Individual and Seasonal Variation in Grizzly Bear Selection for a Railway and other Linear Features in Banff National Park, Canada

by

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Abstract

Mortality caused by collisions with trains affects numerous species globally and has increased recently to threaten the grizzly bear (*Ursus arctos*) population protected in Banff and Yoho National Parks, Canada. Although train collisions are the ultimate cause of mortality, the more proximate processes that cause grizzly bears to use the railway are unclear. No previous study has assessed the relative strength of grizzly bear attraction to the railway compared to other linear features in the study area, including power lines, a secondary road and the right-of-way along the TransCanada Highway fence. According to local knowledge, male bears make greater use of the rail than females, but there has been no quantitative assessment of this putative tendency. I hypothesized that selection for the railway is strongest in spring and fall, when forage resources are limited. I also hypothesized that male bears would select the railway more strongly than females to increase one or more of forage selection, travel efficiency or access to social dominance and mating opportunities. Using GPS collar data collected by Parks Canada, I modeled individual and population-level resource selection functions to compare selection by feature type and season. I also conducted repeated vegetation sampling in each linear feature type and season to quantify the availability of bear forage. Percent cover of vegetation available to grizzly bears was higher in linear features than adjacent forests, lower on the rail than other feature types and lower in the fall than the spring. At the population level, grizzly bears increased selection for the railway in spring and fall and the power line in summer. I did not find evidence of consistent sexual segregation within or among linear features and selection for linear features was highly variable even within classes of individuals. My results suggest that individual experiences and attributes, as well as temporal and spatial features of local landscapes, have greater effects on attraction to the railway than sex or reproductive status. Logical management extensions include a focus on mitigation during the seasons of highest selection for the railway by grizzly bears (spring and fall). Maintenance of power lines should be scheduled to avoid summer months when selection by grizzly bears is strongest, to decrease the potential for human-bear conflict. Integration of this work with other components of a larger project at the University of Alberta will determine whether it is logical and feasible to target mitigation for specific individuals and locations where rail use is highest.

Preface

This thesis is an original work by Alyssa Friesen. Chapter 2 is intended for publication along with co-authors C. C. St. Clair and S. E. Nielsen. The GPS collar data used for this project was collected by the Parks Canada Agency (Banff, Alberta). C. C. St. Clair was the supervisory author and was involved in idea conception and manuscript revision.

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Chapter 1: Introduction

Grizzly bears (*Ursus arctos*) have been extirpated from much of their historic range in North America. As human settlement expanded towards the Western frontier of the continent during the early 1800s, grizzly bears were largely eliminated from their natural prairie habitat. Reduction in the size of populations and the species range occurred due to over-hunting, loss of habitat due to agricultural expansion, reduction of prey availability, and intolerance towards large carnivores. Although attitudes towards grizzly bears and other large carnivores have shifted, many grizzly bears at the edge of the species range exist in small, fragmented populations that are vulnerable to habitat loss and human-related mortality (McLellan et al. 1998). These attributes describe the grizzly bear populations of Alberta which comprise the southeastern fringe of the species range in Canada and are considered threatened (ASRD 2010).

One such population of grizzly bears is protected in Banff and Yoho National Parks, which is among the most highly developed areas where the species exists in North America (Gibeau et al. 2002). Banff National Park (hereafter, Banff), the birthplace of the National Parks system in Canada, is characterized by high human use, with over 3 million visitors to the park each year (Parks Canada 2015). Banff is fragmented by a major transportation corridor (described by Bélisle and St. Clair 2001), which includes the TransCanada Highway and the Canadian Pacific Rail line which was built from 1882 to 1885 and is an integral component of the history of Banff (Holyrod and Van Tighem 1983).

Historically, the majority of reported grizzly bear mortalities have been human-related (Benn and Hererro 2002) and recently railway mortality has increased to become the leading cause of death (Bertch and Gibeau 2010). From 2000 - 2015, 13 individual grizzly bears were struck and killed by trains in Banff and Yoho National Parks (Gilhooly et al. in prep). Continued rail mortality at this rate is a concern for this small population which is naturally rare and wide-ranging (Kušta et al. 2011), has unusually low reproductive rates (Garshelis et al. 2005) and is protein limited (López-Alfaro et al. 2015). Rail mortality is a potential threat to the survival of grizzly bears in

Banff (Bertch and Gibeau 2010), but the behavioral processes that characterize railway use are unclear.

Grizzly bears are likely attracted to the railway for a variety of reasons, including forage availability, increased travel efficiency, or opportunities to exercise social dominance and secure mates, with the ultimate goal of increasing fitness (Berger-Tal et al. 2011). The railway may provide important foraging opportunities for grizzly bears in the form of vegetative enhancement, which is known to occur along roads (Roever et al. 2008a) and power lines (Eldegard et al. 2015). Rail-specific attractants, including grain spilled by trains (Gangadharan et al., in prep) and rail-killed ungulates (Gilhooly et al., in prep), may also be an important food source for this protein-limited population (López-Alfaro et al. 2015). A second reason grizzly bears may use the railway is to increase travel efficiency. The railway follows the bottom of the valley, which is a natural movement corridor for carnivores (Noss et al. 1996). A final reason male grizzly bears may use the railway is to increase access to mating or competitive exclusion opportunities. On the other hand, female grizzly bears with dependent offspring, likely avoid features used by males to protect their cubs from sexually selected infanticide. While these behaviors likely contribute to railway use, none singularly explains the increase in mortality observed in Banff. And although many studies have examined the attraction of roads for grizzly bears (e.g. Roever et al. 2008b; Graham et al. 2010; Northrup et al. 2012), few have investigated selection for the railway.

The University of Alberta Grizzly Bear Research and Mitigation Project, of which this thesis is a component, was developed to identify the root causes of, and effective mitigation for, train strikes on grizzly bears in Banff. The project has four key objectives; (a) quantify environmental variables that contribute to rail strike vulnerability, (b) describe bear behavior that increases vulnerability to collisions with trains, (c) integrate environmental and behavioral components to predict locations and individuals at high risk of rail mortality, and (d) identify management and mitigation strategies to reduce train strikes on grizzly bears. Reducing railway mortality of grizzly bears in Banff will support the persistence of this population, protecting an iconic species for future generations in accordance with a core mandate of the Parks Canada Agency.

My thesis supports the second objective of the University of Alberta Grizzly Bear Research and Mitigation Project by describing grizzly bear selection for linear features in the study area. No assessment has been made of the relative attraction of the railway compared to other linear features that constitute the transportation corridor in Banff. Alternate linear features, including power lines, secondary roads, and the right-of-way along the TransCanada Highway wildlife fence (described by Bélisle and St. Clair 2001), likely afford grizzly bears similar benefits to those attributed to the railway. Comparing grizzly bear selection for the railway with alternate linear features could determine whether the railway is uniquely attractive for grizzly bears and illuminate the importance of rail-specific attractants.

The purpose of this thesis was to investigate grizzly bear use of anthropogenic linear features, thereby comprising one part of the larger study at the University of Alberta (above). My first objective was to compare vegetative enhancement along the railway to rights-of-way along power lines, the Trans-Canada Highway wildlife fence, and a secondary road. My second objective was to compare grizzly bear selection for the railway to other linear features by season. Finally, I investigated whether grizzly bears exhibit sexual segregation in linear feature use. My goal was to determine when and for which grizzly bears the railway is uniquely attractive and the role that vegetation plays as an attractant. I sought to better understand the processes that influence grizzly bear use of the railway to contribute to management recommendations for reducing rail mortalities.

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Chapter 2: Grizzly bear selection for a railway in mountain parks varies by season but not sex[1]

2.1. Introduction

Collisions between vehicles and wildlife on roads and railways negatively impact numerous species globally and may threaten the persistence of small populations of rare species (Kuŝta et al. 2011; Van der Ree et al. 2015). These diverse species include Asiatic elephants (*Elephas maximus*) in India (Dasgupta and Ghosh 2015), mountain pygmy-possums (*Burramys parvus*) in Australia (Van der Ree et al. 2009), great crested newts (*Triturus cristatus*) in Great Britain (Ward et al. 2015) and grizzly bears (*Ursus arctos*) in Canada (Benn and Herrero 2002). For grizzly bears in Banff National Park (hereafter, Banff), rail mortality increased between 2000 and 2010 to become the leading cause of death (Bertch and Gibeau 2010). This population exhibits unusually slow reproductive rates via high age of first reproduction, small litter size and long intervals between litters (Garshelis et al. 2005). In Banff, local knowledge suggests that rail use is higher in spring and fall and higher for male bears, despite similar or higher mortality rates for female bears (Table 1). However, these patterns have not been quantified or compared to selection for other linear features in the area that are used by bears, which include a power line, a secondary road, and the right-of-way along the wildlife fence parallel to the Trans-Canada Highway (described by Bélisle and St. Clair 2001). Comparing selection for the railway to the three other kinds of linear features in the study area could clarify whether the railway is uniquely attractive to grizzly bears, determine the relative importance of rail-specific attractants to collision vulnerability and identify sex-specific differences in selection for the railway. This kind of information will be needed to support mitigation that is both effective and efficient.

One of the most plausible reasons that bears use the railway, despite risk of mortality there, is that it provides important foraging opportunities. Vegetation, including disturbance-tolerant forbs and berry producing shrubs, may be enhanced in rights-of-way along the railway (Gibeau and Herrero 1998) as it is in other linear features, such as roads (Roever et al. 2008a) and power lines (Eldegard et al. 2015). In addition to

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[1] This chapter is intended for publication with primary author A.J. Friesen and co-authors C. C. St. Clair and S. E. Nielsen.

enhanced vegetation, wildlife may be attracted to the railway to forage on spilled grain (Gibeau and Herrero 1998; Gangadharan et al., in prep) and rail-killed ungulates (Gilhooly et al., in prep). In sexually dimorphic species, males and females have different nutrient requirements, which could produce sex-specific habitat selection according to the forage selection hypothesis (Ruckstuhl and Neuhaus 2005). Sexually-dimorphic males invest in growth to increase reproductive success (reviewed by Isaac 2005), with mature male grizzly bears weighing up to 50% more than mature females (Bartareau et al. 2011). Due to their larger size, male mammals require greater quantities of forage than females, which has been documented in African elephants (*Loxodonta Africana*; Shannon et al. 2006) and Australian fur seals (*Arctocephalus pusillus*; Kernaléguen et al. 2015), and potentially better quality forage (e.g., Rode et al. 2001). It follows that male grizzly bears would be especially attracted to enhanced foraging opportunities along a railway. However, enhanced foraging opportunities may also benefit lactating females, which have much higher nutritional demands than non-lactating bears of a similar size (Farley and Robbins 1995; López-Alfaro et al. 2013).This attraction is likely higher for all bears in spring and fall when alternative resources are scarce. During the fall bears also require rapid caloric intake to sustain mass gain prior to hibernation (Gibeau and Herrero 1998, López-Alfaro et al. 2013).

A second reason grizzly bears may use the railway is to increase travel efficiency. Many carnivores, including wolves (*Canis lupus*; Ehlers et al. 2014), cougars (*Puma concolor*; Dickson et al. 2005) and bears (Roever et al. 2010) are believed to use linear features to travel between high quality habitat patches and to search for prey. These features are often constructed along valley bottoms, which are already natural movement corridors for carnivores (Noss et al. 1996; Whittington et al., 2005). Further efficiency of travel on a railway may result from inherent limits on changes in elevation and sinuosity, due to track infrastructure and train length. In sexually dimorphic species, males may have a greater need for travel efficiency than females because they typically have larger home ranges (e.g., Harestad and Bunnell 1979; Dahle and Swenson 2003; Edwards et al. 2013). Male mammals may also support larger home ranges with more flexible movement behavior (e.g., as occurs in African elephants; Shannon et al. 2010) because they are not constrained by offspring mobility. All of these characteristics would be expected to contribute to movement patterns of male grizzly bears, which have home ranges as large as 2740 km^2 that are as much as 26.9 times larger than females (Stevens and Gibeau 2005).

A final reason that grizzly bears may select linear features is to facilitate reproductive and social dominance. For female mammals, offspring predation often includes both inter and intra-specific mortality and, for some species, including bears, sexually-selected infanticide (reviewed by Lukas and Huchard 2014) strongly affects habitat selection (Ruckstuhl and Neuhaus 2005; Steyaert et al. 2013; Steyaert et al. 2016). Females appear to abandon productive foraging habitat used by males to increase security of their offspring in caribou (*Rangifer tarandus*; Jakimchuk et al. 1987) and cougars (Keehner et al. 2015). Related to risk of predation via infanticide is despotism, wherein the highest-ranking bears simply exclude vulnerable individuals, which often includes sub-adults and females with dependent offspring (e.g., Libal et al. 2011; Elfström et al. 2014a). Defensive behaviors appear to peak during the spring mating season when males compete for estrous females (Dahle and Swenson 2003). At that same time, risk of infanticide increases for females with cubs (e.g., Wielgus and Bunnel 1995; Steyaert et al. 2013; Gosselin et al. 2016) and, so, they might be most likely to avoid rail use.

Any one or a combination of these three hypotheses could result in stronger selection by grizzly bears for use of the railway corridor, relative to other linear features. One or more of these hypotheses could also explain variation in selection among seasons and individuals of different sex and reproductive age classes. Based on our hypotheses (above), we predicted that: (a) all bears would increase selection for the rail, during spring and fall when forage availability is low (Gibeau and Herrero 1998); (b) that male bears would select rail corridors more than other linear features to maximize one or more of forage quantity, travel efficiency, and social dominance that could generate mating opportunities; and (c) that female bears with dependent offspring would select features that lacked male bears more strongly than solitary females to increase security. We tested these predictions by: (1) conducting repeated measures of vegetation to quantify and compare vegetative forage cover along four kinds of linear features; (2) comparing selection for the railway and other linear features by grizzly bears based on

GPS telemetry data and (3) comparing selection among three categories of individuals; male, females with dependent offspring and solitary females.

2.2. Materials and methods

The study occurred in Banff and Yoho National Parks in southern Alberta and British Columbia, Canada (51.10º N 115.55 Wº). These parks cover a total of 8178 km^2, encompass the settlements of Banff, Lake Louise, and Field, and are visited by over three million tourists annually (Parks Canada 2015). Banff and Yoho National Parks are bisected by a major transportation corridor (Bélisle and St. Clair 2001; Gibeau et al. 2002), which includes a fenced section of the Trans-Canada Highway, a railway line, power line and an unfenced secondary road, the Bow Valley Parkway, which is used primarily by tourists partly because of frequent and diverse wildlife sightings (Clevenger et al. 2003).

We quantified and compared cover of vegetative bear forage among and between linear feature types by performing repeated vegetation sampling at 28 locations from the East boundary of Banff to Lake Louise during spring, summer and fall in 2015 (Figure 1). At each of the 28 locations, where possible, we paired sample sites within 1500 m of one another on each of the four linear feature types (railway, power line, fence and road) for a total of 109 sites (Figure 1). Each site consisted of three 50 m transects parallel to the linear feature, which we named “middle,” “edge” and “forest” corresponding to their positions. We placed middle transects directly beneath power lines and approximately 1 m from the ballast rock on the railway, paved road surface, or fence. We placed edge transects at forest boundaries and forest transects at least 30 m into the adjacent forest. On each transect, we measured percent cover of 18 bear foods in 4 fixed plots of 1 m^2 and conducted repeated measurements in the same plot locations in each of the three bear seasons (spring, summer, fall).

Within each vegetation plot, we calculated the percent cover of 18 plants that are known to be locally consumed by bears (Table 2, Gunther et al. 2014) and recorded a phenological and reproductive code for each species (based on Dierschke 1972; Bater et al. 2010; Pollock et al., in prep). These codes were used to classify plants as being available, or not, as bear forage (e.g., dandelion is consumed at every phenological stage, whereas sweet vetch is targeted for its roots during early development and senescence; Hamer and Herrero 1987). For each plot and sampling date, we summed percent cover values of available bear food plants to estimate total cover of what we termed “edible bear food.” We compared percent cover of edible bear food among linear feature types, transect positions (middle, edge, and forest), and season and added plot ID as a random effect in regression models fitted with a zero-inflated beta distribution using R 3.1.2 (R Core Team 2014) and the ‘gamlss’ package (Rigby and Stasinopoulos 2005). In addition to main effects, we examined two-way interactions between feature type and each of season and transect position. Additionally, we estimated differences in total area of edible forage (over 100 m) among linear feature types, which differed partly as a function of feature width and infrastructure. We did this by calculating the mean cover of edible bear forage for middle transects and multiplying that value by vegetated area, which was the product of length (100 m) and site-specific width (the distance between middle and edge transect on the fence and double that distance on the road, power line and rail as measured in ArcMap 10.3.1; ESRI 2015).

We measured use of linear features by grizzly bears at the level of both population and individual (below) from a dataset collected by Parks Canada staff, who used culvert traps and free-range darting to capture and fit GPS collars to 26 individual grizzly bears between 2012 and 2015. For each captured bear, staff recorded or estimated body mass, age, and the presence of cubs, and set GPS collars to obtain location fixes every 2 hours, which were subsequently downloaded remotely. We used these locations to model resource selection functions (after Manly et al. 2002) at the level of both individuals and the population-level by examining several environmental variables that might predict habitat selection by grizzly bears and comparing their values for used GPS locations and available points (i.e., similar to Roever et al. 2010; Stewart et al. 2013).

Environmental variables were obtained from GIS layers provided by Parks Canada and extracted with the ‘raster’ package in R 3.1.2 (Hijmans 2015). These layers included a digital elevation model (hereafter elevation) from which we calculated Roughness (via circular moving windows with a 300 m radius) and estimated soil wetness (via the Compound Topographic Index [Gessler et al. 1995]) using the Geomorphometry and Gradient Metrics tool in ArcMap (Evans et al. 2012). We also used a land cover layer generated by the Foothills Model Forest Grizzly Bear Research Program (McDermid 2005) with ten classifications; upland trees, wetland trees, upland herbs, wetland herbs, shrubs, water, barren land, snow, cloud and shadow. We dummy coded each class as a zero or one for land cover classes at each of the available and used points. In addition to the two sets of landscape characteristics, we calculated approximate distances to each linear feature type (railway, power line, fence, and road) and the nearest forest edge, which we estimated by creating a polyline bordering forested and non-forested land cover types. All distance measurements were transformed using a decay function (Nielsen et al. 2009):

$$1 - \exp(-2 * distance(km))$$

This transformation accounted for the decreasing effect of a feature on an animal's behavior as distance to the feature increases, with 95% of the decay occurring within 1.5 km of the feature (Nielsen et al. 2009). Except for land cover classes (above), we standardized explanatory variables using a z-score transformation to enable comparison between variables measured in different units (Gotelli and Ellison 2013). We used Pearson's correlation coefficient to test for collinearity and used within models only variables that were not strongly correlated ($|r| < 0.7$).

We used these environmental variables to model a population-level RSF and included random intercepts for bear, year and season (using the lme4 package in R [Bates et al. 2014]) to identify the habitat variables for inclusion in each individual RSF. We determined the best-fitting population model using Aikake Information Criterion (AIC) (Burnham and Anderson 2002) and then used its covariates to generate a new model for each individual bear. We used individual RSFs because grizzly bears are known to exhibit high individual variation in habitat selection (Nielsen et al. 2002). Individual selection coefficients were then averaged by season (spring, summer, and fall) and sex/status groups (females with dependent offspring, solitary females, and males) to obtain group-level estimates using a two-step approach (after Fieberg et al. 2010). We averaged selection coefficients for each linear feature type using only bears with that particular feature type in their home range and selection coefficient estimates with standard error below 1.0 to obtain bear-season replicates with comparable samples sizes for the railway (n = 74), power line (n = 81), road (n = 56) and fence (n = 70).

To estimate individual models of habitat selection by bears, we separated GPS fixes for each grizzly bear temporally by season; spring (emergence – June 15), summer (June 16 – August 7) and fall (August 8 – hibernation) (Nielsen et al. 2009). Random points were generated within each bear's seasonal home range at a density of 10 points/km^2 to represent available locations. Home range estimates for each individual bear in each year and bear season were calculated as 100% Minimum Convex Polygons. We used bear-season combinations that had at least 100 collar locations in the analysis ($n = 106$).

2.3. Results

Percent cover of 18 types of edible bear foods within plots ranged from 0 – 98%, with an overall mean of 12.2% (Table 2). Significant differences in cover occurred among feature types, transect positions, seasons, and as interactions among these variables (Table 3, Figures 1 and 2). Among feature types, mean cover of edible bear forage was generally higher along the secondary road (15.0 ± 16.7%) and intermediate on power lines (13.6 ± 15.7%) and adjacent to the highway fence (10.8 ± 14.1%) compared to the rail (9.2 ± 14.2%) ($t \geq 6.49$, $P < 0.01$; Table 3, Figure 2). Within feature types, mean cover of edible bear forage was generally highest on edge transects (16.1 ± 17.2%) and intermediate on middle transects (12.9 ± 15.7%) compared to the forest (6.6 ± 10.1%) ($t \geq 19.63$, $P < 0.01$; Table 3, Figure 2). Across feature types and transect positions, edible foods were on average over three times more abundant in spring (16.9 ± 15.4) relative to fall (5.2 ± 11.3) ($t = -5.91$, $P < 0.01$) with intermediate values in summer (14.5 ± 16.4) ($t = 0.27$, $P = 0.78$; Table 3, Figure 3).

Several significant interactions characterized the relationships between feature type and season (Table 3). Edible bear forage was significantly lower during the summer relative to spring on the fence ($t \leq -2.70$, $P < 0.01$). The decrease in edible bear food in the fall relative to the spring was significantly more pronounced for the fence, power line and road than for the rail ($t \leq -2.49$, $P \leq 0.01$) (Table 3, Figure 2). Over a length of 100 m, estimated area of edible bear food was highest along power lines (447 m^2/100 m), followed by the road (240 m^2/100 m), rail (147 m^2/100 m) and fence (131 m^2/100 m).

To evaluate selection for linear features by bears, we analyzed 58 082 GPS collar fixes from 26 individual bears and calculated 106 seasonal home ranges. The average seasonal home range size was 672 km^2 for males (n = 46), 214 km^2 for solitary females (n = 31) and 226 km^2 for females with dependent offspring (n = 29). The most supported population model identified using AIC incorporated elevation, terrain roughness, compound topographic index (CTI) and decayed distance to forest edge (Table 4). Among the 10 land cover types, grizzly bears selected areas comprised of shrubs, upland herbs and upland trees (Table 4). Locations selected by grizzly bears were consistently closer to forest edges and at lower (Table 4). During the spring, grizzly bears selected areas with higher terrain roughness and drier soil wetness (lower CTI) in their home ranges, but they avoided these features in the summer and fall (Table 4).

In a population-level model containing all three seasons and every individual, grizzly bears selected the railway more strongly than the power line or the fence and avoided the road (Table 4). Similar results were obtained by averaging individual models. During the spring, selection for the railway was stronger than selection for any other linear feature type in both the population (Table 4) and average of individual selection coefficients (Figure 4). Two thirds (19/29) of the grizzly bears with railway in their home ranges during spring selected areas closer to the railway. During the summer, selection for the railway decreased, and selection for the power line increased via a similar proportion of bears (23/32 bears with power lines in their summer home range selected for it [Table 4, Figure 4]). During the fall, selection for the railway was stronger than selection for any other linear feature and 10/13 bears with railway in their fall home ranges selected it (Table 4; Figure 4). Despite these population-level tendencies, individual selection coefficients were highly variable among individuals (Figure 5) and exceeded variation that might otherwise have been apparent between categories of sex and reproductive status.

2.4. Discussion

Railways around the world potentially attract wildlife via enhancement of foraging and travel opportunities, but they also carry the risk of collisions with trains. The objectives of this study were to (a) quantify amount of forage vegetation for grizzly bears among four types of linear features, (b) assess whether bears selected railways more than other linear features and (c) determine whether selection for linear features differed with sex and reproductive status. Across seasons, we found that the cover of edible bear food plants was about 8% higher in linear features than the adjacent forest, but it declined among seasons to be about 12 % lower during fall, relative to spring. Relative to the rail, percent cover of edible bear forage was between 2 and 6 % more abundant on the other feature types we measured. Estimated area of edible bear forage over 100 m was highest in power lines, followed by the road, rail, and fence. At the population level, grizzly bears selected the railway preferentially during the spring and fall and the power line during the summer, but we observed no differences in selection by sex or reproductive status. Consequently, we found no support for any of the hypotheses we offered to explain sexual segregation; forage selection, travel efficiency, or social dominance. Rather, grizzly bears exhibited high individual variation in response to linear features, with some individuals exploiting and other avoiding linear features of one or more types within their home ranges.

On average, the vegetation adjacent to linear features provided twice as much edible food for bears than matched sites in the nearby forest. Similar enhancement of graminoids, forbs and shrubs has been documented in power lines (e.g., Eldegard et al. 2015), roads (e.g., Roever et al. 2008a), ski runs (e.g., Burt and Rice 2009), and clearcuts (Nielsen et al. 2004b). This enhancement appears to be most important in spring and bear forage on all linear features decreased from spring to summer, with the lowest relative cover in the fall. Growth of graminoids and forbs are especially likely to be enhanced by earlier snow melt in linear features, which is caused by higher temperatures and greater wind speed (Pohlman et al. 2009). However, these same attributes likely desiccate vegetation more rapidly in the summer to reduce its value to grizzly bears and other herbivores. These desiccating effects are probably increased in railways, where long trains travelling at high speeds generate considerable air turbulence and dark ballast rocks accumulate and retain heat. These effects could explain why vegetative cover in our study was lower along railway than any of the other features.

In global and seasonal population models, grizzly bears selected shrub, upland herb, and upland tree land cover types. Upland tree habitat likely provides hiding cover for grizzly bears (Ciarniello et al. 2007) and is used while bedding and feeding on ungulates (Munro et al. 2006). Grizzly bears have been demonstrated to use upland herb and shrub habitat to access root digging, herbaceous feeding and frugivory opportunities (Munro et al. 2006; Ciarniello et al. 2007). We observed selection for locations at lower elevations, which may enhance herbaceous feeding in the spring and frugivory in the fall as many berry producing shrubs occur at lower elevations (Hamer and Hererro 1987, Nielsen et al. 2004b). Grizzly bears also selected forest edges in our study area, which was consistent with other locations (Nielsen et al. 2004a; Stewart et al. 2013). Interestingly, grizzly bears selected rougher terrain and drier soil wetness during the spring, but avoided these features in the summer and fall. This change in response could occur because bears emerge from their dens, which are at higher elevations (characterized by rougher terrain and drier soils), early in spring before travelling to lower valley bottoms (Milakovich et al. 2012).

At the population level, relative selection by grizzly bears for the four types of linear features differed by season with greater use of the railway during spring and fall, whereas greater use of the power line occurred in summer. Selection for the power line in summer presumably stemmed from the higher abundance of bear foods there, but it may have resulted partly from the tendency for local bears to move to higher elevations in summer to exploit emerging vegetation (Hamer and Herrero 1987). Across our study area, the power line had a slightly higher average elevation (mean = 1481 m) than the railway (mean = 1409 m). The heightened use by bears of the railway in spring and fall aligned with reports by others that grizzly bears make more use of roads in spring (Roever et al. 2008b), or both spring and fall (Graham et al. 2010). Nonetheless, it was surprising that bears selected the railway more strongly than the other linear features in those seasons because it contained less edible forage. The overall avoidance of the road by our study animals suggests that greater forage abundance was not enough to overcome its detrimental features, the primary one likely being a higher probability of encountering people (e.g., Whittington et al. 2005).

An alternative explanation for high use of the railway by bears in spring and fall is that it favored particular forage plants that are highly valued by bears. One likely example is a species of horsetail, *Equisetum arvense*, which thrives in disturbed sites and is a major component of grizzly bear diet in the area (Hamer and Herrero 1987; Munro et al. 2006). This species was more abundant along the railway than other linear features (Table 5), perhaps because snow ploughing in winter increases moisture adjacent to the rail. In addition to the vegetation-based food sources we studied, other rail-based advantages may have supported greater selection for the railway by grizzly bears in the spring and fall when forage resources are limited (Gibeau and Herrerro 1998). These sources, which may be more valuable during the fall when bears require rapid caloric gain (Gibeau and Herrerro 1998), included rail-killed ungulates, which were more prevalent in late winter (Gilhooly et al., in prep) and spilled grain, which increases in fall (Gangadharan et al., in prep). Both these sources are high in protein, which supports rapid mass gain for male bears (Hilderbrand et al. 1999) and the costs of lactation and cub growth in females (Farley and Robbins 1995; Hilderbrand et al. 2000; López-Alfaro et al. 2013). The additional protein sources afforded by the rail may be particularly important to this population of grizzly bears, for which protein appears to be a limiting nutrient (López-Alfaro et al. 2015). These same limitations may also increase the importance of travel efficiency among patches of high habitat quality.

Although each of these advantages is logically associated with the rail, we did not find evidence that they were more valued by bears in different reproductive and sex classes. Contrary to our expectations, there were no differences among these classes in selection for the rail or any other linear feature and, consequently, no evidence in support of hypotheses for sexual segregation based on forage selection (Ruckstuhl and Neuhaus 2005), travel efficiency (Dahle and Swenson 2003), or social dominance (Rode et al. 2006). The absence of such differences was surprising because there is widespread evidence that the life history of grizzly bears is strongly shaped by sexual selection (Dahle and Swenson 2003; Rode et al. 2006; Bartareau et al. 2011) and other studies reported sexual segregation in the use of areas near roads (Gibeau et al. 2002; Chruszcz et al. 2003; Graham et al. 2010) and pipelines (Stewart et al. 2013). It is possible that such differences existed in our study animals, but were obscured by local population demography (e.g., Wielgus and Bunnell 1995), confounding effects of associated human development (e.g., Müller et al. 2004; Steyaert et al. 2016) or other, unmeasured variables.

An alternative interpretation of our results is that sexual selection was actually unimportant in determining use of linear features by grizzly bears because it was swamped by individual differences stemming from other causes. Others have reported similar variability, with selection by grizzly bears varying within age and sex classes from positive to negative values for roads (Roever et al. 2008b; Northrup et al. 2012) and cut-blocks (Nielsen et al. 2002). Large individual differences would be expected to result from different exposure to linear features stemming from landscape context and experience (Nielsen et al. 2013). Additional variation in selection could stem from differences in individual temperament (Réale et al. 2007), which contributed to use of human infrastructure by elk (*Cervus canadensis*, Found and St. Clair 2016). In grizzly bears, variation in use of anthropogenic areas is highly influenced by learning from habituation (e.g., Chruszcz et al. 2003), food conditioning (Elfström et al. 2014b), and maternal rearing (Nielsen et al. 2013).

Our study had several limitations, a primary one of which was the lack of temporal resolution in our RSFs, which typically measure only the effect of static environmental variables on habitat selection (Boyce et al. 2002). Temporal attributes such as changing forage quality, prey availability, human activity, and the presence of conspecifics undoubtedly also contribute to habitat selection (Nielsen et al. 2010). Their omission is likely important because diel patterns of human activity appear to affect use of linear features by grizzly bears (Gibeau et al. 2002; Waller and Servheen 2005), and similar diel responses to anthropogenic features is apparent in cougars (Knopff et al. 2014) and coyotes (*Canis latrans*; Murray and St. Clair 2015). A similar limitation was imposed by the 2 h fix rate of our collars, which may have limited detection of selected features that occurred at smaller spatial and temporal scales (Swain et al. 2008). Because RSFs account for availability, selection may be overestimated due to chance use of a rare feature and underestimated when features are common although they are used frequently (Mysterud and Ims 1998). Measuring grizzly bear use of linear features in addition to selection would improve our ability to detect sexual segregation. A final limitation of our analysis was the parallel orientation and close proximity of the linear features in our study area (Bélisle and St. Clair 2001), despite our use of decayed distances to linear features (Nielsen et al. 2009), and their lack of correlations in our models.

Despite these limitations, our results offer several important insights for mitigating the effects of railways on grizzly bears that may extend to other species and types of linear features. First, we found robust evidence to support others that grizzly bears exhibit seasonal preferences for linear features (Roever et al. 2008b; Graham et al. 2010), which predicts greater need for rail mitigation in the spring and fall when grizzly bears select the railway most strongly and wildlife-vehicle collisions in other locations are most common (Murray and St. Clair 2015; reviewed by Steiner et al. 2014). A second insight is that proactive attention might be warranted for preventing human-bear conflict on power lines in summer. Because summer is the busiest tourist season in Banff (Gibeau et al. 2002), lower rates of human activity on power lines might make them especially attractive to bears in that season (e.g., Northrup et al. 2012). Current widening of the power line may create unexpected encounters between bears and people. A final insight is that the availability of bear forage alone could not explain seasonal patterns of linear feature use, suggesting that many other factors contribute to rail-caused mortality. Understanding the full complement of these factors will be necessary for predicting and mitigating railway use by bears and many other species.

Table 2.1. Count of train collisions with individual grizzly bears in Banff and Yoho National Parks by sex and season from 2000 – 2015. Strikes indicate instances where collisions were reported by Canadian Pacific Railway, but no grizzly bear mortality was confirmed. Mortalities were confirmed by Parks Canada personnel and incidents involving family groups were split to represent the number of individuals killed. Seasons are defined as follows: spring (den emergence – June 15), summer (June 16 – August 7) and fall (August 8 – hibernation).

		Season		
	Spring	Summer	Fall	Total
Mortalities				
Male	1	1	0	2
Female	2	1	3	6
Cub	1	2	2	5
Strikes				
Unknown	2	1	2	5
Total	6	5	7	18

Table 2.2. Range of percent cover of vegetation and percent cover of edible bear forage stages for 18 forage species. Vegetation was deemed edible when the developmental and reproductive stage of the plant indicated it could be consumed by grizzly bears.

Species	Common name	Percent cover (%) Range	Edible bear forage (%) Range
Amelanchier alnifolia	Saskatoon berry	0 - 6	0 - 0
Arctostaphylos uva-ursi	Kinnikinnick	0 - 90	0 - 90
Arnica cordifolia	Heart-leaved arnica	0 - 25	0 - 17
Astragalus ssp.	Milk vetch ssp.	0 - 25	0 - 25
Chamerion angustifolium	Fireweed	0 - 7	0 - 4
Equisetum arvense	Horsetail	0 - 95	0 - 87
Fragaria ssp.	Strawberry ssp.	0 - 48	0 - 37
Hedysarum ssp.	Sweet vetch ssp.	0 - 15	0 - 15
Juncus ssp.	Rushes	0 - 35	0 - 35
Medicago sativa	Alfalfa	0 - 14	0 - 11
Poaceae and Cyperaceae	Grasses and sedges	0 - 99	0 - 75
Ribes lacustre	Gooseberry	0 - 13	0 - 13
Rubus idaeus	Raspberry	0 - 13	0 - 9
Shepherdia canadensis	Buffaloberry	0 - 59	0 - 40
Taraxicum officinale	Dandelion	0 - 55	0 - 55
Trifolium ssp.	Clover ssp.	0 - 40	0 - 25
Vaccinium caespitosum	Dwarf huckleberry	0 - 30	0 - 26
Vaccinium scoparium	Grouseberry	0 - 25	0 - 7

Table 2.3. Zero-inflated beta regression estimates (β) for the effect of linear feature type, transect position and season on percent cover of edible bear forage within plots. Interactions between feature type and season were included in the model. Plot ID was included as a random effect. The rail, spring and forest transect were used as reference categories.

Fixed effects	Proportion of edible bear forage		
Feature type	β	SE	P
Fence	**0.34**	**0.05**	**<0.01**
Power	**0.39**	**0.05**	**<0.01**
Road	**0.50**	**0.05**	**<0.01**
Transect position			
Middle	**0.65**	**0.03**	**<0.01**
Edge	**0.82**	**0.03**	**<0.01**
Season			
Summer	0.02	0.06	0.80
Fall	**-0.46**	**0.08**	**<0.01**
Feature type: Season			
Fence: Summer	**-0.22**	**0.08**	**0.01**
Power: Summer	0.03	0.08	0.71
Road: Summer	-0.05	0.08	0.56
Fence: Fall	**-0.44**	**0.11**	**<0.01**
Power: Fall	**-0.25**	**0.10**	**0.01**
Road: Fall	**-0.44**	**0.10**	**<0.01**

SE, standard error.

Table 2.4. Selection coefficients (β) for population level RSF with random effects for year and individual. The global RSF with all three seasons also had a random effect for season. Bolded values were significant at α = 0.05. For the distance covariates, a positive selection coefficient indicates avoidance, while a negative coefficient indicates selection. Land cover classes were dummy coded.

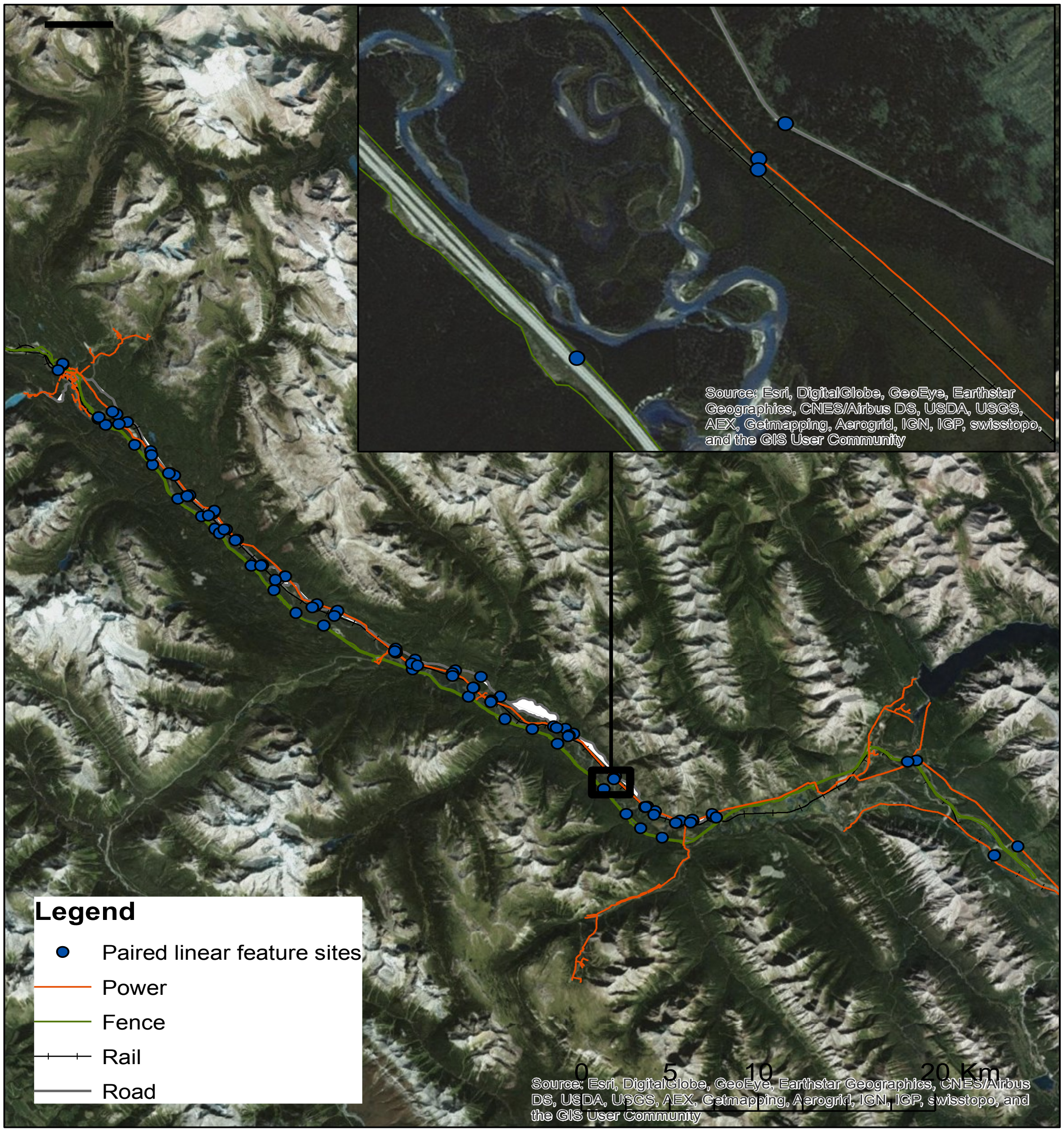
	Global		**Spring**		**Summer**		**Fall**	
	β	SE	β	SE	β	SE	β	SE
Terrain								
elevation	**-0.23**	**0.00**	**-0.28**	**0.01**	**-0.25**	**0.01**	**-0.19**	**0.01**
roughness	**-0.05**	**0.00**	**0.05**	**0.01**	**-0.16**	**0.01**	**-0.03**	**0.01**
CTI	**0.02**	**0.00**	**-0.05**	**0.01**	**0.05**	**0.00**	**0.01**	**0.00**
Land cover class								
shrub	**0.44**	**0.01**	**0.62**	**0.02**	**0.39**	**0.02**	**0.50**	**0.02**
upland herb	**0.62**	**0.01**	**0.69**	**0.03**	**0.48**	**0.02**	**0.76**	**0.02**
upland tree	**0.06**	**0.01**	**0.26**	**0.02**	**0.04**	**0.01**	**0.11**	**0.01**
Decayed distance to:								
forest edge	**-0.30**	**0.00**	**-0.38**	**0.01**	**-0.38**	**0.01**	**-0.21**	**0.00**
road	**0.08**	**0.00**	**0.06**	**0.01**	**0.07**	**0.00**	**0.06**	**0.01**
fence	0.00	0.01	**-0.03**	**0.01**	**-0.06**	**0.00**	**0.24**	**0.01**
power	**-0.07**	**0.00**	**-0.04**	**0.01**	**-0.10**	**0.00**	**-0.02**	**0.01**
rail	**-0.09**	**0.00**	**-0.14**	**0.01**	**0.03**	**0.01**	**-0.23**	**0.01**

SE, standard error.

Table 2.5. Average percent cover and standard deviation of 18 common grizzly bear foods by linear feature type. Calculated using percent cover measured on middle, edge and forest transects during repeated measures vegetation sampling at sites along the railway (28), power line (28), TCH fence (27) and BVP (25).

	Power	Fence	Rail	Road
Species	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Amelanchier alnifolia	0.01 ± 0.21	0.00 ± 0.03	0.01 ± 0.23	0.00 ± 0.08
Arctostaphylos uva-ursi	6.51 ± 11.87	1.79 ± 6.55	4.19 ± 10.83	4.65 ± 11.63
Arnica cordifolia	0.13 ± 0.62	0.29 ± 1.21	0.15 ± 1.40	0.29 ± 1.51
Astragalus ssp.	0.24 ± 0.93	0.53 ± 1.99	0.44 ± 1.70	1.31 ± 2.74
Chamerion angustifolium	0.13 ± 0.53	0.13 ± 0.50	0.04 ± 0.31	0.07 ± 0.41
Equisetum arvense	0.25 ± 1.20	0.96 ± 5.09	1.79 ± 8.07	0.96 ± 6.63
Fragaria ssp.	3.83 ± 4.43	3.09 ± 5.48	2.78 ± 4.32	5.05 ± 5.30
Hedysarum ssp.	0.34 ± 1.34	0.13 ± 0.80	0.10 ± 0.76	0.18 ± 0.95
Juncus ssp.	0.08 ± 0.87	0.00 ± 0.11	0.28 ± 2.53	0.12 ± 1.03
Medicago sativa	0.00 ± 0.03	0.02 ± 0.38	0.16 ± 1.11	0.10 ± 0.76
Poaceae and Cyperaceae	13.71 ± 15.83	11.69 ± 13.69	7.07 ± 10.08	14.54 ± 15.39
Ribes lacustre	0.01 ± 0.12	0.10 ± 0.76	0.06 ± 0.69	0.03 ± 0.39
Rubus idaeus	0.03 ± 0.45	0.10 ± 0.83	0.04 ± 0.56	0.00 ± 0.00
Shepherdia canadensis	1.67 ± 5.32	1.46 ± 4.37	0.60 ± 3.10	1.82 ± 5.63
Taraxicum officinale	0.58 ± 1.93	1.68 ± 3.76	1.14 ± 2.55	1.12 ± 2.25
Trifolium ssp.	0.61 ± 2.00	1.12 ± 3.14	0.89 ± 2.81	1.52 ± 3.25
Vaccinium caespitosum	1.49 ± 3.99	0.44 ± 1.65	0.15 ± 1.06	0.20 ± 1.59
Vaccinium scoparium	0.25 ± 1.52	0.34 ± 1.79	0.10 ± 0.66	0.08 ± 0.87

SD, standard deviation.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 2.1. Map of matched vegetation sample sites at each of the 28 locations throughout the study area.

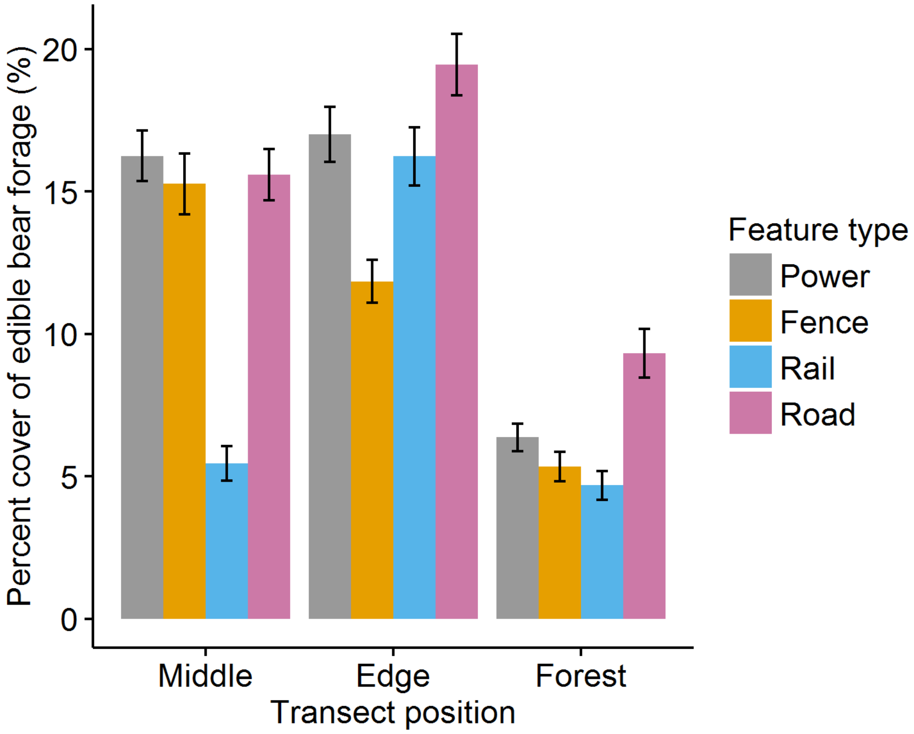


Figure 2.1. Average percent cover of edible bear forage by linear feature type and transect position. All three seasons (spring, summer and fall) were included in averages. Percent cover of 18 bear forage species was calculated in 1 m^2 plots on the power line (n = 941), fence (n = 867), rail (n = 820), and road (n = 851). Error bars represent standard error of the mean.

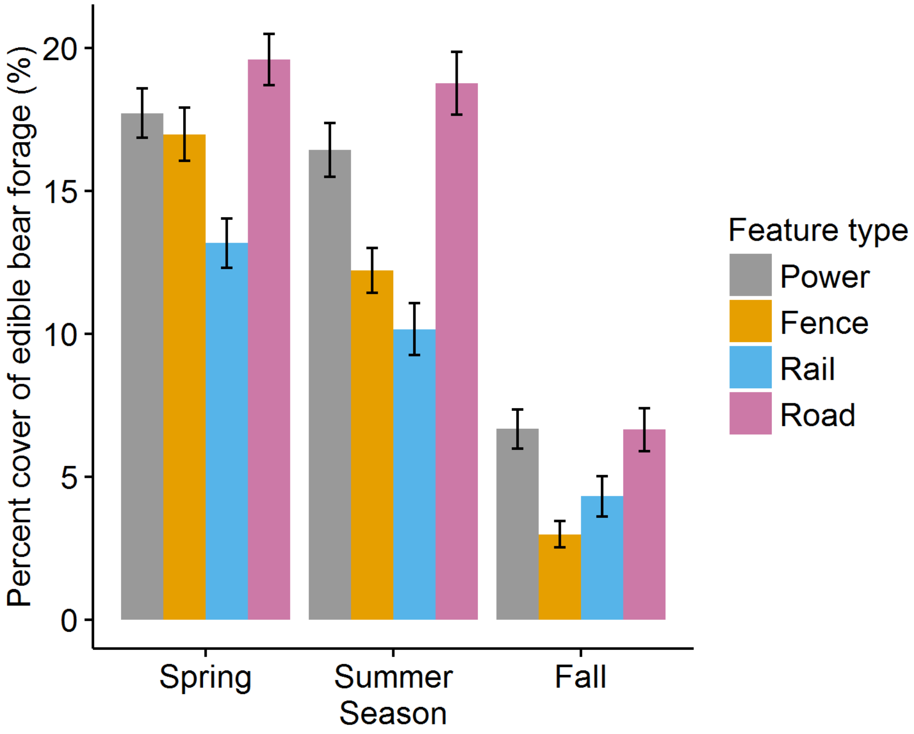


Figure 2.2. Average percent cover of edible bear forage by linear feature type and season. All three transect positions (middle, edge, and forest) were included in averages. Percent cover of 18 bear forage species was calculated in 1 m^2 plots on the power line (n = 941), fence (n = 867), rail (n = 820), and road (n = 851). Error bars represent standard error of the mean.

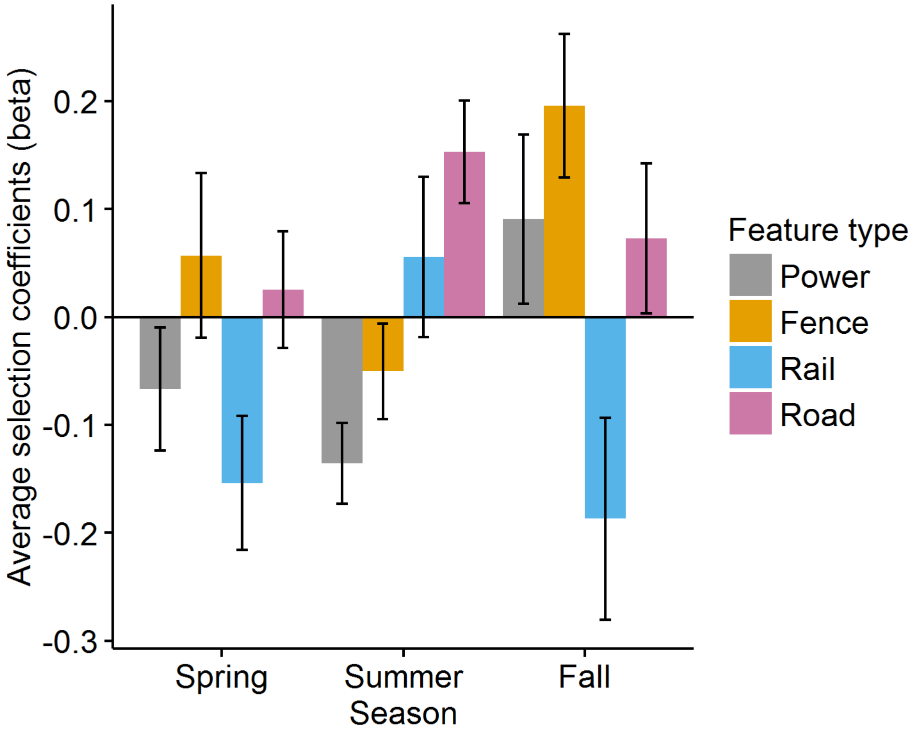


Figure 2.3. Average standardized coefficients (β) by season and linear feature type. Bars represent averages of individual bear selection coefficients and error bars represent standard error of the mean. Note that positive selection coefficients for distances indicate avoidance, while negative coefficients indicate selection.

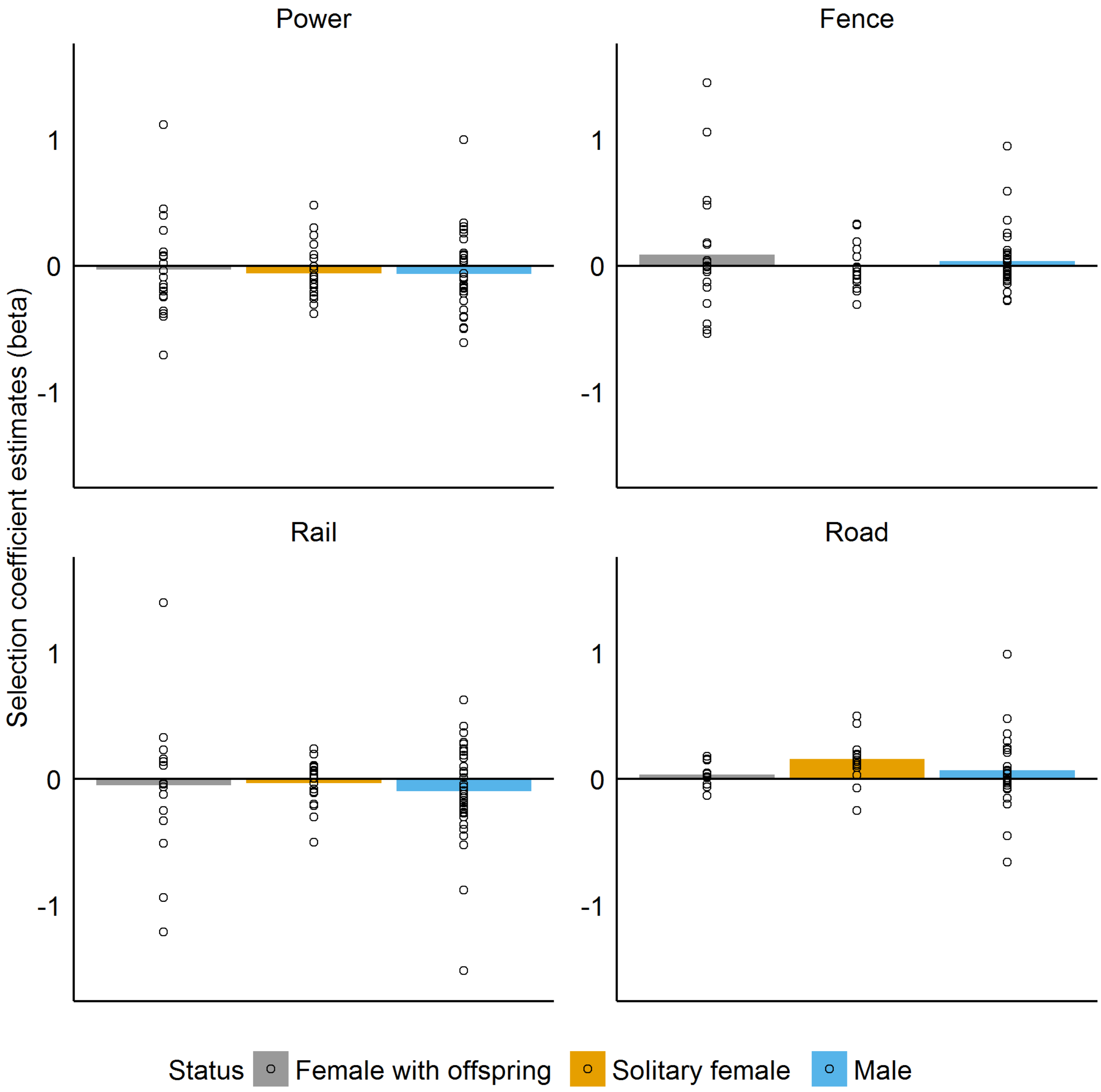


Figure 2.4. Average standardized coefficients (β) by reproductive status and linear feature type. Bars represent group level means of individual selection coefficients and points indicate individual selection coefficients. Error bars represent standard error of the mean. Note that positive selection coefficients for distances indicate avoidance, while negative coefficients indicate selection.

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Chapter 3: General Discussion

This thesis comprised a component of the larger University of Alberta Grizzly Bear Research and Mitigation Project with an overall purpose of describing grizzly bear selection for the railway in relation to other linear features in Banff National Park. My specific objectives were to: (i) quantify and compare vegetative availability in linear features of different types, (ii) compare grizzly bear selection for the railway to other linear features by season, and (iii) determine whether grizzly bears exhibit differences in selection for linear features among sexes. I found that vegetative cover was enhanced by about 8% in linear features compared to adjacent forests and decreased by about 12% in the fall relative to the spring (Chapter 2). Overall, percent cover of edible bear forage was between 2 and 6% higher on the road, power lines and fence than the rail (Chapter 2). Using models constructed from GPS collar data, I found that grizzly bears selected railways most strongly during the spring and fall and power lines during the summer, in accordance with my seasonal hypothesis (Chapter 2). Surprisingly, I did not observe evidence for a second hypothesis, that there would be consistent segregation within or among features by bear sex or reproductive status. Instead, my results showed high individual variation in selection for linear features, which may have resulted from differences in bear temperament and experience, and the temporal and spatial context of individual home ranges (Chapter 2).

My results suggest that although vegetative availability may contribute to selection for the railway, it is likely not the primary attractant for grizzly bears. I recommend that managers focus mitigation efforts during spring and fall when grizzly bears select the railway most strongly. Additional care may also be warranted to avoid human-bear conflict on power lines during the summer. Selection for the railway and other linear features is probably dependent on individual characteristics of grizzly bears as well as spatial and temporal context, making rail mortality difficult to predict.

The results of my study are supported by other studies that have reported similar vegetative enhancement along anthropogenic linear features relative to adjacent forests. Reduced canopy cover there frequently results in increased temperature and wind speed (Pohlman et al. 2009) and these effects likely contribute to the vegetative enhancement that has been demonstrated in power lines (Eldegard et al. 2015), roads (Roever et al. 2008a) and ski runs (Burt and Rice 2009). In highly developed landscapes, particularly where natural vegetation is limited, anthropogenic linear features may provide important foraging opportunities. Rights-of-ways along railways and power lines have even been considered as a conservation tool for bats (Vandevelde et al. 2014), butterflies (Komonen et al. 2013), and native bees (Russell et al. 2005) because of the habitat they provide. Although vegetative enhancement in linear features does not consistently predict grizzly bear selection, these features necessarily increase the availability of open habitats that are limited by fire suppression in Banff (Sachro et al. 2005) to create foraging opportunities for many species.

Differences among species and individuals, in both selection for linear features and vulnerability to vehicle collisions, likely stem at least in part from natural and life history traits. Small populations are more likely to be threatened by vehicle collisions because they are generally more vulnerable to extinction (Caughley 1994). Similarly, rail mortality is more likely to decrease population viability for species that are rare and have large individual home ranges because they exist at lower densities on the landscape (Kušta et al. 2011). A review of road mortality among species suggested that omnivorous and solitary mammals were more vulnerable to vehicle collisions along roadways (Cook and Blumstein 2013). Peaks in vehicle collisions may also be correlated with seasonal behaviors, such as migration, dispersal or mating (e.g. Medinas et al. 2013, Steiner et al. 2014). In my study, grizzly bears selected the railway most strongly in spring and fall (Chapter 2) when food resources are limited (Gibeau and Herrero 1998). Similarly, peaks in mortality of barn owls (*Tyto alba*) along roadways have been demonstrated to correspond with seasons of low resource availability (Grilo et al. 2014). Although I found no consistent evidence of segregation between males and females (Chapter 2), sexual dimorphism strongly shapes the life history of many species. Sex-specific variation has been demonstrated in roadway use by bighorn sheep (*Ovis Canadensis;* Bleich et al. 2016) and jaguars (*Panthera onca;* Conde et al. 2010) and in road mortality of turtles (Aresco 2004).

In addition to life history traits, the results of this study suggest that individual experiences and attributes also contribute to selection responses for linear features (Chapter 2). Although individuals are often pooled to create population-level models, recent studies have highlighted the importance of individual variation in response to roadways by cougars (*Puma concolor*; Knopff et al. 2014) and coyotes (*Canis latrans*; Murray and St. Clair 2015). Although diversity in behavioral responses within a species makes it difficult to identify suitable management actions, that flexibility is extremely valuable for conservation as it increases population persistence amid human disturbance or environmental change (Berger-Tal et al. 2011).

More work is needed to identify the many subtle and overlapping behavioral processes that contribute to the use of linear features by wildlife, thereby supporting clearer direction for mitigating negative effects, such as vulnerability to collisions. Anthropogenic linear features, including roads, railways, power and seismic lines, are ubiquitous around the world and will continue to increase as global transportation systems expand. The most direct of their negative effects, wildlife-vehicle collisions, already affect populations of diverse species that include Asiatic elephants (*Elephas maximus;* Dasgupta and Ghosh 2015), Barred owls (*Strix varia*; Gagné et al. 2015), and northern leopard frogs (*Rana pipiens*; Bouchard et al. 2009). For some carnivores, including Amur tigers (*Panthera tigris;* Kerley et al. 2002) and grizzly bears (Benn and Hererro 2002), proximity to roads and trails is also correlated with human-wildlife conflict and management deaths. Traffic noise may also adversely affect some species because it masks important acoustic signals, such as bird song (e.g., Herrera-Montes and Aide 2011). In addition to these direct effects, linear features can impose negative, indirect effects on wildlife populations. Examples include increasing the prevalence of invasive species (e.g., Mortensen et al. 2009), introducing parasitic species (e.g., Patten et al. 2006), and increasing the efficiency of predators (e.g., Latham et al. 2011, Tigner et al. 2014). These indirect impacts are often characterized as edge-effects, which occur at abrupt natural or anthropogenic boundaries between two ecosystems (Murcia 1995).

The negative effects of railways, roads and other linear features are well documented and have received more attention than their positive effects (e.g., reviewed by Fahrig and Rytwinski 2009; Trombulak and Frissell 2001). However, a number of studies have also examined the diverse positive effects of linear features on wildlife (e.g., reviewed by Morelli et al. 2014). Linear features can provide critical foraging habitat (e.g., Lensu et al. 2011), increase movement efficiency (e.g., Dickson et al. 2005) and facilitate dispersal and gene flow (e.g., Haddad and Tewksbury 2005; Laurence et al. 2013).

A more general conclusion of my own work is that linear features convey both positive and negative effects on wildlife populations that appear to be highly variable among individuals, species and contexts. This variability will make it challenging to generalize mitigation practices for linear features. Studies explicitly attempting to integrate both types of effects will be necessary for conservation planning. One such study demonstrated that roads act as both a barrier and facilitator of gene flow for New England cottontail (*Sylvilagus* transitionalis; Amaral et al. 2016). Another found that roads were selected by wild dogs (*Lycaon pictus*) while travelling, but avoided while resting (Abrahms et al. 2016). Identifying optimal forms of mitigation will often require consideration of the life history and behavior of species most affected by linear features. For grizzly bears in Banff National Park, the net direction of the effect of linear features is not yet clear.

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Appendix I: Vegetation Sampling Design

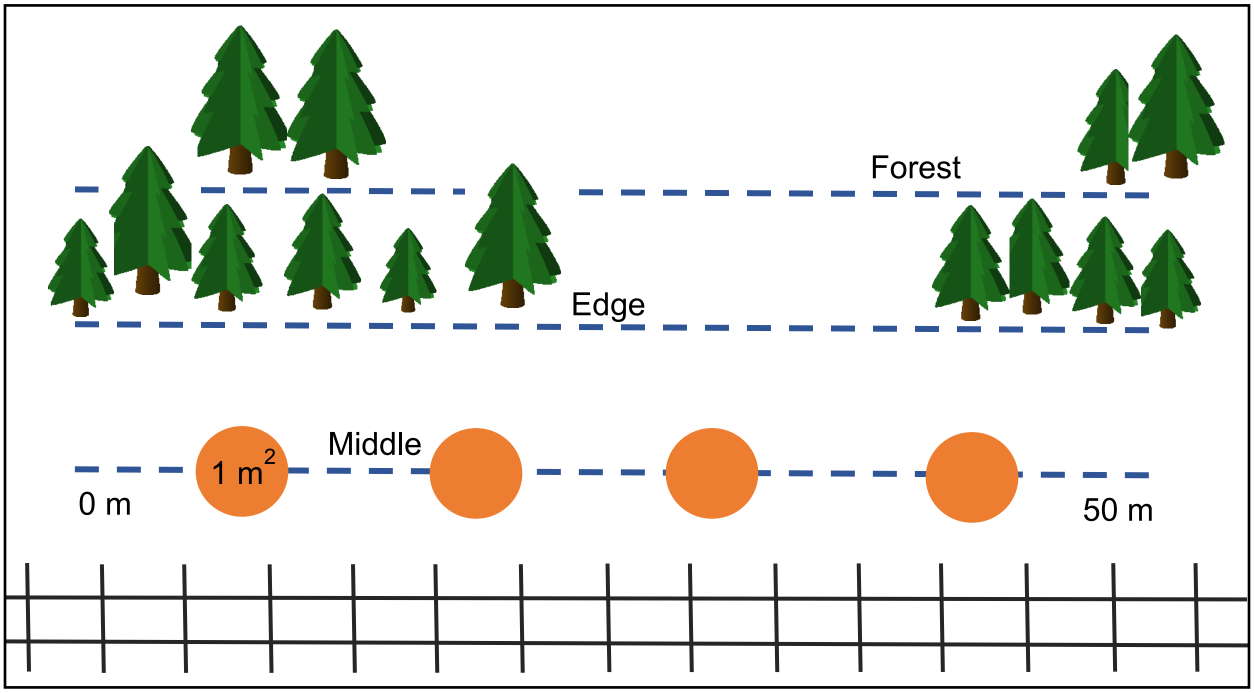

Figure I. 1. Schematic of vegetation sampling design at a matched site on the railway. Each transect position had four fixed 1 m^2 plots as indicated along the middle transect.

Appendix II: Collared Bear Attributes

Table II.1. Attributes and count of GPS telemetry locations for each collared bear from 2012 to 2015.

Bear	Age	Sex	Count of GPS locations 2012	2013	2014	2015	Years with offspring
64	Adult	Female	1689	540	0	0	2012-2013
72	Adult	Female	1596	1448	1801	0	2012-2013
122	Adult	Male	2296	154	0	0	NA
125	Adult	Male	1144	0	0	0	NA
126	Adult	Male	1845	2259	2398	255	NA
128	Sub-adult	Male	0	2215	0	0	NA
130	Adult	Female	461	627	2114	458	2012;2014
131	Adult	Female	1482	1729	0	0	2012-2013
132	Adult	Male	0	0	1605	1475	NA
133	Adult	Female	841	130	0	0	2012
134	Adult	Male	850	0	0	528	NA
135	Adult	Female	1373	987	0	355	2012-2013
136	Adult	Male	1405	755	0	1579	NA
138	Adult	Female	0	934	951	300	2014
140	Adult	Male	0	0	324	0	NA
141	Sub-adult	Female	0	0	1756	736	NA
142	Sub-adult	Female	0	0	584	154	NA
143	Sub-adult	Female	0	0	1812	0	NA
144	Sub-adult	Male	0	0	1374	0	NA
148	Sub-adult	Female	0	0	1667	114	NA
149	Sub-adult	Male	0	0	391	0	NA
155	Sub-adult	Female	0	0	0	1887	NA
156	Sub-adult	Female	0	0	0	1561	NA
158	Adult	Male	0	0	0	1940	NA
160	Sub-adult	Female	0	0	0	1413	NA
161	Adult	Female	0	0	0	1786	NA

Appendix III. Transect Coordinates

Table III.1. Coordinates (UTM) at the start (0 m) of each transect position (ballast, edge, and forest) at each paired site (power, fence, rail, and road) by location.

		Ballast		Edge		Forest	
Location	Feature type	x	Y	x	y	x	y
01-0	Fence	NA	NA	610627	5667828	610381	5667303
01-0	Power	610616	5667825	610631	5667830	NA	NA
01-0	Rail	609263	5667231	609238	5667229	609216	5667224
02-0	Fence	NA	NA	604514	5673219	604522	5673246
02-0	Power	604872	5673250	604868	5673278	604845	5673329
02-0	Rail	604368	5673166	604370	5673167	NA	NA
03-AV-0	Road	591422	5669332	591430	5669341	591434	5669373
03-AV-0	Fence	590516	5668366	590520	5668376	590501	5668407
03-AV-0	Power	591543	5669440	591555	5669459	591580	5669488
03-AV-0	Rail	591266	5669291	591273	5669302	591287	5669345
03-ST-0	Road	593371	5669735	593364	5669733	NA	NA
03-ST-0	Fence	NA	NA	593945	5669631	593913	5669684
03-ST-0	Power	593344	5669854	593373	5669879	593370	5669908
03-ST-0	Rail	593570	5669645	593571	5669651	593563	5669698
03-ST-W1	Road	592232	5669431	592230	5669441	592250	5669464
03-ST-W1	Power	592210	5669499	592204	5669504	592192	5669531
03-ST-W1	Rail	592108	5669308	592116	5669300	592114	5669340
04-0	Road	589699	5670331	589710	5670330	589780	5670321
04-0	Fence	588477	5669855	588478	5669861	588513	5669902
04-0	Power	589536	5670308	589530	5670316	589576	5670315
04-0	Rail	589577	5670312	NA	NA	NA	NA
04-E1	Road	590079	5669902	590070	5669912	590105	5669925
04-E1	Fence	589306	5668954	589304	5668962	589334	5669014
04-E1	Power	590123	5670047	590135	5670049	590170	5670071
04-E1	Rail	590044	5669816	590040	5669822	590053	5669858
04-W1	Road	587860	5672249	587868	5672253	587900	5672298
04-W1	Fence	587214	5671435	587222	5671445	587232	5671460
04-W1	Power	587776	5672127	587780	5672135	587795	5672164
04-W1	Rail	587775	5672089	587774	5672091	NA	NA
05-0	Road	585045	5675285	585053	5675303	585053	5675333
05-0	Fence	583157	5675247	583167	5675261	583220	5675375
05-0	Power	584370	5675436	584376	5675433	NA	NA
05-0	Rail	584539	5675315	584518	5675296	584522	5675300
05-E1	Road	585510	5674959	585518	5674965	585534	5674997
05-E1	Fence	584599	5674327	584607	5674320	584632	5674362

05-E1	Power	585262	5674859	585269	5674862	585310	5674897
05-E1	Rail	585220	5674781	585218	5674826	NA	NA
05-W1	Road	581383	5677328	581377	5677332	581415	5677356
05-W1	Fence	581647	5675887	581638	5675904	581670	5675919
05-W1	Power	580876	5677057	580875	5677078	580896	5677112
05-W1	Rail	580840	5676988	580850	5677007	NA	NA
05-W2	Road	580251	5678554	580245	5678552	580265	5678577
05-W2	Fence	579572	5677308	579570	5677313	579568	5677340
05-W2	Power	579842	5677880	579843	5677879	579920	5677927
05-W2	Rail	579812	5677880	579803	5677875	NA	NA
06-0	Road	575440	5680342	575446	5680346	575481	5680369
06-0	Fence	NA	NA	574838	5679688	574848	5679719
06-0	Power	575466	5680081	575473	5680089	575377	5680133
06-0	Rail	575386	5680197	575339	5680141	NA	NA
06-E1	Road	576552	5679639	576557	5679648	576581	5679660
06-E1	Fence	576397	5679029	576398	5679038	576419	5679059
06-E1	Power	576342	5679407	576336	5679414	576341	5679461
06-E1	Rail	576698	5679287	576698	5679290	NA	NA
06-E2	Road	578807	5678975	578813	5678979	578825	5679021
06-E2	Fence	NA	NA	577274	5678741	577286	5678793
06-E2	Power	578662	5678792	578670	5678802	578698	5678830
06-E2	Rail	578667	5678603	NA	NA	578691	5678654
06-W1	Road	572104	5682681	572105	5682688	572122	5682729
06-W1	Fence	571385	5681828	571390	5681838	571434	5681865
06-W1	Power	572149	5682761	572151	5682768	572151	5682802
06-W1	Rail	571983	5682436	571996	5682439	572014	5682522
06-W2	Road	570917	5683046	570922	5683060	570939	5683079
06-W2	Fence	569809	5682628	569843	5682628	569880	5682667
06-W2	Power	570975	5683187	570984	5683196	571005	5683231
06-W2	Rail	570725	5682956	570735	5682983	570801	5682997
07-0	Road	567895	5685659	567896	5685662	567898	5685706
07-0	Fence	567284	5685631	567285	5685642	567294	5685676
07-0	Power	567844	5685647	567842	5685651	NA	NA
07-0	Rail	567826	5685634	NA	NA	NA	NA
07-E1	Road	569205	5684924	569206	5684933	569202	5684946
07-E1	Fence	568586	5684061	568590	5684063	568635	5684124
07-E1	Power	569225	5684943	569222	5684962	569242	5684998
07-E1	Rail	568646	5684734	568647	5684736	568680	5684758
08-0	Road	NA	NA	565963	5687766	565983	5687780
08-0	Fence	565239	5687963	565242	5687973	565269	5687992
08-0	Power	565894	5687911	565910	5687927	565979	5687933

08-0	Rail	565756	5687913	565829	5687875	565768	5687888
08-E1	Road	566421	5687270	566421	5687276	NA	NA
08-E1	Fence	565486	5687678	565488	5687686	565520	5687721
08-E1	Power	566480	5687279	566483	5687298	566512	5687307
08-E1	Rail	566365	5687238	566368	5687238	NA	NA
08-W1	Road	565125	5688950	565127	5688953	565171	5688983
08-W1	Fence	564481	5688750	564484	5688753	564518	5688794
08-W1	Power	565219	5689096	565224	5689104	565282	5689112
08-W1	Rail	564876	5688791	564873	5688803	564905	5688821
08-W2	Road	563723	5690046	563724	5690051	563757	5690087
08-W2	Fence	563138	5689870	563138	5689876	563165	5689909
08-W2	Power	563792	5690093	563787	5690106	563825	5690113
08-W2	Rail	563647	5690031	563649	5690029	563656	5690075
09-AV-0	Road	561618	5692880	561621	5692883	561640	5692892
09-AV-0	Fence	560696	5693283	560699	5693278	560764	5693316
09-AV-0	Power	561627	5692611	561635	5692602	NA	NA
09-AV-0	Rail	561650	5692625	561659	5692634	561697	5692652
09-AV-E1	Road	562689	5691498	562689	5691495	562714	5691523
09-AV-E1	Fence	561717	5692023	561723	5692022	NA	NA
09-AV-E1	Power	562923	5691338	562919	5691364	562943	5691400
09-AV-E1	Rail	562614	5691486	562629	5691478	NA	NA
09-CL-0	Road	559664	5695255	559668	5695252	559706	5695269
09-CL-0	Fence	558631	5694974	558631	5694985	558673	5694976
09-CL-0	Power	559444	5695402	559450	5695419	559470	5695445
09-CL-0	Rail	558661	5695029	558658	5695025	558690	5695097
09-ST-0	Road	560289	5694728	560289	5694734	560286	5694740
09-ST-0	Fence	559055	5694541	559056	5694545	559792	5694642
09-ST-0	Power	559791	5694599	559794	5694606	559788	5694645
09-ST-0	Rail	593573	5669643	560125	5694646	560142	5694678
10-0	Fence	556629	5698377	556634	5698362	NA	NA
10-0	Power	556634	5698422	556625	5698427	NA	NA
10-0	Rail	556379	5698024	556383	5698002	NA	NA