cover of forage plants as a function of 9 *a priori* candidate models. Models were selected using the Akaike Information Criterion adjusted for small sample sizes (AICc). The top model (in bold) regression estimates and standard errors are displayed in the lower table (b). For transect type, forest was used as the reference category and for season, fall was used as the reference category.

(a)

Model #	Model	*Df*	logLik	AICc	∆AICc	Weights
5	**Transect type * Season**	**11**	**477.00**	**-931.53**	**0.00**	**1.000**
6	Transect type * Elevation	8	449.76	-883.27	48.26	0.000
8	Transect type * Elevation + Elevation^2	9	449.77	-881.22	50.31	0.000
1	Transect type	5	434.49	-858.87	72.67	0.000
2	Season	5	374.61	-739.12	192.41	0.000
7	Season * Elevation	8	374.97	-733.68	197.85	0.000
9	Season * Elevation + Elevation^2	9	375.27	-732.23	199.30	0.000
3	Elevation	4	345.51	-682.95	248.58	0.000
4	Elevation + Elevation^2	5	345.82	-681.53	250.00	0.000

(b)

Final model	B	S.E
Intercept	-1.52	0.13
Transect: Ballast	0.05	0.11
Transect: Edge	1.09	0.12
Season: Spring	-0.68	0.15
Season: Summer	0.08	0.12
Transect: Ballast * Season: Spring	-0.14	0.20
Transect: Edge * Season: Spring	0.12	0.20
Transect: Ballast * Season: Summer	-0.25	0.17
Transect: Edge * Season: Summer	-0.04	0.17

Table 2.S5 (a) Model selection results from beta regression mixed models assessing percent cover of shrubs that were fruiting (18 species) as a function of 9 *a priori* candidate models. Models were selected using the Akaike Information Criterion adjusted for small sample sizes (AICc). The top model (in bold) regression estimates and standard errors are displayed in the lower table (b). For transect type, forest was used as the reference category and for season, summer was used as the reference category.

(a)

Model #	Model	*Df*	logLik	AICc	∆AICc	Weights
5	**Transect type * Season**	**9**	**262.73**	**-506.59**	**0.00**	**0.996**
8	Transect type * Elevation + Elevation^2	10	257.53	-494.01	12.59	0.002
6	Transect type * Elevation	9	256.05	-493.24	13.36	0.001
1	Transect type	6	252.69	-492.99	13.60	0.001
2	Season	5	238.06	-465.85	40.75	0.000
9	Season * Elevation + Elevation^2	8	240.41	-464.13	42.46	0.000
7	Season * Elevation	7	238.49	-462.44	44.15	0.000
4	Elevation + Elevation^2	6	233.98	-455.56	51.03	0.000
3	Elevation	5	232.10	-453.91	52.68	0.000

(b)

Final model	B	S.E
Intercept	-2.61	0.29
Transect type: Ballast	-0.65	0.27
Transect type: Edge	0.66	0.19
Season: Fall	0.53	0.25
Transect type: Ballast * Season: Fall	-0.65	0.33
Transect type: Edge * Season: Fall	0.03	0.28

Table 2.S6 (a) Model selection results from beta regression mixed models assessing percent cover of available shoots (8 species) as a function of 9 *a priori* candidate models. Models were selected using the Akaike Information Criterion adjusted for small sample sizes (AICc). Top models that fell within < 4 AICc (in bold) were averaged and the final model regression estimates and standard errors are displayed in the lower table (b). For transect type, forest was used as the reference category and for season, fall was used as the reference category.

(a)

Model #	Model	*df*	logLik	AICc	∆AICc	Weights
9	**Season * Elevation + Elevation^2**	**10**	**2295.02**	**-4569.84**	**0.00**	**0.416**
7	**Season * Elevation**	**9**	**2293.85**	**-4569.53**	**0.30**	**0.358**
8	**Transect type * Elevation + Elevation^2**	**10**	**2293.71**	**-4567.22**	**2.62**	**0.112**
6	Transect type * Elevation	9	2291.93	-4565.69	4.14	0.053
2	Season	6	2288.59	-4565.10	4.73	0.039
1	Transect type	6	2287.47	-4562.86	6.97	0.013
5	Transect type * Season	12	2292.42	-4560.55	9.29	0.004
4	Elevation + Elevation^2	6	2285.82	-4559.56	10.27	0.002
3	Elevation	5	2284.67	-4559.29	10.55	0.002

(b)

Final averaged model	B	S.E
Intercept	-2.93	0.08
Season: Spring	-0.24	0.08
Season: Fall	-0.10	0.07
Elevation	-0.07	0.08
Elevation^2	0.05	0.03
Elevation * Spring	0.06	0.07
Elevation * Summer	0.21	0.07
Transect type: Ballast	-0.09	0.07
Transect type: Edge	0.12	0.08
Transect type: Ballast * Elevation	-0.16	0.06
Transect type: Edge * Elevation	-0.19	0.08

Table 2.S7 (a) Model selection results from beta regression mixed models assessing percent cover of available roots (2 species) as a function of 9 *a priori* candidate models. Models were selected using the Akaike Information Criterion adjusted for small sample sizes (AICc). Top models that fell within < 4 AICc (in bold) were averaged and the final model regression estimates and standard errors are displayed in the lower table (b). For transect type, forest was used as the reference category.

(a)

Model #	Model	*df*	logLik	AICc	∆AICc	Weights
6	**Transect type * Elevation**	**9**	**647.65**	**-1276.26**	**0.00**	**0.701**
8	**Transect type * Elevation + Elevation^2**	**10**	**647.86**	**-1274.43**	**1.83**	**0.280**
1	Transect type	6	640.33	-1268.18	8.08	0.012
4	Elevation + Elevation^2	6	638.38	-1264.28	11.98	0.002
7	Season * Elevation	9	641.65	-1264.26	12.00	0.002
3	Elevation	5	637.09	-1263.84	12.42	0.001
9	Season * Elevation + Elevation^2	10	642.33	-1263.37	12.89	0.001
2	Season	6	637.47	-1262.45	13.81	0.001
5	Transect type * Season	12	641.93	-1258.02	18.24	0.000

(b)

Final averaged model	B	S.E
Intercept	-4.77	0.20
Transect type: Ballast	-0.06	0.25
Transect type: Edge	0.23	0.12
Elevation	0.44	0.21
Elevation^2	0.07	0.10
Transect type: Ballast * Elevation	-0.83	0.28
Transect type: Edge * Elevation	-0.27	0.11

Table 2.S8 (a) Model selection results for total berry production (single visit) as a function of 5 *a priori* candidate models. Models were selected using the Akaike Information Criterion adjusted for small sample sizes (AICc). Top models that fell within < 4 AICc (in bold) were averaged and the final model regression estimates and standard errors are displayed in the lower table (b). For transect type, forest was used as the reference category.

(a)

Model #	Model	*df*	logLik	AICc	∆AICc	Weights
5	**Transect type * Elevation + Elevation^2**	**10**	**-256.78**	**540.90**	**0.00**	**0.600**
1	**Transect type**	**6**	**-264.44**	**543.36**	**2.46**	**0.176**
4	**Transect type * Elevation**	**9**	**-259.86**	**543.53**	**2.63**	**0.161**
3	Elevation + Elevation^2	6	-265.96	546.39	5.49	0.038
2	Elevation	5	-267.79	547.30	6.40	0.024

(b)

Final averaged model	B	S.E
Intercept	4.58	0.79
Transect: Ballast	1.90	0.50
Transect: Edge	1.06	0.52
Elevation	-0.01	0.36
Elevation^2	-0.48	0.39
Transect type: Ballast * Elevation	0.22	0.41
Transect type: Edge * Elevation	1.07	0.71

Table 2.S9 (a) Model selection results for average sugar content (single visit) as a function of 5 *a priori* candidate models. Models were selected using the Akaike Information Criterion adjusted for small sample sizes (AICc). Top models that fell within < 4 AICc (in bold) were averaged and the final model regression estimates and standard errors are displayed in the lower table (b). For transect type, forest was used as the reference category.

(a)

Model #	Model	*df*	logLik	AICc	∆AICc	Weights
4	**Transect type * Elevation + Week**	**10**	**-94.88**	**218.22**	**0.00**	**0.500**
5	**Transect type * Elevation + Elevation^2 + Week**	**11**	**-93.07**	**218.69**	**0.47**	**0.393**
1	**Transect type + Week**	**7**	**-101.83**	**221.52**	**3.30**	**0.095**
2	Elevation + Week	6	-105.69	226.18	7.96	0.009
3	Elevation + Elevation^2 + Week	7	-104.69	227.24	9.01	0.005

(b)

Final averaged model	B	S.E
Intercept	11.17	4.37
Transect: Ballast	5.99	2.07
Transect: Edge	3.89	1.85
Elevation	-2.77	1.60
Elevation^2	-0.45	0.73
Transect type: Ballast * Elevation	0.81	1.71
Transect type: Edge * Elevation	1.61	2.20
Week	1.66	0.96

Table 2.S10 (a) AICc model selection results for buffaloberry count as a function of 9 *a priori* candidate models. The final model (in bold) regression estimates and standard errors are displayed in the lower table (b). For transect type, forest was used as the reference category and for season, summer was used as the reference category.

(a)

Model #	Model	*df*	logLik	AICc	ΔAICc	Weights
5	**Transect type * Season + Week**	**8**	**1749.94**	**3516.21**	**0.00**	**1.000**
1	Transect type + Week	6	1771.30	3554.80	38.59	0.000
6	Transect type * Elevation + Week	8	1770.74	3557.81	41.60	0.000
8	Transect type * Elevation + Elevation^2 + Week	9	1770.28	3558.99	42.78	0.000
2	Season + Week	6	1774.22	3560.64	44.43	0.000
3	Elevation + Week	6	1774.67	3561.54	45.32	0.000
4	Elevation + Elevation^2 + Week	7	1774.24	3562.74	46.53	0.000
7	Season * Elevation + Week	8	1773.42	3563.17	46.96	0.000
9	Season * Elevation + Elevation^2 + Week	9	1773.01	3564.44	48.22	0.000

(b)

Final model	B	S.E
Intercept	2.37	0.47
Transect: Rail	0.63	0.11
Season: Fall	0.70	0.19
Week	-1.41	0.10
Transect: Rail * Season: Fall	-1.23	0.18

Table 2.S11 (a) AICc model selection results for buffaloberry sugar content as a function of 9 *a priori* candidate models. The final model (in bold) regression estimates and standard errors are displayed in the lower table (b). For transect type, forest was used as the reference category.

(a)

Model #	Model	*df*	logLik	AICc	ΔAICc	Weights
8	**Transect type * Elevation + Elevation^2 + Week**	**9**	**-858.94**	**1736.48**	**0.00**	**0.820**
6	Transect type * Elevation + Week	8	-862.14	1740.75	4.28	0.100
5	Transect type * Season + Week	8	-862.87	1742.22	5.74	0.050
1	Transect type + Week	6	-865.37	1743.03	6.55	0.030
9	Season*Elevation + Elevation^2 + Week	9	-876.65	1771.91	35.43	0.000
4	Elevation + Elevation^2 + Week	7	-878.93	1772.23	35.75	0.000
2	Season + Week	6	-881.17	1774.61	38.13	0.000
7	Season * Elevation + Week	8	-879.46	1775.40	38.92	0.000
3	Elevation + Week	6	-881.72	1775.72	39.24	0.000

(b)

Final model	B	S.E
Transect: Rail	2.85	0.45
Elevation	-2.01	0.68
Week	4.85	0.39
Elevation^2	-1.12	0.55
Transect: Rail * Elevation	0.92	0.44

Figures

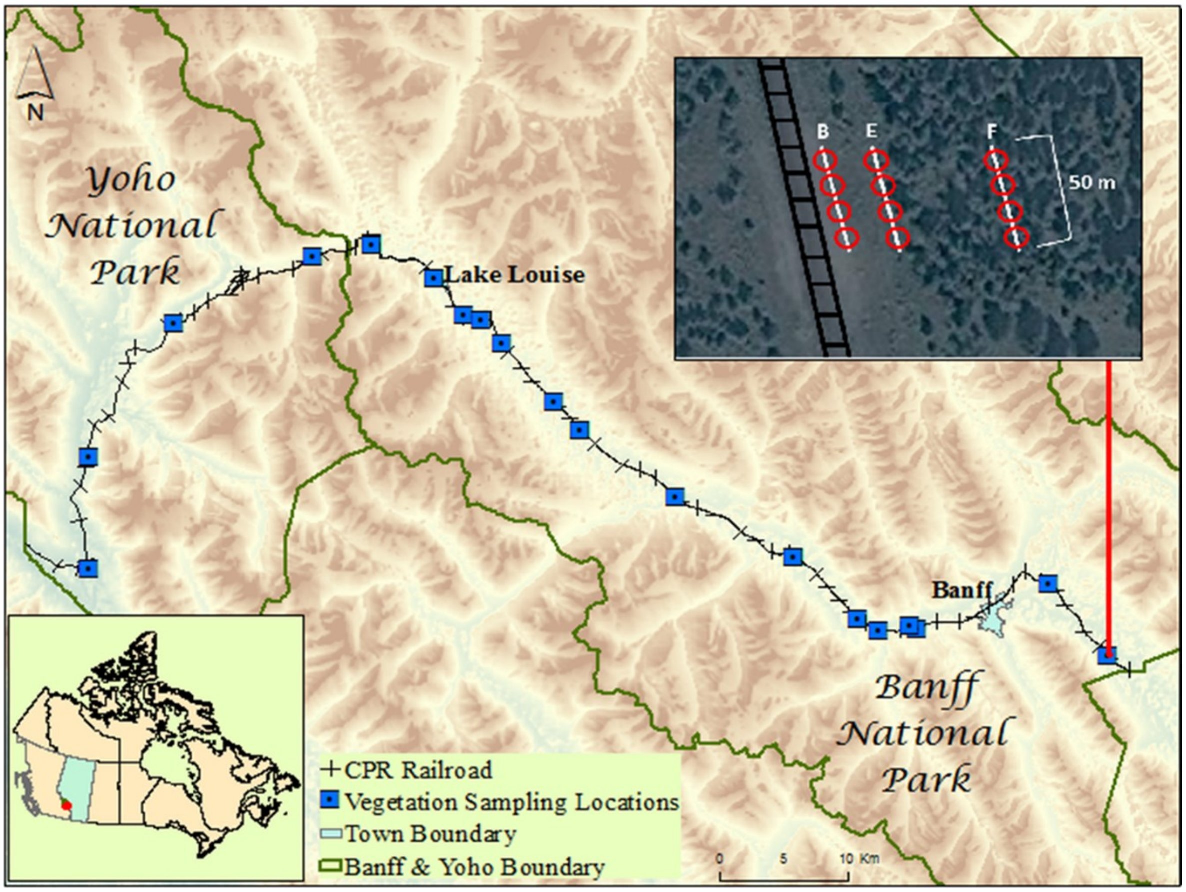

Figure 2.1 Locations of vegetation sampling (n = 19 blue squares) along the Canadian Pacific Railway running through Banff and Yoho National Parks (left inset). The sampling design included three transects parallel to the railway (right inset) with the first ('B') positioned where the ballast meets the vegetation line, the second ('E') along the forest edge, and the third ('F') approximately 50 m into the forest. We placed 4 x 1-m^2 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.

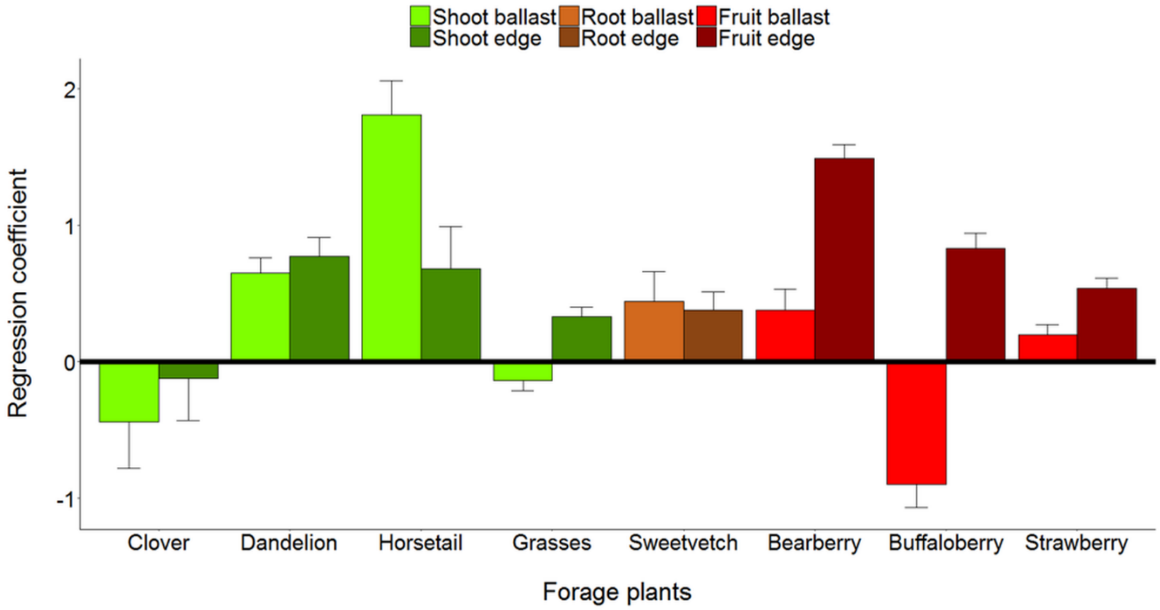

Figure 2.2 Standardized coefficients with standard error from a beta regression mixed effects model describing the percent cover of eight common grizzly bear forage plants. Shoot species are represented by green, root species by brown and fruit species by red, along ballast transects (lighter colours) and edge transects (darker colours) relative to an adjacent forest (black line).

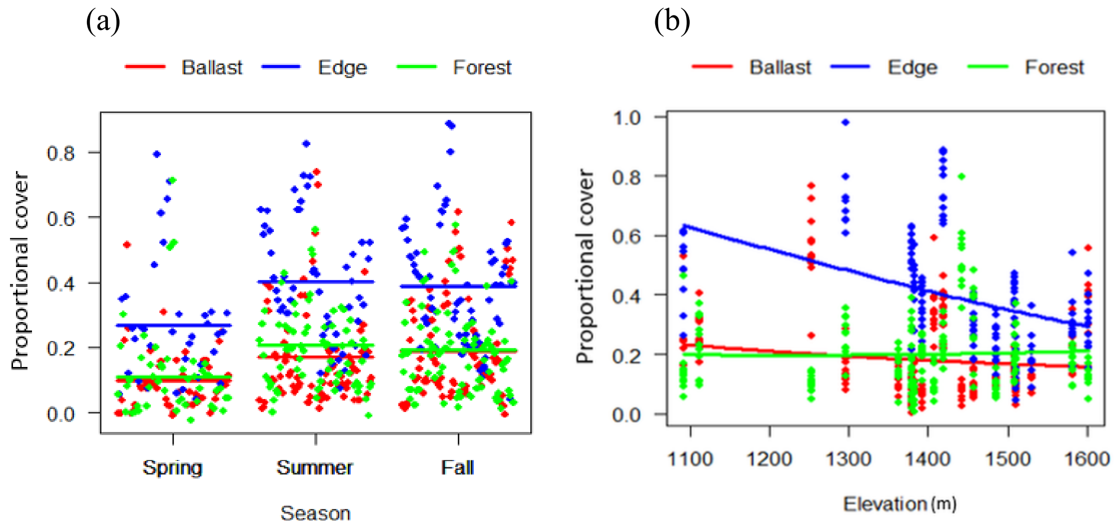

Figure 2.3 Modelled means (lines) and measured values (symbols) for total proportional cover of forage plants averaged across four 1-m^2 circular plots by (a) season (spring, summer, fall) and transect type (ballast, edge, forest) holding elevation constant at its median value and (b) elevation (quadratic) and transect type (ballast, edge, forest) holding the most common season constant (fall).

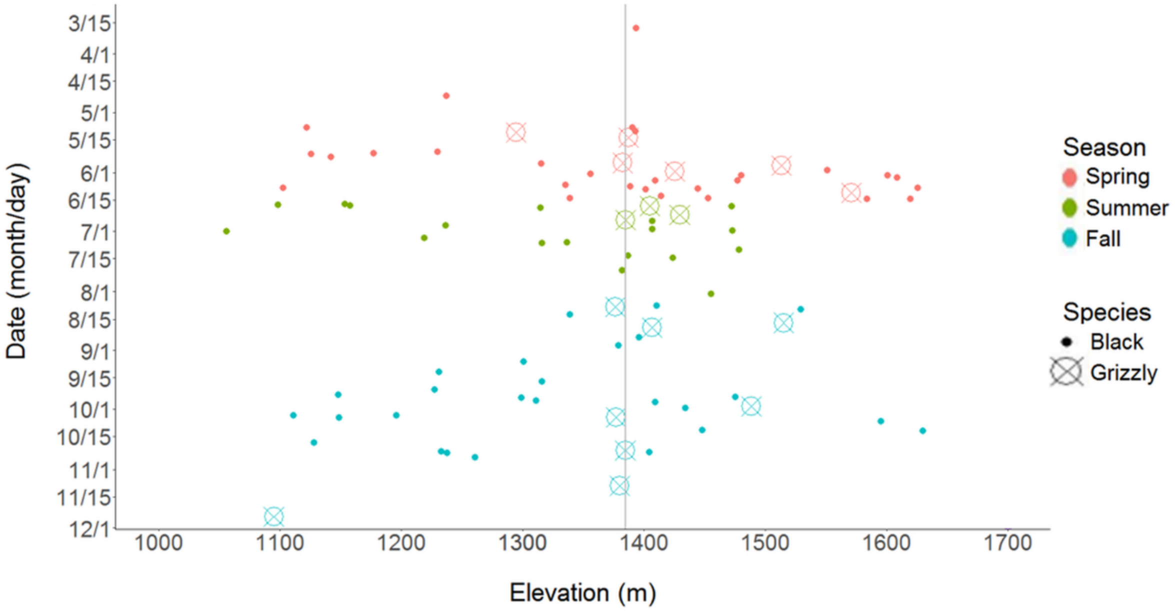

Figure 2.4 Train collision events (symbols) with grizzly and black bears in Banff and Yoho National Parks from 2000 – 2016 by date (month/day), elevation and season (spring, summer, fall). The grey vertical line represents the median elevation for all strikes.

Chapter 3: Spatiotemporal Characteristics of Railway Use by Grizzly Bears in the Canadian Rocky Mountains

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Abstract

Railway networks contribute to the direct mortality of wildlife through collisions with trains, which can threaten wildlife populations even in protected areas. This situation applies to grizzly bears (*Ursus arctos*) in national parks across the Canadian Rocky Mountains where train strikes have become the leading source of human-caused mortality. Mitigation to reduce bear-train collisions requires information about how grizzly bears use the railway spatially and temporally and how particular types of movements might increase collision vulnerability. Using GPS data collected over 12 years from 27 grizzly bears in Banff and Yoho National Parks, we used resource selection functions to relate railway use by bears to variables that described habitat quality, human-use, and topography. We used the same suite of explanatory variables to explore potential differences in sites where three successive GPS points (with 2-hr fix rates) distinguished locations where bears entered, crossed, continued along, or exited the railway corridor with pairwise comparisons that we termed step discrimination functions. We also compared the prevalence of these four step types to the relative frequency of bear-train collisions, predicting that increased railway use would correlate with increased risk of collisions. Overall, 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 (town sites, highways and trails), and in areas with lower habitat quality (within 500 m) and more rugged terrain (within 90 m), and made greater use of the railway in the spring and fall. Among the four step types, bears crossed the railway (27 individuals), twice as often as they entered or exited it (24 individuals) and three times as often as they continued along it (14 individuals). The best-fitting of six step discrimination function differentiated steps that continued along vs. crossed the rail, with greater likelihood of continue movements in areas with rugged terrain (within 300 m) and closer to railway sidings, in the seasons of spring and fall, and associated with steps that were 60% shorter, which may have been indicative of foraging behavior. Despite variation in railway use, we found no correlation between any of overall railway use or the four step types and the frequency of bear-train collisions, although the power of these tests were low. In combination, our results suggest that railway use by bears increased where it provided one or both of increased forage and easier travel through rugged topography, particularly in spring and fall. If increased railway use actually increases strike risk, it might be reduced by removing attractants (e.g., train-spilled grain, rail-side vegetation, and rail-killed ungulates), particularly in areas with rugged topography that constrain movement with an emphasis on attractants that increase in spring and fall.

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

Introduction

Collisions with vehicles are a major source of mortality for wildlife with the potential for population-level effects (reviewed by Fahrig and Rytwinski 2009, Benito-Lopez et al. 2010). Although road mortality is well documented, there is a comparative lack of railway-associated research, despite high rates of wildlife-train collisions (Dorsey et al. 2015, Popp and Boyle 2017, Santos 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 while 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, mitigating vulnerability to train collisions logically requires information on the spatial and temporal factors that are associated with railway use by animals. Similar to roads, railway tracks can intersect important habitat, such as areas associated with forage, cover, or movement routes (reviewed by 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, such as during nocturnal periods when animals avoid human activity (Hebblewhite and Merrill 2008, Schwartz et al. 2010*a*, 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 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 travel continuously along a railway, thereby exhibiting greater dedication to railway use, may be more vulnerable to strikes than animals that cross a railway with briefer encounter durations.

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 areas with adjacent attractants, where bears may be more likely to enter or exit the railway corridor. Others have equated the crossing of linear features to particular landscape characteristics (e.g., Lewis et al. 2011, Sunga et al. 2017), habitat quality (e.g., Chruszcz et al. 2003, Laurian et al. 2008), and human-use (e.g., Whittington et al. 2004, 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 are the leading source of human-caused mortality (Bertch and Gibeau 2010). The bears in this population exhibit unusually low reproductive rates (Garshelis et al. 2005), which appear to stem from food limitation in this mountainous, heavily-forested landscape, where a short growing season further constrains the abundance and productivity of important forage plants (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 (McLellan 2011, Lopez-Alfaro et al. 2015, Nielsen et al. 2016). These factors increase the potential forage opportunities of a railway which, similar to roadsides, enhances growth and productivity of many plant species (Hansen and Clevenger 2005, Roever et al. 2008*a*, 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).

In addition to obtaining food resources, bears and other wildlife may exploit railways as energy-efficient travel corridors. Similar linear features increased the movement rates of red foxes (*Vulpes vulpes*; Adkins and Stott 1998) and wolves (*Canis lupus*; Whittington et al. 2005, Latham et al. 2011), sometimes to increase hunting efficiency (James and Stuart-Smith 2000, Latham 2009, Dickie et al. 2016). This advantage may be especially pronounced in mountainous regions where rugged topography influences animal movement (Noss et al. 1996, Whittington et al. 2004) and for grizzly bears, which are especially wide-ranging (Nielsen et al. 2004*b*, Munro et al. 2006, Schwartz et al. 2010*b*). Relative to roads, railways may be more attractive as travel routes because they are narrower (usually < 30 m width) and contain little human activity (Jalkotzy et al. 1997, Tremblay and St. Clair 2009, Dorsey et al. 2015), features that may increase the relative attraction to and permeability of railways for animal movement (e.g., Jasinska et al. 2014) or travel routes (e.g. Whittington et al. 2005).

More information about which factors predict animal use of railways, how particular movement types relate to motivation for use, and if greater use predicts strike risk could help to identify both locations for and types of railway mitigation. We advanced this broad goal by studying a population of 27 GPS-collared grizzly bears in Banff and Yoho National Parks where 14 grizzly bears have been killed by train strikes at 11 known locations (Fig. 3.1). Seven additional individuals were reported by train staff as struck at six additional locations, but could not be confirmed by the presence of a bear carcass. We compared explanatory variables describing habitat quality, human-use, and topographical features to GPS points from bears within 30 m of the railway to predict the locations with (a) higher overall railway use and (b) each of four specific movement types, to (c) determine whether any of these predicted areas with higher bear mortality. We defined the four movement types using three successive GPS location with 2-hr fix rates as places where bears entered, crossed, continued along or exited the railway corridor (Fig. 3.2). We focused our investigations on three core hypotheses and their associated predictions. (A) If railway use depends on forage quality, travel efficiency, or avoidance of people, relative use should increase in areas with more bear food, in areas with more complex topography, or farther from human infrastructure, respectively. (B) If movement behavior reveals underlying motivation, sustained use (i.e., continue steps) and slower movement (i.e., shorter steps) should have higher associations with beneficial explanatory variables than incidental use (i.e., crossing steps) or faster movement. (C) Finally, if greater railway use conveys a greater risk of mortality, locations with greater overall use and continued movement types should predict sites of past mortality. We used the results of these investigations to offer preliminary recommendations to managers for reducing rail-associated mortality of bears and other wildlife, in this and other regions.

Methods

Study Area

The study was conducted in Banff and Yoho National Parks (Fig. 3.1; 6641 km^2 and 1313 km^2, respectively), which are part of the Canadian Rocky Mountain Parks World Heritage Site. Almost four million people visit these parks each year (Parks Canada 2017b), making them one of the most developed landscapes in the world where grizzly bears and humans continue to coexist (Chruszcz et al. 2003). Banff and Yoho are bisected by the four-lane Trans-Canada

Highway (hereafter highway), which has an estimated traffic volume of over eight million vehicles a year, and the Canadian Pacific Railway (hereafter, railway), which carries 25-35 trains each day (Wells et al. 1999). The railway parallels the highway at an average distance of 416 m (± 1 SD of 325 m) (Dorsey 2011), and passes through both montane and subalpine ecoregions, with elevations ranging from 1100 to 1600 m. The majority of Banff and Yoho Parks occur above treeline in the alpine ecoregion, with some mountain ranges reaching 3500 m. The Parks experience long, cold, snowy winters and short, mild summers (Holland and Coen 1983). The cool climate, along with the rugged and mountainous terrain limits high-quality habitat mostly to lower elevations where the railway and major roads also occur. 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 1987*b*, 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*). Ungulate species like deer (*Odocoileus hemionus; Odocoileus virginianus*), elk (*Cervus canadensis*), and moose (*Alces alces*) inhabit the Parks as well as carnivores such as cougars (*Puma concolor*), wolves (*Canis lupus*), coyotes (*Canis latrans*), and black bears (*Ursus americanus*). Fencing and wildlife crossing structures along the highway have reduced wildlife-vehicle collisions, but no such fencing or structures currently exist for the railroad, and rail-associated mortality remains high for some species, including the grizzly bear (Clevenger et al. 2001, Gilhooly 2016). The study area includes three townsites

(Banff, Lake Louise, and Field), a network of roads and hiking trails, three ski resorts, several campgrounds, and numerous high-volume, day-use areas.

Grizzly Bear Capture and Collaring

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). GPS collars were fitted to 34 individual bears (Vectronic Iridium GPS Plus, Berlin, Germany; Followit Iridium GPS, Lindesberg, Sweden), which recorded GPS locations every two hours from roughly late spring (when collaring took place) to den entry in the late fall. In total, we obtained a twelve-year dataset with 26 bears collared for this project from 2012-2016 and 8 opportunistically collared bears (2000-2004, 2009, 2010). We ran our analyses using the 27 of 34 bears that had at least one GPS location on the railway.

GIS Layers and Modelling

We used ArcMap (version 10.3; ESRI, Redlands, CA) and Geospatial Modelling Environment software (version 0.7.4.0, www.spatialecology.com, accessed 1 Dec 2017) to quantify habitat quality, human-use, and topographical data that we created or received from Parks Canada and hypothesized would influence railway use and movement by grizzly bears in the study area (Table 3.1). We defined a railway-associated GPS location as one that fell within 30 m on either side of the railway corridor. We dummy coded habitat variables which consisted of a land cover layer with 7 classifications: upland tree, wetland tree, upland herb, wetland herb, shrub, water and barren land (Table 3.1; McDermid 2005). We used a digital elevation model and from this calculated a compound topographic index (CTI: ln(upstream contributing area in

m^2/tan(slope)), a proxy for terrain wetness and habitat quality that has a demonstrated correlation with the presence of bear foods (Nielsen et al. 2004*c*). We obtained a layer depicting the percentage of forest canopy cover in the study area and, along with the aforementioned habitat variables, calculated values at four scales: within 30 m of the railway, as well as the average proportion within 100, 200, and 500 m radii. We calculated the Euclidean distance from each rail-associated GPS location to the nearest forest edge, stream, and water body, as well as to seven 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. 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, personal observation). We included gravel pits, former landfills, and ski hills because bears are generally attracted to these sites for their photophilic and disturbance-tolerant vegetation, such as alfalfa (*Medicago* spp.), clover (*Trifolium* spp.), and dandelion (Nielsen et al. 2004*c*, Roever et al. 2008*a*). We transformed each distance measurement (measured in meters) 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 ($-0.002*\text{distance}_{metres}$) resulted in values of 0 at the feature and approached 1 at distances greater than 1000 m (after Nielsen et al. 2009). Lastly, for topography, we calculated the decay distance to wildlife crossing structures and measured terrain ruggedness at two scales (90 m and 300 m) using circular moving windows (ArcMap Vector Ruggedness tool).

Temporal variables consisted of season and time of day. We defined seasons based on regional grizzly bear foraging habits (after Nielsen et al. 2004*a*); spring correlated with the hypophagic period (den emergence - June 14), summer with early hyperphagia (June 15 - August 7), and fall with late hyperphagia (August 8 - den entry). We divided time of day into day, night, and crepuscular periods using the National Research Council of Canada's sunrise/sunset calendar for each date. 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 was calculated as the Euclidean distance between sequential GPS locations and then log-transformed to normalize the distribution.

We used these variables to develop railway-based resource selection functions (Boyce et al. 2002, Manly et al. 2002). We first analysed 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 either 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 four 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 (Fig. 3.2). Within these sequences, the middle position described, over a 6-hr period, locations where bears entered the railway, crossed it, continued along it, or exited the railway. We included only points that were obtained within 5 min of the targeted 2-hr fix rate. We used logistic regression to contrast all six pairwise comparisons of these four 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 vs. 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 Jan 15, 2018). All non-categorical variables were standardized to have a mean of 0 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 Akaike Information Criteria score (AIC) (Burnham and Anderson 2002). Similarly, we assessed linear and quadratic terms and retained habitat variables at the appropriate scale via the lowest univariate AIC score. For each of the 12 habitat and 7 human-use covariates, we ran all model combinations and selected the top model 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 Jan 15, 2018). We then tested combinations of the remaining habitat, human-use, and topographical variables, plus their two-way interactions, using the Akaike Information Criteria for small sample sizes (AICc) (Burnham and Anderson 2002). For the step discrimination functions, we included two-way interactions with temporal variables (season and time of day) and step length. 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 Jan 15, 2018).

To test for correlations between locations with bear mortality and those with concentrated railway use, we conducted decile analyses (similar to Boyce et al. 2002). To do this, we first calculated kernel density estimates for overall railway use and each of the four movement types (enter, cross, continue, and 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. Finally, we recorded for each of 11 bear mortality locations the kernel density estimate associated with railway use and the four movement types and counted the number of mortalities within each decile bin. Within the five use and movement type variables, we obtained a correlation coefficient between the proportion of mortalities in each decile bin and the decile value 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

In total, 34 grizzly bears were fitted with GPS collars set at an approximately 2-hr fix rate over a 12-year span; 15 males and 19 females. Of the 34 collared bears, 27 had at least one railway-associated GPS location (within 30 m of the railway); 13 males and 14 females (Table S1), resulting in 1515 unique railway GPS locations (mean: 56.2 +/- 91.6, range: 1 – 401). Seasonally, 47% of the total railway GPS locations occurred in the spring, 20% in summer, and 33% in fall (Table 3.S2). As diel patterns, 70% occurred during the day, 23% at night, and 7% at crepuscular time periods (Table 3.S2). Three bears used the railway more extensively than others; a large and dominant 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 three times more often than they continued along it, which were, in turn, 24% less prevalent than enter and exit movements. There were 675 railway crossings by 27 grizzly bears (mean per individual = 25 ± 28.1, range: 1 – 117); 304 enter decisions by 24 bears (mean = 12.6 ± 21.3, range: 1 - 84); 231

continue decisions by 14 bears (mean =16.5 ± 35.7, range: 1 - 133); and, 305 exit decisions by 24 bears (mean = 12.7 ± 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 habitat and topographical characteristics. Bears selected the railway at intermediate distances from towns, highways, and trails (as revealed by a better fit of the quadratic term) and in areas that were closer to railroad sidings (Table 3.2**)**. Among the habitat-related variables, bear use of the railway was negatively associated with terrain wetness at a landscape scale (500 m). Grizzly bears selected areas along the railway that had higher shrub cover and that were located closer to water bodies (Table 3.2). Topography was also an important determinant, with bears more likely to use the railway at intermediate distances from wildlife crossings 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 landscape-scale terrain wetness was higher (Table 3.2).

We used the same three suites of explanatory variables in our step discrimination functions to investigate all pairwise comparisons of railway-associated movements, which we defined via the sequence of three steps as entering, crossing, continuing along, and exiting the railway corridor (Table 3.1, Fig. 3.2**)**. The most predictive model distinguishing movement pairs occurred, as we predicted, for movements that continued along vs. crossed the railway (Table 3.3a, AUROC = 0.88). The tendency for bears to continue along the railway was best predicted by topography, via a positive association with terrain ruggedness (300m), which was a covariate in all three models that contrasted continue with the other movement types (Tables 3.3a-c). A better fit of the quadratic term 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 the fall (Table 3.3a). Bears also took smaller steps with continued use of the railway compared to all other movement types (Tables 3.3a-c, Table 3.S3). Step lengths increased in rugged areas and with distance from railroad sidings and human-use trails (Tables 3.3a-c). Compared to crossings, continued use of the railway tended to occur at night ($\beta = 1.04$, 95% CI 0.61 to 1.47).

Railway crossings were defined by four main effects that were associated with habitat, human-use, and topographical variables. Crossing locations had a negative association with herbaceous cover (200 m scale) and occurred further from railroad sidings compared to locations where bears entered or exited the railway (Table 3.3d,e). Crossings were characterized by less rugged terrain at a local 90 m scale (vs. entries) and occurred further from wildlife crossings (vs. exits) (Table 3.3d,e). Our analysis of temporal variables revealed that bears were more likely to cross the railway in the summer, relative to spring (vs. entries: $\beta = 0.62$, 95% CI 0.21 to 1.03; vs. exits: $\beta = 0.59$, 95% CI 0.18 to 0.99) and fall (vs. entries: $\beta = 0.83$, 95% CI 0.35 to 1.32; vs. exits: $\beta = 0.78$, 95% CI 0.30 to 1.26). Bears also travelled more quickly (i.e. longer steps on a log scale) when they crossed the railway (vs. entries: $\beta = 0.14$, 95% CI 0.003 to 0.29; vs. exits: $\beta = 0.32$, 95% CI 0.16 to 0.48) (Table 3.S3).

Enter and exit locations were spatially similar with no habitat, human-use, or topographical variable performing better than the null model, resulting in our least predictive analysis. The only variable that accurately distinguished the two movement types was time of day. We found that bears were more likely to enter the railway during the day and at crepuscular periods and to exit it at night (Table 3.3f).

Based on our decile analysis, there were no strong linear associations between locations of bear mortality (n = 11) and areas of concentrated railway use (Fig. 3.1; 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 3.S4). 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 to 0.23). In a second analysis, we added reported strike sites (n = 6 for a total of 17 locations that included the 11 confirmed mortalities) to determine how their inclusion affected the strength of correlations. Results were similar, with weak associations between collision locations and areas of concentrated railway use (Fig. 3.1; 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 3.S4). However, there was a significant negative relationship between locations of more frequent collisions and continued use of the railway (r = -0.63, p = 0.04). Although neither analysis produced a significant correlation, crossing and overall use sites (which were composed mostly of crossing sites) were unusual in generating a positive correlation coefficient with the sites of greater bear mortality or strikes, whereas the other three 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 (e.g., Kušta et al. 2014, Dorsey et al. 2017, Roy and Sukumar 2017). We sought to determine the spatiotemporal factors associated with habitat, 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 more abundant. Railway use also increased with adjacent rugged topography and poor landscape-scale habitat quality. When we contrasted the rail-associated movements defined by three successive locations as enter, cross, continue, and exit, we found the greatest step discrimination between continue and cross movements. Railway segments containing higher proportions of 17 previous bear-train collisions (both confirmed and unconfirmed) 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 one or more of foraging opportunities, travel efficiency or avoidance of people. Forage-based opportunities were evident in the variables contributing to both overall use, with greater shrub cover, and enter locations, with greater herbaceous cover within 200 m. These variables predicted the presence of several forage plants that are important to bears, including horsetail (*Equisetum* spp.), dandelions (*Taraxacum officinale*) and berry-producing shrubs, which are enhanced along both roads (Nielsen et al. 2004*c*, Roever et al. 2008*a*) and railways (Pollock et al. 2017). The availability of forage along transportation corridors generally promotes higher frequencies of both road crossings (e.g. Chruszcz et al. 2003, Gagnon et al. 2007, Meisingset et al. 2013) and wildlife-vehicle collisions (e.g. Ramp et al. 2005, Ng et al. 2008, Grosman et al. 2009). Interestingly, 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. We were surprised that grizzly bears selected areas where landscape-scale wetness was low because wetness is often correlated with growth in herbaceous plants that are important to bears (Turney and Roberts 2004, Chetkiewicz and Boyce 2009). In addition to forage for bears, this vegetation is attractive to ungulates that also attract bears (Nielsen et al. 2004c, 2017; Munro et al. 2006). The relative lack of selection for wetness may have revealed areas of greater relative attraction for rail-associated attractants, such as horsetail (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 minimizes 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 products of human activity that could attract bears, including disturbance-tolerant plants (Hansen and Clevenger 2005, Rutkovska et al. 2013, Wrzesien et al. 2016), infrastructure and opportunity to accumulate refuse (Raman 2011, Joshi 2013), and petrochemical scents (Derocher and Stirling 1991), while 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. 2001) and use of high human-use areas increases risk of bear mortality (Nielsen et al. 2006, Chruszcz et al. 2003, Lamb et al. 2016). Consistent with this trade-off between risk and reward, bears were more likely to use the railway in closer proximity to people when surrounding habitat quality was low (as measured by low terrain wetness), which may have signalled a greater need for anthropogenic resources (Frid and Dill 2002, Rode et al. 2006). Even the attraction by bears to shrub habitat (above) 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; both overall railway use and locations where bears entered the railway were positively and linearly associated with local (90 m) ruggedness, while bears were more likely to continue along the railway through landscape-scale rugged terrain (300 m). Topography is among the landscape characteristics that can reduce functional connectivity for animals (Belisle 2005) and travel costs are typically higher in structurally-complex landscapes (Parker et al. 1984, Dailey and Hobbs 1989, Shepard et al. 2013) particularly for wide-ranging animals (e.g. Crete and Lariviere 2003, Dickie et al. 2016). Our analyses of step lengths reinforced this interpretation of travel efficiency. Bears demonstrated shorter step lengths on the railway during continue movements and in close proximity to railroad sidings, consistent with foraging behavior both generally (Turchin 1998) and in other studies of grizzly bears (Roever et al. 2010, Graham and Stenhouse 2014, Kite et al. 2016). They demonstrated longer steps where they crossed the railway and in areas with rugged topography, consistent with travel. 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 both 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. 2008*b*; 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 1987*a*, Mace et al. 1999). Spring selection of the railway may therefore reflect early herbaceous feeding opportunities, particularly in forested or mountainous regions, where comparatively heightened temperatures along the railway advances snowmelt and vegetative growth (Munro 2000, Roever et al. 2008*a*, 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 (Robbins et al. 2007, Lopez-Alfaro et al. 2015, 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. 2010*a*, 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 further 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 locations where bears spent more time on the railway (i.e. continue movements), these were significantly negatively correlated with the locations that included both confirmed mortalities and unconfirmed strikes. This pattern might have occurred because continue locations were, in turn, 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 to 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 (Burley 2015, Dorsey et al. 2017) may increase strike risk. 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 (Pengelly and Hamer, unpublished report), use of deterrents (e.g., 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, both in the number of mortality events (11) and the number of bears (3) that frequently used the rail, causing high interpretive reliance on a few individuals. A second limitation stems from the two-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 one-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 over a 12-year period 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 (e.g. Mattson et al. 1992, Baruch-Mordo et al. 2014, Obbard et al. 2014) and our GIS-derived habitat measures would have underestimated fluctuations of plant productivity (Boyce et al. 2002, Nielsen et al. 2010).

Despite these limitations, our study demonstrated strong 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, which reasonably prioritizes mitigation to spring and fall months when trains are most likely to encounter bears. Our results suggest 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 two known hotspots of mortality or areas with high railway use by bears. The influence of landscape-scale habitat variables on railway use and the larger scale of topographical influence emphasizes the large home ranges and associated travel routes of bears. Mitigation at these larger scales logically includes habitat enhancement, such as by forest thinning or prescribed burns, to increase forage productivity and encourage movements away from the railway (e.g. Nielsen et al. 2004*c*, 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 warnings (e.g., via 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; Pengelly and Hamer, unpublished data). We encourage others to analyze and interpret wildlife use and movement in relation to railways as an important part of increasing understanding, and ultimately, improving mitigation of rail-associated wildlife mortality.

Management Implications

Managers might reduce the risk of train strikes on wildlife by reducing attractants on or near the rail, such as spilled grain, rail-killed ungulates, or palatable forage, and target these efforts in areas where (e.g., rugged topography) and times when (e.g., spring and fall) increased railway use may also increase strike risk. Where topography encourages animals to cross or use the railway, managers may lessen collision vulnerability by reducing train speed, providing warnings of approaching trains, and reducing access via a combination of partial exclusion and alternative travel routes.

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The authors of this manuscript declare no conflict of interest.

Tables

Table 3.1 Variables predicted to influence habitat selection and movement by grizzly bears (n=27) on a railway in Banff and Yoho National Parks, Canada.

Category	Variable	Variable Range	Variable Description
Habitat	Canopy Cover[1]	0.00 - 90.00	Proportion of forest cover[2]
	Terrain Wetness[1]	3.55 - 26.03	Compound Topographic Index (CTI); increases with wetter sites[2]
	Land cover	0/1 and 0 - 100	Presence or proportion of land cover in 7 categories[2,3]
	Distance to Edge[1]	0.06 - 0.80	Euclidean distance to nearest forest edge
	Distance to Stream[1]	0.00 - 0.81	Euclidean distance to nearest stream
	Distance to Water bodies[1]	0.00 - 1.00	Euclidean distance to nearest water body
Human-use	Distance to Towns[1]	0.25 - 1.00	Euclidean distance to nearest town
	Distance to Roads[1]	0.00 - 1.00	Euclidean distance to nearest road
	Distance to Highways[1]	0.00 - 0.96	Euclidean distance to nearest highway
	Distance to Railroad Sidings[1]	0.00 - 1.00	Euclidean distance to nearest railroad siding
	Distance to Trails[1]	0.00 - 1.00	Euclidean distance to nearest human-use trail
	Distance to Landfills[1]	0.12 - 1.00	Euclidean distance to nearest landfill
	Distance to Gravel Pits[1]	0.25 - 1.00	Euclidean distance to nearest gravel pit
Topography	Distance to Wildlife Crossing Structures[1]	0.31 - 1.00	Euclidean distance to nearest wildlife crossing
	Terrain Ruggedness[1]	0.00 - 0.18	Terrain Ruggedness Index (TRI)[4]
	Step length	2 - 8289	Distance to successive GPS location (m/2-hr period); log transformed
Movement	Season		Spring (den emergence-Jun14); Summer (Jun15-Aug7); Fall (Aug8-den entry)

Temporal	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)

[1] indicates variables where a quadratic term was tested
[2] indicates variables where multiple scales were tested (100 m, 200 m, 500 m)
[3] 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
[4] indicates where multiple scales were tested (90 m and 300 m)

Table 3.2 Top model results for the resource selection function (RSF) describing characteristics of locations where grizzly bears selected for the railway (versus availability) in Banff and Yoho National Parks, Canada. Parameter estimates, standard error, 95% confidence intervals (CI), and predictive ability of the fitted model (AUROC) are provided. Models were selected using the Akaike Information Criterion for small samples sizes (AIC_c).

RSF

Parameter	Estimate	S.E	95% CI
Intercept	-3.70	0.16	-4.01 to -3.38
Terrain Wetness 500 m	-0.25	0.04	-0.33 to -0.16
Shrub	0.28	0.07	0.14 to 0.41
Distance to Water Bodies	-0.10	0.03	-0.16 to -0.04
Distance to Railroad Sidings	-0.14	0.03	-0.20 to -0.09
Distance to Trails	-0.17	0.04	-0.25 to -0.09
Distance to Trails ^ 2	-0.11	0.04	-0.19 to -0.04
Distance to Towns	-0.17	0.08	-0.32 to -0.02
Distance to Towns ^ 2	-0.45	0.09	-0.64 to -0.26
Distance to Highways	-0.01	0.04	-0.09 to 0.06
Distance to Highways ^ 2	-0.16	0.04	-0.24 to -0.08
Distance to Wildlife Crossings	0.18	0.06	0.06 to 0.31
Distance to Wildlife Crossings ^ 2	0.23	0.05	0.13 to 0.33
Terrain Ruggedness 90 m	0.17	0.03	0.12 to 0.22
Terrain Wetness 500 m × Distance to Towns	0.64	0.10	0.44 to 0.84

AUROC = 0.75

Table 3.3 Top model results for the step discrimination function (SDF) describing characteristics of railway locations where grizzly bears (a) continued vs. crossed, (b) continued vs. entered, (c) continued vs. exited, (d) crossed vs. entered, (e) crossed vs. exited, and (f) entered vs. exited the railway corridor in Banff and Yoho National Parks, Canada. Standardized parameter estimates, standard error, 95% confidence intervals (CI), and predictive ability of the fitted model (AUROC) are provided. Models were selected using the Akaike Information Criterion for small samples sizes (AIC_c).

SDF

(a)

CONTINUE vs CROSS

Parameter	Estimate	S.E	95% CI
Intercept	-4.35	0.62	-5.57 to -3.14
Distance to Railroad Sidings	-0.73	0.44	-1.59 to 0.12
Terrain Ruggedness 300 m	0.43	0.15	0.13 to 0.73
Terrain Ruggedness 300 m ^ 2	0.47	0.14	0.19 to 0.75
Season: Spring (vs. summer)	1.85	0.53	0.80 to 2.89
Season: Fall (vs. summer)	2.41	0.57	1.30 to 3.53
Step Length	-0.52	0.12	-0.74 to -0.29
Distance to Railroad Sidings × Season: Spring (vs. summer)	1.02	0.46	0.11 to 1.93
Distance to Railroad Sidings × Season: Fall (vs. summer)	0.80	0.48	-0.13 to 1.73
Distance to Railroad Sidings × Step Length	0.32	0.12	0.08 to 0.56

AUROC = 0.88

(b)

CONTINUE vs ENTER

Parameter	Estimate	S.E	95% CI
Intercept	-1.31	0.33	-1.96 to -0.66
Distance to Trails	0.33	0.14	0.05 to 0.61
Terrain Ruggedness within 300 m	0.42	0.13	0.16 to 0.68
Terrain Ruggedness within 300 m ^ 2	0.30	0.12	0.06 to 0.53
Step Length	-0.55	0.12	-0.78 to -0.32
Distance to Trails × Step Length	0.26	0.13	0.01 to 0.50

AUROC = 0.77

(c)

CONTINUE vs EXIT

Parameter	Estimate	S.E	95% CI
Intercept	-1.09	0.31	-1.70 to -0.48
Terrain Ruggedness within 300 m	0.46	0.14	0.18 to 0.73
Terrain Ruggedness within 300 m ^ 2	0.43	0.12	0.20 to 0.66
Step Length	-0.31	0.13	-0.56 to -0.06
Terrain Ruggedness within 300 m × Step Length	0.32	0.13	0.07 to 0.57

AUROC = 0.77

(d)

CROSS vs. ENTER

Parameter	Estimate	S.E	95% CI
Intercept	-0.97	0.14	-1.25 to -0.69
Herbaceous Cover within 200 m	-0.21	0.08	-0.36 to -0.05
Distance to Railroad Sidings	0.21	0.08	0.06 to 0.36
Distance to Landfills	0.14	0.07	0.007 to 0.28
Terrain Ruggedness within 90 m	-0.22	0.08	-0.38 to -0.06

AUROC = 0.68

(e)

CROSS vs. EXIT

Parameter	Estimate	S.E	95% CI
Intercept	-1.10	0.15	-1.38 to -0.81
Herbaceous Cover 200 m	-0.19	0.08	-3.38 to -0.34
Upland Tree 200 m	-0.16	0.08	-5.10 to -0.31
Distance to Railroad Sidings	0.22	0.08	0.06 to 3.71
Distance to Wildlife Crossing Structures	0.17	0.10	0.02 to 3.69
Step Length	0.25	0.09	0.09 to 4.21
Distance to Wildlife Crossing Structures × Step Length	0.24	0.10	0.04 to 4.34

AUROC = 0.69

(f)

ENTER vs EXIT

Parameter	Estimate	S.E	95% CI
Intercept	-0.60	0.18	-0.96 to -0.25
Day (vs. night)	0.73	0.21	0.33 to 1.14
Crepuscular (vs. night)	1.74	0.42	0.91 to 2.57

AUROC = 0.60

Table 3.S1 Grizzly bear ID, sex, and number of monitoring days spent on the rail out of the total number of railway days in each of three seasons by 27 grizzly bears on the Canadian Pacific Railway in Banff and Yoho National Parks, Canada. Collared bears that did not use the railway were not included.

Bear ID	Sex	Rail Days: Spring	Rail Days: Summer	Rail Days: Fall	Rail Days: All	Percent of Total Rail Days
30	Female	5	5	0	10	1.46
45	Male	0	2	0	2	0.29
56	Female	24	0	7	31	4.54
59	Female	18	6	0	24	3.51
64	Female	8	9	0	17	2.49
68	Male	1	0	0	1	0.15
72	Female	9	26	0	35	5.12
122	Male	22	2	38	62	9.08
125	Male	3	1	0	4	0.59
126	Male	74	22	9	105	15.37
128	Male	17	16	61	94	13.76
130	Female	9	18	2	29	4.25
132	Male	2	3	0	5	0.73
133	Female	2	3	1	6	0.88
134	Male	1	14	0	15	2.20
136	Male	12	7	4	23	3.37
138	Female	2	0	0	2	0.29
141	Male	43	3	0	46	6.73
142	Female	17	11	0	28	4.10
143	Female	6	8	0	14	2.05
144	Male	8	2	2	12	1.76
148	Female	10	24	11	45	6.59
149	Male	10	0	0	10	1.46
156	Female	6	3	0	9	1.32
158	Male	13	3	0	16	2.34
160	Female	10	2	4	16	2.34
161	Female	10	12	0	22	3.22
Total		342	202	139	683	100.00

Table 3.S2 Temporal distribution (season and time of day) of railway-associated GPS points (within 30 m of the railway) from collared grizzly bears in Banff and Yoho National Parks, Canada.

	Railway Pts	Total Railway Pts	Percentage
Spring	712	1515	47.00
Summer	303	1515	20.00
Fall	500	1515	33.00
Day	1062	1515	70.10
Night	348	1515	22.97
Crepuscular	105	1515	6.93

Table 3.S3 Step lengths (km/2-hr GPS fix rate) by grizzly bears along the Canadian Pacific Railway in Banff and Yoho National Parks, Canada. Mean step lengths +/- SD for each rail-associated step type (enter, cross, continue along, exit) are given by season and time of day.

Step Type	Spring	Summer	Fall	Day	Night	Crepuscular	Mean +/- SD
Enter	0.97 +/- 1.22	1.38 +/- 1.26	1.31 +/- 1.29	1.24 +/- 1.30	0.82 +/- 1.10	0.87 +/- 1.05	1.14 +/- 1.26
Cross	1.15 +/- 1.43	1.37 +/- 1.29	1.11 +/- 0.92	1.25 +/- 1.26	1.03 +/- 1.42	1.16 +/- 1.26	1.21 +/- 1.29
Continue	0.76 +/- 1.27	1.66 +/- 1.77	0.74 +/- 0.96	1.03 +/ - 1.19	0.47 +/- 0.96	0.48 +/- 0.63	0.77 +/- 1.11
Exit	0.83 +/- 1.03	1.00 +/- 1.11	0.96 +/- 1.04	1.05 +/- 1.14	0.59 +/- 0.74	0.52 +/- 0.49	0.90 +/- 1.05

Table 3.S4 Results from decile analyses that investigate correlations between locations of bear mortality (n = 11) and collisions (n = 17; includes both confirmed mortalities and reported strikes) and each of five kinds of movement: overall use and sequences of three steps (at 2-hr fix rates) where bears enter, cross, continue along, or exit the Canadian Pacific Railway in Banff and Yoho National Parks, Canada.

			Use				
Decile	Available Pts (100 m)	Mortality (n=11)	Collision (n = 17)	Prop. Mortality	Prop. Collision	**Corr. Mortality**	**Corr. Collision**
1	130	1	2	0.008	0.015	**r = 0.107**	**r = 0.039**
2	130	0	0	0.000	0.000	**p = 0.77**	**p = 0.89**
3	130	0	0	0.000	0.000		
4	130	2	4	0.015	0.031		
5	130	1	2	0.008	0.015		
6	130	4	4	0.031	0.031		
7	130	1	1	0.008	0.008		
8	130	0	1	0.000	0.008		
9	130	1	2	0.008	0.015		
10	130	1	1	0.008	0.008		
			Enter				
Decile	Available Pts (100 m)	Mortalities (n=11)	Collisions (n = 17)	Prop. Mortality	Prop. Collision	**Corr. Mortality**	**Corr. Collision**
1	130	1	2	0.008	0.015	**r = -0.383**	**r = -0.542**
2	130	2	4	0.015	0.031	**p = 0.27**	**p = 0.11**
3	130	3	3	0.023	0.023		
4	130	1	1	0.008	0.008		
5	130	0	1	0.000	0.008		
6	130	1	1	0.008	0.008		
7	130	0	1	0.000	0.008		
8	130	3	3	0.023	0.023		
9	130	0	0	0.000	0.000		
10	130	0	1	0.000	0.008		
			Cross				
Decile	Available Pts (100 m)	Mortality (n=11)	Collision (n = 17)	Prop. Mortality	Prop. Collision	**Corr. Mortality**	**Corr. Collision**
1	130	1	1	0.008	0.008	**r = 0.397**	**r = 0.302**
2	130	0	2	0.000	0.015	**p = 0.26**	**p = 0.40**
3	130	0	0	0.000	0.000		

4	130	1	1	0.008	0.008		
5	130	0	0	0.000	0.000		
6	130	0	1	0.000	0.008		
7	130	5	7	0.038	0.054		
8	130	1	1	0.008	0.008		
9	130	1	2	0.008	0.015		
10	130	2	2	0.015	0.015		

Continue

Decile	Available Pts (100 m)	Mortality (n=11)	Collision (n = 17)	Prop. Mortality	Prop. Collision	**Corr. Mortality**	**Corr. Collision**
1	130	2	4	0.015	0.031	**r = -0.362**	**r = -0.634**
2	130	0	1	0.000	0.008	**p = 0.30**	**p = 0.04**
3	130	0	1	0.000	0.008		
4	130	4	4	0.031	0.031		
5	130	2	2	0.015	0.015		
6	130	2	2	0.015	0.015		
7	130	1	2	0.008	0.015		
8	130	0	1	0.000	0.008		
9	130	0	0	0.000	0.000		
10	130	0	0	0.000	0.000		

Exit

Decile	Available Pts (100 m)	Mortality (n=11)	Collision (n = 17)	Prop. Mortality	Prop. Collision	**Corr. Mortality**	**Corr. Collision**
1	130	1	2	0.008	0.015	**r = -0.322**	**r = -0.405**
2	130	1	3	0.008	0.023	**p = 0.36**	**p = 0.24**
3	130	1	1	0.008	0.008		
4	130	4	5	0.031	0.038		
5	130	0	0	0.000	0.000		
6	130	1	1	0.008	0.008		
7	130	2	2	0.015	0.015		
8	130	1	2	0.008	0.015		
9	130	0	0	0.000	0.000		
10	130	0	1	0.000	0.008		

Figures

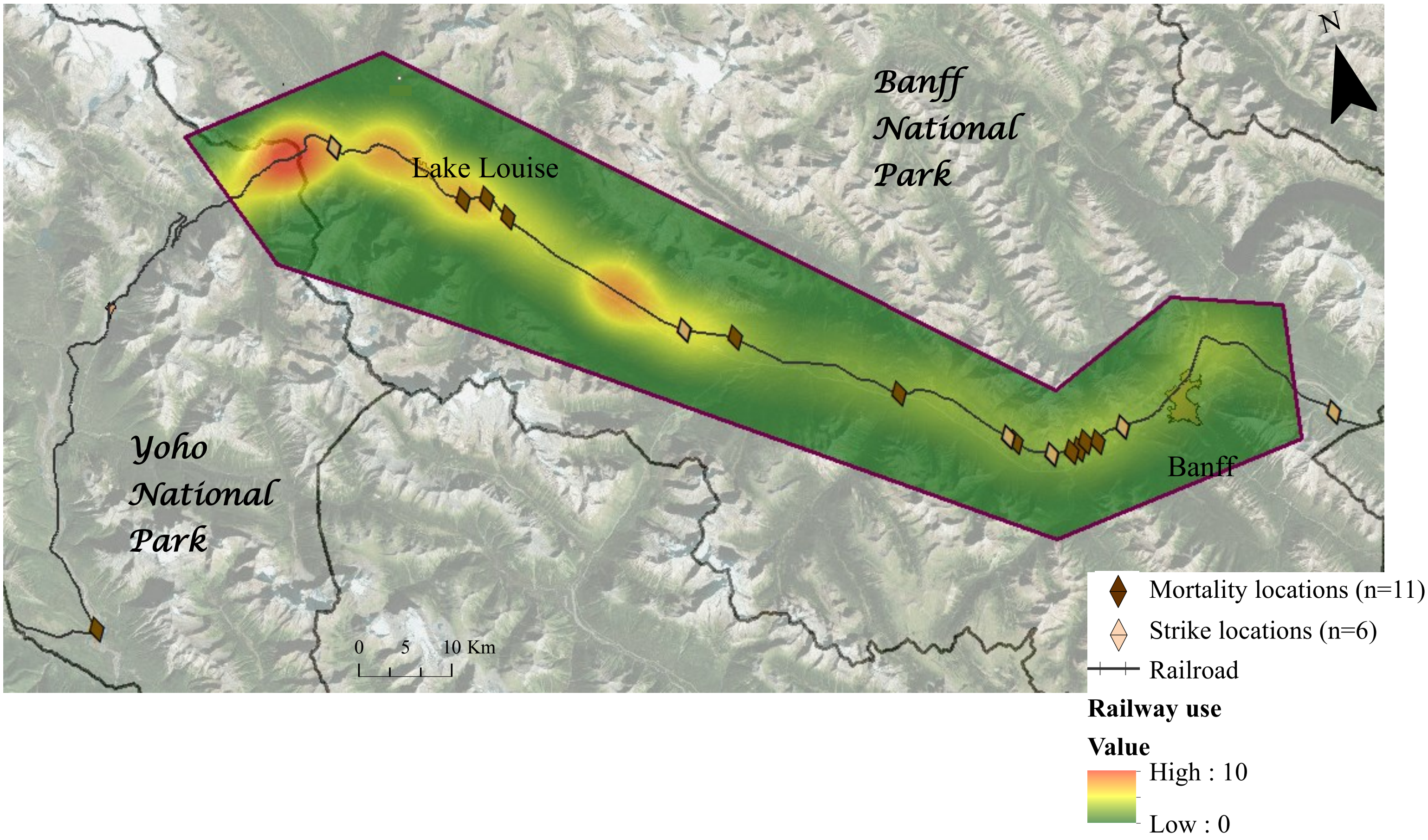

Figure 3.1 The study area where we investigated railway use and associated movement by grizzly bears in Banff and Yoho National parks in Western Canada. A subsection of the Canadian Pacific Railway through Banff National park is provided in colour to illustrate the kernel density values of railway use by GPS-collared grizzly bears (red areas = highest use; see inset legend). Data was collected intermittently from 2000-2016. 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. The town sites of Lake Louise and Banff are labelled on the map.

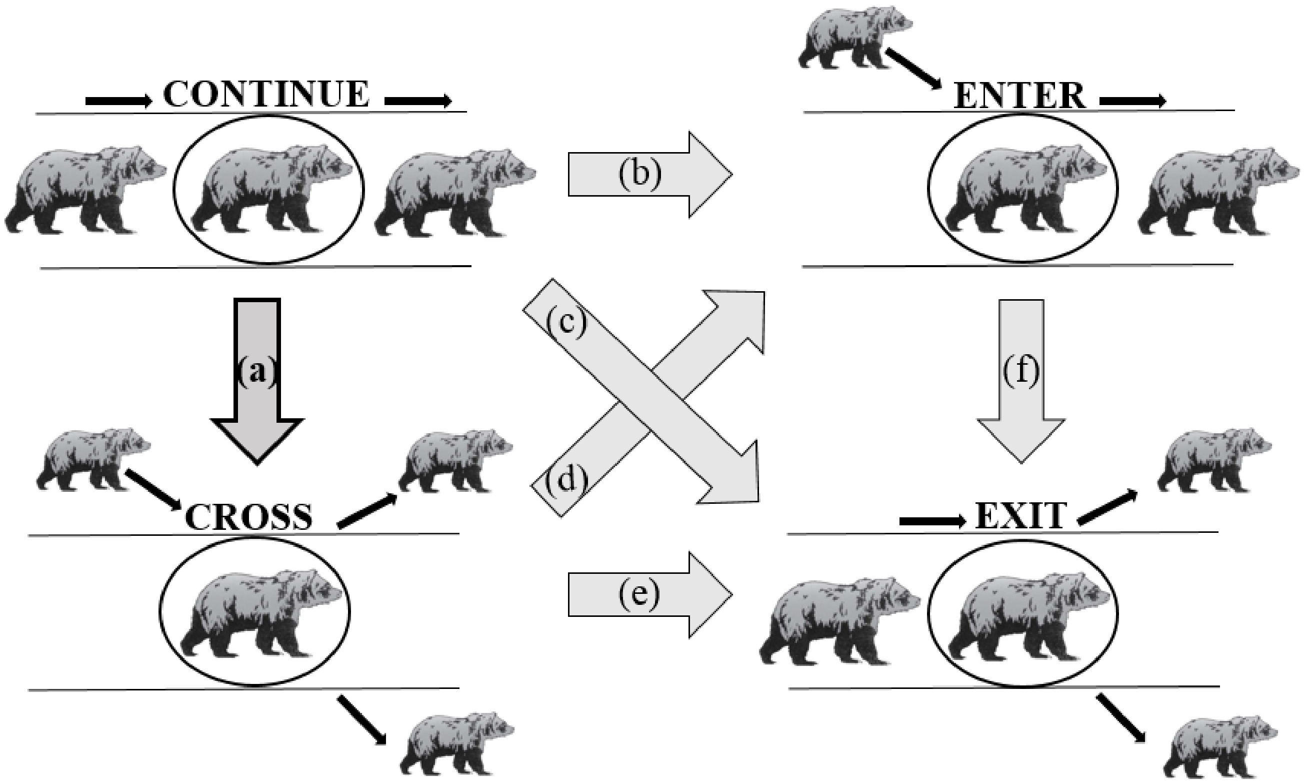

Figure 3.2 Schematic for step discrimination functions, in which we contrasted locations along the Canadian Pacific Railway in Banff and Yoho National Parks, Canada, where grizzly bears exhibited three successive GPS locations. For each contrast, the second point (depicted with circles) denotes four types of rail use: continue, cross, enter, and exit. We were primarily interested in the difference between (a) continued vs. crossed movements, but also analyzed each of the remaining pairwise contrasts of (b) continued vs. entered, (c) continued vs. exited, (d) crossed vs. entered, (e) crossed vs. exited, and (f) entered vs. exited.

Figure 3.S1 Two male grizzly bears (M126 and M128; Table S1) on the Canadian Pacific Railway in Banff National Park, Canada.

Chapter 4: Railway-Associated Attractants as Potential Toxicants for Wildlife

Sonya Z. Pollock and Colleen C. St. Clair

Abstract

The adverse effects of railways on wildlife are little studied in comparison to roads and have mainly addressed mortality from train collisions. Wildlife-train collisions are of particular concern for sensitive populations in protected areas, such as grizzly bears (*Ursus arctos*) in Canada's Rocky Mountain Parks where train collisions are the leading cause of recorded mortality. Food attractants along the rail, which include spilled grain and invasive plants, appear to increase strike risk for bears and other wildlife, but they may also affect wildlife as sources of rail-associated pollutants. We estimated such exposure by comparing concentrations of heavy metals and polycyclic aromatic hydrocarbons (PAHs) in rail-associated samples of grain and dandelions (*Taraxacum officinale*) to reference sources, additionally measuring mycotoxins in grain and heavy metals in bear hair. We predicted that metal concentrations in grizzly bear hair would be correlated with high rail use by bears (measured with GPS collars), or other anthropogenic features. Relative to reference samples, rail-associated vegetation contained 0.3 to 3.1 times the concentration of heavy metals and 1.5 to 34.6 times the concentration of PAHs, train-spilled grain contained 4.0 to 759.4 times the concentration of heavy metals and 80.1 to > 500,000 times the concentration of PAHs. However, grain exhibited low levels of mold-caused mycotoxins. Concentrations for several metals and PAHs exceeded regulatory standards set for purposes of maximum tolerable thresholds or soil remediation guidelines, particularly for grain. The hair of male bears had higher mean metal concentrations than females, but higher concentrations of metals in hair did not correlate with greater frequency of rail use. However, metal concentrations near the hair root, were correlated with bear use of ski hills in the fall. Our results suggest that wildlife exposure to rail-associated toxicants could be reduced by removal of spilled grain and regular maintenance of railway lubricating stations, actions that may be particularly important in protected areas. Our work also encourages investigation of metal contamination on ski hills, which may relate to vegetation restoration, snow-making, or other anthropogenic activity.

Keywords: Dandelion, Grizzly bear, Habitat selection, Hair analysis, Metals, Polycyclic aromatic hydrocarbons, Railway, *Taraxacum officinal*e, Train-spilled grain, *Ursus arctos*, Vegetation

Introduction

Railways exert negative effects on wildlife comparable to those of roads, but they have not been similarly studied (Benito-Lopez et al. 2010, Dorsey et al. 2015, Popp and Boyle 2017, Santos et al. 2017). More attention is warranted partly because railway use and infrastructure continues to grow (Fuller et al. 2001, Steenhof et al. 2006, Hanaoka and Regmi 2011). To date, most of the attention to the negative effects of railways has addressed mortality from collisions with trains, which occur at high frequencies in some locations (Wells et al. 1999, Kusta 2011) and can exceed rates of mortality on nearby roads (Waller and Servheen 2005). This source of mortality is especially problematic in protected areas and for species that are threatened or endangered, such as elephants in India (*Elephus maximus*, Joshi and Singh 2007, Palei et al. 2013, Dasgupta and Ghosh 2015, Roy and Sukumar 2017) and grizzly bears in North America (*Ursus arctos*, Waller and Serveen, 2005, Bertch and Gibeau 2010). Few studies have addressed other detrimental effects of railways on wildlife, including environmental pollutants and toxicants that could jeopardize the health of adjacent ecosystems and wildlife (Levengood et al. 2015, Wierzbicka et al. 2015).

This lack of attention is unfortunate because railway transportation is a major producer of both heavy metals and polycyclic aromatic hydrocarbons (hereafter, ‘PAHs’), which originate from several sources including incomplete fossil fuel combustion, material abrasion, machine grease and oils, and creosote-treated railway ties (Malawaska and Wilkomirski 2001, Moret et al. 2007, Wilkomirski et al. 2011). These railway-associated toxicants can accumulate in the surrounding soil and vegetation through wet or dry deposition and are resistant to degradation (Martinez and Motto 2000, Abdel-Shafy and Mansour 2016), creating an exposure pathway to vegetation and herbivores that may bioaccumulate in animals at higher trophic levels (Awofolu 2005, Dan-Badjo et al. 2008). Like roadsides, vegetation near railways may act as sinks for transportation-derived toxic heavy metals, such as cadmium, chromium, lead, and zinc (Zhang et al. 2012, 2016), and carcinogens, such as polycyclic aromatic hydrocarbons (hereafter PAHs) like benzo[a]pyrene (Azhari et al. 2011). These pollutants are typically most concentrated in soils and plants nearest to transportation corridors (Moret et al. 2007, Liu et al. 2009, Wilkomirski et al. 2011) and have well-demonstrated but varied toxic effects on wildlife (reviewed by Acevedo-Whitehouse and Duffus 2009, Jaishankar et al. 2014, Tchounwou et al. 2012).

Exposure to both heavy metals and PAHs can reduce the condition and fitness of individuals, with the potential for population-level effects (Derocher et al. 2003, Baos et al. 2012), particularly for species that have small or declining populations, e.g. polar bears (*Ursus maritimus*; Oskam et al. 2003, Villa et al. 2017) and killer whales (*Orcinus orca*; Jepson et al. 2016, Mongillo et al. 2016). Fitness consequences can result from exposure to even low concentrations of some pollutants via changes in behaviour, growth, metabolism, or reproduction (Tierney and Kennedy 2008, Rhind et al. 2010, Jaishankar et al. 2014). The toxic metal cadmium, for example, is known to affect male reproductive function at low level exposures via reduced sperm concentration and mobility (Wirth and Mijal 2010), whereas exposure to PAHs can induce DNA-damaging adducts leading to developmental effects, with *in utero* exposure substantially increasing risk (Perera et al. 2005, Ewa and Danuta 2017).

Railways could expose wildlife to associated pollutants in at least two ways; via enhancement of adjacent vegetation and exposure to train-spilled agricultural products, such as cereal grains. Like other transportation features, railways enhance the growth and abundance of disturbance-tolerant and light-sensitive vegetation, including many species that are palatable to wildlife (Pollock et al. 2017). Ubiquitous examples of these species include dandelion (*Taraxacum officinale*), horsetail (*Equisetum arvense*) and several berry-producing shrubs (Hansen and Clevenger 2005, Roever et al. 2008a, Pollock et al. 2017). Agricultural products that leak from railway cars (Dorsey 2011) can sum to large quantities over time and space (Gangadharan et al. 2017) and are consumed by wildlife (Murray et al. 2017) to generate risk of collisions (above) but also exposure to toxicants. These could include compounds that emanate from train wheels and undercarriages, such as the petrochemicals in wheel grease, as well as mycotoxins produced by decomposing grain. Mycotoxins are secondary metabolites of fungus that are commonly associated with the improper storage or transport of cereal grains (Yiannikouris and Jouany 2002) and may contaminate as much as 25% of the world's annual grain production (Charmley et al. 1995). Long-term exposure to even small concentrations of mycotoxins can degrade immune systems to compromise the health of wildlife consuming decomposing anthropogenic food (Murray et al. 2016).

Rail-associated toxicants from any source are especially concerning when they occur in protected areas and involve threatened populations. These contexts apply to grizzly bears (*Ursus arctos*) in Canada's Rocky Mountain Parks, where train collisions are the leading cause of recorded mortality (Bertch and Gibeau 2010). Some bears in the region make extensive use of the railway (Pollock et al. in review), which offers forage opportunities in the form of spilled grain (Gangadharan et al. 2017) and vegetation (Pollock et al. 2017) that are consumed by grizzly bears (Murray et al. 2017). This population has among the lowest densities and reproductive rates in North America (Garshelis et al. 2005), which may increase its vulnerability to the detrimental effects of rail-associated toxicants.

The objectives of the study were to determine (a) whether forage in the form of rail-associated vegetation and train-spilled grain potentially exposes bears and other wildlife to toxicants consisting of one of more of heavy metals, PAHs, and mycotoxins; and (b) if metal concentrations measured in the hair of individual bears is correlated with their frequency of railway use. To support additional interpretation of toxicant signatures in bear hair, we also compared their metal concentrations to use of other anthropogenic features. Stemming from the mechanisms of potential contamination described above, we predicted that toxicants associated with railway operation (metals and PAHs) or decomposing grain (mycotoxins) would occur in higher concentration in samples collected from railway vegetation and grain, respectively, relative to reference samples from other locations. We also predicted that bears that use the railway more frequently would have higher comparative levels of metals in their fur. Further, we predicted that males and adult bears would exhibit higher metal concentrations than females and sub-adults, stemming from accumulating exposure over space (via home range size) and time (via age), respectively.

Methods

Study area and target species

Our study was conducted in Banff and Yoho National Parks in Western Canada with focus on the Canadian Pacific Railway (hereafter railway) that bisects both parks. The railway runs approximately parallel to the busy, four-lane Trans-Canada Highway through both montane and subalpine ecosystems. This major transportation corridor sees approximately 25-35 trains a day and over six million cars each year (Wells et al. 1999, Stantec 2016). Trains running through the parks carry grain from the prairies out to the coast for export, where 15 million tonnes are received annually (AARD 2013). Various agricultural grains are inadvertently spilled along the railway during transport and are known to attract wildlife such as wheat (*Triticum aestivum*), barley (*Hordeum vulgare)*, canola (*Brassica* spp.), flax (*Linum usitatissimum*), lentils (*Lens culinaris*), peas (*Pisum sativum*), and soybean (*Glycine max*) (Gangadharan et al. 2017). Several bear-attracting plants are seasonally available along the railway, roads, and other human-disturbed areas, e.g. ski hills, such as dandelion (*Taraxacum officinale*), horsetail (*Equisetum arvense*), graminoids (grasses, sedges, rushes), and various fruits, like buffaloberry (*Shepherdia canadensis*) (Hansen and Clevenger 2005, Roever et al. 2008, Pollock et al. 2017). Banff National Park is among the most heavily human-dominated landscapes in the world where grizzly bears still exist (Gibeau and Herrero 1998, Gibeau et al. 2002), with more than 4 million tourists visiting each year (Parks Canada 2017b). The study area includes three townsites (Banff, Lake Louise, and Field), a network of roads, three ski resorts, and numerous high-volume, camping, hiking, and day-use areas.

Our target species for railway-associated pollutant testing included dandelions growing along the rail and wheat spilled from hopper cars. We chose dandelion because of its association with human-disturbed areas such as railways and roadsides (Hansen and Clevenger 2005, Roever et al. 2008, Pollock et al. 2017), its wide geographic distribution, its importance as a forage plant to bears (Hamer and Herrero 1987a, Munro et al. 2006, Gunther et al. 2014), and its recognition as a hyperaccumulator and bioindicator (Czarnowska and Milewska 2000, Ligocki et al. 2011). For grains, we collected mainly wheat owing to its high abundance (Gangadharan et al. 2017) and potential to mould for mycotoxin testing (reviewed by Schaarschmidt and Fauhl-Hassek 2018).

For all metal analyses (grain, vegetation, and bear hair), we investigated concentrations of 10 heavy metals associated with transportation pollution (aluminum, cadmium, chromium, copper, iron, lead, manganese, molybdenum, nickel, and zinc). For PAHs (grain and vegetation), we investigated 16 that are deemed 'priority pollutants' by the U.S. Environmental Protection Agency and the Canadian Environmental Protection Act due to their toxicity (EPA 1982 and CEPA 1999; see Table 4.2). We were particularly interested in examining concentrations of the PAH Benzo[a]pyrene, a well-studied toxicant and known carcinogen (EPA 1982).

Collection and analysis of vegetation and grain samples

We identified four locations for sampling of dandelions and five locations for sampling of wheat corresponding approximately to miles 77 (grain only), 86, 105, 113, and 136 (westward from the Calgary, Alberta CPR railyard), which were among 15 sites used previously to estimate the rate of deposition for agricultural products (Gangadharan et al. 2017). Within each location, we collected dandelion leaves within 3 m of the railway along a 100 m transect and combined them to form an aggregate sample at each location. Dandelion reference samples were collected along a parallel 100 m transect approximately 50 m from the railway within the adjacent forest.

Grain samples taken from between the rails at five locations were similarly collected along a 100 m transect and combined to form an aggregate sample at each location. We dried these samples to a constant volume and stored them in labelled and sealed glass jars in a refrigerator. These samples were used to measure metals and PAHs (below). Because there was no opportunity to collect wheat in the park except in association with trains or the railway, we purchased two separate samples (white and red wheat) from a store (Nutter's Bulk and Natural Foods) to serve as reference values for subsequent measurements. For measurement of mycotoxins, we targeted samples collected from two types of locations; places on the tracks where trains had stopped and piles of grain had accumulated (n = 8) and the back sills of hopper cars where grain accumulates during loading (n = 7). Both sources are targeted by foraging bears (Parks Canada, personal communication) and appeared to exhibit some decomposition via visible mould, which we did not see in grain scattered on the railway at low densities. We placed grain samples in labelled and sealed plastic bags and froze them at -20°C until analysis. We compared our mycotoxin results to standards set by the Canadian Food Inspection Agency.

To support analyses for metals and PAHs, we dried each sample of dandelion and rail-collected grain for 48 hours at 70°C in a scientific oven and then placed into a labelled, 150 ml glass jar and sent to ALS Environmental Laboratories for metal analyses (Edmonton, Alberta, Canada). The methods were conducted following the protocol outlined by the Province of British Columbian for assessment of metals in animal and plant samples (Government of BC 2014) with instrumental analysis by inductively coupled plasma mass spectrophotometry (modified from EPA Method 6020A). Instrumental analysis for polycyclic aromatic hydrocarbon (PAH) testing was conducted for both vegetation and grain samples by a different ALS Environmental Laboratories (Burlington, Ontario, Canada) using soxhlet extraction and analyzed by gas chromatography coupled with low resolution mass spectrometry. Specific methodology is described by ALS Environmental Laboratories (ALS 2018).

To support analyses of mycotoxins, we placed the frozen grain samples collected from spills and train sills on dry ice for transport to Trilogy Analytical Laboratories (Washington, Missouri, USA). Tests assessed the concentrations for five mycotoxins that are common in cereal crops (Aflatoxin, Fumonisin, DON, Zearalenone, Ochratoxin A; Pascale 2009) using high-performance liquid chromatography. To ensure extraction accuracy, samples were compared to reference samples with known toxin concentrations as described by Trilogy Analytical Laboratories (Trilogy Analytical Laboratory 2017).

Collection and analyses of bear hair

Samples of grizzly bear hair were obtained from Parks Canada Agency, which were collected from bears that were captured for fitting of GPS collars in spring 2012 - 2015 to support several research projects associated with a joint initiative for grizzly bear conservation. From this sample, we selected 20 bears (10 females and 10 males) with home ranges in Banff and/or Yoho National Parks and used one to two guard hairs from each bear to determine metal concentrations. Metal concentrations were measured for individual sections of hair using laser ablation (below). Segmental hair analysis permits investigation into retrospective and chronological exposure to contaminants (D'Urso et al. 2017) because metal concentrations in hair reflect the blood or body burden of metals during the period of hair growth (Solgi and Ghasempouri 2015). Grizzly bear hair grows from approximately June through October with an estimated growth rate of ~ 1.5 – 2.0 cm / month (Christensen et al. 2005, Noel et al. 2015, Mowat et al. 2017). Because our guard hair samples were collected in the spring, we expected to correlate metal concentrations at the root with habitat use in the previous fall, concentrations near the tip with habitat use in the previous summer, and average concentrations along the length of the hair with average habitat use for the previous year. We defined seasons according to regional bear feeding habits after Nielsen et al. (2004); spring (start of sampling season to June 14), summer (June 15 to August 7), and fall (August 8 – end of sampling season).

We sent bear hair samples for segmental hair analysis using laser ablation by Stantec Consulting (Sidney, BC, Canada) using the methods described by Noel et al. (2015) which included the standard washing procedure developed for human hair by the International Atomic Energy Agency (Ryabukin 1978). Laser ablation was conducted along 2 mm longitudinal sections at approximately 1 cm intervals along each hair starting at the root. Values therefore represented an average of measured elemental concentrations (in parts per million, ppm) along the 2 mm scans. The instrument used to run the samples was a Thermo X-Series 2 quadrupole ICP-MS coupled with UV laser ablation system (University of Victoria, Victoria, BC, Canada; as in Noel et al. 2015).

Railway use by bears

To determine variation in rail use by bears, we obtained GPS locations for the 20 individuals in the year preceding hair sampling (n = 6 individuals) or the year following it (n = 14 individuals). We compared these locations to transportation, human-use, and topographical features using geographical information system (GIS) layers from Parks Canada. We used ArcMap (version 10.3; ESRI, Redlands, CA) to quantify individual bear use of five anthropogenic features: the major transportation corridor [including the highway and railway], secondary roads, ski hills, gravel pits, and old landfill sites. We combined the highway and railway into one classification referred to hereafter as the transportation corridor because of their close proximity and parallel orientation throughout the parks. GPS locations from collared bears were recorded every two hours from emergence from hibernation or capture (typically early spring) to den entry in the late fall. We quantified anthropogenic habitat use as the proportion of GPS locations that fell within 30 m of each feature for each bear and season (spring, summer, and fall). Because some pollutants are more likely to condense at the cold temperatures associated with high elevations (Bing et al. 2016), we also recorded the mean elevation recorded for each bear-season combination.

Statistical analysis

To evaluate metal and PAH concentrations in railway-associated forage, we conducted a principal component analysis (PCA) using the statistical software Past (Hammer 1999-2018). Metal and PAH concentrations were first log-transformed to normalize their distributions. We used PCA based on a covariance matrix to synthesize variation in heavy metal concentrations, first for vegetation samples (railway and forest), and second for grain samples (railway and store-bought) for 10 heavy metals: aluminum, cadmium, chromium, copper, iron, lead, manganese, molybdenum, nickel, and zinc (Table 4.1). We did the same for the 16 priority PAHs (Table 4.2). We then regressed the resultant principal component scores for each contaminant (metals and PAHs) and forage type (vegetation and grain) as a function of their proximity to the railway (i.e. railway samples versus reference samples) using linear models ('lme4' version 1.1-12; R version 3.2.1). For all analyses, we considered predictor variables to be significant if their beta coefficients did not overlap zero.

We examined differences in metal concentrations for 10 heavy metals in bear hair in relation to categories of sex, age (adult ≥ 8 yrs and subadult ≤ 5 yrs), mean elevation, and proportionate use of the major transportation corridor as well as four other anthropogenic features thought to influence metal exposure (secondary roads, ski hills, old landfills, and gravel pits). We conducted separate analyses for each section of hair (tip, root, averaged) regressed with corresponding seasons of habitat use (summer, fall, combined). Statistical analyses were performed in R 3.2.1 (R Core Team 2015).

To understand the complex relationship between metal concentrations in bear hair and habitat use, we conducted a PCA using the same methodology described above, but for each section of hair (averaged, tip, root). We then regressed the resultant principal component scores for each individual bear and section of hair with their corresponding seasonal use of each anthropogenic feature and mean elevation as well as sex and age class using linear models ('lme4' version 1.1-12; R version 3.2.1). All non-categorical variables were standardized to have a mean of 0 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 Akaike Information Criteria score (AIC) (Burnham and Anderson 2002). We addressed our objectives by running all model combinations and selected the top model for each analysis using Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson 2002) ('MuMIn' version 1.15.1; R version 3.2.1). If models were within ΔAICc<2, we considered them to be competitive and averaged their coefficients (Burnham and Anderson 2002). We reported standardized regression coefficients, their confidence intervals, and an adjusted R^2 metric to evaluate effect sizes and measure model fit.

Results

We used principal component analysis to test our predictions that metal and PAH concentrations would be higher in railway-associated samples of vegetation and grain. For vegetation samples, metal concentrations were represented by a one-component model that explained approximately 80% of the variance in the data set. Component 1 was highly correlated with molybdenum (0.75), and to a lesser extent iron (0.35), lead (0.30), and cadmium (0.29). Component 1 had a negative association with nickel (-0.33) (Table 4.4). Our regression of component 1 scores demonstrated significantly higher values in rail-side dandelion samples when compared to forest references (Table 4.6; β = 1.44, CI = 0.81, 2.08). For PAH concentrations in vegetation samples, we again obtained a one-component model describing approximately 88% of the variance in the data set. Component 1 was most correlated with PAHs anthracene, chrysene, fluoranthene, fluorene, phenanthrene, and pyrene (loadings 0.32 – 0.38) (Table 4.4). Our regression of component 1 scores demonstrated significantly higher values in rail-side dandelion samples when compared to forest references (Table 4.6; β = 3.34, CI = 1.51, 5.17).

For grain samples, metal concentrations were represented by a one-component model that explained approximately 97% of the variance in the data set. Component 1 was most correlated with lead (0.49), iron (0.48), and chromium (0.45) (Table 4.5). Our regression of component 1 scores demonstrated significantly higher values in train-spilled grain samples when compared to store-bought references (Table 4.6; β = 5.75, CI = 4.58, 6.91). For PAH concentrations in grain samples, we again obtained a one-component model describing approximately 99% of the variance in the data set. Component 1 had several PAHs with similar loadings (between 0.25 and 0.30), with the three highest being fluoranthene (0.30), pyrene (0.29), and benzo[a]anthracene (0.28) (Table 5). Our regression of component 1 scores demonstrated significantly higher values in train-spilled grain samples when compared to store-bought references (Table 4.6; β = 16.82, CI = 11.57, 22.07). Grain samples had a larger percentage of hazardous high molecular weight

PAHs (4-6 rings) on average ($\bar{x}$ = 72.7 % +/- 9.7) than vegetation ($\bar{x}$ = 51.7 % +/- 6.9). Seven high weight PAHs that are considered carcinogenic were present in all railway-associated samples (benzo[a]anthracene, benzo[a]pyrene, Benzo[b]fluoranthene, Benzo[k]fluoranthene, Chrysene, Dibenzo[a]anthracene, and indeno[1,2,3-cd]pyrene; IARC 2018), constituting ~15 % of grain (~7 % of dandelion) total PAH content.

Among the 15 grain samples collected from spills on the railway (n = 8) and train sills (n = 7), three (20%), all from spills, tested positive for the presence of one or more mycotoxins. Two of the three samples contained both deoxynivalenol and ochratoxin A, and the third sample contained deoxynivalenol only. Despite detectable presence, the concentrations for deoxynivalenol (0.1, 0.1, and 0.3 ppm) and ochratoxin A (5.3 and 15.6 ppb) were well below the maximum tolerable limit for swine feed set by the Canadian Food Inspection Agency at 1 ppm and 200 ppb, for deoxynivalenol and ochratoxin, respectively (CFIA 2017).

We found evidence of pollutants in bear hair with average sums of 10 heavy metals along the length of the hair ranging from approximately 139.07 to 1867.49 mg/kg for female bears and 113.84 to 4900 mg/kg for male bears (Table 4.3). Males bears had significantly higher concentrations of 10 metals, both overall (β_{males} = 0.23, CI = 0.05, 0.39), and for the individual elements of chromium (β_{males} = 0.58, CI = 0.32, 0.85), iron (β_{males} = 0.46, CI = 0.21, 0.70), nickel (β_{males} = 1.01, CI = 0.73, 1.30), and molybdenum (β_{males} = 1.68, CI = 1.19, 2.17), but not the other metals ($\beta \leq 0.36$ and CIs overlapped zero for the rest). Metal concentrations were highly variable among bears with coefficients of variation for each element ranging from 50.9 (zinc) to 271.0 (lead) (Table 4.3). The coefficients of variation were not significantly different between males and females (β_{males} = -6.65, CI = -54.71, 68.01). There were no differences in the concentrations of heavy metals in bear hair as a function of age class (β_{adult} = 0.10, CI = -0.27, 0.07) or the interaction between age and sex (β = 0.01, CI = -0.33, 0.36).

We used principal component analysis to test hypotheses relating heavy metal concentrations in hair to the proportion of time spent within 30 m of the transportation corridor, secondary roads, ski hills, gravel pits, and old landfill sites, as well as mean elevational use and age and sex classes of grizzly bears. Averaged metal concentrations along the length of the guard hair could be grouped into a two-component model that explained approximately 80% of the variance in the data set (Table 4.4a). Component 1 was most correlated with molybdenum (0.94), whereas component 2 was most correlated with cadmium and lead (0.67 and 0.53, respectively) (Table 4.4b). Similar results occurred for metal concentrations at the tip of the guard hair where 2 components explained 80% of the variation in the data (Table 4.4a). Again, component 1 was most correlated with molybdenum (0.88) and component 2 was most correlated with cadmium and iron (0.66 and 0.41, respectively) (Table 4.4c). The two-component model for metal concentrations at the root of the guard hair accounted for the most variance (~84%; Table 4a). Its component 1 was most correlated with molybdenum (0.48), lead (0.46), and manganese (0.41) while component 2 was most correlated with cadmium (0.40) (Table 4.4d).

We used these two PCA components as response variables to examine the effects of habitat use, sex and age classes for each of hair averages, tips, and roots. For hair averages, component 1 was significantly predicted by sex with greater values for male bears (Table 4.5). For hair tips, which reflected summer growth, component 1 also increased for male bears. For hair roots, which reflected fall growth, component 1 increased with the proportion of time spent on ski hills. Also for hair roots, component 2 increased slightly with use of ski hills, and elevation, but declined slightly with use of the transportation corridor and secondary roads, which were contrary to our predictions. In this model, the 95% confidence intervals for all three coefficients overlapped zero, inviting caution for interpretation.

Discussion

Grizzly bears are among the wildlife that make extensive use of railways for which one hazard may be ingestion of rail-associated toxicants that might result from transportation pollutants or decomposition of spilled grain. We tested this possibility by measuring metals and PAHs in rail-associated vegetation and spilled grain, mycotoxins in grain that was spilled on the rail or grain cars, and metal concentrations in bear hair. As predicted, we found that railway samples for dandelion and grain demonstrated significantly higher concentrations in 10 heavy metals and 16 priority PAHs when compared to their respective references. Mycotoxins (deoxynivalenol and ochratoxin A) occurred in 20% of our decomposing grain piles, but at very low levels. Male bears had significantly higher metal concentrations than females, but with large variation in concentrations among individuals. Contrary to our primary hypothesis, metal concentration in bear hair were not higher in animals that spent more time in the vicinity of the transportation corridor; in fact, they were slightly lower for some metals. We found some evidence that metal concentrations increased with time spent near ski hills for bear hair grown in the fall. There was also a weak positive effect of elevation on bear habitat use for hair grown in the fall.

The availability of dandelion along railways can pose a strong attraction for bears coming out of winter hibernation because it is one of the earlies species available in the spring, is ubiquitous in the railway environment, and is an important and favoured food for grizzly bears (Hamer and Herrero 1987a, Munro et al. 2006, Pollock et al. 2017). We found elevated levels of metals and PAHs in our railway-associated dandelion samples compared to references. For metals, the strongest correlation for rail-side dandelion occurred for molybdenum (mean 10.6 mg/kg +/- 4.7), with levels approximately 10 times higher than typical concentrations in terrestrial plants (~1.0 mg/kg; Barceloux and Barceloux 1999). Dandelion has been demonstrated to accumulate high concentrations of molybdenum in aboveground parts due to the efficient translocation from roots to shoots (Curlik et al. 2016). Although not seemingly a threat to bear health, molybdenum concentrations in railway-associated dandelion were above the maximum tolerable level established for cattle (5.0 mg/kg) due to molybdenosis, a molybdenum-induced copper deficiency which affects both domesticated and wild ruminants (e.g. moose *Alces alces*, Frank 1998; Tibetan gazelle *Procapra picticaudata*, Shen et al. 2010). Sources of molybdenum in the railway environment are likely attributed to molybdenum disulphide formulations that are used in lubricating greases, brake pads, and linings (Barceloux and Barceloux 1999).

For PAHs, all 16 measured were present in rail-side dandelion, with the three highest correlations for anthracene (mean 9.62 ng/g +/- 12.5), a low-weight PAH, fluoranthene (mean 108 ng/g +/- 103.1) and pyrene (64.1 ng/g +/- 87.5), both high-weight PAHs. We found a higher overall proportion of volatile low molecular weight PAHs in dandelion samples, which is characteristic of contamination from aerial deposition and therefore likely to originate from railway emission particulates (Malawaska and Wilkomirski 2001). All three of these PAH concentrations found in rail-side dandelion were well below toxicity thresholds (anthracene: 2500 ng/g, fluoranthene: 8200 ng/g, pyrene 10720 ng/g; Brooks 2004).

Bears are known to forage along the railway for grain deposits in North America and the attraction is acknowledged to contribute to bear-train collisions (Waller and Servheen 2005, Hopkins et al. 2014, Dorsey et al. 2015). In our study area, railway use by bears increases in the spring and fall months, which has been proposed to correlate with herbaceous foraging opportunities (Munro 2000, Roever et al. 2008, Pollock et al. 2017) and an increase in fall export of grains (Gangadharan et al. 2017). In concurrent studies within the study area, half of bear scats collected within 150 m of the railway contained grain (Murray et al. 2017) and grain spillage was approximated at 110 tonnes per year, providing a nutritious and dependable food resource to bears (Gangadharan et al. 2017). We found high concentrations of metals and PAHs in train-spilled grain when compared to both references and rail-side dandelion. For metals, the strongest correlations for train-spilled grain were for lead (mean 30.4 mg/kg +/- 12.3), iron (mean 27880 mg/kg +/- 20865.8), and chromium (mean 91.9 mg/kg +/- 72.7). When compared to the Alberta soil guidelines, our lead levels were below (70 mg.kg), and chromium levels above (64 mg/kg) remediation values (AEP 2016). However, in relation to maximum tolerable levels (MTL) for swine, horse, and poultry, lead concentrations in train-spilled grain were about 3 times higher (10 mg/kg; NRC 2005), with chromium concentrations slightly below the MTL (100 mg/kg; NRC 2005). Lead, a priority pollutant, is of particular concern due to its high toxicity and potential for population-level effects in various species, e.g. condors (*Gymnogyps californianus)* and eagles (*Haliaeetus leucocephalus, Aquila chrysaetos;* Fisher et al. 2006), including sublethal effects such as damage to organs, the immune and reproductive systems, and neurological impairment (Rattner et al. 2008). Although we found no set soil remediation guidelines for iron, iron concentrations in train-spilled grain were ~ 55 times higher than the MTL specified for cattle (500 mg/kg; NRC 2005).

The strongest correlations in train-spilled grain occurred for high molecular weight PAHs fluoranthene (119657.5 ng/g +/- 136219.9), pyrene (82192.5 ng/g +/- 92837.8), and benzo[a]anthracene (14088 ng/g +/- 17240.1). These three PAHs were approximately 15, 8, and 5 times higher than toxicity thresholds, respectively (fluoranthene: 8200 ng/g, pyrene 10720 ng/g, benzo[a]anthracene 2500 ng/g; Brooks 2004). High weight PAHs tend to be characterized by a longer term, cumulative deposit found closer to the emission source, and in the context of the railway are thought to originate from machine grease, oils, and creosote compounds (Moret et al. 2007, Wilkomirski et al. 2011). Not only are PAH concentrations in grain much higher than rail-side dandelion, but a higher proportion of high weight PAHs can be more harmful to organisms because they are less water soluble, have lower vapour pressures, and can partition more easily into organic matter (Abdel-Shafy and Mansour 2016). For benzo[a]pyrene, a priority pollutant, concentrations were about six times higher in our grain samples ($\bar{x}$ = 4.66 mg/kg, range 0.81 – 13.0) than the recommended concentration in residential soils and areas with high ecological value such as national parks (≥ 0.7 mg/kg; CCME 1999). We compared the sum of 16 PAHs to standard limits set for agricultural soil contamination and found that our railway grain samples were classified as 'heavily polluted' (> 1.0 mg/kg), whereas our dandelion samples were considered 'weakly polluted' (0.2 - 0.6 mg/kg), with one sample classified as 'polluted' (0.6 - 1.0 mg/kg) (Maliszewska-Kordybach 1996, Wilkomirski et al. 2011, Jiao et al. 2017).

Mycotoxin concentrations were largely below detection limit which was surprising due to the apparent signs of decomposition in our grain samples. The samples that tested positive contained deoxynivalenol (DON) and/or ochratoxin A; two toxins that commonly infect wheat, are able to grow in temperate climates, are highly stable, and are both considered toxic and carcinogenic to animals (Rachon et al. 2016, Schaarschmidt and Fauhl-Hassek 2018). The negligible levels of mycotoxins detected in observably moldy grain could be due to environmental factors at the railway that were not suitable for mycotoxin production, e.g. large temperature or moisture fluctuations (Rachon et al. 2016). Further, although absent in the literature, the high contamination of railway grain with metals or PAHs could inhibit the formation of mycotoxins, an interesting area for future research. Based on our sample concentrations, mycotoxins do not appear to be a threat to the health of wildlife who forage on train-spilled grain in the region.

As hypothesized, male bears in our study area had higher overall metal concentrations in their fur than female bears. There are several reasons why this may be the case; female bears are able to transfer contaminants to their offspring via milk, e.g. maternal transfer of mercury and PCBs in polar bears (Knott et al. 2012). Male bears have much larger home ranges and therefore access to diverse human land uses with a higher probability of exposure to metal pollution (Stevens and Gibeau 2005). Further, male bears spend less time hibernating than female bears and their larger body mass requires an increased nutritional demand, both factors potentially heightening exposure (Pigeon et al. 2016, Rode et al. 2006). Sexual segregation of bears commonly results in adult male bears dominating areas with high quality food resources (Rode et al. 2006), even if these areas may increase the risk of contamination or mortality. We found the strongest sex differences in concentrations of molybdenum, with male bears having the highest levels. Exposure to molybdenum in this context will occur mainly through ingestion, with foods derived from above-ground plants generally having higher concentrations of molybdenum than roots, tubers, or animal tissue (Barceloux and Barceloux 1999). We found evidence for a high requisition of molybdenum in our own samples of railway-associated dandelion (above). It could be that male bears are ingesting higher quantities of forage that have accumulated molybdenum throughout the study area. Major anthropogenic sources of molybdenum on a broad-scale are from fossil fuel combustion, sewage sludge, and agricultural, industrial or mining operations (Barceloux and Barceloux 1999). Our mean molybdenum concentrations in hair samples from male bears (12.4 mg/kg +/- 29.2) were about three times higher than other studies which measured ruminant hair of animals displaying signs of molybdenosis (Tibetan yak *Bos grunniens*

4.61 +/- 1.61, Shen et al. 2006; Tibetan gazelle 4.71 mg/kg +/- 1.72, Shen et al. 2010). Molybdenum concentrations for black bears (*Ursus americanus*) in Big Bend National Park ranged from 0.09 to 0.45 mg/kg (Shanks et al. 2008).

Some contaminants accumulate with age, e.g. PCB levels in polar bears (Bernhoft et al. 1997), however contrary to our predictions, we did not find this with metal concentrations in bear hair. Of the metals we tested, cadmium and lead tend to increase with age in many species due to a slow rate of elimination and accumulation in tissues, even with low level exposures (Komarnicki 2000, Rautio et al. 2010, Hermoso de Mendoza Garcia et al. 2011). The lack of age effect for this study may be due to our use of principal components analysis as opposed to individual metal investigations. Further, the large variation in metal concentrations could be related to behavioural differences in habitat selection and foraging habits that are not age-dependent.

We did not find that metal concentrations in bear hair correlated with the frequency of use of the transportation corridor. The lack of correlation was unexpected as we found evidence for the contamination of railway-associated foods, particularly for train-spilled grain. Additionally, we observed contaminated areas along the railway (e.g. grease lubricating stations) that would occasionally contain grain-filled bear scats and heard reports that ‘railway bears’ would sometimes exhibit oil on their fur (Parks Canada, personal communication). It could be that use of the transportation corridor and consumption of associated foods is minimal overall when considering habitat selection on the broader landscape. Although foods growing along transportation corridors may be a strong attractant, several factors may limit exposure time, like repeated human disturbance from cars, trains, noise, and personnel. Because the magnitude of metal contamination depends on many factors including the frequency, dose, and duration of exposure (Tchounwou et al. 2012), it is possible that none of these are at levels high enough to correlate metal concentrations in bear hair with these types of habitat use. Alternatively, it is possible that not one specific type of habitat use is responsible for the variation in metal exposure, it may be a combination of several different sources through time and space in this heavily human-dominated landscape. It is difficult to identify specific sources of contamination for wide-ranging animals who have broad diets like grizzly bears. In the case of high molybdenum concentrations, we may not have estimated the appropriate type of habitat that would result in heightened exposure. Lastly, it was necessary to combine both the railway and highway into one variable due to their close proximity and parallel orientation throughout the parks, however doing so may have diluted the effect of one or the other as an identifiable source of contamination.

We found a correlation with the fall use of ski hills by grizzly bears and an increased concentration of metals in bear hair, particularly for aluminum, cadmium, iron, lead, manganese, and molybdenum. Metal concentrations nearest the root of the hair are most reliably linked to internal contamination through diet due to new growth and minimal exposure to external contamination. Bears in the study area and other regions are known to frequent ski hills which offer high quality habitat due to various bear-attracting plants that grow in the maintained ski runs (Mueller 2001; Parks Canada, personal communication). The consistent presence of bears on ski hills has contributed to a growing number of summer bear viewing tours for many resorts (e.g. Whistler Mountain; Needham et al. 2004). Vegetation growing on ski hills has the potential to harbour metals from various sources including the use of fertilizers and chemical additives for snow hardening, herbicide application, snowmaking operations (including pumping systems, alloy pipes, and potentially contaminated water sources), and general machinery operations such as grooming and machine or mechanical ski run clearing (Parks Canada 2015, Pintaldi et al. 2017). Metal concentrations correlating with fall habitat selection of ski hills could be related to fall berry consumption and/or that bears are in a hyperphagic period when they gorge on foods, more than doubling their summer caloric intake to build fat reserves in preparation for winter hibernation (Nielsen et al. 2004, Stenvinkel et al. 2013). The high intake of forage during the fall months may reflect the higher correlation with metal exposure at that time. Future work investigating contaminant levels and mechanisms of contamination for ski hill ecosystems would be highly valuable.

We found some evidence that bears that used higher elevations, on average, had higher cadmium concentrations in their fur. Metals can be transported long distances adsorbed onto particulate matter and deposited at high elevations due to the cold condensation effect (Wegmann et al. 2006, Bing et al. 2016). An elevation-dependent accumulation in soil or sediment has been demonstrated for several metals, including cadmium (Li et al. 2018, Magnani et al. 2018). In addition to aerial deposition at higher altitude, other important factors that affect cadmium uptake by plants and are influenced by elevation are soil properties like pH and plant species (Smoulders 2001).

In sum, our results offer some mitigation suggestions that could reduce wildlife exposure to toxicants. Train-spilled grain harboured comparatively higher levels of both heavy metals and PAHs making it a priority for removal. Removal should be focused in areas like railway sidings where trains are stopped for extended periods and can accumulate both grain and pollutants. Lubricating stations along railways should be regularly monitored and maintained to reduce attraction and the spread of grease, a known source of PAHs. Partial exclusion fencing can reduce wildlife access in areas of concern. Further, the use of organic herbicides and pesticides should be encouraged along railways, roadsides, ski hills, and other areas that wildlife frequent. We encourage monitoring of soil and plant contamination on ski hills, including sources of water used for snowmaking. Prohibiting access, e.g. electric fencing, in areas where operations are concentrated may be warranted to reduce contaminant exposure to wildlife.

Tables

Table 4.1 The average concentrations (mg/kg) +/- SD and range (min-max) of 10 heavy metals found in samples of grain collected from the rail (n = 5) or purchased (n = 2), and dandelions growing along the rail (n = 4) or ~50 m inside the adjacent forest (n = 4). Rail samples were collected along the Canadian Pacific Railway in Banff and Yoho National Parks, Canada.

Metal	Grain (rail)	Grain (purchased)	Dandelion (rail)	Dandelion (forest)
Al	571.4 +/- 415.5 (248-1150)	*10 (10, 10)	26.5 +/- 8.89 (19-38)	23.5 +/- 8.19 (13-30)
Cd	0.30 +/- 0.18 (0.11-0.59)	0.04 (0.04, 0.05)	0.20 +/- 0.10 (0.08-0.31)	0.10 +/- 0.06 (0.03-0.16)
Cr	91.9 +/- 72.7 (37.9-215)	*0.2 (0.2, 0.2)	1.74 +/- 0.58 (1.19-2.43)	1.22 +/- 0.34 (0.78-1.58)
Cu	47.4 +/- 24.9 (26.4-86.7)	4.34 +/- 1.04 (3.6, 5.07)	11.8 +/- 1.38 (10-13.1)	12.0 +/- 3.57 (8.46-16.6)
Fe	27880 +/- 20866 (12100-62700)	40.7 +/- 3.68 (38.1, 43.3)	388 +/- 136.5 (192-508)	123.5 +/- 38.9 (74.1-158)
Pb	30.4 +/- 12.3 (9.07-40.2)	*0.04 (0.04, 0.04)	0.51 +/- 0.36 (0.14-0.98)	0.19 +/- 0.07 (0.13-0.26)
Mn	309.4 +/- 190.3 (129-569)	39.2 +/- 10.4 (31.8, 46.5)	26.8 +/- 7.40 (18-36.1)	37.8 +/- 15.8 (23.5-60.3)
Mo	30.8 +/- 18.4 (13.7-62)	0.69 +/- 0.26 (0.5, 0.87)	10.6 +/- 4.70 (6.52-17.3)	0.77 +/- 0.31 (0.34-1.05)
Ni	19.1 +/- 9.73 (8.05-32.7)	0.38 +/- 0.17 (0.26, 0.5)	0.67 +/- 0.13 (0.55-0.82)	2.37 +/- 0.48 (1.8-2.85)
Zn	111.9 +/- 54.2 (73.7-183)	28.3 +/- 11.3 (20.3, 36.3)	49.5 +/- 17.2 (34.8-73.6)	44.7 +/- 16.4 (27.5-64.4)

*Detection Limit, samples were < D.L.

Table 4.2 The average concentrations (ng/g) +/- SD and range (min-max) of 16 polycyclic aromatic hydrocarbons (PAHs) found in samples of grain collected from the rail (n = 5) or purchased (n = 2), and dandelions growing along the rail (n = 4) or ~50 m inside the adjacent forest (n = 4). Rail samples were collected along the Canadian Pacific Railway in Banff and Yoho National Parks, Canada.

PAH	Grain (rail)	Grain (purchased)	Dandelion (rail)	Dandelion (forest)
Acenaphthene	10827.2 +/- 14454.8 (394-30100)	0.12 (0.11, 0.12)	3.2 +/- 4.13 (0.3-9.27)	0.31 +/- 0.09 (0.24-0.44)
Acenaphthylene	187.12 +/- 217.1 (23-490)	*0.10 (0.10, 0.10)	0.35 +/- 0.28 (*0.20-0.77)	*0.20 (0.20-0.20)
Anthracene	7871.6 +/- 10070.2 (455-22300)	*0.10 (0.10, 0.10)	9.62 +/- 12.5 (2.01-28.2)	0.28 +/- 0.11 (0.28-0.43)
Benzo(a)anthracene	14088 +/- 17240.1 (1390-41200)	*0.10 (0.10, 0.10)	1.80 +/- 1.43 (0.89-3.94)	0.35+/- 0.29 (*0.20-0.78)
Benzo(a)pyrene	4655.2 +/- 5153.2 (805-13000)	*0.10 (0.10, 0.10)	0.99 +/- 0.96 (0.16-1.05)	0.27 +/- 0.13 (*0.20-0.46)
Benzo(b)fluoranthene	7284 +/- 7578.6 (1300-19500)	*0.10 (0.10, 0.10)	2.86 +/- 1.90 (1.03-5.49)	0.69 +/- 0.78 (*0.20-1.83)
Benzo(ghi)perylene	1316.8 +/- 1176 (400-3260)	*0.10 (0.10, 0.10)	0.93 +/- 0.68 (0.21-1.65)	0.34+/- 0.21 (*0.20-0.64)
Benzo(k)fluoranthene	5558 +/- 5550.5 (1080-14000)	*0.10 (0.10, 0.10)	2.04 +/- 1.72 (0.66-4.54)	0.45 +/- 0.44 (*0.20-1.11)
Chrysene	19145 +/- 17591.4 (2460-42100)	0.14 +/- 0.05 (0.10, 0.17)	9.85 +/- 7.73 (4.84-21.3)	1.07+/- 1.22 (*0.20-2.86)
Dibenzo(ah)anthacene	434.4 +/- 330.2 (132-900)	*0.10 (0.10, 0.10)	0.30 +/- 0.11 (*0.20-0.43)	*0.20 (0.20-0.20)
Fluoranthene	119657.5 +/- 136219.9 (7630-298000)	0.23 (0.23, 0.23)	108 +/- 103.1 (31.7-260)	5.12 +/- 2.88 (3.37-9.41)
Fluorene	12654.2 +/- 16885.9 (558-35700)	0.21 (0.20-0.21)	20.7 +/- 27.0 (4.55-61.1)	0.86 +/- 0.13 (0.68-1.00)
Indeno(1,2,3cd)pyrene	1781.4 +/- 2006.9 (401-5220)	*0.10 (0.10, 0.10)	0.92 +/- 0.70 (0.22-1.73)	0.30+/- 0.20 (*0.20-0.59)
Naphthalene	136.58 +/- 161.2 (19.5-400)	1.71 +/- 0.19 (1.57, 1.84)	1.88 +/- 0.28 (1.62-2.19)	2.00 +/- 0.19 (1.81-2.26)
Phenanthrene	91610 +/- 105914.2 (4210-223000)	0.81 +/- 0.08 (0.75, 0.86)	148.5 +/- 140.8 (62.6-359)	6.45 +/- 1.93 (4.95-9.28)
Pyrene	82192.5 +/- 92837.8 (5270-204000)	0.30 +/- 0.04 (0.27, 0.32)	64.05 +/- 87.5 (12.8-195)	2.82 +/- 1.80 (1.65-5.50)

*Detection Limit, samples were < D.L.

Table 4.3 Average metal content (mg/kg) +/- SD, range (min-max), and coefficient of variation (CV) in grizzly bear hair samples by sex. Hair samples were collected during spring captures for GPS-collaring for another study in Banff and Yoho National Parks, Canada (2012-2015).

Element	Females (*n* = 10)	Males (*n* = 10)
Al	167.1 +/- 116.9 (11.9 - 543.7) CV = 70.0	227.7 +/- 226.8 (4.22 - 1264.0) CV = 99.6
Cd	1.14 +/- 1.97 (0.007 - 17.2) CV = 172.1	1.11 +/- 1.68 (0.03 - 7.33) CV = 150.7
Cr	1.35 +/- 2.62 (0.11 - 22.7) CV = 194.7	2.34 +/- 2.91* (0.17 - 15.4) CV = 124.3
Cu	8.75 +/- 4.63 (2.61 - 30.6) CV = 52.9	10.9 +/- 10.2 (0.22 - 63.7) CV = 93.6
Fe	153.3 +/- 118.9 (9.38 - 581.4) CV = 77.6	281.6 +/- 362.3* (8.04 - 2683.0) CV = 128.7
Mn	39.8 +/- 37.3 (0.31 - 205.3) CV = 93.9	37.7 +/- 40.8 (0.81 - 231.4) CV = 108.3
Mo	0.75 +/- 1.71 (0.03 - 9.57) CV = 227.0	12.4 +/- 29.2* (0.03 - 166.1) CV = 235.9
Ni	0.95 +/- 1.18 (0.06 - 7.50) CV = 123.7	2.73 +/- 3.44* (0.06 - 28.4) CV = 125.9
Pb	1.80 +/- 4.88 (0.03 - 41.3) CV = 271.0	1.91 +/- 3.07 (0.01 - 24.6) CV = 161.0
Zn	129.5 +/- 80.9 (53.6 - 662.3) CV = 62.5	131.4 +/- 66.9 (42.6 - 565.4) CV = 50.9
Average Sum	504.3 +/- 279.2 (139.1 - 1867.5) CV = 55.4	709.8 +/- 661.1* (113.8 - 4900.1) CV = 93.1

* Asterixed values represent significantly higher concentrations (CI's did not overlap zero)

Table 4.4 Principal components analysis of metal and PAH concentrations in dandelion leaves collected within 3 m of the Canadian Pacific Railway and ~50 m into the adjacent forest at 4 locations in Banff and Yoho National Parks, Canada.

Dandelion Metals	PC 1 (79.6% of variance)
Al	0.09
Cd	0.29
Cr	0.12
Cu	0.04
Fe	0.35
Mn	-0.09
Mo	**0.75**
Ni	-0.33
Pb	0.30
Zn	0.07

PAHs	PC 1 (88.3% of variance)
Acenaphthene	0.23
Acenaphthylene	0.08
Anthracene	**0.38**
Benz(a)anthracene	0.23
Benzo(a)pyrene	0.16
Benzo(b)fluoranthene	0.24
Benzo(ghi)perylene	0.14
Benzo(k)fluoranthene	0.22
Chrysene	**0.32**
Dibenzo(ah)anthacene	0.05
Fluoranthene	**0.35**
Fluorene	**0.33**
Indeno(1,2,3 cd)pyrene	0.15
Naphthalene	-0.01
Phenanthrene	**0.34**
Pyrene	**0.35**

Table 4.5 Principal components analysis of metal and PAH concentrations in grain samples collected along the Canadian Pacific Railway at 5 locations in Banff and Yoho National Parks, Canada, as well as 2 store-bought reference samples.

Grain Metals	PC 1 (97.0% of variance)
Al	0.29
Cd	0.14
Cr	**0.45**
Cu	0.18
Fe	**0.48**
Mn	0.15
Mo	0.27
Ni	0.29
Pb	**0.49**
Zn	0.10

PAHs	PC 1 (98.8% of variance)
Acenaphthene	0.26
Acenaphthylene	0.18
Anthracene	0.26
Benz(a)anthracene	**0.28**
Benzo(a)pyrene	0.26
Benzo(b)fluoranthene	0.27
Benzo(ghi)perylene	0.23
Benzo(k)fluoranthene	0.26
Chrysene	**0.28**
Dibenzo(ah)anthacene	0.20
Fluoranthene	**0.30**
Fluorene	0.25
Indeno(1,2,3 cd)pyrene	0.24
Naphthalene	0.10
Phenanthrene	0.26
Pyrene	**0.29**

Table 4.6 Models describing metal and PAH concentrations in dandelion leaves collected within 3 m of the Canadian Pacific Railway versus ~50 m into the adjacent forest as well as grain collected along the Canadian Pacific Railway versus store-bought reference samples. Models where confidence intervals do not overlap zero are in bold.

Model Forage / Contaminant	Response	Predictor	Beta	95% CI	Adjusted R^2
Dandelion / Metals	PC1[1]	**Railway**	**1.44**	**0.81, 2.08**	0.81
Dandelion / PAHs	PC1[2]	**Railway**	**3.34**	**1.51, 5.17**	0.73
Grain / Metals	PC1[3]	**Railway**	**5.75**	**4.58, 6.91**	0.96
Grain / PAHs	PC1[4]	**Railway**	**16.82**	**11.57, 22.07**	0.92

[1] molybdenum
[2] anthracene, chrysene, fluoranthene, fluorene, phenanthrene, and pyrene
[3] iron, lead, chromium
[4] fluoranthene, pyrene, benzo[a]anthracene, chrysene

Table 4.7 Principal components analysis of metal concentrations in different sections of grizzly bear hair (average, tip, root). Hair samples were collected during spring GPS-collaring for another study in Banff and Yoho National Parks, Canada (2012-2015).

Hair Section	Component 1	Component 2	Cumulative %
Average	55.33%	24.75%	80.08%
Tip	53.73%	26.06%	79.79%
Root	51.25%	32.71%	83.96%

Average

Metals	PC 1	PC 2
Al	0.00	0.23
Cd	-0.21	**0.67**
Cr	0.16	0.21
Cu	0.07	0.17
Fe	0.09	0.33
Mn	0.02	0.15
Mo	**0.94**	-0.02
Ni	0.06	-0.02
Pb	0.15	**0.53**
Zn	0.06	0.09

Tip

Metals	PC 1	PC 2
Al	0.17	0.32
Cd	-0.15	**0.66**
Cr	0.26	0.33
Cu	0.09	0.07
Fe	0.24	**0.41**
Mn	0.12	0.04
Mo	**0.88**	-0.23
Ni	0.05	-0.03
Pb	0.14	0.35
Zn	0.01	0.10

Root

Metals	PC 1	PC 2
Al	**0.35**	0.18
Cd	0.33	**0.40**

Cr	0.11	-0.04
Cu	0.07	0.06
Fe	**0.37**	0.06
Mn	**0.41**	0.27
Mo	**0.48**	**-0.84**
Ni	0.00	0.00
Pb	**0.46**	0.16
Zn	0.02	0.04

Table 4.8 Top models describing metal concentrations in different sections of grizzly bear hair (average, tip, root) as a function of sex, age class, habitat use (major transportation corridor, secondary roads, ski hills, gravel pits, and old landfill sites) and mean elevation by season (combined, summer, fall). Models where confidence intervals do not overlap zero are in bold.

Model Hair/Habitat Use	Response	Predictor	Beta	95% CI	Adjusted R^2
Average/Combined	PC1[1]	**Sex (male)**	**0.97**	**0.30, 1.64**	0.30
	PC2[2]	Null	-	-	-
Tip/Summer	PC1[3]	**Sex (male)**	**1.24**	**0.52, 1.96**	0.39
	PC2[4]	Null	-	-	-
Root/Fall	PC1[5]	**Ski Hills**	**0.53**	**0.08, 0.98**	0.24
	PC2[6]	Ski Hills	0.27	-0.07, 0.68	0.38
		Elevation	0.26	-0.33, 0.59	
		Transportation Corridor	-0.30	-0.68, 0.26	
		Secondary Roads	-0.41	-0.71, 0.01	

[1] molybdenum

[2] cadmium and lead

[3] molybdenum

[4] cadmium and iron

[5] aluminum, iron, lead, manganese, and molybdenum

[6] cadmium

Chapter 5: General Discussion

The motivation for this study stemmed from an increase in bear-train collisions in the last two decades in Canada's Rocky Mountain Parks. My research is a component of the broader Grizzly Bear Conservation Initiative, a collaborative project with the University of Alberta, Canadian Pacific Railway, and Parks Canada to identify and mitigate the causes of bear-train collisions. Broadly, my dissertation objectives were to increase understanding on how railways influence grizzly bears in Banff and Yoho National Parks in Western Canada and provide mitigation suggestions to reduce railway-associated mortality. To do this, I (a) investigated the abundance and phenology of bear attracting plants near the railway, (b) identified spatiotemporal factors associated with grizzly bear railway use and movement and investigated if these areas were correlated with locations of past bear-train collisions, and (c) measured metal and PAH concentrations in railway-associated forage and investigated if bears who frequented the railway had comparatively higher concentrations of these contaminants in their fur. In this final chapter, I will summarize and interpret the main results from chapters 2-4 and then discuss the corresponding management implications for grizzly bear conservation in the region. I will conclude with some limitations of the study, suggestions for future research, and a final synthesis of the dissertation.

Summary of Results

The abundance of palatable forage near the railway may attract bears and other wildlife, including ungulates. For bears, collisions with trains could result from an attraction to both vegetation and carcasses that result from train strikes on other animals. Further, the availability of forage may change with season and elevation which could contribute to the timing and location of railway use for bears and other wildlife. In chapter 2, I found that the forest edge next to the railway had increased species diversity, richness, and total cover of forage plants as well as accelerated phenology compared to an adjacent forest. I also found that fruiting species produced comparatively more berries near the railway, particularly early in the season and at higher elevations. Buffaloberry, a major fall food source for bears in the region, demonstrated earlier ripening and higher sugar content proximal to the railway, but this relationship was negatively associated with elevation.

The identification of spatiotemporal factors that contribute to use of the railway and risks of mortality by bears has received limited study to date. This information could be useful in developing mitigation recommendations that would reduce collision vulnerability for bears and other wildlife. In chapter 3, I found that there was strong seasonality in railway use, with highest use occurring primarily in the spring and then fall. Bears tended to use the railway in daylight hours versus at night or crepuscular periods. I identified that railway use increased in areas with lower landscape-scale habitat quality, where terrain was locally rugged, close to railway sidings (a low-speed section of track), and at intermediary distances from towns, highways, and trails. In the analysis of movement types, I found that bears were more likely to enter the railway where there was high habitat productivity, close to railway sidings, and in locations constrained by local rugged terrain. For bears that demonstrated prolonged use of the railway (i.e. continue movements), they tended to do so where terrain was rugged on a broad scale. Lastly, I established that step lengths were consistently shorter when bears were on versus off the railway.

The contamination of railway-associated forage by metals, PAHs, or mycotoxins could exert negative effects on wildlife who forage near railways. Although little studied, exposure to these contaminants could be particularly detrimental in protected areas where wildlife and habitats are more vulnerable. In chapter 4, I found that metal and PAH concentrations were higher for rail-side dandelion and train-spilled grain compared to reference samples that were taken away from the railway. For metals, this difference was most pronounced for molybdenum in dandelion, and lead, iron, and chromium in grain. I also found that train-spilled grain contained a higher proportion of hazardous high weight PAHs on average than rail-side dandelion. Mycotoxin production in grain samples was uncommon and occurred at very low levels. For the examination of metal concentrations in grizzly bear hair, I found that male bears had higher mean concentrations than females, and this difference was greatest for molybdenum. I did not find that bears who frequented the railway had higher levels of metal concentrations in their fur, but I did find a significant positive association for the use of ski hills in the fall, particularly for the metals aluminum, iron, lead, manganese, and molybdenum.

Contribution of Research and Interpretation of Results

A primary contribution of my research is that I found an increase in the abundance, phenology, and productivity of bear forage plants located near the railway relative to the adjacent forest (chapter 2). This vegetation enhancement is a potential attractant to bears which may increase the risk of train strikes. Light, heat, and disturbance from the railway enhances vegetative growth for some species, which is particularly influential in the mountain parks where dense forest cover persists from historic fire suppression (Sachro et al. 2005). Several other studies have demonstrated similar vegetative enhancement along linear features such as roadsides (Gelbard and Belnap 2003, Rentch et al. 2005, Roever et al. 2008), power lines (Eldegard et al. 2015, Lampinen et al. 2015, Friesen 2016), and trails (Ballantyne and Pickering 2015), as well as other human-use areas associated with disturbance like ski hills (Burt and Rice 2009) and clear-cuts (Nielsen et al. 2004b). Specifically, vegetative growth along forest edges are known to attract bears, in part due to the proximity to hiding cover (Nielsen 2004a, Merkle et al. 2011, Stewart et al. 2013). However, forest edges are also known to increase the risk of human-caused mortality, for example, edges that are associated with roads, forestry, and agriculture (Nielsen et al. 2006, Northrup et al. 2012, Takahata et al. 2014).

Habitat selection by grizzly bears changes seasonally and is largely dictated by the phenology of forage plants (Hamer and Herrero 1987a, Turney and Roberts 2004). Plant availability is particularly important for bears in the mountain parks who are comparatively reliant on vegetation and considered protein-limited (López-Alfaro et al. 2015). The availability of railway-associated plants may therefore reflect the strong seasonal pattern in railway selection by bears in the spring and fall when food resources are otherwise limited on the landscape (Gibeau and Herrero 1998, Friesen 2016, Pollock et al. In review). Due to a relative lack of open habitats in the mountain parks, the railway may be one of the first snow-free locations where important early season plants like dandelion, horsetail, and grasses grow (Munro 2000; Roever et al. 2008a,b). Horsetail, a plant I found in high abundance near the railway, may be particularly beneficial to bears in the spring, when its protein content can exceed 20% and structural fiber is low, increasing its digestibility (Hamer and Herrero 1987a, Munro et al. 2006). Bears, post-hibernation, can be highly motivated to obtain these spring food resources, as demonstrated by the selection of habitats near roads at this time of year (Mace et al. 1996, Roever et al. 2008a, Graham et al. 2010).

I found high berry productivity near the railway, most notably for buffaloberry, likely due to the strong negative association between fruit production and canopy cover (Hamer 1996). Buffaloberries are the main late season food source for grizzly bears in the region because they are high in soluble carbohydrate, allowing bears to increase fat reserves for winter hibernation (Hamer and Herrero 1987a, McLellan and Hovey 1995, Munro et al. 2006). Although habitats with berry production generally increase fitness for grizzly bears, this is not the case when these habitats occur in close proximity to humans (McLellan 2015). A bear's dependency on berry consumption in the fall generally increases the likelihood of human-bear encounters, which contributes to various sources of human-caused mortality (Benn and Herrero 2002, Lamb et al. 2016). Similarly, fruit productivity along railways could create ecological traps for bears which may be demonstrated by a peak in grizzly bear–train collisions in the fall.

At lower elevation locations, I found that better conditions for berry production occurred at the forest edge, whereas at higher elevations, availability was extended closer to the railway. This result was likely due to temperature differences affecting early maturation and senescence of fruits. In contrast, the enhancing effect of the rail was generally greater at lower elevations for spring forage plants. Bears in mountainous landscapes will follow the availability of forage plants from low to high elevations as the summer progresses in an effort to access foods at optimal phenological stages (Hamer and Herrero 1987a, Waller and Mace 1997, Munro et al. 2006). Contrary to my prediction, I did not find that greater train strikes occurred at lower elevations in the spring and at higher elevations in the fall. However, if rail-side vegetation enhances the growth of critical foods at critical times, it may increase the attraction and therefore collision risk for bears.

Another major contribution of my research is that I found spatial and temporal characteristics associated with grizzly bear railway use (Chapter 3), which can help to identify times and places where railway mitigation may be most beneficial. Primarily, bears selected for the railway in areas where there was evidence for forage availability (natural or anthropogenic). As established in Chapter 2, there are various bear-attracting plants that are seasonally available near the railway (above), which may account for increased railway use in the spring and fall by bears in the study area. The selection for railway locations with increased shrub and herbaceous cover provide support that bears are seeking out areas with higher plant forage. I identified a strong and consistent selection for railway sidings, likely because leaking grain accumulates where trains slow down (Gangadharan et al. 2017), which occurs most predictably at railway sidings where trains stop to allow another train to pass. In a concurrent study, train-spilled grain was most abundant in the fall and winter months, which correlated with higher export rates (Gangadaharan et al. 2017). The attraction to spilled grain may be another reason why bears select for the railway in the fall. Spilled grains such as wheat and lentils could offer an important supplementary food source to this population of bears (Garshelis et al. 2005, Lopez-Alfaro et al. 2015, Gangadharan et al. 2017). I found that bears used the railway in areas with low landscape-scale terrain wetness. Terrain wetness has been used an indicator of bear occurrence (Turney and Roberts 2004, Chetkiewicz and Boyce 2009) because it can influence the availability of major foods for grizzly bears, e.g. herbaceous plants and ungulates (Nielsen et al. 2004c, 2017; Munro et al. 2006). The use of the railway in areas with low terrain wetness at the landscape-scale suggests that bears may perceive the railway as comparatively high-quality habitat in a resource deficient area.

I found that bears used shorter steps when they were on versus off the railway and when near railway sidings, which supports the hypothesis that bears are attracted to the railway for foraging opportunities. Shorter steps are frequently associated with foraging behaviour, both generally (Turchin 1998), and in other studies of grizzly bears (Roever et al. 2010, Graham and Stenhouse 2014, Kite et al. 2016). Shorter step lengths denote foraging because animals tend to persist in habitats where they can meet their nutritional needs (McLoughlin et al. 2000), whereas longer step lengths are indicative of travel and directed movement (Turchin 1998). I found that bears exhibited comparatively longer step lengths as they moved through more rugged terrain which may suggest a perception of risk in these areas. An increase in travel speed can occur in part as a behavioural response to fear (Dussault et al. 2007, Leblond et al. 2013), such as when crossing transportation corridors (Dussault et al. 2007, Roever et al. 2010, Leblond et al. 2013), when moving near urban areas (Karelus et al. 2017), and as distance from hiding cover increases (Brown et al. 2018).

Alternatively, bears may be using the railway as an energy-efficient travel route through rugged terrain. In mountainous regions, rugged areas can form narrow corridors, which can constrain wildlife movement (Alexander and Waters 2000, Whittington et al. 2004). Bears who need to navigate these areas while avoiding people may achieve this by travelling along a relatively flat railway. Wolves have been shown to use the railway for travel, predominantly in the winter months when snow depths are high (Callaghan and Paquet 1996, Whittington et al. 2004, 2005). Similarly, ungulates such as elk and moose use railways to avoid deep snow conditions and conserve energy (Huggard 1993, Eriksson 2014). Like bears, wolves and ungulates have a high mortality rate along the railway in the mountain parks (Wells et al. 1999, Gilhooly 2016, Dorsey et al. 2017).

I did not expect the lack of correlation between locations where animals are most likely to use or move along the railway and locations of past bear-train strikes. Identifying where animals concentrate their use and movement has been effective at reducing road-associated mortality (Dussault et al. 2007, Lewis et al. 2011, Baigas et al. 2017) as evidenced through the placement of highway crossing structures (Clevenger et al. 2002, Schuster et al. 2013, Loraamm and Downs 2016) and areas designated for speed reductions and warning systems (Baigas et al. 2017, Backs et al. 2017, Seiler and Olsson 2017). Interpretations for the lack of correlation between railway use and train strikes in my study area may be that other spatiotemporal factors are more important contributors to collision vulnerability, e.g. track curvature and poor site lines, which may limit train detection (Burley 2015). Secondly, it could be that bears that frequently use the railway have learned to exploit it effectively and safely.

A final major contribution of my research is that I identified railway-associated attractants as potential toxicants for bears (Chapter 4), which resulted in some specific mitigation suggestions to reduce contaminant exposure in the mountain national parks. As discussed in Chapter 2, dandelion is an important food source for grizzly bears and, like several other bear forage plants, is ubiquitous in the railway environment (Hamer and Herrero 1987a, Munro et al. 2006, Pollock et al. 2017). In Chapter 3, I discussed that in addition to rail-side herbaceous forage, bears are known to seek out train-spilled grain and frequent railway sidings to do so. The elevated levels of metals and PAHs that I found in both food sources, but most notably for train-spilled grain, could pose a health risk for bears and other wildlife that repeatedly ingest contaminated forage.

Specifically, dandelion tends to accumulate molybdenum in aboveground parts, both generally, and in this study (Wilkomirski et al. 2011, Curlik et al., 2016). These levels do not appear to cause problems for animals with single stomachs, like bears, but mean concentrations in dandelion at the railway could cause molybdenosis for ruminants with repeated exposure (Frank 1998, Shen et al. 2010). For train-spilled grain, mean lead levels were approximately three times higher than maximum tolerable levels (MTL) established for swine (NRC 2005), yet below soil remediation guidelines (AEP 2016). Lead is highly toxic with varying adverse effects on organisms (Rattner et al. 2008) and is well known for its decimating influence on eagles and other scavenging raptor populations (Mateo 2009, Nadjafzadeh et al. 2013, Isomursu et al.

2018). Demonstrating an opposite trend, mean chromium levels in train-spilled grain were slightly below swine MTL (NRC 2005), yet above proposed soil remediation guidelines (AEP 2016). Federal government agencies have named chromium and lead as priority pollutants, meaning that their toxicity to the environment and organisms impose regulatory limits in both the US (EPA 1982) and Canada (CEPA 1999). I found high levels of polycyclic hydrocarbons (PAHs), another set of priority pollutants, in train-spilled grain. Several PAHs were at concentrations above toxicity thresholds (Brooks 2004). For benzo[a]pyrene, a well-studied PAH and known carcinogen, mean concentrations were ~ 6 times higher than recommended in soils for areas with high ecological value such as national parks (CCME 1999).

The lack of correlation between metal concentrations in bear hair and the frequency of railway use was unexpected considering I found elevated levels of metals in railway-associated forage. It is possible that because grizzly bears are opportunistic omnivores that use a wide variety of habitats (Noss et al. 1996), the consumption of railway foods is minimal overall when considering bear diet on the broader landscape. In addition, due to their wide-ranging nature, it could be that several different habitat-types are contributing to the variation in metal concentrations. Further, the magnitude of contamination and hence toxicity to wildlife depends on several factors such as the frequency, dose, and duration of exposure to the contaminant (Tchounwou et al. 2012, Mayfield et al. 2013). It may be that none of these factors were at levels that would demonstrate a correlation with this specific type of habitat use. For example, bears feeding along the railway are undoubtedly disturbed by the repeated passing of trains and potentially railway personnel, which can limit both the frequency and duration of exposure. In addition, the contaminant dose may vary spatially as evidenced by the high variation in our samples. Locations along the railway like railway sidings, where trains are stopped for extended periods, may have higher contamination than other areas along the railway (see Wilkomirski et al. 2011). Plant species that grow along the railway and hyperaccumulate metals would change through both space and time (Giacomino et al. 2016) as would the deposition of grain (Gangadharan et al. 2017), both influencing exposure by bears.

The correlation I found between the use of ski hills by bears and metal concentrations in their fur is a novel finding with management implications for ski resorts, particularly in national parks and protected areas. The correlation occurred for metal concentrations specifically at the root of the hair, which is considered most reliably linked to internal contamination through diet because hair segments further from the root have had longer contact with exogenous sources (e.g. Godfrey et al. 2012). Although bear viewing tours are popular for many ski resorts in North America (Needham et al. 2004, Parks Canada 2015), it is likely that bears are ingesting contaminated vegetation while foraging there. However, the correlation I found was for fall use of ski hills only. This could be due to seasonal, species-specific contamination, e.g. berry-producing plants (Barcan et al. 1998), or simply that bears are doubling their caloric intake during the hyperphagic period (Nielsen et al. 2004, Stenvinkel et al. 2013). There are several potential sources for metal contamination on ski hills including the use of fertilizers and herbicides, snowmaking operations including contaminated water sources, and general machinery operations such as grooming and ski run clearing (Eydal 1997, Parks Canada 2015, Pintaldi et al. 2017). Future work investigating contaminant levels for vegetation growing on ski hills and mechanisms of contamination offers an exciting area for future research.

Management Implications and Recommendations

The results from my dissertation support several management recommendations that will assist with grizzly bear conservation in the region, both through the reduction of railway-associated mortality and through a reduction in exposure to contaminants in the national park. My results demonstrate that the railway can increase plant diversity, abundance, productivity, and accelerate the phenology of important bear foods, potentially increasing strike risk. Although location-based mitigation suggestions may be difficult due to species-specific and variable responses of vegetation, vegetation enhancement along the railway emphasizes the need to monitor and manage the growth of bear-attracting plants, particularly in high risk areas like mortality hotspots and at locations where other factors increase the risk of collisions (Rea et al. 2003, 2010, Meisingset et al. 2014). Encouraging the growth of non-palatable vegetation at the railway may minimize attraction, both for bears and for ungulates, which bears may target as scavenging opportunities. Vulnerability to train collisions by bears may be further reduced by improving the quality and quantity of grizzly bear forage away from the railway in safer locations, such as by forest thinning, the creation of forest gaps, the intentional planting of fruiting shrubs, or prescribed fire (Nielsen et al. 2004, Block et al. 2016, Braid et al. 2016).

Secondly, my results provided some strong spatial and temporal patterns of railway use and movement by grizzly bears. Bears are most likely to use the railway in the spring and fall months, in locations where foraging opportunities occur (natural or train-spilled grain), in areas with rugged topography, and where there is poor landscape-scale habitat quality. Seasonality in railway use by bears prioritizes mitigation to the spring and fall when trains are most likely to encounter bears (e.g. Kasworm and Manley 1990). Further, the removal of railway attractants such as vegetation (above) and train-spilled grain in areas where collision risk is heightened, e.g. mortality hotspots, or in areas with high railway use by bears, e.g. railway sidings. The selection of sidings by bears highlights the necessity to monitor and promptly remove grain spills at these locations due to a higher deposition rate (Gangadharan et al. 2017). In locations where bears are known to use the railway such as in rugged terrain where there are few alternate travel routes, train-based mitigation (reducing speed, sounding horns; Carvalho et al. 2017) or track-based mitigation (warning systems; Backs et al. 2017) should be considered. A complementary approach is to create safe, alternate travel corridors where functional movement is constrained near the railway and to limit human-use trails and other developments in these areas (Whittington et al. 2004; Pengelly and Hamer, unpublished data). Lastly, because bears tended to use the railway in areas where landscape-scale habitat quality was lower, managers should consider mitigation measures at broader scales, such as improving habitat to encourage movements away from the railway (above).

My final chapter revealed elevated metal and PAH concentrations in railway-associated forage, especially for train-spilled grain. The removal of train-spilled grain should be prioritized, particularly at railway sidings where a) bears frequent, b) deposition is greater, and c) contamination is likely higher (see Wilkomirski et al. 2011). In addition, efforts to reduce or prohibit the growth of plants that hyperaccumulate metals along railways would not only benefit bear health but could also reduce risks for ungulate species (e.g. molybdenosis; Shen et al. 2010). Although, railways have implemented methods to reduce grain spills like hopper car refurbishments (Dorsey 2011), I urge the continuation of monitoring programs and regular train car maintenance. Due to the high levels of PAHs in railway grain and the attraction by bears and other wildlife to it, trains passing through national parks and protected areas should not only be regularly monitored for the leakage of grain, but also for the leakage of lubricants, grease, and oils, which are known sources of PAHs (Wilkomirski et al. 2011). Further, lubricating stations along railways should be maintained to minimize the spread of grease. In areas of repeated contamination, e.g. railway sidings, partial exclusion fencing could be considered to prohibit wildlife access. In protected areas, the use of organic herbicides and pesticides should be encouraged where wildlife are known to forage (Dayan et al. 2009). The novel finding of metal exposure via ski hill-associated forage leads to the necessity to understand mechanisms of contamination, including testing of soil, plants, and water sources. Prohibiting access to wildlife where ski hill operations are concentrated may be warranted to limit exposure to various contaminants.

Limitations and Future Research

In the following section, I summarize the main limitations from my work and suggest ideas for future research. A primary limitation in my study was low sample size across chapters. For chapter 3, both in the number of collision events (17) and the number of bears (3) that frequently used the rail (> 10% of railway GPS locations). For chapter 4, both in the number of aggregate samples collected for dandelion (8) and grain (7) and the number of bears used for the metal analysis (20). These low sample sizes cause high interpretive reliance on a few individuals or samples, which may not represent the broader population or system as a whole. However, many wildlife studies are characterized by low sample size, particularly for wide-ranging animals such as bears (Bissonette 1999). A more generalized determination of the factors that contribute to railway use and mortality by grizzly bears may be through a collaborative approach to synthesize data across railways and regions. Although sample size was low and variation was high in contaminant concentrations for grain and vegetation samples, I was nonetheless able to determine which contaminants were present and conclude that, for grain in particular, railway attractants have the potential to harbor high concentrations of both metals and PAHs. More intensive testing of grain and vegetation samples taken from the railway would give a better indication of the risk these foods pose to bear health and may also help to predict locations for higher risk of contamination, e.g. railway sidings (Wilkomirski et al. 2011). Similarly, a way to further enhance understanding of bear habitat use and exposure to metals would be to collect additional hair samples from collared bears in other regions. This future work would be relatively easy to undertake as only one or two guard hairs are required and hair samples are routinely taken from bears during the collaring process. Lastly, I am intrigued by the prospect of contaminant testing on ski hills. I unfortunately did not collect vegetation samples that would support my finding that bears that forage on ski hills have higher metal contamination, but I suggest this could be an interesting project for another researcher.

A second limitation that I realized in hindsight, is the absence of important explanatory variables that would have allowed for more predictive models on railway use and mortality. In chapter 2, I did not measure several variables that are important to plant growth and community structure, such as soil conditions (Molina-Venegas 2016) and climatic variables (Smith-Ramirez and Armesto 1994, Schroder et al. 2014). Future work that includes location-based covariates like these would help to identify the fine-scale mechanisms behind enhanced species-specific plant growth and help to identify locations of higher mortality risk for bears via vegetation attractants. Following from this, railway selection results from chapter 3 would have been strengthened to include field-based vegetation measures. My use of GIS-derived habitat variables would have underestimated fluctuations of plant productivity (Boyce et al. 2002, Nielsen et al. 2010) that undoubtedly changed over the data collection period that could affect railway use by bears. For example, bears can select habitats near humans more often in years of poor food availability (e.g. Mattson et al. 1992, Baruch-Mordo et al. 2014, Obbard et al. 2014). Including measures of rail-based attractants in railway selection and mortality models would provide a more accurate picture of strike risk for grizzly bears.

Summary

In summary, my results suggest that the attraction to and use of the railway by grizzly bears in Canada’s Rocky Mountain Parks involves many interacting factors that can both benefit and threaten the persistence of this vulnerable population. The first factor is that bears use the railway to forage via vegetation enhancement at the railway through increased diversity, abundance, productivity, and phenology of plants consumed by bears. An additional attractant that draws bears to the railway is train-spilled grain which was reflected in their persistent selection of railway sidings, areas for potential grain accumulation. The seasonal fluctuation of these attractants likely correlates with the strong seasonality in railway use by bears. The second factor is that bears use the railway as an easy travel corridor through rugged terrain, which further highlights how landscape-scale variables can influence specific areas of railway use and movement. Threats to bears can emanate from each of these seemingly-beneficial factors, i.e. forage opportunity and travel efficiency, if they increase the risk of mortality from collisions, or if they increase exposure to railway-based contaminants. These threats are likely to be most severe when multiple forms converge in space or time. Given the global occurrence of wildlife-train collisions and the increasing demand of railway transport, I encourage others to examine wildlife use of railways to broaden understanding, and ultimately, to mitigate railway-associated mortality. Mitigating train collision vulnerability will contribute to the conservation of grizzly bears in North America and many other species worldwide.

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