Food availability and grizzly bear (*Ursus arctos*) selection of post-fire and thinned forests in the mountain national parks of Canada

by

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Abstract

Human-caused mortality and habitat loss have led to the extirpation of grizzly bears (*Ursus arctos*) across much of their North American range. Today, these factors continue to limit extant grizzly bear populations as productive habitats often occur in areas with elevated mortality risk creating ecological traps. Maintaining viable grizzly bear populations and preventing further range loss requires minimizing human-caused mortality and maintaining, or enhancing, productive habitats in secure locations.

The objectives of this study were to evaluate the effects of post-fire and forest thinning on grizzly bear habitat quality in Banff, Yoho, and Kootenay national parks to assess whether these disturbances enhance grizzly bear habitat. Specifically, I first estimated grizzly bear selection of post-fire habitats across different spatial and temporal scales using data from 26 radio-collared grizzly bears. Factors that influenced grizzly bear selection of burns were then used to predict locations (map) where prescribed burning will most effectively create habitat attractive to bears. Second, I compared the presence and abundance of 25 known grizzly bear foods between burns, thinned forests, and adjacent undisturbed forests testing which factors (climate, terrain, or disturbance) most contributed to their occurrence thus informing future burn or thinning prescriptions.

Grizzly bear selection of burns was scale dependant. Burns did not affect home range selection (placement) within the study area but were selected within their home range across the active season (April to November). Compared to thinned or forested areas, burns provided a greater abundance of important early spring, summer, and fall food resources, whereas thinned areas had more abundant green, herbaceous vegetation that is favoured by bears in late spring and early summer. This study provides a more comprehensive understanding of grizzly bear food

resources and habitat use of burned and thinned areas and supports the use of prescribed fire and thinning for enhancements of grizzly bear habitat in remote, secure areas of the parks. Models from this thesis can assist with planning the locations of future prescribed fires and forest thinning treatments in the region.

Preface

This thesis is an original work by Charles McLellan. Chapter 2 and 3 are intended for publication along with co-authors S.E. Nielsen and J. Park. I contributed to the concept formation, study design, and led work on field data collection, data analysis, and manuscript composition. Scott E. Nielsen and Jane Park contributed to the concept formation, study design, data analysis, and thesis edits. The GPS collar data used for this project was collected by the Parks Canada agency under capture permit number LL-2012-10975.

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This thesis would not have been possible without the field staff whom hiked or bushwhacked thousands of kilometers to collect data for this project. I will forever look back at those long days, cold creek crossings, and blistered feet with fond memory. Thank you: Kate Johnson, Leah Pengelly, Gavin Hurd, Brigitte Dreger, Tyler Bateman, Andrew Braid, and many others.

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Table of Contents

Abstract ii
Preface iv
Acknowledgements v
Table of Contents vi
List of Tables viii
List of Figures ix
List of Appendices xii
Chapter 1: General Introduction 1
1. Literature Cited 7
Chapter 2: Multi-scale selection of post-fire habitats by grizzly bears in Banff, Yoho, and Kootenay National Parks, Canada 13
1. Introduction 13
2. Methods 16
2.1 Study Area 16
2.2 Landscape mapping and covariate descriptions 17
2.3 Grizzly bear habitat use 20
2.4 Multi-scale resource selection and predictive mapping 22
3. Results 25
3.1 Influence of recent burns, older burns, and human-use habitats on grizzly bear home range selection (second-order scale) 26
3.2 Seasonal selection of burns, older burns and human-use habitats within home range (third-order scale) 26
3.3 Seasonal within-patch selection of recent burns (fourth-order scale) 29
4. Discussion 31
5. Conclusion 36
6. Literature Cited 39
Chapter 3: Grizzly bear (*Ursus arctos*) food production in post-fire and forest-thinned habitats in Banff, Yoho, and Kootenay National Parks, Canada 57
1. Introduction 57
2. Methods 60

2.1 Study Area 60
2.2 Grizzly bear foods 61
2.3 Field Sampling 63
2.4 Comparing grizzly bear food occurrence among burns, thinned and control areas 64
2.5 Grizzly bear food productivity 65
3. Results 66
3.1 Grizzly bear food occurrence in burned and thinned areas 66
3.4 Distribution of grizzly bear foods in burns 67
3.5 Distribution of grizzly bear foods in thinned areas 67
3.6 Abundance of grizzly bear foods in burns and forested controls 68
3.7 Abundance of grizzly bear foods in thinned areas and forested controls 69
3.8 Abundance of grizzly bear foods between burns and thinned areas 69
4. Discussion 69
5. Literature Cited 78
Chapter 4: General Discussion 95
1. Literature Cited 102
Appendices 105

List of Tables

Table 2.1: Hypophagia season coefficients (β), standard errors (S.E.), significance levels (*p*), and odds ratios (OR) for selection (3rd order) of burns, old burns, and human use areas. Individual models created using logistic regression while sex, age, and population models created from generalized linear mixed effects models (GLMM) with a random intercept for individual bears..... 47

Table 2.2: Early hyperphagia estimated coefficients (β), standard errors (S.E.), significance levels (*p*), and odds ratios (OR) for selection (3rd order) of burns, old burns, and human use areas. Individual models created using logistic regression while sex, age, and population models created from generalized linear mixed effects models (GLMM) with a random intercept for individual bears. 48

Table 2.3: Hyperphagia estimated coefficients (β), standard errors (S.E.), significance levels (*p*), and odds ratios (OR) for selection (3rd order) of burns, old burns, and human use areas. Individual models created using logistic regression while sex, age, and population models created from generalized linear mixed effects models (GLMM) with a random intercept for individual bears..... 49

Table 2.4: Estimated coefficients (β), standard errors (S.E.), and significance levels (*p*) for climate and terrain models created within burn patches (4rd order) for each season. Predictive climate covariates include: mean annual precipitation (MAP), end of frost free period (EFFP), beginning of frost free period (BFFP), climate moisture deficit (CMD), and minimum temperature in January (TMN_01). Terrain covariates include: slope, elevation (elev), distance to water (dwater) and heat-load index (hli). Validation for each model is illustrated by Spearman rank correlation (r_s) between the model training and model testing data. Models were built following a purposeful model building approach using generalized linear mixed effects models (GLMM) with a random intercept for individual bears. 50

Table 2.5: Estimated coefficients (β), standard errors (S.E.), and significance levels (*p*) for fire and terrain models created within burn patches (4rd order) for each season. Predictive fire covariates include: burn severity (severity), distance to fire edge (dist_fire), fire size (area), and time since fire (tsf). Terrain covariates include: slope, elevation (elev), distance to water (dwater) and heat-load index (hli). Validation for each model is illustrated by Spearman rank correlation (r_s) between the model training and model testing data. Models were built following a purposeful model building approach using generalized linear mixed effects models (GLMM) with a random intercept for individual bears. 51

Table 3.1: Akaike's Information Criteria (AIC) top selected model that best describe the occurrence of 18 grizzly bear foods within burned habitats of Banff area. AIC scores (w_i) for the null model and top ranked model, likelihood ratio (LR) χ^2 tests, and their significance (p), as well as area under the curve (AUC), and percent deviance explained are provided.. 86

Table 3.2: Akaike's Information Criteria (AIC) top selected model that best describe the occurrence of 18 grizzly bear foods within thinned habitats of Banff area. AIC scores (w_i) for the null model and top ranked model, likelihood ratio (LR) χ^2 tests, and their significance (p), as well as area under the curve (AUC), and percent deviance explained are provided.. 87

Table 3.3: Average fruit density, green forb dry weight, root density, ungulate pellet groups, and ant colonies per hectare for 19 grizzly bear foods in burned habitats (n = 113) and adjacent non-disturbed forest habitats (n = 103). Mann-Whitney U-tests were used to investigate significant (p) differences between burns and the adjacent forested controls for each species. 88

Table 3.4: Average fruit density, green forb dry weight, root density, ungulate pellet groups, and ant colonies per hectare for 16 grizzly bear foods in thinned habitats (n = 44) and adjacent forested controls (n = 39). Mann-Whitney U-tests were used to investigate significant (p) differences between thinned areas and the adjacent forested controls for each species..... 89

Table 3.5: Average fruit density, green forb dry weight, root density, ungulate pellet groups, and ant colonies per hectare for 19 grizzly bear foods in burned habitats (n = 113) and thinned areas (n = 44). Mann-Whitney U-tests were used to investigate significant (p) differences between burns and thinned areas for each species. 90

Table H.6: Percent occurrence for 18 grizzly bear foods in burns (n = 111) and adjacent non-disturbed forests (n = 103). Beta coefficients (± S.E.), significance levels (p), and odds ratios (OR) of finding grizzly bear foods within burns compared to non-disturbed forests are reported from logistic regression models. 116

List of Figures

Figure 2.1: Location of the study area encompassing Banff, Yoho, and Kootenay National Parks in the south Canadian Rocky Mountains. Wild and prescribed fires that occurred between 1960 and 2012 are indicated by red polygons. Older wildfires that occurred between 1886 and 1959 are indicated by orange polygons. 52

Figure 2.2: Spearman rank (r_s) correlations between the percent of locations within human use areas (HUA) and either burn, or old burn patches. (A) hypophagia burn and human use area; (B) hypophagia old burn and human use area; (C) early hyperphagia burn and human use area; (D) early hyperphagia old burn and human use area; (E) hyperphagia burn and human use area and (F) hyperphagia old burn and human use area. 53

Figure 2.3: Maps predicting grizzly bear selection during hypophagia season (May 1st to June 14th) that illustrate the relative effectiveness of prescribed fire for generating habitat that grizzly bears will select during this season. (A) predictive map across the study area masked only by rock and ice habitats. (B) predictive map across the study area illustrating the burn patches used to create spatial predictions and areas masked because they do not match the modelling environment, or they are rock or ice. 54

Figure 2.4: Maps predicting grizzly bear selection during early hyperphagia season (June 15th to August 7th) that illustrate the relative effectiveness of prescribed fire for generating habitat that grizzly bears will select during this season. (A) predictive map across the study area masked only by rock and ice habitats. (B) predictive map across the study area illustrating the burn patches used to create spatial predictions and areas masked because they do not match the modelling environment, or they are rock or ice. 55

Figure 2.5: Maps predicting grizzly bear selection during hyperphagia season (August 8th to October 31st) that illustrate the relative effectiveness of prescribed fire for generating habitat that grizzly bears will select during this season. (A) predictive map across the study area masked only by rock and ice habitats. (B) predictive map across the study area illustrating the burn patches used to create spatial predictions and areas masked because they do not match the modelling environment, or they are rock or ice. 56

Figure 3.1: Study area encompassing Banff, Yoho and Kootenay National Parks in the southern Canadian Rocky Mountains. Locations where grizzly bear food sampling occurred within burns (n = 111), adjacent burn controls (n = 103), thinned areas (n = 45), and adjacent thinned controls (n = 39) are illustrated. Wild and prescribed fires that occurred between 1960 and 2012 are indicated by red polygons. 91

Figure 3.2: Estimated coefficients from logistic regression models describing the occurrence of 18 grizzly bear foods within burns compared to non-disturbed forests. Positive coefficients indicate a greater occurrence within burns whereas negative coefficients indicate a greater occurrence within non-disturbed controls. Odds ratios (OR) illustrated above bars represent the odds of finding grizzly bear foods within burns compared to non-disturbed forests. 92

Figure 3.3: Estimated coefficients from logistic regression describing the occurrence of 19 grizzly bear foods within thinned areas compared to non-disturbed forests. Positive coefficients indicate a greater occurrence within thinned areas whereas negative coefficients indicate a great occurrence within non-disturbed controls. Odds ratios (OR) illustrated above bars represent the odds of finding grizzly bear foods within thinned areas compared to non-disturbed forests. 92

Figure 3.4: Estimated coefficients from logistic regression describing the occurrence of 18 grizzly bear foods between burns and thinned areas. Positive coefficients indicate a greater occurrence within burns whereas negative coefficients indicate a great occurrence within thinned areas. Odds ratios (OR) illustrated above bars represent the odds of finding grizzly bear foods within burns compared to thinned areas. 93

Figure 3.5: Bar graphs illustrating differences of similar groups of important grizzly bear foods (per hectare) between burns, thinned areas (treatments), and adjacent non-disturbed areas (controls). (A) illustrates differences of fruit (berry) density from 15 fruiting species. (B) illustrates differences of dry weight of three species of green herbaceous vegetation (*Taraxacum officinale, Triffolium* spp. and *Equisetum arvense*). (C) illustrates differences in sweetvetch (*Hedysarum alpin*ium and *Hedysarum sulphurescens*) stem density. (D) illustrates the differences pellet group density from six ungulate species. (E) illustrates the differences in *Formicidae* colony density. 94

List of Appendices

Appendix A: Grizzly bear identification, sex, age class (adult: > 5 yrs; sub-adult: 2-4 yrs), multi-annual 100% minimum convex polygon (MCP) home range size (km^2), percent (%) of burn, old burn and, human use area (HUA) patches in home ranges, and the number of radio-telemetry locations for each season (hypophagia, early hyperphagia, and hyperphagia). .. 105

Appendix B: Influence of recent burns, older burns, and human-use habitats on grizzly bear home range selection (second-order scale). 106

Appendix C: Covariates used to model grizzly bear selection within burned habitats of Banff, Yoho, and Kootenay National Parks. 108

Appendix D: List of grizzly bear foods examined in burns, thinned areas, and adjacent controls as well as their percent occurrence and description. 109

Appendix E: Description of burn and forest thinned features where grizzly bear food data was collected. 110

Appendix F: Environmental covariates used to model the distribution of grizzly bear foods in burns and thinned areas in Banff area. Variable code, category, unit, and source are presented. 115

Appendix G: Name and structure of the five a priori candidate models used for assessing the distribution of grizzly bear foods within burns and thinned areas of Banff area. Disturbance model includes covariates include: tree cover (Tree_cov), regenerating tree cover (Regen_cov), time since disturbance (Age) and disturbance size (Area). The terrain model includes covariates: compound topographic index (CTI), elevation (ELEV) and heat-load index (HLI). The summer climate model includes covariates: average summer precipitation (PPT_SM) and temperature (TAV_SM). The winter climate model includes covariates: average winter precipitation (PPT_WT) and temperature (TAV_WT). The annual climate model includes covariates: mean annual precipitation (MAP) and temperature (MAT). ... 115

Appendix H: Occurrence of grizzly bear foods between burns, thinned areas and adjacent non-disturbed forests. 116

Appendix I: Occurrence of fruit on plants in burns and thinned areas. 119

Chapter 1: General Introduction

Habitat loss and degradation are primary factors that reduce biodiversity (Butchart et al. 2010; Rands et al. 2010). An important and common strategy for moderating these impacts is to protect areas as reserves, parks, or under other designations with the objective of maintaining ecological processes and native species (Chape et al. 2005; Possingham 2006). While protected areas (PAs) are important for conservation, they rarely, if ever represent the multitude of environments that exist in a region (Rodrigues et al. 2004). Additionally, PAs are usually of insufficient size, lack connectivity (Peres 2005; Defries et al. 2005; Naughton-Treves et al. 2005), are often influenced by external activities (Woodroffe and Ginsberg 1998; Hansen and DeFries 2007), and are still susceptible to habitat loss and degradation (Liu et al. 2001; Curran et al. 2004). Increasing the size of PAs is usually difficult because surrounding land is often developed (Gude et al. 2007; Wittemyer et al. 2008), while establishing new PAs is also difficult given the economic, political, social, and cultural dependence of land and resources (Peluso 1993; Adams et al. 2004; Cernea and Schmidt-Soltau 2006). As the human population and associated developments continue to expand, maintaining functional PAs is increasingly important, but also increasingly challenging. The role of effective PAs for conserving biodiversity is especially important for certain groups of species. Wide-ranging carnivores are particularly vulnerable to habitat loss and human-caused mortality (Cardillo et al. 2005; Ripple et al. 2014, but see Linnell et al. 2001).

In North America, habitat loss and degradation occurred rapidly over the last two centuries (Dobson et al. 1997), which has negatively influenced many species, including the grizzly bear (*Ursus arctos* L.; McLellan 1998; Mattson and Merrill 2002). Prior to European settlement, grizzly bears maintained a continuous distribution in western North America, except perhaps some deserts (Mattson and Merrill 2002), ranging from the Arctic Ocean to Central Mexico and

from the Pacific Ocean to the state of North Dakota (Herrero 1972; Schwartz et al. 2003). Since then, increased human density, habitat loss, and human-caused mortality reduced North American grizzly bear populations, as well as their distribution (Mattson and Merrill 2002). In the contiguous United States and Mexico, their distribution was reduced by over 98% (Servheen 1998), which prompted listing grizzly bears as a threatened species in the United States under the Endangered Species Act in 1975. In Canada, grizzly bears have been extirpated from prairie habitats of Manitoba, Saskatchewan, and Alberta. Today, local grizzly bears density varies in British Columbia, western Alberta and the Yukon, Northwest and Nunavut territories. In total, there are roughly 26,000 grizzly bears in Canada (Ross 2002) and are listed as a species of special concern (COSEWIC 2012). This status is largely due to the factors of having a low reproductive rate, low local population density, large range size, and vulnerability to habitat loss and human-mortality (Purvis et al. 2000).

Sustaining viable grizzly bear populations along the fringe of their current distribution is particularly challenging because along the occupied/extirpated interface, habitat fragmentation and mortality results in low density, isolated, sub-populations with lower genetic diversity (McLellan 1998; Paetkau et al. 1998; Proctor et al. 2012). The province of Alberta encompasses most of the eastern grizzly bear distribution of Canada and conserving these populations is necessary to minimize additional range loss. Alberta bears are exposed to resource development that has fragmented habitat and increased both human access and conflict (Nielsen et al. 2009; Northrup et al. 2012). These stresses contributed to listing grizzly bears as a threatened species in Alberta in 2010 (Alberta Environment and Parks, 2016). With resource development continuing to increase, conservation efforts attempt to minimize their negative effects by maintaining core areas where road density and access are limited (Nielsen et al. 2009). While these efforts are

necessary, it is also important that PAs in Alberta maintain viable grizzly bear populations that can, when needed, act as source populations to offset adjacent non-protected areas that may at times be sinks (Northrup et al. 2012, Lamb et al. 2017).

Adjacent to much of Alberta's threatened grizzly bear distribution is one of the largest contiguous PAs in North America with four national parks, eight provincial parks and multiple wilderness areas comprising over 27,500 km^2 of protected land. With large parts of this area (e.g. Banff National Park) being protected from hunting, industrial development and associated habitat loss for over a century, it is often assumed that they support high density or increasing populations of grizzly bears. Unfortunately, this generalization isn't necessarily true. For example, grizzly bears in the Bow Valley of Banff National Park (BNP), have a relatively low population density and considered to be at carrying capacity (Garshelis et al. 2005; Sawaya et al. 2012). With PAs providing a fundamental base in the long-term conservation of threatened species (Margules and Pressey 2000), it is necessary to identify factors that limit grizzly bear populations in these PAs and implement management strategies to augment these populations.

With 9,000 human residents and over three million annual visitors, BNP it is one of the busiest areas in North America where both humans and grizzly bears co-exist and consequently Banff bears suffer from human-caused mortality (Benn and Herrero 2002; Nielsen et al. 2004a; Bertch and Gibeau 2009), and the loss and fragmentation of habitat (Gibeau 1998; Gibeau et al. 2002; Garshelis et al. 2005). Over the last four decades, human-caused mortality has accounted for over 80% of the known grizzly bear deaths with most occurring near townsites and along highways or rail-lines (Benn and Herrero 2002; Nielsen et al. 2004a; Bertch and Gibeau 2009). During this period, management strategies to reduce mortality have been successful (Benn and Herrero 2002; Bertch and Gibeau, 2009) and contributed to Banff grizzlies high survival rates

(Garshelis et al. 2005). Banff area grizzly bears are also limited by bottom-up processes. Relatively poor habitat is the primary factor causing low reproductive rates in Banff area grizzlies (Garshelis et al. 2005), as well as smaller body sizes and condition (Nielsen et al. 2013). This suggests that to enhance grizzly bear populations in Banff and adjacent parks, it is necessary to secure or enhance habitat in areas where human conflict is minimal. With current national park priorities to increase visitation and maintain visitor experiences (Parks Canada 2017), enhancing grizzly bear habitat far from people using methods that maintain Parks Canada's commitment to sustain ecological integrity, may be critical for the future of these bears.

Grizzly bear habitat in the Rocky Mountains generally consists of a mosaic of forest and open areas that are often maintained by wildfire, avalanche, or other natural disturbances (Herrero 1972). These ecosystems are favoured by grizzly bears because open areas provide a greater abundance of foods such as ungulates, roots, herbaceous vegetation, and high-energy fruit (Martin 1983; Hamer 1999; Nielsen et al. 2004b, McLellan 2011). Adjacent forested areas, in turn, offer cover that is utilized for bedding, thermal regulation and security (Blanchard 1983; McLellan 1990; Munro et al. 2006; Moe et al. 2007). Throughout the Canadian Rocky Mountains, fire prevention and suppression has reduced wildfire, early successional habitats, and landscape heterogeneity (Tande 1979; White, 1985; Rhemtulla 2002; Van Wagner et al. 2006). The loss of early successional habitats is more pronounced in PAs than non-protected areas because non-protected areas are disturbed by forestry, mining, energy extraction, and the access roads they require. In Alberta, sites disturbed by industry provide increased quantities of critical grizzly bear foods (Nielsen et al. 2004b; Roever et al. 2008a; Cristescu et al. 2015) and consequently grizzly bears use these sites (Nielsen et al. 2004c; Roever et al. 2008b; Cristescu et al. 2016) even though they are associated with elevated mortality risk (Benn and Herrero 2002;

Nielsen et al. 2006). In PAs where resource extraction is absent, high human use areas, such as railways, roadways, and townsites, provide early seral habitat for grizzly bears (Pollock et al. 2017) and given the elevated risk of mortality (Benn and Herrero 2002; Nielsen et al. 2004a), are likely ecological traps (Naves et al. 2003; Nielsen et al. 2006; Lamb et al. 2017). Furthermore, the wildfire deficit has resulted in a non-natural build up of forest fuels (Keane et al. 1990; see however; Schoennagel et al, 2004), which has prompted the clearing and thinning of vegetation around townsites and other developments to mitigate the consequences of wildfire. These thinning applications have the potential to enhance grizzly bear habitat near townsites and other high human use areas so may also set an ecological trap.

To address the reduced frequency of wildfire, Parks Canada started prescribed burning in the early 1980's to restore the role of fire on ecosystem structure and function. Since the first prescribed fire in 1983, thousands of hectares have been burned to address more specific objectives including: reducing fuels to decrease wildfire potential, reducing the susceptibility of forests to insects and disease, restoring grasslands, and to enhance wildlife habitat. Early research and observations in BNP suggested that grizzly bears use post-burn habitats (Hamer and Herrero 1987) because these areas provided important grizzly bear foods (Hamer 1996; Hamer 1999; Pengelly and Hamer 2006; 2014). As a result, numerous prescribed fires have been implemented with the objective of enhancing grizzly bear habitat, but their effectiveness has not been evaluated. Grizzly bear habitat quality in forest thinning treatments has also not been assessed. It is important that we improve our understanding of how prescribed fire and forest thinning change community structure and ultimately reshape grizzly bear habitat.

The overall objective of this thesis is to provide empirical information on the influence of post-fire and post-thinning habitats on grizzly bear food resources and habitat selection so future

management practices can more effectively enhance habitat in secure locations while minimizing habitat enhancements where grizzly bear mortality is elevated. This thesis includes four chapters, including an introduction and conclusion, with chapter's two and three organized into independent, but complementary manuscripts. Excluding specific University of Alberta guidelines, the format for chapter two and three follow author submission guidelines for the *Journal of Wildlife Management.*

In chapter two, I investigated grizzly bear selection of post fire habitats at three spatial scales to: (1) evaluate if grizzly bears selected post-fire habitats across a range of temporal and spatial scales; (2) test factors predicted to influence grizzly bear selection within burned patches; and (3) developed prescriptive maps to predict where prescribed fire will be most effective for enhancing grizzly bear habitat. In chapter three, I quantified differences in the occurrence and abundance of 25 known grizzly bear foods between burns, thinned areas, and adjacent non-disturbed habitats (forested-controls) and compared models to evaluate what group of factors (climate, terrain or disturbance) contribute most to the occurrence of grizzly bear foods in both burns and thinned areas.

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Chapter 2: Multi-scale selection of post-fire habitats by grizzly bears in Banff, Yoho, and Kootenay National Parks, Canada

1. Introduction

The North American distribution and population of grizzly bears (*Ursus arctos L.*) was significantly reduced in the late 1800's and early 1900's (Mattson and Merrill 2002). Today, grizzly bears are relegated to remote, often mountainous locations, or protected areas where human-caused mortality and habitat loss is less pronounced. The current range of the species in Alberta constitutes most of the eastern edge of their Canadian distribution, so the conservation of these populations is essential to halt further range loss. Grizzly bears in Alberta continue to be affected by expanding resource development and human access, which has contributed to habitat loss and increases in human-caused mortality (Nielsen et al. 2004a; Nielsen et al. 2006). In 2010, grizzly bears were listed as a threatened species in Alberta (Alberta Environment and Parks 2016). Even in protected areas, such as Banff National Park (hereafter Banff), populations are small and at carrying capacity (Garshelis et al. 2005; Sawaya et al. 2012). Animals in Banff have been protected from legal wildlife harvest and resource extraction for almost a century, although grizzly bears in Banff still suffer from high rates of human-caused mortality (Benn and Herrero 2002; Nielsen et al. 2004a) and insufficient quality habitat (Gibeau 1998; Garshelis et al. 2005). Grizzly bears in Banff have apparent nutritional limitations (López-Alfaroa et al. 2015) resulting in small body sizes (Nielsen et al. 2013) and low reproductive rates (Garshelis et al. 2005) with small average litter sizes (1.84 cubs), long inter-birth intervals (4.4 years), and late age of first surviving litters (8.4 years). This has contributed to bears in Banff having one of the lowest reproductive rates of any studied grizzly (brown) bear population (Garshelis et al. 2005), while human-causes have been the single largest mortality factor over the past 35 years (Benn and

Herrero 2002; Berch and Gibeau 2009). To promote a long-term positive or stable population trend, management and conservation can focus on minimizing mortality and/or increasing productivity of habitats. Primary factors affecting mortality and the location of mortality sinks for grizzly bears in Banff are known (Benn and Herrero 2002; Nielsen et al. 2004a) and management strategies continue to be implemented to reduce mortality events (Bertch and Gibeau 2009). Our understanding, however, is more limited on what habitat factors limit local population abundance and which specific management actions can be used to enhance or protect these habitats.

Primary grizzly bear habitat in the central Rocky Mountains has been described as areas composed of a mosaic of forest and open regions which are typically maintained by disturbance agents such as fire or avalanche (Herrero 1972). Fire history studies suggest that wildfire was common in Banff prior to the twentieth century (White 1985; Rogeau and Gilbride 1994), but since then, fire prevention and suppression has dramatically decreased the fire cycle from approximately 60-70 years in the montane ecoregion to over 280 years (Van Wagner et al. 2006). The reduction of fire has altered natural ecosystems throughout the Rocky Mountains with fire-dependent, successional habitats being replaced with homogenous, mature forest stands (Tande 1979; White 1985; Rhemtulla et al. 2002).

The consequence of reduced early successional habitat on grizzly bears in Banff is difficult to quantify because the effects of fire suppression are tied to natural fire regimes that are temporally and spatially variable (Arno 1980; Agee 1993). Research investigating grizzly bear foods in the Rocky Mountains suggest that fruit (Martin 1983; Hamer et al. 1991; Hamer 1996; Braid and Nielsen 2015; Barber et al. 2016; Denny and Nielsen 2017), roots (Hamer 1999; Pengelly and Hamer 2006), and ungulates (Hamer and Herrero 1991; Mattson 1997) are positively associated

with post-fire/early seral stands. In a study 200 km south of Banff in the Flathead valley of British Columbia, McLellan and Hovey (2001) reported that bears favored old burns during the late summer and early fall period over that of other habitat types. When feeding in these burns, bears rapidly deposited the fat needed for hibernation and reproduction (McLellan 2011).

A widespread reduction of fire may also negatively affect grizzly bears by increasing the relative attractiveness to human disturbed sites that increase mortality risk. In other parts of the Canadian Rockies where natural fire regimes have been altered, grizzly bears select clearcuts (Wielgus and Vernier 2003; Nielsen et al. 2004b) and road edges (Roever et al. 2008), despite elevated risk of mortality (McLellan and Shackleton 1988; Benn and Herrero 2002; Nielsen et al. 2004a). In Banff, over 80% of the recorded grizzly bear deaths between 1971 and 2008 were directly caused by people and occurred near town sites, roads, or railways (Benn and Herrero 2002; Nielsen et al. 2004a; Berch and Gibeau 2009). There has been a considerable amount of research evaluating grizzly bear selection of human disturbances including clearcuts (Weilgus and Vernier 2003; Nielsen et al. 2004b; Stewart et al. 2012), roads (Mace et al. 1996; Gibeau et al. 2002; Roever et al. 2008), agricultural lands (Northrup et al. 2012), mine sites (Critescu et al. 2016), and oil and gas infrastructure (Laberee et al. 2014; Mckay et al. 2014). However, there is little research focused on the use of post-fire habitats despite the fact that prescribed fire may be considered one of the few tools available to enhance habitat without promoting access and associated mortality.

To address reduced wildfire frequency, Parks Canada commenced a prescribed fire program in 1983 to reinstate fire as a primary ecological disturbance. Since then, the proficiency and operational application of prescribed fire has increased and is now considered a primary method for enhancing secure grizzly bear habitat. However, to effectively enhance grizzly bear habitat

with prescribed fire, it is important to first determine if grizzly bears use (select) burned patches and evaluate the factors contributing to which burns or parts of burns are most favored by bears. The objectives of this work were to therefore: (1) evaluate if grizzly bears selected burned habitats in Banff, Yoho, and Kootenay National Parks across a range of temporal and spatial scales, (2) test climate, terrain, and burn factors predicted to influence grizzly bear selection within burned patches, and (3) develop prescriptive maps that predict where prescribed fire would be most effectively used to enhance grizzly bear habitat. I also investigated if individual grizzly bears that selected burns had reduced use (selection) for areas where human-caused mortality was more likely, thus suggesting direct interactions with the management of grizzly bear mortality.

2. Methods

2.1 Study Area

The study encompassed Banff, Yoho, and Kootenay National Parks (hereafter Banff area; Figure 2.1), which form a contiguous protected area within the southern Canadian Rocky Mountains (51°40 N, 116° 00' W). Together these parks cover approximately 9,360 km^2 straddling the continental divide including parts of Alberta and British Columbia. Topography consists mainly of rugged mountains, steep ravines, and occasionally flat, wide valley bottoms. Elevations range from 890 m in the southwest corner to over 3500 m along the continental divide. Precipitation is related to an orographic effect with the west side of the divide receiving greater annual precipitation (~616 mm/year) than the east side (~472 mm/year). Average daily maximum temperature in the valley bottoms are 9° C with average minimum temperatures of -3° C. The large elevation gradient, variable topography, soil, and local climate influence the diversity of vegetation communities. In general, the vegetation associations can be classified into the

following three ecoregions based on elevation: montane (900-1,600 m), subalpine (1,600-2,300 m), and alpine (> 2,300 m). The montane region is dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), Douglas fir (*Pseudotsuga menziesii*), and aspen (*Populus tremuloides*) forest with a dry grass or wet shrub understory. Subalpine regions are forested with Engelmann spruce (*Picea engelmanii*), subalpine fir (*Abies lasiocarpa*), subalpine larch (*Larix lyallii*), and mature lodgepole pine. Low shrubs, herbs, grasses, and lichens characterize alpine areas.

Historically, the fire cycle was largely influenced by the precipitation gradient across the divide. Between the years 1340 and 1840, areas in the west burned on average every 90-100 years, while areas east of the divide burned every 60-70 years (Van Wagner et al. 2006). Fire frequency in both regions has been significantly reduced since that time. On the east side of the divide, between 1760 and 1940, the fire cycle increased by roughly 175 years with only 1% of the forests burning naturally since 1940 (Van Wagner et al. 2006). Fire history data since 1840 are more variable on the west side of the divide (Van Wagner et al. 2006), however in Kootenay National Park, Masters (1990) describes a fire cycle of 60 years prior to 1788 to an almost complete absence of fires between 1928 and 1988. Since Master's research, a wildfire burned more than 17,000 ha in Kootenay National Park in 2003. Parks Canada's current objective in the mountain national parks is to manage fire to 50% of the historic fire cycle.

2.2 Landscape mapping and covariate descriptions

Burns

I categorized burns within the study area into two classes based on age and precision of burn perimeters. Data for recent burns (1960-2015) were derived from direct post-burn mapping and

Landsat imagery. Data from many older burns (i.e., 1896-1959) have lower spatial accuracy because they were derived from fire history work in the area (Masters 1990; Rogeau and Gilbride 1994) and in some cases, direct post-burn mapping. Grizzly bear selection for these historic burns were analysed at broad spatial scales to investigate the possible long-term value of post-fire habitats. Duration was of interest because grizzly bear foods, such as huckleberry (*Vaccinium membranaceum*) and buffaloberry (*Shepherdia canadensis*), may not reach maximum fruit productivity until >50 years after disturbance (Martin, 1979; Hamer 1996) with some cases bears demonstrating selection for older post-fire habitats (e.g., Hamer and Herrero 1987b; McLellan and Hovey 2001). Research in the late 1970's, from within the study area, suggested that bears readily used these older burns that occurred between 1868 and 1936 (Hamer and Herrero 1987b). I incorporate these older burns in the analysis to evaluate if bears continue to utilize these habitats or if forest succession over the past 40 years has reduced their habitat value to bears.

Burn severity

Because burn severity affects post-fire vegetation responses (Turner et al. 1999; Keeley 2009), I evaluated whether burn severity influenced grizzly bear habitat selection within post-fire habitats. The severity of some recent, larger burns (post-1990; >100 ha) were mapped using differenced Normalized Burn Ratio (dNBR; Key and Benson 2006). These methods utilize the Landsat Thematic Mapper (TM) remote sensing satellites to establish Normalized Burn Ratio's (NBR) that are described as the ratio between Landsat TM bands 4 and 7, which are sensitive to vegetation and exposed soil cover (Key and Benson 2006). Burn severity is measured by comparing a pre-fire NBR image with a post-fire NBR image with the difference (dNBR) indicating changes to vegetation and soil resulting from the fire. For the analyses, I compared

images taken one year before fires to those taken two years after the fire. The processed burn severity estimates were summarized in ArcGIS 10.2 (Environmental Systems Research Institute 2013) with a pixel resolution of 30 m.

Human-use

I tested whether individual bears that selected burn patches had reduced selection for areas with high human use. To quantify this, I developed a human-use area (HUA) polygon that encompassed sites where mortality risk is elevated and previously identified as mortality sinks (Benn and Herrero 2002; Nielsen et al. 2004a; Bertch and Gibeau 2009). HUA's included a 1000 m buffer around the townsites of Banff, Lake Louise, and Field, and a 100 m buffer on each side of highways, other primary roads, and the Canadian Pacific rail-line. I did not include areas such as trails, ski-hills, campgrounds, or outlying commercial accommodations because in the last two decades these areas have not contributed to grizzly bear mortality events (Bertch and Gibeau 2009).

Climate, terrain, and distance measures

I considered 26 climate, 4 terrain, and 2 distance covariates that have been used in other grizzly bear habitat selection studies in the region (Apps et al. 2004; Nielsen et al. 2004b; Milakovic et al. 2012) or used to describe the distribution of important bear foods (Nielsen et al. 2003; 2010; Roberts et al. 2014; Braid and Nielsen 2015). Terrain variables included elevation, slope, heat-load index, and a compound topographic index. Heat-load index (HLI) measures annual solar radiation by combining slope, aspect, and latitude (McCune 2007), while the compound topographic index (CTI) represents a wetness index that describes moisture and drainage and has been found to be correlated with numerous soil attributes (Moore et al. 1991; Gessler et al.

1995). I also incorporated measures of distance to burn patch edge and distance to waterbody as these have been associated with grizzly bear habitat selection elsewhere (McLellan and Hovey 2001; Stewart et al. 2013). Climate data were obtained from ClimateWNA, a software that generates monthly, seasonal and annual climate variables (Wang et al. 2012). The climate data were derived at a 300 m resolution.

2.3 Grizzly bear habitat use

Between 2012 and 2015, 14 female and 12 male grizzly bears (See Appendix A for details) were captured by Parks Canada personnel using culvert traps or ground darting techniques that were approved under Parks Canada research collection permit number LL-2012-10975. To minimize animal stress, capture costs, and to facilitate other research objectives, all captures occurred during the spring, in valley bottoms, and near roads or access points. Bears were fitted with ATS (Advanced Telemetry Systems), Followit, or Vectronic brand GPS radio collars that were programmed to acquire locations at 2 or 4 hour intervals. Without accounting for missing GPS fixes that occurred from collar malfunction, GPS acquisition rates were >85% and therefore I did not account for GPS radio telemetry bias (Frair et al. 2004). Locations outside the study area (2.2%) were removed because of inconsistent mapping of burn polygons and availability of other covariate data. The multi-annual home range of each bear was delineated using 100% minimum-convex-polygons (MCP's) using Minimum Bounding Geometry in ArcGIS 10.2 (Environmental Systems Research Institute, 2013). Random points were generated at a density of 5 locations per km^2 in ArcGIS across each home range and across the entire study area to estimate either available or use locations depending on the scale of analysis (see description of scales below).

Selection of burn patches was evaluated using resource selection functions (RSF's; Manly et al. 2002) following a used/available design where grizzly bear "use" was compared to "available"

locations bounded by spatial extents (Boyce 2006). I implemented a multi-scale approach to evaluate each of the specific objectives and to account for dependence of RSF results on spatial scale parameters (Boyce 2006; Meyer and Thuriller 2006; Ciarneillo et al. 2007). I developed seasonal RSF models at Johnson's (1980) second-order (homerange; See Appendix B), third-order (within home range), and fourth-order (within patch) scales to account for spatial and temporal effects on selection variability (Boyce 2006). At the second-order scale (Appendix B), I evaluated if grizzly bears establish their home ranges relative to recent burns (1960-2012), old burns (1886 -1959), or human-use areas. At the third-order scale I examined if bears demonstrate selection for these three habitat types during different seasons, and if individuals who select burn or old burn patches have lower selection for human-use areas. At the fourth-order scale, I modelled covariates that predict grizzly bear locations within burn patches. I then extrapolated these models across the study area to produce prescriptive management maps that predict locations where prescribed fire would be most effective relative to generating productive grizzly bear habitat based on patterns of habitat selection of existing burns.

At the broadest scale, the influence of season was not investigated; however, at finer scales, telemetry data were divided into three seasons to account for differences in diet (Hamer and Herrero 1987a; Hamer et al. 1991, McLellan and Hovey 1995; Munro et al. 2006) and habitat use (Nielsen et al. 2003; 2010). The first season, hypophagia, included telemetry locations from May 1st to June 14th. During hypophagia, bears in the region typically feed on sweetvetch (*Hedysarum* spp.) roots, ungulates, and green herbaceous plants such as clover (*Trifolium* spp.), dandelions (*Taraxacum officinale*), and horsetails (*Equisetum arvense*). The second season, or early hyperphagia, included telemetry locations from June 15th to August 7th. During early hyperphagia bears continue to feed on herbaceous matter but also focus on cow-parsnip

(*Heracleum lanatum*), sedges, grasses, and ants (*Formicidae* spp.). The last season, hyperphagia, included telemetry locations from August 8th to October 31st. During hyperphagia bears focus on huckleberries, blueberries, grouseberries (*Vaccinium* spp.), and buffaloberries (*Shepherdia canadensis*), and prior to hibernation return to feeding on sweetvetch roots and ungulates. Variation in burn selection between sex and age classes was evaluated at the second and third-order scales. Individuals with an average age >5 years were classified as adults, while sub-adults consisted of those bears between 2-5 years of age during the study.

2.4 Multi-scale resource selection and predictive mapping

2.4.1 Seasonal selection of burn patches within home ranges (third-order scale)

To test if grizzly bears selected burned habitats during each season, I followed a design III structure (Thomas and Taylor 1990) at the third-order scale (Johnson 1980) where the use of burns was compared to availability of burns within individual home ranges. At this scale, I also investigated selection for old burns (1896-1960) and human-use areas to consider if post-fire habitats draw bears away from these areas where the probability of mortality is elevated (Benn and Herrero 2002; Nielsen et al. 2004a). During each season, use locations of an individual (1) were compared to randomly generated locations across their home range (0) following the univariate RSF logistic model:

$$w(x) = \exp(\beta_1 x_1) \qquad \text{(eqn1)}$$

where $w(x)$ is the resource selection function and β_1 is the selection coefficient for the predictor variable x_1 (Manly et al. 2002). For this analysis, predictor variable x_1 indicated whether locations fell within (1) or outside (0) burn polygons and β coefficients were assessed using

generalized linear models (GLM) with a binomial distribution and logit-link function using R statistical computing package (R development core, 2008).

Population-level assessments included pooling sex and age-classes and all individuals for an overall assessment. For each of these analyses I used generalized linear mixed models (GLMM) where a random intercept accounted for unbalanced sampling of individual grizzly bears and autocorrelation (Gillies et al. 2006; Hebblewhite and Merrill 2008). The RSF with random effects extend equation 1 to the form:

$$w(x) = \exp(\beta_o + \beta_1 x_{1ij} + \gamma_{0x}) \qquad \text{(eqn2)}$$

where β_o is the mean intercept, β_1 is the selection coefficient for the predictor variable x_1 (in this case: burn patch), and γ_{0x} is the random intercept (Gillies et al. 2006). To estimate β coefficients I used generalized linear mixed-effects modelling using Laplace approximation with R package lme4 (R development core, 2008; Bates et al. 2013).

To test if individual grizzly bears that select burned habitats showed reduced selection for human use locations, I investigated correlation between the percent of locations within burns and old burns to the percent of locations within human use areas for each bear. I used Spearman rank correlation (r_s) with negative and significant values indicating that bears that select burns or old burns have a lower affinity for human use areas.

2.4.2 Seasonal within-burn patch selection (fourth-order scale)

I followed a design III structure (Thomas and Taylor 1990) at the fourth-order scale (Johnson 1980) to measure the importance of covariates to predict locations grizzly bears selected within burns during each season. I compared locations for each individual that were within burns (use)

to randomly generated locations within burns (available) that were in their home range. To maintain adequate sample sizes for model building and validation, I only partitioned data by season and did not evaluate sex and age class influences.

I followed a purposeful model building approach (Hosmer et al. 2013) which began by analysing each predictor variable (See Appendix C for details) in a univariate GLMM as described by equation 2. Predictor variables were then ranked by their significance (z- values) and all significant ($p \leq 0.25$), non-collinear ($r < |0.7|$) predictor variables were fit into the multivariate RSF logistic model:

$$g(x) = \exp(\beta_o + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k + \gamma_{0k}) \quad \text{(eqn 3)}$$

where β_o is the mean intercept, x_k are a vector of predictor variables and γ_{0x} is the random intercept (Gillies et al. 2006). Predictor variables in this multivariate model that were not significant ($p \geq 0.05$) were removed and the "new" model was compared to the "previous" model using log likelihood (Hosmer et al. 2013). This process was iterated until the best fitting "main effects model" was established.

Model validation and mapping

I used a *k*-fold cross-validation to evaluate the predictive capability of each seasonal model (Boyce et al. 2002) by randomly withholding 20% (i.e., $k = 5$) of grizzly bear location data and used this data partition to validate the model that was created with the remaining 80% of the 'training' data. Predictions are evaluated based on the frequency of observed locations in predicted ranked bins of habitat quality from 1 to 10; if the RSF model had high predictive power, then the frequency of grizzly bear locations would be greater in higher ranked bins

(Boyce et al. 2002). Spearman's rank correlation (r_s) was used to assess goodness-of-fit with high positive values indicating good predictive capacity.

The seasonal models that were most supported by the data were extrapolated into study-area maps using the Raster Calculator function in the Spatial Analyst extension of ArcGIS. To reduce bias and problems of inference associated with extrapolating models from a patch to a landscape spatial scale (Boyce 2006), I masked locations across the study area that did not match the burn patch sampling environment for each covariate in the model. For comparison and management planning, I present two maps for each season, one with and one without the sampling environment mask.

2.4.3 Burn severity and terrain modelling

To evaluate the influence fire and terrain variables on grizzly bear selection of burns, I followed the same modelling approach described above, but only for seven burns that were mapped for burn severity. The intent of these models was to identify specific burn factors that influence grizzly bear selection so they can be implemented when developing fire prescriptions to enhance grizzly bear habitat. In these models, I maintained a random-intercept for individual bears but also included one for each of the seven burns to account for a lack of independence of burn predictors, including time since fire and burn area. These models were also validated using *k*-fold cross-validation (Boyce et al. 2002).

3. Results

3.1 Influence of recent burns, older burns, and human-use habitats on grizzly bear home range selection (second-order scale).

At the population level, recent burns (1960-2012) had no significant effect on grizzly bear home range location, however, both sub-adults and females had more recent burns within their home range than available. Old burns (1896-1959) were negatively associated with the locations of grizzly bear home ranges while human use areas had a positive association. For each of these three habitat types there was considerable variability among individuals (See Appendix B for additional details).

3.2 Seasonal selection of burns, older burns and human-use habitats within home range (third-order scale)

3.2.1 Hypophagia

A total of 8,996 bear locations were collected during hypophagia (May 1-June 14). Of these 1,055 (11.7%) occurred in recent burns, that on average covered 5.6% of the home ranges. An additional 782 (8.6%) occurred in old burns that on average covered 6.7% of the home ranges, while 2,184 (24.3%) occurred within human use areas that on average covered only 3.4% of the home ranges. During this season, 7 individuals selected burns, 8 avoided burns (7 were never located in a burn), and 4 bears neither selected nor avoided burn patches (Table 2.1).

At a population-level, bears positively selected for burn patches with an odds ratio (OR) of 2.39 (2.4 times more likely in burns than non-burns). Bears, as a population, also selected older burns (OR 1.60) with 11 bears selecting, 5 avoiding (4 were never located in an old burn), and 6 bears neither selecting nor avoiding old burns. Human-use areas were selected for during hypophagia with 18 bears selecting human-use areas with only 3 bears having neutral selection of human-use

areas. The odds ratio for selecting areas of human-use versus areas without human-use was high at 9.66. Sub-adults had neutral selection for burns and old-burns, while adults and both sex classes demonstrated positive selection for all three habitats during the hypophagia.

During the hypophagia season there was a negative and significant correlation between individual bear percent selection of burns and human use areas (Figure 2.2A). However, there was also a positive, non-significant, correlation between old burns and human use areas (Figure 2.2B).

3.2.2 Early hyperphagia

During early hyperphagia (June 15th to Aug. 7th), 19,909 bear locations were collected. Of these 2,297 (11.5%) occurred in burns, 998 (5.0%) were in old burns, and 3,374 (16.9%) were in human use areas. During this period, burn habitats were selected by 9 bears and avoided by 9 bears (2 were never located in a burn), while 4 bears neither selected nor avoided burns (Table 2.2). Old burns were selected by 8 bears, avoided by 11 (1 was never located in an old burn) and 6 bears had neutral selection. Human use areas continued to be highly selected with 19 bears selecting areas of human use, 4 neither selecting nor avoiding, and only 2 bears avoiding these habitats. At the population level, bears selected burns and human use areas more than expected based on availability; however, they had a significant avoidance of old burned habitats (Table 2.2). In contrast to the hypophagia period, selection for burned habitat increased slightly (OR: 2.46), whereas selection in both old burns (OR: 0.734) and human use areas (OR: 6.27) decreased. Evaluating age or sex-classes independently did not reveal any specific variation with both classes selecting for burns and human use areas and avoiding old burn habitats.

There was a negative, non-significant, correlation between percent selection of burns by individual bears and human use areas during the early hyperphagia season (Figure 2.2C). For this season, individual bear selection of old burn patches and human use areas continued to be positively correlated, however, they were not significant (Figure 2.2D).

3.2.3 Hyperphagia

During hyperphagia (Aug. 8th to Oct. 31st) 24,770 bear locations were collected with 4,636 (18.7%) in burns, 3,377 (13.7 %) in old burns, and 1,408 (5.6%) in human use areas. During this period, burn habitats were selected by 14 bears, avoided by 6 bears (3 were never located in burns), and only 1 individual had neutral selection for burn patches (Table 2.3). Old burns were also selected during this season with 13 bears selecting, 4 avoiding (1 was never located in an old burn), and 5 neither selecting nor avoiding these habitats. Only 7 bears selected human use areas during this season, while 14 avoided (6 were never located in human use areas), and 3 neither selected nor avoided these sites. At the population level, bears still had a positive selection for all three habitats. In comparison to previous seasons, there was a notable increase in the selection of burn and old burns, while there was a reduction in selection of human use areas. During hyperphagia estimated odds ratios were 4.48 for burns, 2.43 for old burns and 1.98 for human use areas. The reduced selection of human use areas during hyperphagia was largely attributed to female bears avoiding these habitats. In contrast, an evaluation of differences among age-classes did not reveal any variation in selection from population-level results.

During the hyperphagia season, the correlation between the percent of locations within burn patches and human use areas for each individual remained negative but non-significant (Figure

2.2E). This measure for old burns and human use areas was negative during the hyperphagia season but also remained non-significant (Figure 2.2F).

3.3 Seasonal within-patch selection of recent burns (fourth-order scale)

3.3.1 Hypophagia

The climate and terrain variables that best predicted the 1,005 grizzly bear locations that occurred within burn habitats during hypophagia included: mean annual precipitation (MAP), distance to water (dwater), end of frost free period (eFFP), slope, and elevation (Table 2.4). During the season of hypophagia, grizzly bears selected steep sites at lower elevations that were further from water as compared to available burn habitat. Burn locations with lower annual precipitation and a late date of frost on-set also contributed to which burns, and where within the burns, bears selected. Model validation was good with a positive Spearman rank correlation (r_s = 0.93; SD = 0.03). Maps extrapolating this model provide predictions of priority sites for prescribed fire that should create or enhance grizzly bear habitat for the hypophagia period (Figure 2.3).

The fire and terrain model assembled from a subset of fires and grizzly bear locations (n = 496) that had the best model performance included the fire covariates: severity, time since fire (TSF), area, and distance to fire (Table 2.5). Terrain covariates that increased model performance included elevation (elev) and heat-load index (HLI). During this season bears selected older and larger burns and sites closer to the edge of fires with lower burn severity. These sites were located at lower elevations with elevated heat-load (solar radiation). This model also had good predictive accuracy with significant and positive Spearman rank (r_s = 0.92, SD= 0.03).

3.3.1 Early hyperphagia

During the season of early hyperphagia, the climate and terrain variables that best predicted the 2,297 grizzly bear locations occurring within burn patches included: mean annual precipitation (MAP), end of frost free period (eFFP), heat load index (HLI), distance to water (dwater), and slope (Table 2.4). During this season grizzly bears selected burned areas in warmer and wetter sites with flatter terrain and further from water sources. Validation indicated this model fit well with a positive Spearman rank correlation (r_s = 0.92, SD= 0.03). Study area-wide maps extrapolated from this model indicated priority areas for creating or enhancing early hyperphagia grizzly bear habitat with prescribed fire (Figure 2.4).

The fire and terrain model that best described grizzly bear selection inside burn patches included elevation, heat-load index (HLI), burn area, and slope (Table 2.5). This model was based on 1,791 grizzly bear locations that occurred within burns where burn severity was mapped. During early hyperphagia, burn severity did not predict grizzly bear locations; however, bears did select for smaller burns. In these burns they also selected for flatter, lower elevations with a lower heat-load index. This model also had good predictive accuracy with significant and positive Spearman rank rho (r_s = 0.93, SD=0.04).

3.3.2 Hyperphagia

During the season of hyperphagia, the 4,636 grizzly bear locations that occurred within burns were best predicted by the terrain variables: elevation, slope, and compound topographic index (CTI), and the climate variables: climate moisture deficit (CMD), beginning of frost free period (bFFP), and mean coldest month temperature (MCMT; Table 2.4). During this period, bears selected low angled and dry slopes at high elevations within burns in locations that were cold in the winter and where frost persisted late in the spring. Validation indicated this model had

relatively good predictive capacity with a positive Spearman rank correlation (r_s = 0.87, SD =0.06). A study area-wide map extrapolated from this model indicates priority areas for creating or enhancing hyperphagia bear habitat with prescribed fire (Figure 2.5).

The fire and terrain covariates that best explained grizzly bear locations (n = 3,195) within the subset of burns included elevation, distance to water, slope, and burn severity (Table 2.5). During hyperphagia, grizzly bears preferred high elevation, low angle slopes that burned at high severity, and that were further from water. This model had lower predictive accuracy than fire and terrain models from previous seasons; but still a positive Spearman rank rho (r_s =0.70, SD=0.07).

4. Discussion

These results support the Canadian Rocky Mountain parks long term management idea that burned habitats provided important habitat for grizzly bears. Previous knowledge of grizzly bear selection of burned habitats in the Banff area was based primarily on field observations and qualitative assessments (Hamer and Herrero 1987a). Here, I demonstrated that grizzly bears in the study did not adjust (select) home ranges based on locations of burns, but they did select burned patches within their home range. I also determined that selection of these habitats varied among individuals, temporally, and at different spatial scales. Previous analyses have emphasised individual (McLellan and Hovey 2001; Nielsen et al. 2002), seasonal (McLellan and Hovey 2001; Nielsen et al. 2003; 2004b), and spatial (McLoughlin et al. 2002; Ciarniello et al. 2007) variation in grizzly bear habitat selection. This research supports the importance of addressing these factors.

I also found grizzly bears selected human-use areas at all scales and seasons. This result was anticipated given that bears were captured within, or near such sites. This biased capture

distribution likely also influenced the selection of burn patches, particularly at the home range scale (2nd order). Fire suppression over in the last century has occurred throughout the study area, however, fire suppression efforts were greater and their effects most pronounced in the main valleys where bears were captured (White 1985). Fire suppression resulted in less burned habitats in and around the bear capture sites and therefore fewer burned patches within home ranges centered near their capture location. Randomly capturing bears across the study area would decrease the bias associated with capture location (Roever et al. 2008), however, without more secondary roads in the study area, unbiased capture would require helicopter darting or snaring that would increase costs and may cause a bias towards burned habitats because helicopter-based capture is most effective in open areas, including burns.

Grizzly bears selected burn patches within their home ranges (i.e. 3rd order) during each season and this is the scale that best tests if grizzly bears select burned patches (Johnson 1980; Boyce et al. 2003; Boyce 2006). The selection of burned habitat during spring (hypophagia) or early summer (early hyperphagia) has rarely been documented. About 10% of the bears monitored by McLellan and Hovey (2001) used burned habitats during spring more than were available in their study area. Immediately to the west of Banff area, Munro (1999) found both male and female grizzly bears used burns more than available during spring, although not nearly to the degree that they selected avalanche chutes. To the northeast of this study, Nielsen et al. (2002) found bears avoid burns during this season. I presume selection of burns early in the year is because roots of sweetvetch are larger, more abundant, and easier to dig in burned areas than elsewhere (Hamer 1999; Pengelly and Hamer 2006) and this is a major food during spring (Hamer and Herrero 1987a; 1987b; McLellan and Hovey 1995; Munro et al. 2006). The within-burn model for the hypophagia season found bears selecting steeper and drier sites that are characteristic of

locations bears dig yellow sweetvetch (*Hedysarum sulphurescens*; Holcroft and Herrero 1984), but also feed on other early season foods such as bearberry (*Arctostapstaphylos uva-ursi*) and ants (Hamer and Herrero 1987a). Burn patches may also provide more opportunity for bears to kill or scavenge on ungulates because these habitats are selected by ungulates (Boyce et al. 2003; Gillingham and Parker 2008; Allred et al. 2011), as well as wolves targeting ungulates (Robinson et al. 2012).

Bears continued to select burns during early hyperphagia, but switched from areas with low precipitation to areas with higher precipitation, perhaps coinciding with the feeding transition to green herbaceous vegetation, grasses, and sedges (Hamer and Herrero 1987a; McLellan and Hovey 1995; Munro et al. 2006). Differences in snowpack between low and high precipitation sites likely contribute to this transition as well, with dry sites being selected early because they are snow-free sooner than areas with a greater snowpack. The absence of alternative forest-opening disturbances, such as logging in Banff area, likely contribute to burn patch selection during early hyperphagia, whereas outside protected areas, bears avoided burns (Nielsen et al. 2002), but selected cut-blocks (Nielsen et al. 2004b).

As anticipated, selection of burns peaked when bears were in hyperphagia which is consistent with McLellan and Hovey (2001), who analyzed habitat selection of 63 radiocollared grizzly bears over 16 years and found burns were selected over other habitats between 1 August and 20 September. Grizzly bears throughout the Canadian Rockies feed primarily on fruiting plants during hyperphagia (Hamer and Herrero 1987a; McLellan and Hovey 1995; Munro et al. 2006) and increased fruit production occurring in burns (Martin 1983; Hamer et al. 1991; Hamer 1996; Pengelly and Hamer 2014) likely explains elevated selection of burn patches during this period. Old burn patches (1896-1959) that were avoided in early hyperphagia were selected during

hyperphagia, including the burns that occurred in 1928 and 1936 and grizzly bears used in the late 1970's (Hamer and Herrero 1987b). This result suggests that burns have the capacity to provide productive habitats for multiple generations of grizzly bears. In the Flathead Valley of British Columbia, similar high-elevation burns from severe wildfires during the droughts of the 1930's produced sufficient huckleberries to keep that grizzly bear population at high densities in the 1980's despite heavy hunting pressure and intensive industrial development (McLellan and Hovey 2001, McLellan 2011; 2015). The selection models during the hyperphagia season from more recent burns (1960-2012) support a similar phenomenon with bears selecting higher elevation sites that burned at increased severity. I hypothesize that these covariates are predictors for grizzly bear selection because they promote productive berry fields. In montane zones of the Banff area, a high severity fire will replace lodgepole pine stands at lower elevations and Engelmann spruce and subalpine fir forests at higher elevations (Arno 1980). At lower elevations, post-fire lodgepole pine regeneration occurs rapidly, often at high stem density because of serotinous cones that open and germinate quickly after a fire (Turner et al. 1999; Schoennagel et al.2003). However, at higher elevations natural regeneration is typically gradual and occurs at lower stem density because Engelmann spruce and subalpine fir rely on seed dispersal from burn edges or surviving trees (Johnson and Miyanishi 1991). This delayed conifer regeneration allows for increased and prolonged productivity of fruiting plants that are important to grizzly bears, particularly because buffaloberry (*Shepherida canadensis*) and *Vaccinium* species reproduce primarily from rhizomes that, being underground, are often resistant to fire (Miller 1977; Noste and Bushy 1987).

The selection of burn patches during hyperphagia suggests that use of prescribed fire can enhance habitat and stimulate the low reproductive rates of grizzly bears in Banff area because it

is during this period grizzly bears rapidly deposit fat (McLellan 2011), thus influencing reproductive capacity (Hilderband et al. 2000; Robbins et al. 2012). Additionally, during hyperphagia when burn patches were highly selected, grizzly bear selection of human-use areas declined by almost 5 and 3-times in comparison to hypophagia and early hyperphagia respectively. Females; however, had their greatest affinity for burn patches during hypophagia and selected burns half as much as males during hyperphagia. A greater selection of these habitats by males supports previous research that suggests females are displaced from highly productive habitats to avoid intraspecific predation (Wielgus and Bunnell 1994). Even with the lower rates of human-use selection during hyperphagia I did not observe a significant negative correlation between individual selection of burns and human-use areas during hyperphagia. This was likely influenced by bears returning to human use areas from burn patches after fruiting resources diminished. Partitioning the hyperphagia season into two classes, berry season and post-berry season, as others have done (McLellan and Hovey 2001), would help identify the late season return to human use areas.

I suggest caution when interpreting differences in selection by sex at various scales because of different home range sizes. At the broadest scale, home range delineated “use”, and bears with large home ranges (males) could have a negative association, while bears with smaller home ranges (females) have a positive association when having the same burn patches within their home range. At a finer spatial scale, however, the influence of home range size switches because home range now delineated “available” habitat. At this scale if males and females, for example, had the same burn patches within their home range and used these patches the same, male selection would be greater because this habitat covers a smaller proportion of their larger home ranges. This emphasises the application of hierarchical, multi-scale approach when investigating

habitat selection following a use-availability design (Boyce 2006; Meyer and Thuiller 2006). Differences in home range size and availability of burn patches within home ranges likely contributes to a functional response (Mysterud and Ims 1998) of these habitats where preference of burn patches changes with the proportion of burn patches available (Matthiopoulos et al. 2011). I did not investigate or account for a possible functional response, as others have done elsewhere for other species (Hebblewhite and Merrill 2008; Godvik et al. 2009). Research investigating a functional response could help guide targets for amount of area burned and prescribed fire locations that best achieve an optimal proportion of burn patches across the landscape that most benefit grizzly bears.

Due to differences of spatial scale between burn patches where models were generated and the study area where they were extrapolated, I suggest care in the use of predictive maps with on-the-ground evaluations needed prior to implementing prescribed fires. I controlled for potential "scaling-up" model extrapolation errors by masking study area locations that failed to match the environment sampled in my study, but factors influencing selection that were not captured by my models are not accounted for in prescriptive maps. I suggest the models could be improved further by incorporating geomorphic covariates that address spatial differences of substrate and soil composition as these have important associations with vegetation communities, particularly in areas such as Banff where limestone, granitic, and quartzitic soils occur (Goldin 1977). Although there are some limitations with this study, it demonstrates that grizzly bears select burn patches in Banff area and provides park managers information to more effectively increase limited grizzly bear habitat through the application of prescribed fire.

5. Conclusion

This study demonstrates that grizzly bears select burned patches within home ranges during all active seasons, particularly during hyperphagia when they rapidly deposit fat in preparation for hibernation and successful pregnancy (McLellan 2011). Bears also selected for 55-110 year-old burns at this time of year indicating the long-term value of burns as habitat for bears. Based on climate, terrain, and fire factors, I developed models that predicted where prescribed fire and wildfire would increase grizzly bear habitat. This should assist fire managers in selecting locations where prescribed fire will most enhance habitat for bears. I also identify factors that, if implemented in fire prescriptions, should increase habitat quality for bears. I do note that grizzly bears in this study also selected for human-use areas (highways, railways and townsites) where over 80% of the known mortality has occurred in the last 30 years (Benn and Herrero 2002; Berch and Gibeau 2009). Grizzly bears selection for these risky habitats notably decreased during the hyperphagia period when burns were selected most.

With the Banff grizzly bear population at low density, at carrying capacity (Sawaya et al. 2012; Whittington and Sawaya 2015), and with one of the slowest reproductive rates of any population studied (Garshelis et al. 2005), this study provides optimism that prescribed fire can help stimulate bottom-up factors by enhancing and creating important habitat and at the same time, reduce top-down factors by drawing bears away from areas of high human use. Analytical methods that tie habitat selection to survival (Nielsen 2011), reproduction (McLoughlin et al. 2007), and abundance (Boyce and McDonald 1999; Nielsen et al. 2005; Nielsen et al. 2010; Boyce et al. 2016) have grown considerably in recent years and have the potential to increase our understanding of how forest fires (natural and prescribed) affect bear populations. Additional research in Banff area on the demographics of grizzly bears should examine the effect of prescribed fires on population growth. Given the substantial decrease of fire disturbance in these

ecosystems over the last century (White 1985; Van Wagner et al. 2006), I encourage continued and increased use of prescribed fire in Banff area and additional evaluation of its importance to grizzly bears by measuring the foods produced, use by bears, and vital rates of bears before and after prescribed fire is applied.

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Table 2.1: Hypophagia season coefficients (β), standard errors (S.E.), significance levels (*p*), and odds ratios (OR) for selection (3rd order) of burns, old burns, and human use areas. Individual models created using logistic regression while sex, age, and population models created from generalized linear mixed effects models (GLMM) with a random intercept for individual bears.

	Recent burns (1960-2012)				Old burns (1896-1959)				Human use areas			
	β	**S.E.**	***p***	**OR**	**β**	**S.E.**	***p***	**OR**	**β**	**S.E.**	***p***	**OR**
Individual												
F64	-0.048	0.404	0.906	0.953	0.915	0.234	<0.001	2.496	1.730	0.109	<0.001	5.641
F72	-0.053	0.146	0.716	0.948	1.289	0.163	<0.001	3.628	2.174	0.106	<0.001	8.791
M122	0.915	0.141	<0.001	2.497	0.246	0.230	0.283	1.279	2.082	0.139	<0.001	8.019
M125	[a]avoid				2.995	0.228	<0.001	19.979	3.727	0.260	<0.001	41.567
M126	-1.826	0.338	<0.001	0.161	1.322	0.099	<0.001	3.750	3.326	0.078	<0.001	27.836
M128	[a]avoid				0.697	0.209	<0.001	2.009	4.029	0.150	<0.001	56.210
F130	2.984	0.152	<0.001	19.771	-0.022	0.274	0.936	0.978	0.162	0.132	0.219	1.176
F131	2.261	0.116	<0.001	9.589	[a]avoid				1.191	0.241	<0.001	3.292
M132	0.445	0.134	<0.001	1.560	-2.075	0.324	<0.001	0.126	0.766	0.164	<0.001	2.151
†F133	-	-	-	-	4.430	0.436	<0.001	83.915	1.319	0.453	0.004	3.739
F135	2.297	0.142	<0.001	9.942	[a]avoid				0.168	0.484	0.728	1.183
M136	1.605	0.119	<0.001	4.978	0.112	0.182	0.537	1.119	1.170	0.149	<0.001	3.222
†F138	-	-	-	-	-0.876	1.081	0.418	0.416	1.409	0.279	<0.001	4.091
M140	-0.435	0.269	0.105	0.647	1.158	0.205	<0.001	3.182	1.229	0.767	0.109	3.417
M141	-0.078	0.124	0.529	0.925	1.011	0.068	<0.001	2.749	2.497	0.057	<0.001	12.149
F142	[a]avoid				3.163	0.197	<0.001	23.637	3.926	0.192	<0.001	50.709
F143	[a]avoid				-0.829	0.464	0.074	0.437	1.441	0.180	<0.001	4.223
M144	[a]avoid				[a]avoid				3.457	0.163	<0.001	31.715
F155	1.338	0.174	<0.001	3.812	[a]avoid				1.151	0.489	0.019	3.162
F156	[a]avoid				2.935	0.178	<0.001	18.827	3.305	0.231	<0.001	27.239
M158	[a]avoid				1.194	0.226	<0.001	3.301	2.484	0.254	<0.001	11.988
†F161	-	-	-	-	[a]avoid				2.064	0.361	<0.001	7.876
Sex class												
female	1.339	0.051	<0.001	3.816	0.359	0.064	<0.001	1.432	1.719	0.050	<0.001	5.580
male	0.243	0.066	<0.001	1.275	0.551	0.055	<0.001	1.734	2.659	0.042	<0.001	14.287
Age class												
adult	1.096	0.043	<0.001	2.991	0.643	0.047	<0.001	1.903	2.187	0.037	<0.001	8.904
subadult	0.038	0.094	0.684	1.039	-0.113	0.094	0.230	0.893	2.570	0.071	<0.001	13.063
Population	0.869	0.038	<0.001	2.385	0.467	0.042	<0.001	1.595	2.268	0.033	<0.001	9.663

† no burn patches in home range

[a]Perfect avoidance: parameter estimate not available

Table 2.2: Early hyperphagia estimated coefficients (β), standard errors (S.E.), significance levels (*p*), and odds ratios (OR) for selection (3rd order) of burns, old burns, and human use areas. Individual models created using logistic regression while sex, age, and population models created from generalized linear mixed effects models (GLMM) with a random intercept for individual bears.

	Recent burns (1960-2012)				Old burns (1896-1959)				Human use areas			
	β	**S.E.**	***p***	**OR**	**β**	**S.E.**	***p***	**OR**	**β**	**S.E.**	***p***	**OR**
Individual												
F64	-0.389	0.469	0.407	0.678	0.954	0.231	<0.001	2.596	1.925	0.106	<0.001	6.856
F72	0.574	0.083	<0.001	1.776	0.930	0.132	<0.001	2.533	1.724	0.087	<0.001	5.609
M122	1.963	0.088	<0.001	7.123	-0.836	0.274	0.002	0.434	2.008	0.109	<0.001	7.446
M125	1.570	0.428	<0.001	4.806	1.456	0.304	<0.001	4.290	2.345	0.380	<0.001	10.432
M126	1.329	0.082	<0.001	3.779	0.157	0.128	0.221	1.170	2.451	0.077	<0.001	11.604
M128	-1.225	0.384	0.001	0.294	-2.524	0.580	<0.001	0.080	2.413	0.100	<0.001	11.166
F130	1.446	0.166	<0.001	4.247	0.074	0.214	0.731	1.076	1.405	0.084	<0.001	4.076
F131	2.622	0.088	<0.001	13.770	-3.377	0.359	<0.001	0.034	0.037	0.250	0.883	1.037
M132	-1.157	0.168	<0.001	0.314	-0.739	0.127	<0.001	0.478	-1.656	0.301	<0.001	0.191
†F133	-	-	-	-	-0.036	0.168	0.830	0.965	0.555	0.258	0.031	1.743
M134	1.082	0.128	<0.001	2.950	-0.100	0.147	0.495	0.905	2.037	0.106	<0.001	7.666
F135	0.733	0.102	<0.001	2.081	-1.090	0.127	<0.001	0.336	-1.401	0.530	0.008	0.246
M136	-0.610	0.221	0.006	0.543	-1.270	0.264	<0.001	0.281	1.899	0.098	<0.001	6.678
†F138	-	-	-	-	1.810	0.459	<0.001	6.107	1.176	0.263	<0.001	3.241
M141	1.402	0.167	<0.001	4.065	-0.605	0.202	0.003	0.546	-0.051	0.256	0.842	0.950
F142	-0.547	0.244	0.025	0.579	0.867	0.228	<0.001	2.379	2.135	0.146	<0.001	8.457
F143	-0.397	0.172	0.021	0.672	0.659	0.175	<0.001	1.933	1.459	0.131	<0.001	4.301
M144	-0.225	0.468	0.630	0.798	[a]avoid				2.685	0.250	<0.001	14.660
F148	0.099	0.266	0.709	1.104	-0.538	0.356	0.131	0.584	2.719	0.104	<0.001	15.163
M149	[a]avoid				1.782	0.138	<0.001	5.940	3.026	0.157	<0.001	20.616
F155	0.068	0.153	0.659	1.070	-1.470	0.161	<0.001	0.230	-0.415	0.565	0.462	0.660
F156	-0.634	0.307	0.039	0.530	0.993	0.157	<0.001	2.698	0.736	0.269	0.006	2.088
M158	[a]avoid				-2.559	0.712	<0.001	0.077	1.293	0.246	<0.001	3.643
F160	-2.570	1.008	0.011	0.077	0.321	0.327	0.326	1.379	2.184	0.187	<0.001	8.882
†F161	-	-	-	-	-2.003	0.718	0.005	0.135	0.340	0.365	0.352	1.405
Sex class												
female	0.934	0.039	<0.001	2.544	-0.364	0.049	<0.001	0.695	1.685	0.039	<0.001	5.395
male	0.854	0.045	<0.001	2.348	-0.235	0.055	<0.001	0.791	1.976	0.037	<0.001	7.216
Age class												
adult	1.266	0.033	<0.001	3.546	-0.412	0.047	<0.001	0.662	1.767	0.032	<0.001	5.853
subadult	-0.566	0.080	<0.001	0.568	-0.132	0.059	0.026	0.876	2.006	0.051	<0.001	7.431
Population	0.899	0.029	<0.001	2.456	-0.309	0.037	<0.001	0.734	1.836	0.027	<0.001	6.272

† no burn patches in home range

[a]Perfect avoidance: parameter estimate not available

Table 2.3: Hyperphagia estimated coefficients (β), standard errors (S.E.), significance levels (*p*), and odds ratios (OR) for selection (3rd order) of burns, old burns, and human use areas. Individual models created using logistic regression while sex, age, and population models created from generalized linear mixed effects models (GLMM) with a random intercept for individual bears.

	Recent burns (1960-2012)				Old burns (1896-1959)				Human use areas			
	β	**S.E.**	***p***	**OR**	**β**	**S.E.**	***p***	**OR**	**β**	**S.E.**	***p***	**OR**
Individual												
F64	-1.623	0.720	0.024	0.197	-1.045	0.463	0.024	0.352	0.658	0.123	<0.001	1.931
F72	1.229	0.075	<0.001	3.417	1.452	0.121	<0.001	4.272	-1.160	0.184	<0.001	0.314
M122	0.828	0.087	<0.001	2.290	0.768	0.112	<0.001	2.155	2.839	0.082	<0.001	17.096
M125	[a]avoid				1.914	0.110	<0.001	6.779	1.560	0.220	<0.001	4.760
M126	3.450	0.060	<0.001	31.513	0.273	0.104	0.009	1.314	0.071	0.122	0.562	1.073
M128	[a]avoid				-0.141	0.154	0.360	0.869	2.380	0.086	<0.001	10.803
F130	2.273	0.168	<0.001	9.710	[a]avoid				-1.726	0.310	<0.001	0.178
F131	1.322	0.081	<0.001	3.749	0.460	0.084	<0.001	1.584	[a]avoid			
M132	-3.202	-0.413	<0.001	0.041	0.355	0.091	<0.001	1.426	-4.217	1.003	<0.001	0.015
†F133	-	-	-	-	0.329	0.154	0.033	1.390	-0.947	0.472	0.045	0.388
M134	0.541	0.272	0.046	1.717	3.324	0.123	<0.001	27.767	2.225	0.159	<0.001	9.255
F135	0.123	0.104	0.239	1.130	1.310	0.077	<0.001	3.707	[a]avoid			
M136	0.372	0.120	0.001	1.451	2.007	0.070	<0.001	7.441	-1.029	0.243	<0.001	0.358
†F138	-	-	-	-	1.689	0.459	<0.001	5.415	[a]avoid			
M141	2.960	0.111	<0.001	19.297	-2.081	0.338	<0.001	0.125	-3.254	1.003	0.001	0.039
F142	0.697	0.224	0.002	2.007	0.445	0.366	0.223	1.561	-0.476	0.428	0.265	0.621
F143	-0.078	0.134	0.564	0.925	0.603	0.158	<0.001	1.828	-2.528	0.457	<0.001	0.080
M144	1.988	0.089	<0.001	7.302	-0.443	0.329	0.178	0.642	-0.681	0.205	<0.001	0.506
F148	1.496	0.157	<0.001	4.462	0.428	0.212	0.043	1.534	1.636	0.100	<0.001	5.136
F155	-1.259	0.201	<0.001	0.284	1.201	0.085	<0.001	3.322	[a]avoid			
F156	1.727	0.159	<0.001	5.623	0.160	0.186	0.388	1.174	[a]avoid			
M158	[a]avoid				-2.559	0.712	<0.001	0.077	1.293	0.246	<0.001	3.643
F160	2.787	0.136	<0.001	16.229	[a]avoid				0.047	0.213	0.824	1.049
†F161	-	-	-	-	1.162	0.176	<0.001	3.197	[a]avoid			
Sex class												
female	1.086	0.036	<0.001	2.961	0.843	0.036	<0.001	2.323	-0.013	0.055	0.815	0.987
male	1.790	0.030	<0.001	5.990	0.935	0.035	<0.001	2.548	1.170	0.042	<0.001	3.221
Age class												
adult	1.766	0.028	<0.001	5.848	1.050	0.030	<0.001	2.856	0.525	0.044	<0.001	1.691
subadult	0.860	0.043	<0.001	2.362	0.508	0.047	<0.001	1.662	0.922	0.053	<0.001	2.514
Population	1.500	0.023	<0.001	4.481	0.889	0.025	<0.001	2.433	0.684	0.034	<0.001	1.981

† no burn patches in home range

[a]Perfect avoidance: parameter estimate not available

Table 2.4: Estimated coefficients (β), standard errors (S.E.), and significance levels (*p*) for climate and terrain models created within burn patches (4rd order) for each season. Predictive climate covariates include: mean annual precipitation (MAP), end of frost free period (EFFP), beginning of frost free period (BFFP), climate moisture deficit (CMD), and minimum temperature in January (TMN_01). Terrain covariates include: slope, elevation (elev), distance to water (dwater) and heat-load index (hli). Validation for each model is illustrated by Spearman rank correlation (r_s) between the model training and model testing data. Models were built following a purposeful model building approach using generalized linear mixed effects models (GLMM) with a random intercept for individual bears.

Hypophagia				**Early hyperphagia**				**Hyperphagia**			
Covariate	**β**	**S.E.**	***p***	**Covariate**	**β**	**S.E.**	***p***	**Covariate**	**β**	**S.E.**	***p***
† MAP	-0.340	0.032	<0.001	slope	-0.048	0.005	<0.001	†elev	0.121	0.022	<0.001
† dwater	0.061	0.017	<0.001	EFFP	0.087	0.007	<0.001	BFFP	0.111	0.012	<0.001
EFFP	0.014	0.004	<0.001	† hli	-0.055	0.014	<0.001	†CMD	-1.534	0.105	<0.001
slope	0.041	0.006	<0.001	† MAP	0.126	0.021	<0.001	MCMT	0.093	0.009	<0.001
† elev	-0.167	0.039	<0.001	TMN_01	1.203	0.080	<0.001	slope	-0.065	0.004	<0.001
				† dist_water	0.065	0.013	<0.001	cti	-0.033	0.017	0.051
Validation	[a]r_s *0.93 SD 0.03*			**Validation**	[a]r_s *0.92 SD 0.03*			**Validation**	[a]r_s *0.87 SD 0.06*		

† estimated coefficients and standard errors 100 times their actual value

[a] k-fold cross-validation using 10 testing/training sets and 10 bins

Table 2.5: Estimated coefficients (β), standard errors (S.E.), and significance levels (*p*) for fire and terrain models created within burn patches (4rd order) for each season. Predictive fire covariates include: burn severity (severity), distance to fire edge (dist_fire), fire size (area), and time since fire (tsf). Terrain covariates include: slope, elevation (elev), distance to water (dwater) and heat-load index (hli). Validation for each model is illustrated by Spearman rank correlation (r_s) between the model training and model testing data. Models were built following a purposeful model building approach using generalized linear mixed effects models (GLMM) with a random intercept for individual bears.

Hypophagia				**Early hyperphagia**				**Hyperphagia**			
Covariate	**β**	**S.E.**	***p***	**Covariate**	**β**	**S.E.**	***p***	**Covariate**	**β**	**S.E.**	***p***
† severity	-0.130	0.040	0.001	† elev	-0.149	0.024	<0.001	†dwater	0.029	0.014	0.040
† elev	-0.326	0.049	<0.001	† hli	-0.113	0.020	<0.001	elev	0.260	0.019	<0.001
† hli	0.092	0.020	<0.001	area	-0.018	0.006	0.002	slope	-0.049	0.004	<0.001
† dist_fire	-0.036	0.015	0.017	slope	-0.040	0.006	<0.001	tsf	-0.181	0.038	<0.001
tsf	0.203	0.096	0.035					†severity	0.047	0.015	0.002
area	0.513	0.239	0.032								
Validation	[a]r_s *0.92 SD 0.03*			**Validation**	[a]r_s *0.93 SD 0.04*			**Validation**	[a]r_s *0.70 SD 0.07*		

† estimated coefficients and standard errors 100 times their actual value

[a] k-fold cross-validation using 10 testing/training sets and 10 bins

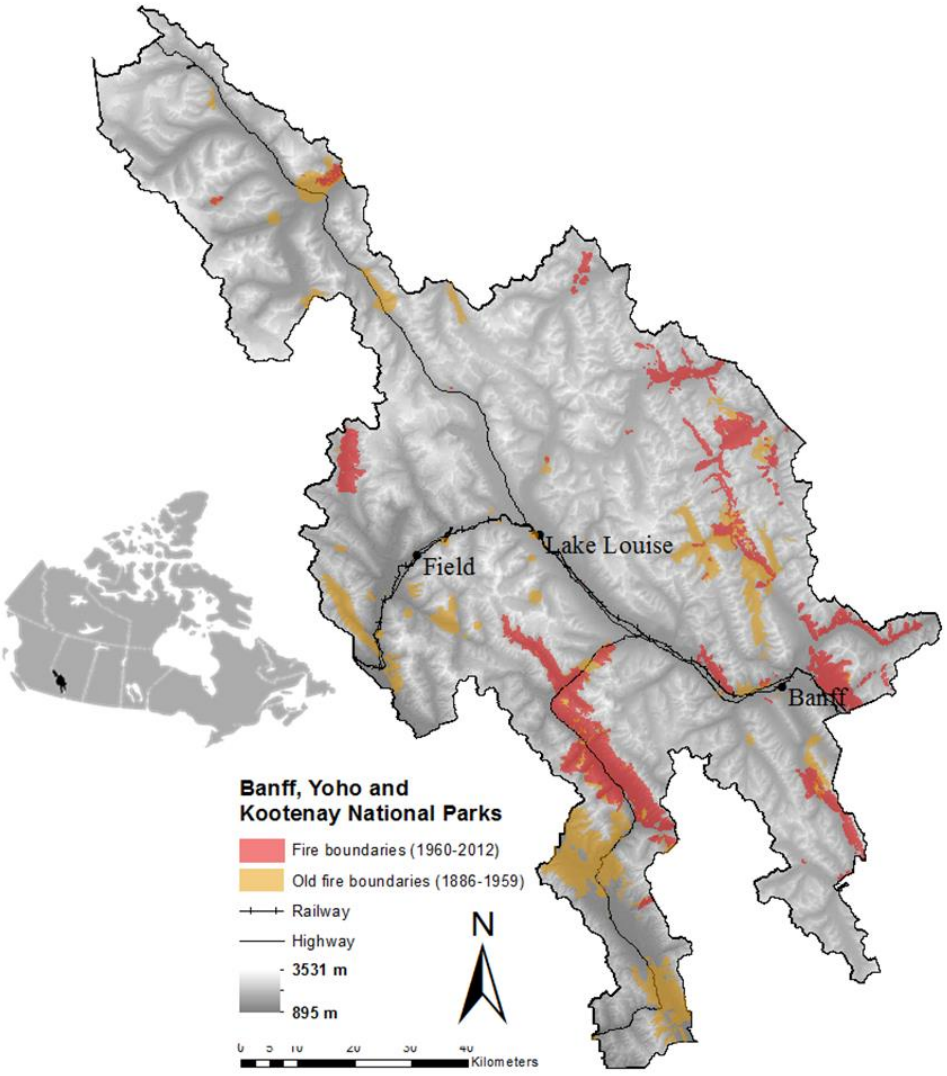

Figure 2.1: Location of the study area encompassing Banff, Yoho, and Kootenay National Parks in the south Canadian Rocky Mountains. Wild and prescribed fires that occurred between 1960 and 2012 are indicated by red polygons. Older wildfires that occurred between 1886 and 1959 are indicated by orange polygons.

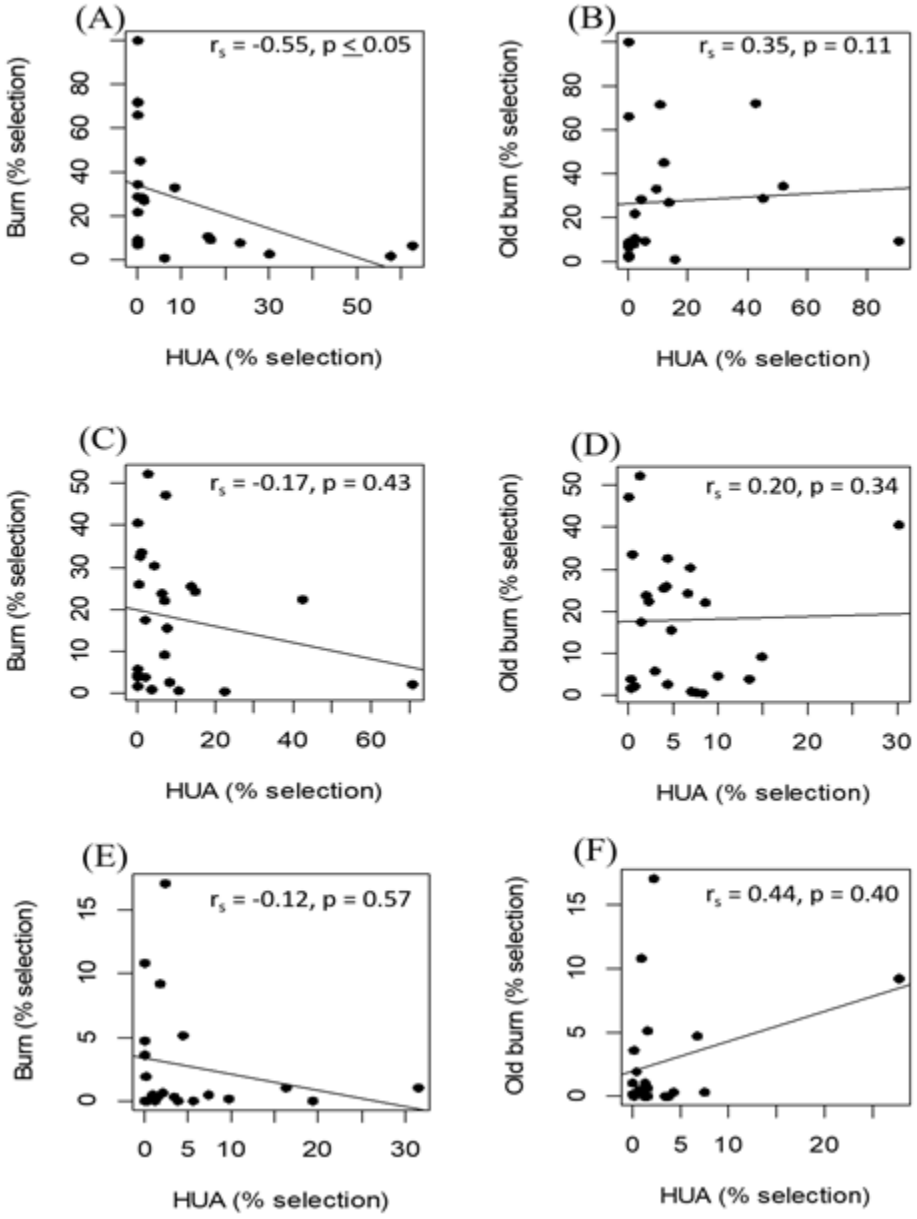

Figure 2.2: Spearman rank (r_s) correlations between the percent of locations within human use areas (HUA) and either burn, or old burn patches. (A) hypophagia burn and human use area; (B) hypophagia old burn and human use area; (C) early hyperphagia burn and human use area; (D) early hyperphagia old burn and human use area; (E) hyperphagia burn and human use area and (F) hyperphagia old burn and human use area.

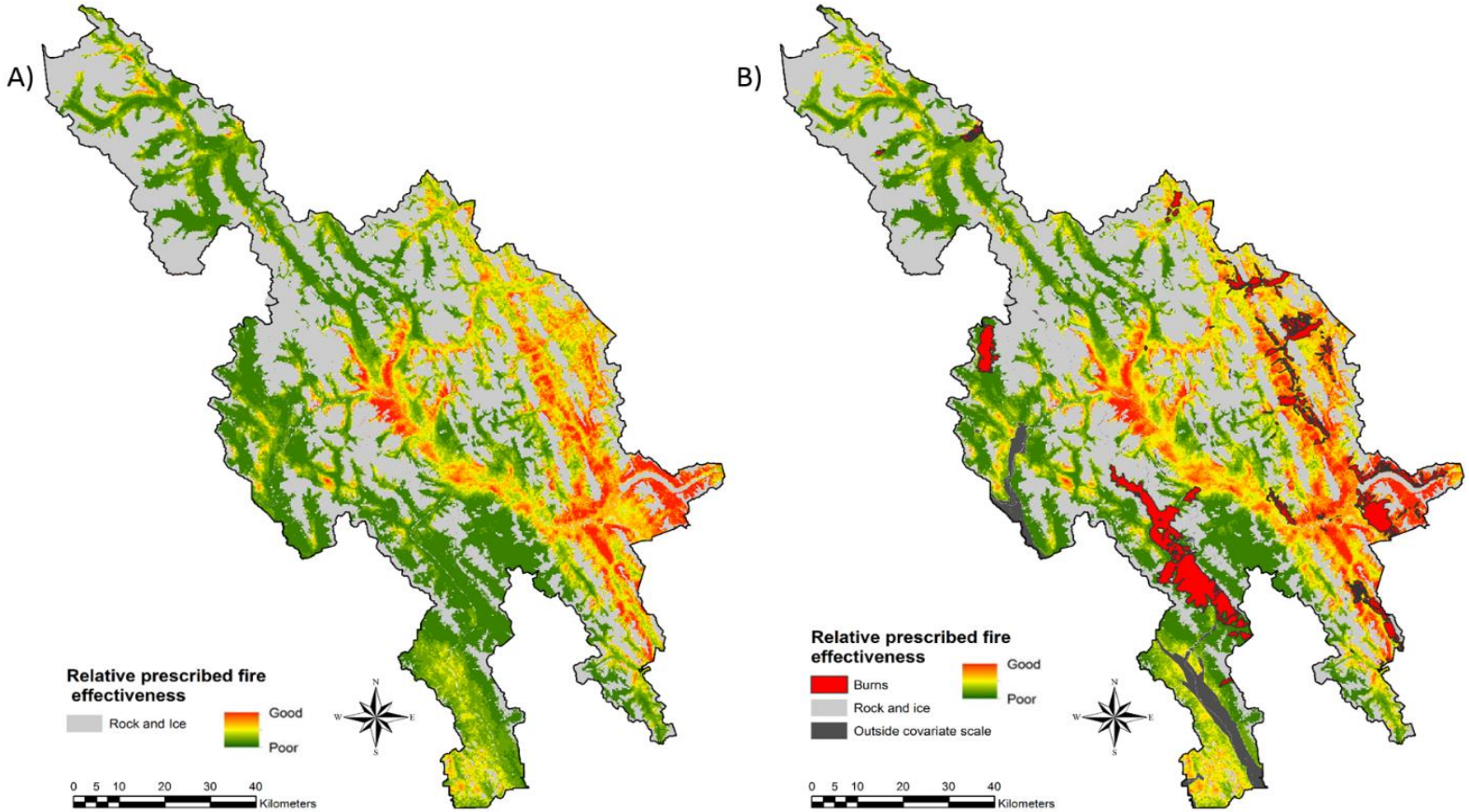

Figure 2.3: Maps predicting grizzly bear selection during hypophagia season (May 1st to June 14th) that illustrate the relative effectiveness of prescribed fire for generating habitat that grizzly bears will select during this season. (A) predictive map across the study area masked only by rock and ice habitats. (B) predictive map across the study area illustrating the burn patches used to create spatial predictions and areas masked because they do not match the modelling environment, or they are rock or ice.

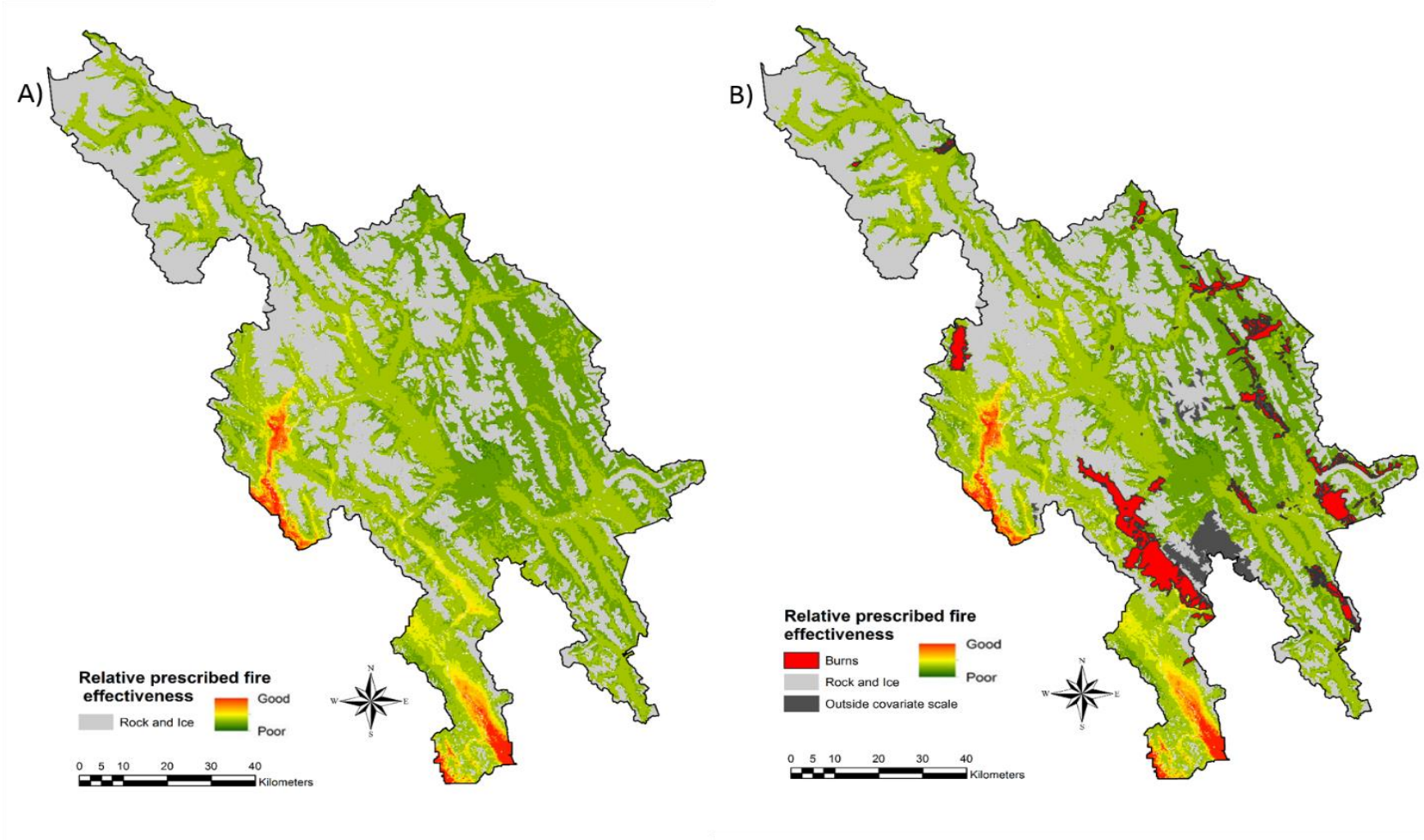

Figure 2.4: Maps predicting grizzly bear selection during early hyperphagia season (June 15th to August 7th) that illustrate the relative effectiveness of prescribed fire for generating habitat that grizzly bears will select during this season. (A) predictive map across the study area masked only by rock and ice habitats. (B) predictive map across the study area illustrating the burn patches used to create spatial predictions and areas masked because they do not match the modelling environment, or they are rock or ice.

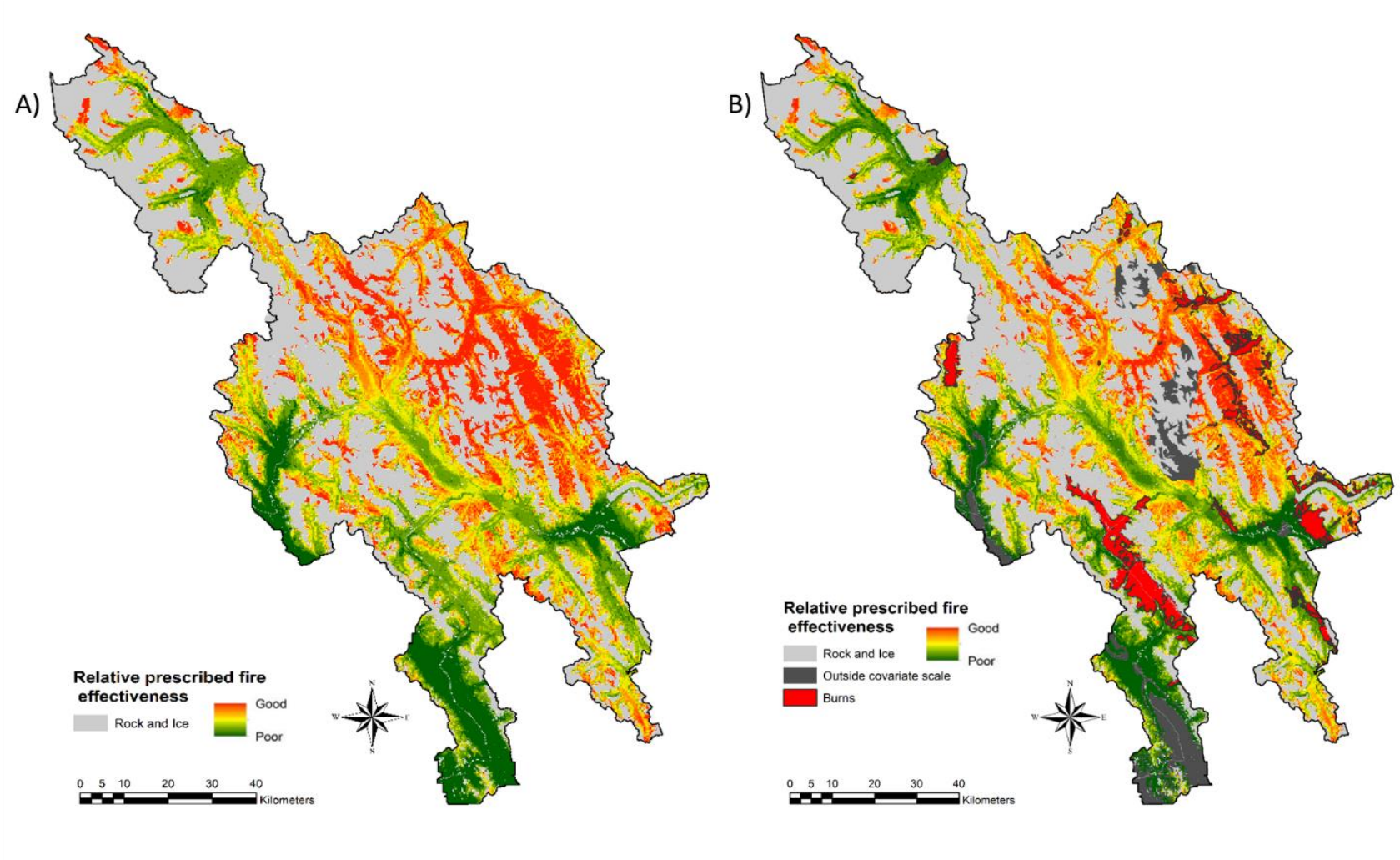

Figure 2.5: Maps predicting grizzly bear selection during hyperphagia season (August 8th to October 31st) that illustrate the relative effectiveness of prescribed fire for generating habitat that grizzly bears will select during this season. (A) predictive map across the study area masked only by rock and ice habitats. (B) predictive map across the study area illustrating the burn patches used to create spatial predictions and areas masked because they do not match the modelling environment, or they are rock or ice.

Chapter 3: Grizzly bear (*Ursus arctos*) food production in post-fire and forest-thinned habitats in Banff, Yoho, and Kootenay National Parks, Canada

1. Introduction

Human-caused mortality and habitat loss are the primary factors that limit wildlife populations and contribute to species extinctions (Fahrig1997; Woodroffe 2000). In North America, human-caused mortality was the primary factor leading to the extirpation of grizzly bears (*Ursus arctos*) from much of their range between 1850 and 1970 (Mattson and Merrill 2002). By the 1970's grizzly bears mainly occupied protected areas or remote regions where human-caused mortality was less pronounced. Since the 1970's, conservation efforts have focused on reducing human-caused mortality by limiting or prohibiting hunting, minimizing bear attractants, restricting access, and educating the public (Mattson et al. 1996). These efforts have effectively recovered populations in many areas (Harris et al. 2007; Eberhardt and Breiwick 2010; Mace et al. 2012), but elsewhere grizzly bear populations continue to decline (Boulanger and Stenhouse 2009; McLellan 2015) and their long-term sustainability is an increasing concern. For these populations, continuing to minimize mortality while also maintaining, enhancing, or creating productive and secure habitat is required.

Mortality (top-down) has typically been considered the primary factor limiting grizzly bear populations (McLellan et al. 1999; Boyce et al. 2001; Harris et al. 2006), however, research on food resources (bottom-up) and population demographics identify the importance of productive habitats for grizzly bear conservation (Hilderbrand et al. 1999; Nielsen et al. 2010; McLellan 2011; Mowet et al. 2013; Nielsen et al. 2017). Human-caused mortality and food productivity are also linked; human-bear conflicts and mortality often increase during times when food availability declines (Mattson et al. 1992; Gunther et al. 2004). In addition, grizzly bears are

particularly susceptible to ecological traps or attractive sink habitat where productive habitat occurs in areas with elevated mortality risk (Nielsen et al. 2006; Schwartz et al. 2010; Northrup et al. 2012; Lamb et al. 2017). Effective grizzly bear conservation requires both reducing mortality and maintaining productive habitats. If productive habitat is secured, enhanced, or created in remote, roadless areas where human/bear conflict and thus grizzly bear mortality is low, then bear populations will increase by stimulating bottom-up growth parameters and suppressing top-down mortality parameters (Lamb et al. 2018). Research on grizzly bear diet (Hamer and Herrero 1987a; Mattson et al. 1991; McLellan and Hovey 1995; Munro et al. 2006), nutritional optimization (Robbins et al. 2007; Coogan et al. 2014), and foods that contribute to increases in grizzly bear abundance and density (Hilderbrand et al. 1999; Nielsen et al. 2010; 2017; McLellan 2011; Mowat et al. 2013; López-Alfaro et al. 2015) are well documented. Knowledge on practices and applications to enhance or establish productive habitats that contain these critical grizzly bear food resources is limited.

Banff National Park, Canada has had no hunting or resource development for over a century, yet grizzly bears still suffer from human-caused mortality (Benn and Herrero 2002; Nielsen et al. 2004a) and a lack of productive habitat (Gibeau 1998; Garshelis et al. 2005). Over the last 35 years, more than 80% of known grizzly bear deaths were human-caused, with railway and road collisions being the primary causes (Benn and Herrero 2002; Berch and Gibeau 2009). With Banff having only moderately productive habitat (Gibeau 1998), and a large expanse of rock and ice, grizzly bears have low population density, small body sizes, very low reproductive rates, and are considered at carrying capacity (Garshelis et al. 2005; Sawaya et al. 2012; Nielsen et al. 2013). Unlike measuring human caused mortality, it is difficult to quantify the degree to which grizzly bear habitat quantity and quality has changed within protected areas. Using a cumulative

effects analysis, Gibeau (1998), suggested that human developments, such as townsites, trails, roads, and the railway in Banff, more than doubled the number of management units that were described as "low realized productivity." This assessment, however, did not consider the influence that effective fire suppression and loss of early seral habitat has had on grizzly bear habitat quality.

Grizzly bear habitat in the Rocky Mountains is often categorized by a mosaic of forested and open habitats that are usually maintained by disturbance events, notably wildfire (Hererro 1972; Zager et al. 1983). Fire history studies throughout the Canadian Rockies, including Banff, suggest fire suppression has contributed to significant declines in fire frequency during the last century (Tande 1979; White 1985; Rogeau and Gilbride 1994; Van Wagner et al. 2006; Rogeau et al. 2016; Davis et al. 2016) and an increase of mature, homogenous forests (Chavardes and Daniels 2016). The effect of reduced fire frequency on grizzly bear habitat quality is difficult to quantify, however, after an analysis of grizzly bear feeding ecology in Banff, Hamer and Herrero (1987b) anticipated a decline in grizzly bear density in the absence of recurring fire. This observation prompted additional research where many of the more important grizzly bear foods were found to be associated with post-fire/early seral ecosystems; including buffaloberry (*Shepherida canadensis*; Hamer 1996), grouseberry (*Vaccinium scoparium*; Pengelly and Hamer 2006), yellow sweetvetch (*Hedysarum sulphurescens*; Hamer 1999), and ungulates (Hamer and Herrero 1991). The implications of reduced fire frequency and resulting homogenous forest stands encouraged the introduction of prescribed fire in 1983 to maintain ecological integrity (including grizzly bear habitat) and reduce the potential for more catastrophic, landscape-level wildfires (White 1985). In addition to prescribed fire, forest thinning projects have been

implemented to reduce fuels around town-sites, accommodations, transportation corridors, and for prescribed fire guards.

Prescribed fire and forest thinning have the potential to increase the productivity of grizzly bear foods (Hamer and Hererro 1991; Hamer 1996; Hamer 1999; Nielsen et al. 2004b; Pengelly and Hamer 2006) and influence grizzly bear habitat selection (McLellan and Hovey 2001; Nielsen et al. 2004c). It is, therefore, important to understand the relationships between prescribed fire, forest thinning and grizzly bear foods so these practices can maximize bear food productivity in remote and secure areas, while minimizing productivity near humans to avoid generating an ecological trap (Nielsen et al. 2006; Northrup et al. 2012; Lamb et al. 2016) where mortality risk is heightened.

Here I investigate the influence of fire (wildfire and prescribed fire) and forest thinning on the occurrence, abundance, and distribution of important grizzly bear foods. Specifically, my objectives were to: (1) quantify differences in the occurrence and abundance of 25 known grizzly bear foods between burns, thinned areas, and adjacent non-disturbed habitats (forested-controls), and (2) compare models to evaluate what group of factors (climate, terrain or disturbance) contribute most to the occurrence of grizzly bear foods so future applications of forest thinning and prescribed fire can more effectively enhance, in secure areas, grizzly bear habitat, while reducing grizzly bear habitat quality in areas with elevated mortality risk.

2. Methods

2.1 Study Area

Grizzly bear food data were collected across a 9,360 km^2 study area comprised of Banff, Yoho, and Kootenay National Parks (hereafter “Banff area”) located in the southern Rocky Mountains

of Canada (51°40 N, 116° 00’ W; Figure 3.1). These parks span the continental divide and are characterized by mountainous topography (elevation: 890 m to 3600 m), short dry summers, and long cold winters. Precipitation is greater to the west (~616 mm/year) than the east (~472 mm/year) of the continental divide that affects vegetation communities and fire regimes. Forests are dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), Douglas fir (*Pseudotsuga menziesii*) and aspen (*Populus tremuloides*) in montane areas and Engelmann spruce (*Picea engelmanii*), subalpine fir (*Abies lasiocarpa*), subalpine larch (*Larix lyallii*) in subalpine areas. The major valleys in the parks have high human disturbance with three townsites (Banff, Lake Louise, and Field), major highways, a transcontinental rail-line, and over three million visitors per year in Banff park alone (Figure 3.1; Parks Canada 2010).

The historical fire regime in the Banff area is influenced by elevation and longitude with fires traditionally being more frequent in the montane (valley bottoms) and east of the continental divide (generally 60-70 years) compared to the sub-alpine and west of the divide (generally 90-100 years; Van Wagner et al. 2006). During the last century fire has been less frequent, primarily because of effective fire suppression (Tande 1979; White 1985; Van Wagner et al. 2006; Rogeau et al. 2016; Davis et al. 2016). I collected bear food samples in wildfires that occurred between 1960 and 2012, prescribed fires conducted between 1983 and 2012, and areas thinned between 1988 and 2010.

2.2 Grizzly bear foods

Twenty five grizzly bear foods (Appendix D) were investigated based on previous feeding and diet studies in the Rocky Mountains (Hamer and Herrero 1987a; Mattson 1991; McLellan and Hovey 1995; Munro et al. 2006), but only species that occurred at >5% of the sample sites were analysed. From den emergence until green-up (April and May) grizzly bears in the region feed

primarily on *Hedysarum* (sweetvetch) roots, ungulates and to a lesser extent overwintered *Arctostaphylos uva-ursi* (bearberry) fruit. After green-up (June to mid-July) bears continue to feed on unglutes, but focus more on green herbaceous plants such as gramanoids, *Taraxacum officinale* (dandelions), *Trifolium* species (clover) and *Equisetum* species (horse tail). Once available (mid-July to October), fruits dominate the grizzly bear diet. Most abundant and important in Banff area is *Shepherdia canadensis* (buffaloberry) followed by *Vaccinium* species, specifically: *Vaccinium membranaceum* (black huckleberry), *Vaccinium scoparium* (grouseberry) and *Vaccinium myrtillus* (bilberry). Other fruiting species that occur at lower density and therefore are consumed more rarely include: *Vaccinium caespitosum* (dwarf blueberry), *Vaccinium myrtilloides* (velvet leaf blueberry), *Amelanchier alnifolia* (Saskatoon berry), *Ribes* species (gooseberry and currants), *Lonicera involucrata* (black twinberry), *Viburnum* species (cranberry), *Rubus* species (raspberry and thimbleberry) and *Fragaria virginiana* (wild strawberry). Three *Vaccinium* species (*Vaccinium membranaceum, Vaccinium caespitosum* and *Vaccinium myrtilloides)* occur infrequently in Banff area, but given their regional importance (McLellan and Hovey 1995; Munro et al. 2006; McLellan et al. 2011; Lamb et al. 2017) I combined them into a *Vaccinium* species complex for analyses. During this period of hyperphagia, *Formicidae* species (ants) consumption also peaks. In the late fall prior to denning, bears typically return to feeding on ungulates, *Hedysarum* roots and *Arctostaphylos uva-ursi* fruit. Although not prevalent in other regional grizzly bear dietary analyses of western Alberta, *Pinus albicaulis* (whitebark pine) seeds are likely an important late season food in Banff area (Hamer and Pengelly 2015). Based on regional grizzly bear diet analyses (McLellan and Hovey 1995; Munro et al. 2006), feeding habits in Banff area (Hamer and Herrero 1987a; Hamer and Herrero 1991; Hamer 1996; Hamer 1999; Pengelly and Hamer 2006), and nutritional value

of food species (Coogan et al. 2014; López-Alfaro et al. 2015), I grouped species into four categories (low, moderate, high, and critical) based on their predicted importance to grizzly bears in Banff area (Appendix D).

2.3 Field Sampling

During the growing seasons (June – September) of 2012 and 2013, I collected grizzly bear food data at 113 burn, 44 thinned, and 142 adjacent non-disturbed control plots (See Appendix E for details of burn and thinned areas where sampling occurred). All plots were randomly selected within three terrain strata: elevation, heat-load index (HLI), and compound topographic index (CTI) derived from a geographic information system (GIS; Esri 2013). This categorization was done to ensure plots within burns or thinned areas were matched to adjacent, non-disturbed control plots based on terrain variables that have previously predicted grizzly bear food occurrence (Nielsen et al. 2004b; Braid and Nielsen 2015). HLI measures annual solar radiation by combining slope, aspect, and latitude (McCune 2007), while CTI represents a wetness index that describes moisture and drainage and often correlates with numerous soil attributes (Moore et al. 1991; Gessler et al. 1995).

At each plot, one 100 m transect running south to north was established and the presence or absence of all 25 grizzly bear foods were tallied within a 2-m wide belt transect (200 m^2). Also, within this 2-m belt, the number of ungulate pellet groups, ant colonies and for certain food items, stems counts were collected. I used ungulate pellet groups for ungulate occurrence (Loft and Kie 1988; Edge and Marcum 1989; Mansson et al. 2011) and abundance (Marques et al. 2001; Alves et al. 2013) measures, but recognise potential biases in local patterns where they deficate (Collins and Urness 1981). Also, within the 2-m belt transect, the number of berries from shrub species were counted for a maximum of 12 fruiting shrubs of each species during the

fruiting season (June 15- Sept.15). When additional fruiting shrubs were present, fruit abundance was estimated from the mean number of berries on the 12 counted plants. Fruit for herbaceous plants was counted and averaged from eight 1-m^2 quadrats which were evenly spaced along the 100 m transect. Within these quadrats I also collected and oven dried portions of green herbaceous plants to estimate the average dry-weight for each green herbaceous species. Line intercept was used along the 100 m transect to calculate percent cover for bear foods, as well as tree (≥ 1.3 m height) and regenerating tree cover (< 1.3 m height), which are important predictors of the occurrence and abundance of fruit (Minore 1984; Hamer 1996; Nielsen et al. 2004b).

2.4 Comparing grizzly bear food occurrence among burns, thinned, and control areas

I first compared the occurrence of 25 grizzly bear foods within burns and thinned areas to corresponding non-disturbed control sites. I then compared burned to thinned areas so I could evaluate if one of these applications increases the odds of bear food occurrence. Finally, I re-iterated these steps to compare the occurrence of fruit for 5 shrubs and 8 fruiting herbs (Appendix G). For each of these analyses I used logistic regression and report results as odds ratios (Hosmer et al. 2013). Odds ratios can be interpreted as the odds of a grizzly bear food resource occurring in burns or thinned areas compared to non-disturbed controls. Odds ratio values > 1 indicate a greater presence of the bear food in burns or thinned areas, whereas odds ratio values < 1 indicate greater presence of the bear food in the non-disturbed control.

To evaluate if climate, terrain, or disturbance (from the burning or thinning process) factors (Appendix E) best predicted the presence of grizzly bear foods in burned and thinned areas, I compared logistic regression models (0 – bear food item absent; 1 – bear food item present) from five hypothesized a priori candidate groups (Appendix F) for both burns (n = 111) and thinned areas (n = 45). For these models, I included random intercepts for each burn or thinned area and

sampling year (2012 or 2013) to account for spatial autocorrelation and non-independence (lme4 package in R; Bates et al. 2014). The first group, named the *terrain model*, included terrain factors: elevation (ELEV), heat load index (HLI), and compound topographic index (CTI). The second group, named the *disturbance model*, included burned or thinned treatment factors: time since disturbance (age), area of disturbance (area), tree cover (Tree_cov), and regenerating tree cover (Regen_cov). The remaining three groups were based upon seasonal climatic factors. These were named the *annual climate model* that included mean annual precipitation (MAP) and mean annual temperature (MAT); the *winter climate model* that included average winter precipitation (PPT_WT) and average winter temperature (TAV_WT); and the *summer climate model* that included summer precipitation (PPT_SM) and average summer temperature (TAV_SM). The variables within each group were not correlated (Pearson correlations $r < |0.7|$) and Akaike's information criteria (AIC) was used to evaluate which models best predicted grizzly bear food occurrence in burns and thinned areas (Burnham and Anderson 2002). For fruiting food groups, this process was re-iterated to analyse which climatic, terrain, or disturbance groups best predicted the presence of fruit in burned and thinned patches.

2.5 Grizzly bear food productivity

For bear food productivity measures, I used Mann-Whitney U-tests ($p \leq 0.5$) to compare the estimated average density per hectare or dry-weight per hectare among burns, thinned areas, and their associated non-disturbed controls. For fruiting plants, I compared the average density of berries (berries/hectare) for plots visited only during the fruiting period (June 15- Sept.15) with one exception. *Arctostaphylos uva ursi* fruit productivity was collected for all plots, regardless of the date, because these fruits over-winter and remain countable in the early spring, which is when bears typically fed on them (McLellan and Hovey 1995; Munro et al. 2006). For green

herbaceous plants I compared dry-weights, while for rooting species of *Hedysarum*, I compared stem density as measure of the number of tap roots in which bears forage, although I recognize that each tap root can give rise to more than one stem (Hamer 1999). *Formicidae* colonies that occurred in stumps, logs, or mounds were pooled regardless of the substrate, colony size, or *Formicidae* species. Similarly, ungulate pellet groups were pooled regardless of the ungulate species.

3. Results

3.1 Grizzly bear food occurrence in burned and thinned areas

Six grizzly bear foods had greater presence in burns compared to adjacent non-burned sites (Figure 3.2; Appendix H). These included: *Amelanchier alnifolia, Ribes oxycanthoides, Rubus idaeus, Arctostaphylos uva-ursi, Taraxacum officinale,* and *Formicidae. Rubus idaeus* was present in over 25% of burn plots, but in less than 1% of control plots resulting in an odds ratio of 35.7. Although less prominent, *Taraxacum officinale, Amelanchier alnifolia, Formicidae,* and *Ribes oxycanthoides* had odds ratios of 6.8, 4.4, 4.1 and 2.9 respectively, while *Arctostaphylos uva-ursi* had an odds ratio of 2.0. Only the *Vaccinium* complex that combined *V. membranaceum, V. caespitosum,* and *V. myrtilloides* had greater presence in non-burned sites with an odds ratio of 2.6.

Only two grizzly bear foods, *Taraxacum officinale* and *Rubus idaeus*, had greater presence in thinned areas than adjacent control sites with odds ratios of 7.1 and 4.4 respectively (Figure 3.3; Appendix H). When comparing burns to thinned areas, only *Taraxacum officinale* presence differed and occurred in thinned areas about three times more often than burns, while *Trifolium* species occurred in over 15% of the thinned plots but were never recorded in a burn (Figure 3.4; Appendix H).

3.4 Distribution of grizzly bear foods in burns

There was considerable variation in model rankings among the 18-different grizzly bear foods modelled. Based on AIC weights, the disturbance model ranked highest for seven species including the important *Shepherdia canadensis*, while the terrain model ranked highest for four species (Table 3.1). Of the three climate models, the winter model fit the data best for four foods, including the important *Hedysarum sulphurescens* root (Table 3.1). The summer climate ranked highest for ungulates and *Virburnum edule*, while the annual climate only ranked highest for *Ribes oxyacanthoides* (Table 3.1). All three *Vaccinium* species, including the combined *Vaccinium* species model, were all best supported by the disturbance model. Using likelihood ratio (LR) χ^2 tests, all models were significant ($\alpha < 0.05$), except those for *Formicidae* and *Taraxacum officinale* (Table 3.1). The percent deviance explained, represented by the reduction in the log-liklihood from the null model, ranged from as low as 3.3% for *Taraxacum officinale* to as high as 33.1% for *Arctostaphylos uva-ursi*. Classification accuracy, based on area-under the curve (AUC) was good (AUC: 0.7 – 0.9) for 13 grizzly bear foods, but poor (AUC: 0.5 – 0.7) for the remaining five (Table 3.1).

3.5 Distribution of grizzly bear foods in thinned areas

Of the 17-different grizzly bear foods modelled in thinned areas the winter climate model was the top ranked (AIC weights) for over half, including the more important foods of *Shepherdia canadensis*, *Hedysarum sulphurescens*, and ungulates (Table 3.2). The disturbance model ranked highest for four species, whereas both the summer and annual climate models ranked highest for one species each (Table 3.2). These models were not as predictive as the burn models with only seven significant overall (likelihood ratio χ^2 tests; $\alpha < 0.05$) and generally with low deviance explained (from 1% to 8.3%). Classification accuracy, based on area-under the curve (AUC),

was good (AUC: 0.7 – 0.9) for 11 grizzly bear foods, but was poor (AUC: 0. 5 – 0.7) for the remaining six (Table 3.2). The *Formicidae* and the *Rubus idaeus* disturbance models were the strongest of all models tested, whereas the *Taraxacum officinale* and the *Ribes oxyacanthoides* models were the weakest.

3.6 Abundance of grizzly bear foods in burns and forested controls

Amelanchier alnifolia, Arctostaphylos uva-ursi, and *Rubus idaeus* fruit were more abundant in burns than adjacent forested controls (Table 3.3). In addition to these three species, the total average of fruit (all species combined) was greater in burns (Figure 3.3) with an average of over a third more fruit (60,503 fruit/ha) compared to the forested controls (17,909 fruit/ha; Table 3.3).

Of the three green herbaceous forbs evaluated, *Taraxacum officinale* was the only species that had a greater dry weight in burns than forested controls (Table 3.3). When the three green herbaceous forbs were pooled, they collectively had greater abundance in burns (3,744 g/ha) than forested controls (922 g/ha; Figure 3.5). Similarly, neither *Hedysarum sulphurescens* or *Hedysarum alpinium* alone were different between burns and forested controls, however, the combined density of the two species was greater in burns (Figure 3.5) with an average of 2,891 stems/ha in burns and 1,693 stems/ha in the forested controls (Table 3.3).

Formicidae colony density was greater in burns with an average of over five times more in burns (10.8 colonies/ha) compared to forested controls (1.9 colonies/ha; Table 3.6). Even though ungulate pellet groups occurred at higher density in burns (46.9 pellet groups/ha) compared to forested controls (25.2 pellet groups/ha; Figure 3.5), this difference was non-significant (Table 3.3).

3.7 Abundance of grizzly bear foods in thinned areas and forested controls

The difference in bear food abundance between thinned areas and their adjacent forested controls was not as distinct as it was in burns. Only *Taraxacum officinale* and *Trifolium* species were greater in thinned areas with *Taraxacum officinale* averaging over 750 g/ha in thinned areas but under 44.9 g/ha in forested controls, while *Trifolium* was absent from the forested samples but had almost 2000 g/ha in thinned areas (Figure 3.5; Table 3.4).

3.8 Abundance of grizzly bear foods between burns and thinned areas

When comparing burns directly with thinned areas (Table 3.5), *Arctostaphylos uva-ursi* fruit was significantly greater in burns, whereas *Trifolium* species and all green herbaceous species combined had a greater dry weight in thinned areas (Table 3.5). Overall, burns were generally about one-third more productive for fruit and three-times more productive for roots and ants, whereas thinned areas were about one-third more productive for green herbaceous plants.

4. Discussion

Like other animals, grizzly bears trade off foraging efficiency with risk (Stephens et al. 2006). If the best foraging sites are in remote mountains, then bear survival will be higher than if the best feeding sites are in valley bottoms near highways, railways, and human settlements. In areas such as Banff, decades of fire suppression have likely reduced foraging opportunities in remote areas with bears now more often found in valleys where they are more vulnerable. In this study, I investigated the response of bear foods to burns and forest thinning with the goal of learning ways to create quality foraging opportunities in remote areas, far from the variety of human activities in major valley bottoms.

When comparing burns, thinned areas and forested controls, burns provided the greatest potential for producing early spring, late summer, and fall grizzly bear foods, while thinned areas provided

the most potential for early summer foods. *Amelanchier alnifolia, Rubus ideaus, Arctostaphylos uva-ursi, Taraxacum officinale,* and *Formicidae* occurred at greater frequency and provided a greater abundance of food in burns than forested areas. These findings are consistent with previous post-fire succession studies that also reported increases in these species after prescribed or wildfires (Lentile et al. 1997; Anderson and Baily 1979; Whitney 1982; Rowe 1983; Wood 2004; Andersen 1991).

In Banff and other parts of the Rocky Mountains, grizzly bears fed primarily on *Hedysarum* roots, ungulates, and to a lesser extent *Arctostaphylos uva-ursi* fruit in the early spring after den emergence and again in the late fall prior to denning (Hamer and Herrero 1987a; Mattson 1991; McLellan and Hovey 1995; Munro et al. 2006). I found the occurrence of *Hedysarum* stems and ungulate pellet groups at similar frequency in burns and thinned areas, but were both over one-third more abundant in burns. While investigating *Hedysarum sulpherescens* abundance in two Banff prescribed fires, Hamer (1999) also found greater abundance in the burns compared to adjacent forested areas. Other research in Banff also documented extensive digging of *Hedysarum* species by grizzly bears within burns compared to the adjacent forest (Hamer 1999; Pengelly and Hamer 2006).

I also found about twice the odds of *Arctostaphylos uva-ursi* occurring in burns compared to forested areas and the abundance of fruit on this plant was over 18-fold higher in the burned habitats. Given the general paucity of food available during the early spring and late fall, the abundance of *Arctostaphylos uva-ursi* fruit within burns is promising. Diet analysis of black bears in Banff indicted that *Arctostaphylos uva-ursi* fruit accounted for over 21% of their scat volume between September 16th and October 31st (Raine and Kansas 1990) which supports the need for additional research on the use of these fruits by grizzly bears in Banff.

Protein from ungulates is typically the most important pre-and-post hibernation food for grizzly bears in this region (McLellan and Hovey 1995; Munro et al. 2006). Ungulates may be an important factor contributing to reproductive success (López-Alfaro et al. 2015) and local density (Nielsen et al. 2017), although stable isotope analysis suggest male bears consume more than females (McLellan 2011). I observed an increased number pellet groups in burns compared to forested areas, but the difference was small and could have been due to sampling variation. Sachro et al. (2005), however, reported that prescribed fires in Banff increased summer carrying capacity of elk from 8 to 28 individuals/100 km^2 based on forage availability, while other studies document ungulate selection of burned habitats (Boyce et al. 2003; Gillingham and Parker 2008; Allred et al. 2011). Additional research on ungulate selection and population response to Banff area burns would complement the importance of these habitats for grizzly bears.

In late summer and early fall (hyperphagia), grizzly bears in the Canadian Rockies feed primarily on fruit (Hamer and Herrero 1987a; McLellan and Hovey 1995; Munro et al. 2006) and then rapidly deposit fat (McLellan 2011) which increases their reproductive capacity (Hilderband et al. 2000; Robbins et al. 2012). As hypothesized, four fruiting species occurred at greater frequency and three species had greater abundance of fruit in burns compared to the controls. When all fruiting species were combined, the abundance of fruit in burns was over three-times greater than in the adjacent forested areas. The most numerous and important fruiting species for bears in Banff area, *Shepherdia canadensis*, was one and a half times more likely to occur in burns and had over one and half times more fruit than in the adjacent forested stands, however, variation was considerable, and these differences were not significant. Previous research on *Shepherdia canadensis* in Banff found a negative association between fruit production and canopy cover in burned habitats but did not make comparisons to non-burned habitats (Hamer

1996). To the north and south of Banff, both the amount of canopy and type of canopy (conifer or deciduous) explained patterns in buffaloberry abundance (Barber et al. 2016; Denny & Nielsen 2017). The disturbance model, that included tree cover, regeneration cover, time since fire, and fire size, was the best predictor of both the occurrence of *Shepherdia canadensis* and its fruit with both being negatively correlated with tree cover and regenerating tree cover. Thus, local variations in overstory tree cover, including patterns in post-fire severity, or tree regeneration following disturbance increases local variability in fruit production. Fires and thinning that maintain more semi-open canopy conditions will therefore most favor fruit production for this species.

Only the *Vaccinium* complex that included *Vaccinium membranaceum, Vaccinium caespitosum* and *Vaccinium myrtilloides* occurred more frequently in controls than they were in burns, however, fruit occurrence and abundance was similar. This result was unexpected because previous studies have reported positive responses of *Vaccinium* species after fire (Miller 1976; Foster 1985; Flinn and Wein 1988). The disturbance model fit well for *Vaccinium* spp. occurrence within burns and suggests potential mechanisms as to why these species occurred more frequently in forested habitats. Time since fire had the largest influence, with the odds of *Vaccinum* spp. occurring in a burn increasing by 1.14 (OR) for each year after the burn. The lower occurrence of *Vaccinium* spp. within burns may have been because many of the burns were recent and of high severity resulting in the loss of shallow rhizomes with recolonization from those that survived yet to occur. I did not include burn severity in the models because few burns within the study area had this quantified. Additional sampling in burns where burn severity is measured would help evaluate the association between burn severity, time since fire, and the occurrence of *Vaccinium* species, as well as other foods. Fruit abundance for the *Vaccinium*

species complex was similar between burns ($\bar{x}$ = 1138 / ha) and forested controls ($\bar{x}$ = 1168 / ha), however, these amounts were minor compared to areas north (Nielsen et al. 2004b) and south (Barber et al. 2016; McLellan 2015) of Banff area.

Each of the five different candidate models supported a least one grizzly bear food within burns suggesting that not all foods will respond in the same areas to the same treatment. Or, when using prescribed fires to enhance grizzly bear foods, for some foods it is more important to focus on the location of the burn (terrain or climate characteristics), while for others the burn prescription (factors influencing the burn size and tree cover) is more important. Based on previous research (Nielsen et al. 2004b; Nielsen et al. 2017), I hypothesised that climate and terrain variables would better predict the occurrence of grizzly bear food plants, whereas the disturbance models would better predict the occurrence of fruit. My data supported this hypothesis for *Arctostaphylos uva-ursi* and *Rubus ideaus*, but not for *Vaccinium scoparium* and *Fragaria virginiana* where the opposite occurred. The disturbance model was the best predictor for both plant and fruit occurrence for *Shepherdia canadensis, Vaccinium myrtillus* and the *Vaccinium* species complex. With the documented influence of these fruits on grizzly bear density (McLellan 2015; Nielsen et al. 2017), increasing their abundance and fruit production are important for enhancing grizzly bear habitat with prescribed fire. With a few exceptions, all models of bear food occurrence had relatively good model fit and predictive accuracy indicating that spatial model inputs (climate and terrain) could be used to map priority areas for enhancing grizzly bear foods, whereas the disturbance model inputs could be incorporated into specific burn prescriptions with the aim of increasing specific bear food and fruit occurrences.

Thinned treatments had the highest occurrence and abundance of green herbaceous vegetation that make up most of grizzly bears diet in the early summer (Hamer and Herrero 1987a; Mattson

1991; McLellan and Hovey 1995; Munro et al. 2006). The exotic species *Taraxacum officinale* and *Trifolium* spp., were seven times more likely to occur within thinned areas than the forested controls. When comparing logged cut-blocks to upland forests northeast of Banff, Nielsen et al. (2004b) reported similar results for *Trifolium* spp. while the odds of *Taraxacum officinale* in cutblocks was almost 14 times greater than in upland forests. When I compared burns to thinned areas, both *Taraxacum officinale* and *Trifolium* species occurred more frequently in thinned areas and collectively provided almost 2 kg/ha more than in burns. The increased occurrence of these exotics in thinned areas is likely because these treatments were closer to the main transportation corridors from where they have spread (Hansen and Clevenger 2005). Many thinning blocks also used machinery and skid roads that are known to disperse exotics (Pauchard and Alaback 2006). These species are often introduced in seed mixes during rehabilitation processes.

In the thinned areas, the winter climate model best predicted the occurrence for nine of the 17 bear foods evaluated. This model included mean winter precipitation and mean winter temperature. All models supported at least one grizzly bear food emphasising the importance of addressing climate, terrain, and disturbance factors when thinning areas. As hypothesised (Nielsen et al. 2004b; Nielsen et al. 2017), the climate and terrain variables better predicted the occurrence of fruiting species, whereas the disturbance model better predicted fruit occurrence. Of the seven-fruiting species evaluated, *Ribes oxycanthoides, Shepheridia canadensis*, and *Fragaria virginiana* occurrence was best predicated by the winter or terrain models, while the occurrence of fruit was best predicted by the disturbance model. There was little consistency between both plant or fruit occurrence models for each species between burns and thinned areas. This result highlights the importance of specific burn or thinning parameters and how they affect

both the occurrence of species and their fruit. Had the disturbance mechanisms had little influence, similar model results would be expected between these two treatments.

Compared to burned areas, the thinned area models overall had poorer fit and predictive accuracy. The fruit occurrence models performed poorly compared to the burn models with only two of seven having good fit and five having good predictive accuracy. The lack of fit for many of these species is likely associated with the smaller sample size in thinned areas, as opposed to the lack of climatic, terrain, or disturbance variable prediction. As more areas continue to be thinned in Banff area, additional data, particularly if collected at permanent plots pre- and post-thinning, will increase understanding of the factors that encourage growth of bear foods in remote areas but also reduce foods in high risk areas.

Overall, the grizzly bear habitat in Banff area has limited productivity compared to other areas (Gibeau 1998; Garshelis et al. 2005) and the frequent absence or low density of grizzly bear foods in the plots presents challenges for predicting their occurrence and abundance within burns or thinned areas. Additional sampling using a stratified design to sample only highly productive sites would assist in identifying factors contributing to the most productive habitats.

For each food or combination of foods, there will be a threshold of abundance, below which foods are too scarce for bears to efficiently feed. Many of my comparisons may be at sites below this threshold and so are meaningless to bears. To investigate if bear food abundance in the treatment areas is sufficient for a bear to forage in, grizzly bear telemetry locations should be used to focus data collection to areas that are of sufficient quality to be used by grizzly bears. In addition, a much longer study design would be of value given the inter-annual variability in fruit

production (McLellan 2015), and associated grizzly bear feeding response (Hamer and Herrero 1987a).

Without a comprehensive diet analysis conducted across the Banff area, the importance of each food investigated was based only on previous research. A dietary analysis would provide important insight to which foods are most critical to Banff grizzly bears. For example, both McLellan and Hovey (1995) and Munro et al. (2006) did not report whitebark pine (*Pinus albicaulis*) seeds in grizzly bear scats in their nearby study areas, but in Yellowstone National Park it is a critical food resource (Mattson et al. 1991; Gunther et al. 2014). In Banff, Hamer and Pengelly (2015) detected grizzly bear feeding on whitebark pine seeds, but the importance of this food resource remains unknown and may be localized to certain bears where they overlap with this limited resource. In addition, diet knowledge is particularly important for examining influences of grizzly bear foods on population demographics (McLellan 2011, 2015; Nielsen et al. 2017) which is fundamental for identifying factors limiting populations. Combining information from stable isotopes (Hilderbrand et al. 1999, Hobson et al. 2000), scat analysis, and correction factors (Hewitt and Robbins 1996) would enable a comprehensive diet analysis in Banff area and address this critical knowledge gap.

Grizzly bears in Banff appear to be caught in similar ecological traps as other bear populations (Nielsen et al. 2006; Lamb et al. 2016) where they are attracted to productive habitats associated with elevated human caused mortality (Nielsen et al. 2004a; Pollock et al. 2017). These attractive sinks contribute to Banff grizzly bears having low population density and limits population growth (Garshelis et a. 2005; Sawaya et al. 2012) even though extensive research and effort have focused on reducing mortality (Berch and Gibeau 2009; Backs et al. 2017). Grizzly bear densities in nearby areas, with similar habitats, were influenced more by bottom-up food

resources than top-down mortality factors (McLellan et al. 2015; Nielsen et al. 2017) even though these areas have higher mortality rates than Banff (Garshelis et al. 2005; Boulanger and Stenhouse 2009; Sawaya et al. 2012). Maintaining or enhancing productive habitat that provide grizzly bears with the combination of macronutrients to facilitate growth and reproduction (Erlenbach et al. 2014; Coogan et al. 2014) is essential for maintaining or increasing grizzly bear densities (Nielsen et al. 2017), particularly if these habitats are in secure, road-less areas without elevated mortality (Schwartz et al. 2010; Lamb et al. 2018). Here I demonstrate that many important grizzly bear foods, occur more frequently and at higher density in burns than forested or thinned habitats and identify groups of factors that influence the occurrence of grizzly bear foods. This provides promise for Banff area grizzly bears and other low-density populations because prescribed fire can be applied in remote, secure, road-less areas where human-caused mortality is rare or even absent. Given the importance of burns for grizzly bear foods and many other ecological functions (Agee 1996), land use planning in areas that lack protected areas should limit fire suppression or conduct prescribed fires in remote areas where timber resources and other values are at limited risk, as these are also the best areas for enhancing grizzly bear habitat.

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Table 3.1: Akaike's Information Criteria (AIC) top selected model that best describe the occurrence of 18 grizzly bear foods within burned habitats of Banff area. AIC scores (w_i) for the null model and top ranked model, likelihood ratio (LR) χ^2 tests, and their significance (p), as well as area under the curve (AUC), and percent deviance explained are provided.

Grizzly bear food item		**Null model**	**Top selected model**					
Type	**Name**	**AIC (w_i)**	**Model**	**AIC (w_i)**	**LR χ^2**	***p***	**AUC**	**% Dev. Exp.**
shrub-fruit	*Amelanchier alnifolia*	99.05	Terrain	83.54	21.51	<0.001	0.81	10.75
	Lonicera involucrata	75.73	Winter climate	52.46	27.27	<0.001	0.74	13.63
	Ribes oxycanthoides	147.90	Annual climate	126.20	25.73	<0.001	0.69	12.87
	Shepherdia canadensis	102.30	Disturbance	80.41	29.92	<0.001	0.84	14.96
	Viburnum edule	75.73	Summer climate	60.75	18.98	<0.001	0.72	9.49
herb or	*Arctostaphylos uva-ursi*	149.10	Winter climate	87.00	66.10	<0.001	0.90	33.05
dwarf-shrub	*Fragaria virginiana*	155.30	Disturbance	147.90	15.39	0.004	0.62	7.69
fruit	*Rubus idaeus*	131.50	Winter climate	103.90	31.58	<0.001	0.74	15.79
	Rubus parviflorus	75.73	Terrain	58.15	23.58	<0.001	0.79	11.85
	Vaccinium myrtillus	71.21	Disturbance	62.78	16.43	0.002	0.83	8.21
	Vaccinium scoparium	114.10	Disturbance	87.06	35.07	<0.001	0.78	17.54
	Vaccinium spp. complex	88.13	Disturbance	73.47	22.66	<0.001	0.85	11.32
forb	*Equisetum arvense*	61.49	Disturbance	54.86	14.63	0.006	0.43	7.32
	Hedysarum alpinium	65.36	Disturbance	58.83	14.53	0.006	0.84	7.27
	Hedysarum sulphurescens	154.60	Winter climate	101.30	57.33	<0.001	0.88	28.67
	Taraxacum officinale	105.60	Terrain	105.10	6.53	0.088	0.67	3.27
protein	*Formidae* spp.	95.56	Terrain	94.40	7.12	0.068	0.68	3.58
	Ungulate spp.	147.90	Summer climate	131.20	20.70	<0.001	0.76	10.35

Table 3.2: Akaike's Information Criteria (AIC) top selected model that best describe the occurrence of 18 grizzly bear foods within thinned habitats of Banff area. AIC scores (w_i) for the null model and top ranked model, likelihood ratio (LR) χ^2 tests, and their significance (p), as well as area under the curve (AUC), and percent deviance explained are provided.

Grizzly bear food item		**Null model**	**Top selected model**					
Type	**Name**	**AIC (w_i)**	**Model**	**AIC (w_i)**	**LR χ^2**	***p***	**AUC**	**% Dev. Exp.**
shrub-fruit	*Amelanchier alnifolia*	36.98	Terrain	34.79	8.19	0.042	0.79	4.10
	Lonicera involucrata	39.34	Winter	40.78	2.56	0.279	0.67	1.28
	Ribes oxycanthoides	59.69	Winter	61.77	1.92	0.383	0.66	0.96
	Shepherdia canadensis	35.39	Winter	34.46	4.93	0.085	0.68	2.47
	Viburnum edule	39.38	Disturbance	37.48	9.90	0.042	0.89	4.95
herb or	*Arctostaphylos uva-ursi*	58.10	Winter	51.02	11.08	0.003	0.65	5.54
dwarf-shrub	*Fragaria virginiana*	56.19	Terrain	58.02	4.18	0.243	0.68	2.09
fruit	*Rubus idaeus*	51.54	Disturbance	42.77	16.77	0.002	0.88	8.38
	Vaccinium myrtillus	35.40	Disturbance	38.06	5.33	0.255	0.80	2.67
	Vaccinium scoparium	49.02	Annual	47.18	5.85	0.054	0.71	2.92
	Vaccinium spp. combined	39.34	Summer	41.01	2.32	0.313	0.73	1.18
forb	*Equisetum arvense*	39.34	Winter	40.03	3.32	0.191	0.72	1.66
	Hedysarum alpinium	34.26	Winter	33.06	5.20	0.074	0.78	2.60
	Hedysarum sulphurescens	65.83	Winter	58.44	11.39	0.003	0.70	5.69
	Taraxacum officinale	63.67	Winter	65.32	2.35	0.310	0.57	1.17
protein	*Formidae* spp.	26.04	Disturbance	17.48	16.56	0.002	0.99	8.28
	Ungulate species	65.83	Winter	58.19	11.64	0.002	0.75	5.82

Table 3.3: Average fruit density, green forb dry weight, root density, ungulate pellet groups, and ant colonies per hectare for 19 grizzly bear foods in burned habitats (n = 113) and adjacent non-disturbed forest habitats (n = 103). Mann-Whitney U-tests were used to investigate significant (p) differences between burns and the adjacent forested controls for each species.

Grizzly bear food		**Burn**		**Forest**		***p***
Type	**Name**	**mean (#/ ha)**	**S.E.**	**mean (#/ ha)**	**S.E.**	
shrub-fruit	*Amelanchier alnifolia*	304.0	234.7	0.0	0.0	0.018
	Lonicera involucrata	54.5	33.5	0.0	0.0	0.055
	Ribes oxycanthoides	1703.0	874.3	119.2	57.7	0.288
	Shepherdia canadensis	24751.0	6585.1	13979.7	3870.9	0.836
	Viburnum edule	265.5	144.9	74.2	51.9	0.599
herb or	*Arctostaphylos uva-ursi*	13975.0	4275.9	755.5	319.1	0.0057
dwarf-shrub	*Fragaria virginiana*	412.5	250.0	27.5	27.5	0.209
fruit	*Rubus idaeus*	3762.5	2084.1	0.0	0.0	0.010
	Rubus parviflorus	787.5	562.6	0.0	0.0	0.098
	Vaccinium myrtillus	3400.0	1615.4	123.6	73.2	0.348
	Vaccinium scoparium	7437.5	5814.9	755.5	495.7	0.340
	Vaccinium spp. complex	1137.5	590.8	1167.6	800.1	0.322
total -fruit	All fruiting species	60503.0	9800.6	17909.3	3991.8	0.0028
green - forb	*Equisetum* spp.	3035.6	2435.9	845.1	534.4	0.366
green - forb	*Taraxacum officinale*	306.3	127.0	31.6	31.6	<0.001
green - forb	*Trifolium* spp.	432.4	432.4	44.9	42.5	0.529
total - forbs	All green forbs	3774.3	2470.4	921.6	538.3	0.0038
forb - root	*Hedysarum alpinium*	477.0	207.9	92.7	66.9	0.315
forb - root	*Hedysarum sulphurescens*	2413.5	360.6	1600.5	317.0	0.111
total - root	Hedysarum combined	2890.5	396.9	1693.2	324.8	0.0472
protein - animal	Ungulate pellet groups	46.8	8.5	25.2	5.2	0.127
protein - insect	*Formidae* spp. colonies	10.8	3.4	1.9	1.0	0.00779

Table 3.4: Average fruit density, green forb dry weight, root density, ungulate pellet groups, and ant colonies per hectare for 16 grizzly bear foods in thinned habitats (n = 44) and adjacent forested controls (n = 39). Mann-Whitney U-tests were used to investigate significant (p) differences between thinned areas and the adjacent forested controls for each species.

Grizzly bear food		**Thinned**		**Forest**		***p***
Type	**Name**	**mean (#/ ha)**	**S.E.**	**mean (#/ ha)**	**S.E.**	
shrub-fruit	*Amelanchier alnifolia*	176.3	123.0	379.4	353.1	0.879
	Ribes oxycanthoides	2067.5	1390.3	261.8	161.6	0.615
	Shepherdia canadensis	10052.5	3953.7	15394.1	7181.8	0.841
	Viburnum edule	91.3	78.0	1.5	84.9	0.376
herb or	*Arctostaphylos uva-ursi*	2906.3	2598.0	955.9	517.2	0.554
dwarf-shrub	*Fragaria virginiana*	406.3	211.8	73.5	51.2	0.470
fruit	*Rubus idaeus*	3000.0	2557.0	330.9	330.9	0.390
	Vaccinium myrtillus	10000.0	5733.3	0.0	0.0	0.062
	Vaccinium spp. complex	0.0	0.0	477.9	355.4	0.127
total -fruit	All fruiting species	39231.3	15889.9	25117.7	8396.2	0.384
green - forb	*Equisetum* spp.	2319.4	1169.0	2298.1	1616.8	0.622
green - forb	*Taraxacum officinale*	753.6	349.2	44.9	38.8	<0.001
green - forb	*Trifolium* spp.	1944.4	1837.5	0.0	0.0	0.01927
total - forbs	All green forbs	5017.5	2439.0	2342.9	874.8	0.113
forb - root	*Hedysarum alpinium*	220.0	143.6	20.5	15.3	0.208
forb - root	*Hedysarum sulphurescens*	764.4	165.2	1370.5	339.1	0.238
total - root	Hedysarum combined	984.4	294.4	1391.0	342.4	0.580
protein - animal	Ungulate pellet groups	46.7	11.4	53.8	18.4	0.697
protein - insect	*Formidae* spp.colonies	3.3	1.9	5.1	3.1	0.841

Table 3.5: Average fruit density, green forb dry weight, root density, ungulate pellet groups, and ant colonies per hectare for 19 grizzly bear foods in burned habitats (n = 113) and thinned areas (n = 44). Mann-Whitney U-tests were used to investigate significant (p) differences between burns and thinned areas for each species.

Grizzly bear food		**Burn**		**Thinned**		***p***
Type	**Name**	**mean (#/ ha)**	**S.E.**	**mean (#/ ha)**	**S.E.**	
shrub-fruit	*Amelanchier alnifolia*	304.0	234.7	176.3	123.0	0.859
	Lonicera involucrata	54.5	33.5	0.0	0.0	0.204
	Ribes oxycanthoides	1703.0	874.3	2067.5	1390.3	0.813
	Shepherdia canadensis	24751.0	6585.1	10052.5	3953.7	0.451
	Viburnum edule	265.5	144.9	91.3	78.0	0.790
herb or	*Arctostaphylos uva-ursi*	13975.0	4275.9	2906.3	2598.0	0.029
dwarf-shrub	*Fragaria virginiana*	412.5	250.0	406.3	211.8	0.185
fruit	*Rubus idaeus*	3762.5	2084.1	3000.0	2557.0	0.934
	Rubus parviflorus	787.5	562.6	0.0	0.0	0.886
	Vaccinium myrtillus	3400.0	1615.4	10000.0	5733.3	0.383
	Vaccinium scoparium	7437.5	5814.9	0.0	0.0	0.153
	Vaccinium spp. complex	1137.5	590.8	0.0	0.0	0.375
total -fruit	All fruiting species	60503.0	9800.6	39231.3	15451.0	0.154
green - forb	*Equisetum* spp.	3035.6	2435.9	2319.4	1169.0	0.204
green - forb	*Taraxacum officinale*	306.3	127.0	753.6	349.2	0.097
green - forb	*Trifolium* spp.	432.4	432.4	1944.4	1837.5	<0.001
total - forbs	All green forbs	3774.3	2470.4	5017.5	2439.0	0.002
forb - root	*Hedysarum alpinium*	477.0	207.9	220.0	66.9	0.383
forb - root	*Hedysarum sulphurescens*	2413.5	360.6	764.4	317.0	0.095
total - root	Hedysarum combined	2890.5	396.9	984.4	324.8	0.109
protein - animal	Ungulate pellet groups	46.8	8.5	46.7	5.2	0.467
protein - insect	*Formidae* spp.colonies	10.8	3.4	3.3	1.0	0.173

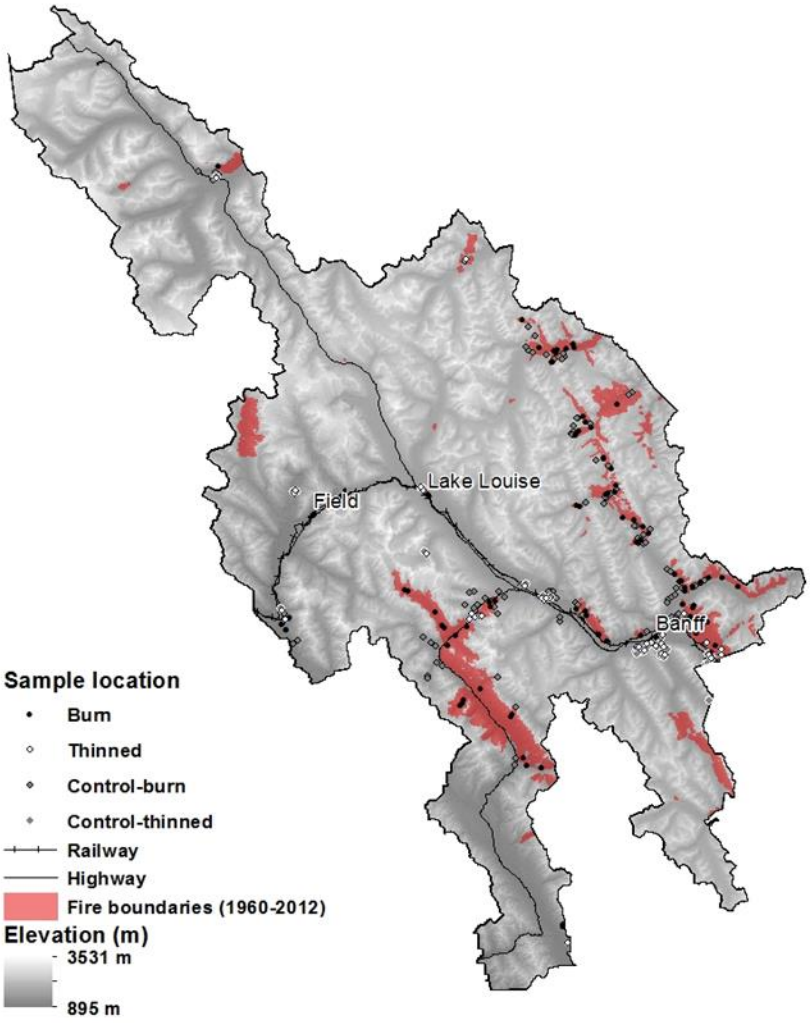

Figure 3.1: Study area encompassing Banff, Yoho and Kootenay National Parks in the southern Canadian Rocky Mountains. Locations where grizzly bear food sampling occurred within burns (n = 111), adjacent burn controls (n = 103), thinned areas (n = 45), and adjacent thinned controls (n = 39) are illustrated. Wild and prescribed fires that occurred between 1960 and 2012 are indicated by red polygons.

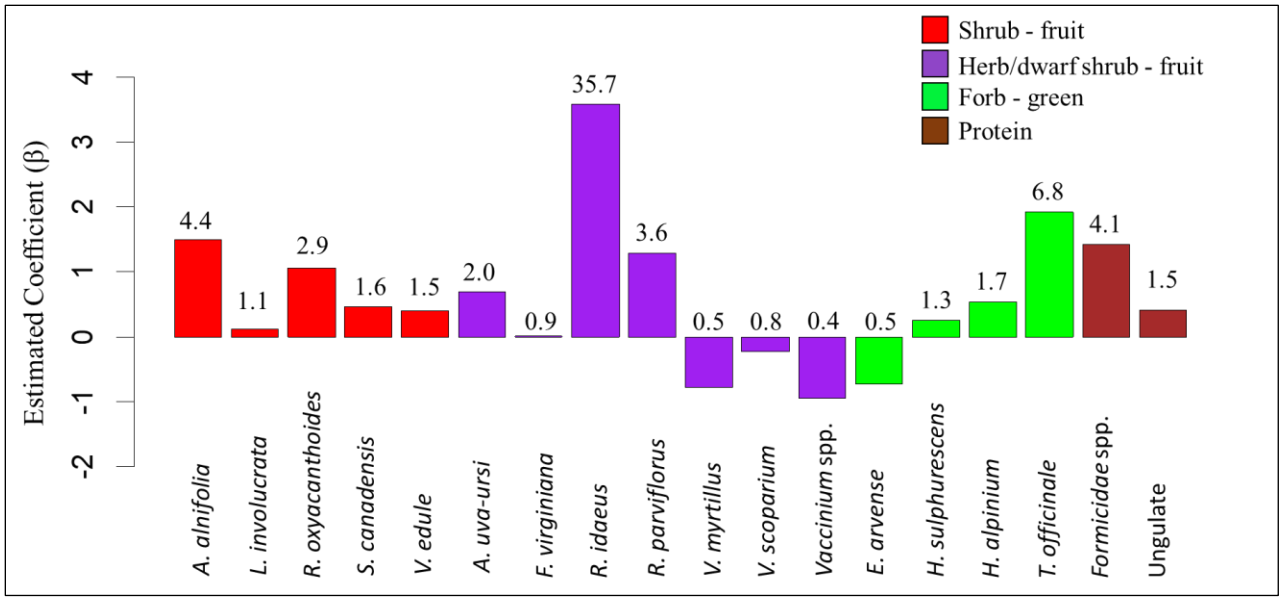

Figure 3.2: Estimated coefficients from logistic regression models describing the occurrence of 18 grizzly bear foods within burns compared to non-disturbed forests. Positive coefficients indicate a greater occurrence within burns whereas negative coefficients indicate a greater occurrence within non-disturbed controls. Odds ratios (OR) illustrated above bars represent the odds of finding grizzly bear foods within burns compared to non-disturbed forests.

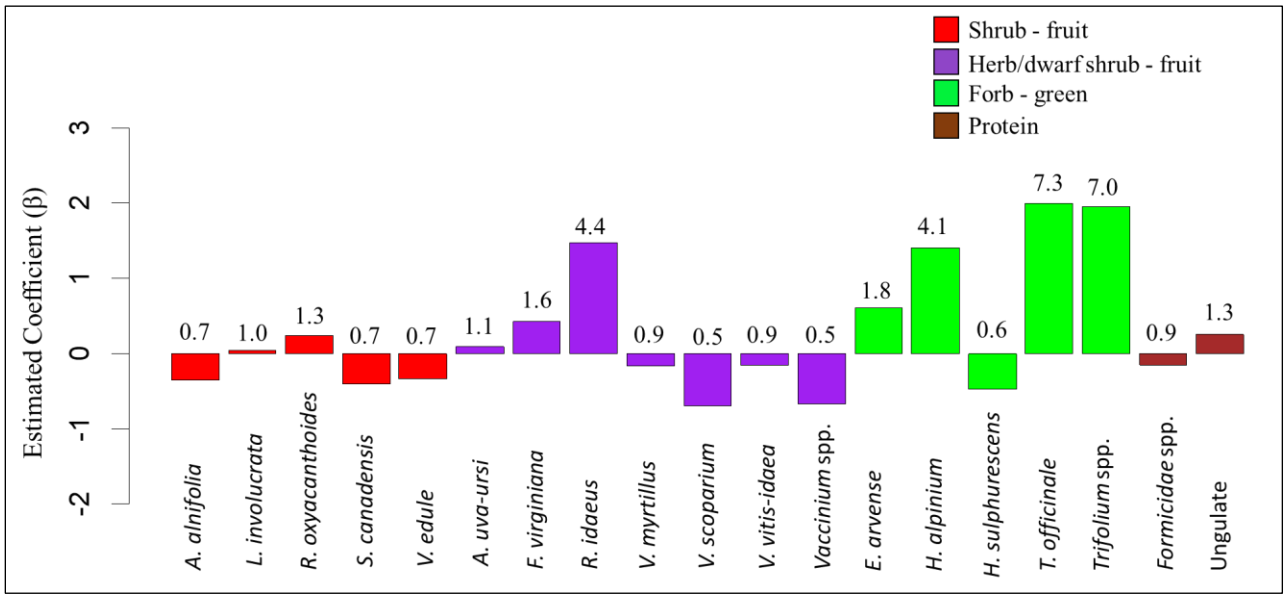

Figure 3.3: Estimated coefficients from logistic regression describing the occurrence of 19 grizzly bear foods within thinned areas compared to non-disturbed forests. Positive coefficients indicate a greater occurrence within thinned areas whereas negative coefficients indicate a great occurrence within non-disturbed controls. Odds ratios (OR) illustrated above bars represent the odds of finding grizzly bear foods within thinned areas compared to non-disturbed forests.

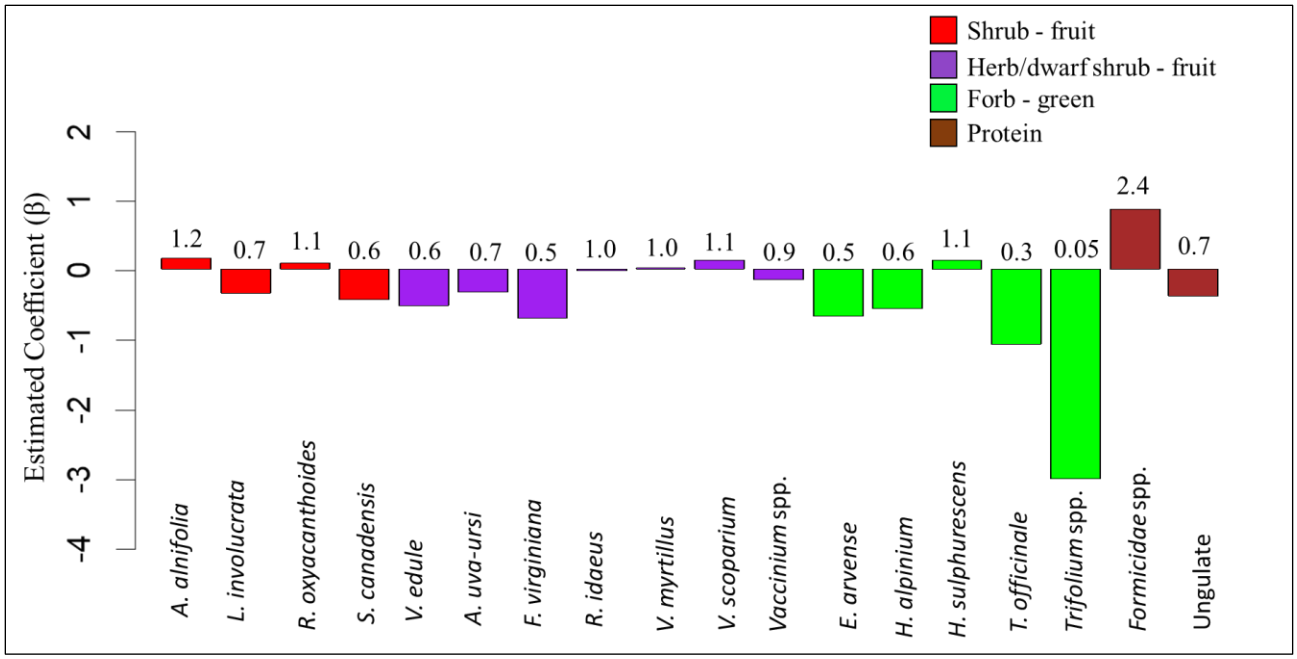

Figure 3.4: Estimated coefficients from logistic regression describing the occurrence of 18 grizzly bear foods between burns and thinned areas. Positive coefficients indicate a greater occurrence within burns whereas negative coefficients indicate a great occurrence within thinned areas. Odds ratios (OR) illustrated above bars represent the odds of finding grizzly bear foods within burns compared to thinned areas.

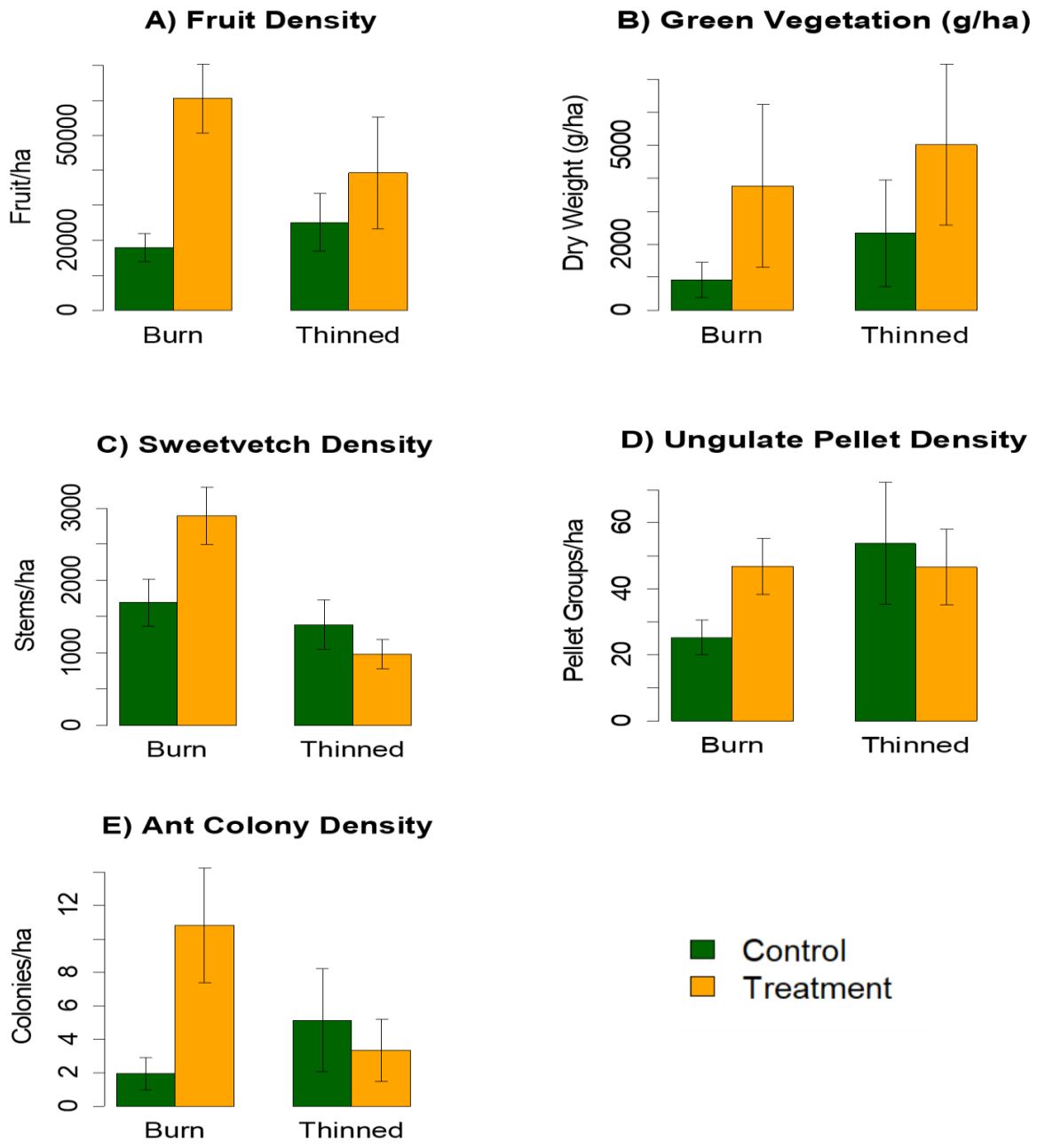

Figure 3.5: Bar graphs illustrating differences of similar groups of important grizzly bear foods (per hectare) between burns, thinned areas (treatments), and adjacent non-disturbed areas (controls). (A) illustrates differences of fruit (berry) density from 15 fruiting species. (B) illustrates differences of dry weight of three species of green herbaceous vegetation (*Taraxacum officinale, Triffolium* spp. and *Equisetum arvense*). (C) illustrates differences in sweetvetch (*Hedysarum alpin*ium and *Hedysarum sulphurescens*) stem density. (D) illustrates the differences pellet group density from six ungulate species. (E) illustrates the differences in *Formicidae* colony density.

Chapter 4: General Discussion

In the interior mountains of North America, grizzly bear densities are typically greatest where high quality habitat coincides with low human density (Apps et al. 2004; Lamb et al. 2018). When high quality grizzly bear habitat occurs near areas with high human density, ecological traps are often established as grizzly bears are often attracted to areas that are also associated with high mortality risk (Nielsen et al. 2006; Northrup 2012; Boulanger et al. 2014; Lamb et al 2017). Grizzly bear conservation has attempted to address this issue by restricting human access, often by limiting road density in areas of high quality grizzly bear habitat or areas where bears are known to frequent (Nielsen et al. 2009; Alberta Environment and Parks 2016). While these restrictions are important for grizzly bears, they are often difficult to implement and enforce given the economic and social interest of access. In the future, pressure to develop and permit access to areas of high quality grizzly bear habitat will likely increase as demands for resources and recreation rise along with the human population. In mountainous regions, where large tracks of land still exist without road access, an alternative approach to their conservation is to enhance habitat in areas distant from resource developments and human access. This approach, as opposed to restricting resource development and access, has lower associated economic and social impact. A major challenge with generating high quality grizzly bear habitat is understanding and implementing methods that do not require roads.

Prescribed fire is one possible tool that can enhance grizzly bear habitat since both grizzly bears and their critical food resources often occur in post-fire habitats (Hamer and Herrero 1987; Hamer 1999; McLellan and Hovey 2001; Apps et al. 2004). From an economic and social perspective, prescribed fire is easier to apply in remote areas because some of the negative impacts associated with burning are reduced, such as smoke and timber loss. Another potential

method to enhance grizzly bear habitat is forest clearing or thinning. Again, grizzly bears in some areas have demonstrated selection for cutblocks (Nielsen et al. 2004a) because of elevated food resources (Nielsen et al. 2004b).

The primary objective of this thesis was to evaluate the effectiveness of prescribed fire and forest thinning for enhancing grizzly bear habitat, so these practices can more effectively be used in remote, secure locations or to reduce habitat quality when conducted near known mortality sinks. To address this objective, I quantified and evaluated grizzly bear selection of post-fire habitats and the frequency and density of important grizzly bear foods within post-fire habitat and thinned forests. An additional objective was to identify environmental and site factors that most contribute to increases in grizzly bear habitat quality after fires to map and prescribe locations of future burns with the objective of most effectively enhancing grizzly bear habitat. My thesis expanded on decades of work in Banff National Park that focused on the relationship between grizzly bear use of post-fire habitats and bear food production (Hamer and Hererro 1987; Hamer 1996; Hamer 1999; Pengelly and Hamer 2006). Unlike the previous studies that occurred primarily in Cascade and Panther valleys (~ 250 km^2) of Banff National Park, this research looked at post-fire and forest thinned habitats throughout Banff, Yoho, and Kootenay National Parks (9,360 km^2) from 1110 m to 2267 m elevation gradient. Results reported in Chapter 2 of this thesis expand on the findings of Hamer and Herrero (1987), both spatially and temporally, but also by the number of grizzly bears tracked. In this Chapter, I concluded that grizzly bears, as a population, selected post-fire habitats throughout their active period (April – November). These results are already being used by managers. Maps generated from factors that predicted grizzly bear selection within post-fire habitats have been incorporated into prescribed fire plans with the objective of enhancing grizzly bear habitat. To increase our understanding of the association of

prescribed fires and grizzly bear habitat and use by bears, it is important that grizzly bear food and use data are collected prior to, and after these burns (before-after design), to increase our understanding of what factors contributed to improved grizzly bear habitat in a post-burn ecosystem.

Overall, the results in Chapter 3 did not support previous studies in the Cascade and Panther valleys of Banff that found greater density of *Shepherdia canadensis* and *Vaccinium scoparium* fruit (Hamer 1999; Pengelly and Hamer 2014), and *Hedysarum* roots (Hamer 1999; Pengelly and Hamer 2006) in burns than in non-disturbed areas. I examined a much greater diversity of burns and this variety, at different successional stages and elevations, caused high variation between burns. However, when I pooled all fruiting species together, and similarly the two *Hedysarum* species, I found greater amounts of both fruit and roots in burns compared to adjacent forest controls. Of the 25 grizzly bear food resources I examined, *Arctostaphylos uva-ursi*, *Taraxacum officinale*, and *Formicidae* species had the greatest increase in burns and thinned areas when compared to adjacent, non-disturbed controls. A comprehensive diet analysis of grizzly bears in Banff, Yoho, and Kootenay would help identify the relative importance of these, and other foods for grizzly bears in this region.

Like some other grizzly bear populations in North America, bears in the Banff area suffer from ecological traps where attractive habitat occurs in areas with high mortality risk (Nielsen et al 2004c; Pollock et al. 2017). Over 80% of known grizzly bear mortality in Banff in the last 30 years has been human caused with the rail-line being the primary mortality source in more recent years (Benn and Herrero 2002; Bertch and Gibeau 2009). Disturbances (burns, forest clearing, excavations, etc.) adjacent to areas with elevated mortality sources should attempt to minimize grizzly bear attractants. To reduce the effects of catastrophic wildfire, forest thinning and fuel

reduction are occurring in and around townsites, highways, and railways, as well as in remote areas where new landscape fuel breaks are being added. In Chapter 3, I identified factors that contributed to increased foods in forest thinned areas and these should be addressed to minimize habitat quality near townsites, highways, and railways and to increase habitat quality in remote or secure areas. Future thinning practices in Banff, Yoho, and Kootenay National Parks should be carefully monitored prior to, and after thinning, to evaluate methods that restrict or enhance grizzly bear foods. For example, both Zager et al. 1983 and Nielsen et al. (2004b) reported that scarification after clearcutting reduced numerous important grizzly bear foods. Unfortunately, thinning and fuel reduction records in Banff, Yoho, and Kootenay between 1988 and 2012 were recorded inconsistently and limited the ability to detect the influence of specific treatments on grizzly bear foods. Overtime, areas that have been thinned will require maintenance to sustain their effectiveness of reducing fire spread. Research on maintenance methods (mechanical vs. chemical) that most efficiently enhance or restrict thinned areas from becoming high quality habitat should be addressed. When grizzly bear habitat is enhanced adjacent to high mortality areas, the attraction to these ecological traps should be offset by generating habitat in remote secure areas. Because grizzly bears are wide-ranging animals and their diet changes throughout their active season, addressing spatial and temporal factors to minimize their use of ecological traps by enhancing habitat in remote areas requires additional study. Knowing the optimal distance to enhance habitat from known mortality sources would be beneficial, but given grizzly bears follow maternal knowledge of habitat selection and conflict behavior (Nielsen et al. 2013; Morehouse et al. 2016), reducing their use of ecological traps may take generations. If habitat enhancements in secure areas stimulate reproductive rates of bears in remote areas that typically

avoid areas with increased human caused mortality, an overall positive population growth would be expected even with continued human-caused mortality in sink locations.

Although inferences from this thesis are difficult to extrapolate outside of Banff, Yoho, and Kootenay National Parks, the importance of post-fire habitats for grizzly bears is likely more pronounced in more mesic areas where *Vaccinium membranaceum* is more common. Throughout much of interior British Columbia, *Vaccinium membranaceum* is the primary hyperphagia food source for grizzly bears (McLellan and Hovey 1995; McLellan 2015; Lamb et al. 2017) and is often associated with post-fire habitats (Martin 1979; Zager et al. 1983; McLellan 2015). In the Flathead Valley of British Columbia, high severity burns that occurred during drought years in the 1930's generated huckleberry fields at higher elevations that have been productive for decades and have promoted high grizzly bear reproductive rates, and high bear densities, despite high rates of mortality (McLellan and Hovey 2001; McLellan 2011; McLellan 2015). In these unprotected areas, the decrease of early-seral habitat from intensive fire suppression is less pronounced than in national parks because extensive logging has maintained early successional communities. Unfortunately, these practices have also created a network of roads and thus the establishment of ecological traps (Lamb et al. 2017). Updating wildfire management practices in both B.C. and Alberta that would restrict fire suppression in remote areas, particularly in non-drought years, might stimulate grizzly bear populations by promoting *Vaccinium membranaceum* and other important food production in secure areas. Under the current fire suppression model in B.C., Alberta, and elsewhere in the Rocky Mountains, fires in remote areas are usually suppressed quickly and it is only during exceptionally hot, dry summers that fires escape early suppression efforts and become large (Dennison et al. 2014; Rogeau et al. 2016). Salvage logging and replanting also typically occurs in burned areas which promotes access and

minimizes early successional habitats and their associated ecological benefits (Lindmayer and Noss 2006; Swanson et al. 2010).

Of all the human influences in the Rocky Mountains that have altered ecosystem function in the last two centuries, fire exclusion and suppression often go unnoticed and remain under researched (Arno et al. 2000) even though they alter ecosystems in remote areas where people have little other influence. Ecosystem alteration from clearcut logging, mining, road building, and other industrial activities occur quickly, have visible consequences, and are easily quantified. In contrast, changes from fire exclusion and suppression occur gradually, go un-noticed and their impacts are difficult to quantify. For these reasons it is difficult to assess if human-caused changes to fire regimes have altered grizzly bear carrying capacity, or if fire exclusion and suppression have contributed to grizzly bear mortality sinks that also limit their populations. While these are important questions, they are difficult to answer given the spatial and temporal scales that fire exclusion, grizzly bears, and ecosystems operate. While additional research is necessary and important, we currently have a good understanding of the primary factors that limit grizzly bear populations; human caused mortality and the lack of productive habitat. Grizzly bear conservation efforts that focused on reducing mortality in the last 40 years have been effective (Mace et al. 2012) and after over a century of decline, grizzly bears are now increasing in many areas along the fringe of their distribution (Mace et al. 2012; Morehouse and Boyce 2016). Humans are learning to co-exist with grizzly bears and now their long-term persistence relies on ensuring we maintain the large-tracks of productive habitat that they require. As time progresses, resource extraction, agriculture, and recreation will continue to expand, and the persistence of grizzly bears will depend on how well we balance these interests and those of bears. If we fail to maintain this balance, protected areas will become even more

vital to grizzly bear conservation and it is fundamental that these areas provide them with the diversity of productive habitats that they require.

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Appendices

Appendix A: Grizzly bear identification, sex, age class (adult: > 5 yrs; sub-adult: 2-4 yrs), multi-annual 100% minimum convex polygon (MCP) home range size (km^2), percent (%) of burn, old burn and, human use area (HUA) patches in home ranges, and the number of radio-telemetry locations for each season (hypophagia, early hyperphagia, and hyperphagia).

Bear				Habitat % in MCP			Radiotelemetry locations			
ID	sex	ageclass	MCP (km^2)	burn	oldburn	HUA	hypophagia	early hyperphagia	hyperphagia	total
F64	female	adult	894.9	2.1	1.8	6.7	597	598	817	2,012
F72	female	adult	825.0	9.5	2.8	5.6	702	2,001	1,997	4,700
M122	male	adult	2298.5	9.9	5.3	3.9	327	616	994	1,937
M125	male	adult	1581.2	1.6	3.7	1.1	80	87	566	733
M126	male	adult	2327.5	4.1	3.6	2.7	1,336	1,880	2,871	6,087
M128	male	subadult	1723.7	3.7	6.6	4.3	251	627	989	1,867
F130	female	adult	764.8	2.5	1.9	7.0	977	1,727	815	3,519
F131	female	adult	486.1	16.3	17.9	1.5	417	1,082	1,239	2,738
M132	male	subadult	614.3	11.8	13.4	4.9	514	1,140	1,218	2,872
F133	female	adult	364.3	0.0	9.8	2.2	64	500	471	1,035
M134	male	adult	1951.3	2.5	4.9	2.5	-	1,114	323	1,437
F135	female	adult	416.9	13.8	22.9	1.7	262	983	1,330	2,575
M136	male	adult	2264.5	4.5	5.3	3.0	615	1036	1,606	3,257
F138	female	adult	240.4	0.0	0.5	1.9	479	806	906	2,191
M140	male	adult	254.7	9.5	4.7	0.2	282	-	-	298
M141	male	adult	1359.6	2.2	9.3	2.8	738	623	878	2,239
F142	female	adult	397.2	7.7	3.5	5.9	191	449	194	834
F143	female	subadult	421.1	8.7	4.6	5.9	242	644	949	1,835
M144	male	subadult	693.9	8.9	2.0	5.8	208	70	937	1,215
F148	female	subadult	639.5	3.8	2.0	6.1	-	688	1,011	1,699
M149	male	subadult	459.9	0.0	6.5	3.0	-	391	-	391
F155	female	subadult	315.6	13.8	25.6	1.1	204	636	1,007	1,847
F156	female	subadult	345.3	4.4	5.6	1.8	196	639	726	1,561
M158	male	adult	955.6	0.1	3.6	1.1	181	637	1,009	1,827
F160	female	subadult	332.8	5.1	2.8	3.4	-	282	909	1,191
F161	female	adult	570.3	0.0	2.4	1.1	134	637	1,008	1,779
			^{A}903.8	**^{A}5.6**	**^{A}6.7**	**^{A}3.4**	**^{T}8,997**	**^{T}19,909**	**^{T}24,770**	**^{T}53,676**

- no locations for season
^{A} average; ^{T} total

Appendix B: Influence of recent burns, older burns, and human-use habitats on grizzly bear home range selection (second-order scale).

At the population level, recent burns (1960-2012) had no significant effect on grizzly bear home range selection (Table B.1). There was, however, variability among individuals. Ten bears had more recently burned habitat, while 11 bears had less recently burned habitat in their home range compared to that which was available across the study area. Four bears showed neither preference nor avoidance. Age and sex-class accounted for some of the individual variability with sub-adult and female home ranges selected for more burned habitat, while adults and males selected home ranges with a similar proportion of burned habitat that was available across the study area.

At the population level, grizzly bear home range had less old (1896-1959) burned habitats than the study area (Table B.1). There was less individual variability compared with new burns, with only 5 individuals positively selecting old burns, while 20 individuals had negative home range selection in old burned habitats. Age or sex did not have a significant influence on selection of old burns.

Human-use areas were positively associated with locations of grizzly bear home ranges (Table B.1). Only 5 bears had a smaller proportion of human-use areas in their home range than was available across the study area. In contrast, 17 bears had more human-use areas within their home range than across the study area, while 3 bears were similar to that which was available in the study area.

Table B.1: Estimated coefficients **(β),** standard errors (S.E.), significance levels (*p*), and odds ratios (OR) for home range selection (2rd order) of burns, old burns, and human use areas. Individual models created using logistic regression while sex, age, and population models created from generalized linear mixed effects models (GLMM) with a random intercept for individual bears.

	Recent burns (1960-2012)				**Old burns (1896-1959)**				**Human use areas**			
Sex/ID	**β**	**S.E.**	***p***	**OR**	**β**	**S.E.**	***p***	**OR**	**β**	**S.E.**	***p***	**OR**
Individual												
F64	-1.423	0.138	<0.001	0.241	-1.466	0.117	<0.001	0.231	1.422	0.073	<0.001	4.145
F72	0.647	0.060	<0.001	1.909	-1.009	0.098	<0.001	0.365	1.207	0.081	<0.001	3.342
M122	0.693	0.041	<0.001	2.000	-0.346	0.047	<0.001	0.707	0.814	0.065	<0.001	2.256
M125	-1.209	0.070	<0.001	0.299	-0.616	0.046	<0.001	0.540	-0.562	0.092	<0.001	0.570
M126	-0.204	0.053	<0.001	0.816	-0.759	0.055	<0.001	0.468	0.549	0.070	<0.001	1.731
M128	-0.295	0.062	<0.001	0.745	-0.234	0.051	<0.001	0.791	0.974	0.068	<0.001	2.649
F130	-1.210	0.135	<0.001	0.298	-1.433	0.124	<0.001	0.239	1.507	0.076	<0.001	4.514
F131	1.218	0.062	<0.001	3.380	1.056	0.057	<0.001	2.875	0.250	0.146	0.087	1.284
M132	0.857	0.063	<0.001	2.357	0.734	0.057	<0.001	2.084	1.185	0.091	<0.001	3.272
F133	[a]avoid				0.418	0.080	<0.001	1.519	0.486	0.151	<0.001	1.625
M134	-0.599	0.067	<0.001	0.549	-0.298	0.050	<0.001	0.743	0.350	0.079	<0.001	1.418
F135	0.993	0.071	<0.001	2.700	1.272	0.058	<0.001	3.568	-0.027	0.178	0.881	0.974
M136	-0.256	0.055	<0.001	0.774	-0.371	0.048	<0.001	0.690	0.622	0.069	<0.001	1.862
F138	[a]avoid				-2.714	0.410	<0.001	0.066	0.093	0.219	0.673	1.097
M140	0.653	0.101	<0.001	1.921	-0.267	0.125	0.033	0.766	-1.688	0.502	<0.001	0.185
M141	-0.566	0.049	<0.001	0.568	-0.462	0.040	<0.001	0.630	0.503	0.060	<0.001	1.653
F142	0.445	0.089	<0.001	1.561	-0.889	0.133	<0.001	0.411	1.105	0.112	<0.001	3.018
F143	0.748	0.077	<0.001	2.113	-0.451	0.106	<0.001	0.637	1.360	0.100	<0.001	3.898
M144	0.624	0.065	<0.001	1.867	-1.411	0.129	<0.001	0.244	1.274	0.084	<0.001	3.573
F148	-0.752	0.119	<0.001	0.471	-1.207	0.122	<0.001	0.299	1.447	0.082	<0.001	4.252
M149	[a]avoid				-0.041	0.086	0.629	0.959	0.669	0.125	<0.001	1.953
F155	0.774	0.087	<0.001	2.168	1.544	0.061	<0.001	4.682	-0.575	0.263	<0.001	0.563
F156	-0.276	0.129	0.032	0.759	-0.274	0.108	0.011	0.760	0.136	0.181	0.452	1.146
M158	-4.409	0.578	<0.001	0.012	-0.622	0.078	<0.001	0.537	-0.418	0.144	0.004	0.659
F160	-0.104	0.122	0.391	0.901	-0.855	0.142	<0.001	0.425	0.837	0.135	<0.001	2.310
F161	[a]avoid				-1.178	0.127	<0.001	0.308	-0.405	0.183	0.027	0.667
Sex class												
female	0.094	0.042	0.027	1.098	0.015	0.038	0.695	1.015	0.844	0.063	<0.001	2.325
male	-0.079	0.043	0.067	0.924	-0.289	0.036	<0.001	0.749	0.631	0.068	<0.001	1.879
Age class												
adult	-0.098	0.037	0.009	0.907	-0.236	0.032	<0.001	0.790	0.608	0.057	<0.001	1.836
subadult	0.203	0.051	<0.001	1.226	0.041	0.045	0.359	1.042	0.985	0.079	<0.001	2.678
Population	0.010	0.030	0.739	1.010	-0.140	0.026	<0.001	0.869	0.748	0.046	<0.001	2.113

[a] Perfect avoidance-no burn patch in home range (parameter estimate not available)

Appendix C: Covariates used to model grizzly bear selection within burned habitats of Banff, Yoho, and Kootenay National Parks.

Category	Variable	Code	Unit	Source
Climate	Annual heat-to-moisture index	ahm	unitless	Wang et al., 2012
	Beginning of frost-free period	bffp	day of year	Wang et al., 2012
	Climatic moisture deficit	cmd	mm	Wang et al., 2012
	Climate moisture index	cmi	unitless	Wang et al., 2012
	Climate moisture index (June, July, and August)	cmijja	unitless	Wang et al., 2012
	Degree-days below 0 °C	dd0	degree days	Wang et al., 2012
	Degree-days above 5 °C	dd5	degree days	Wang et al., 2012
	Ending of frost-free period	effp	day of year	Wang et al., 2012
	Est. extreme minimum temperature, 30-yr normal	emt	°C	Wang et al., 2012
	Reference atmospheric evaporative demand	eref	mm	Wang et al., 2012
	Frost-free period	ffp	days	Wang et al., 2012
	Mean annual precipitation	map	mm	Wang et al., 2012
	Mean annual temperature	mat	°C	Wang et al., 2012
	Mean coldest-month temperature	mcmt	°C	Wang et al., 2012
	Mean May-to-September precipitation	msp	mm	Wang et al., 2012
	Mean warmest-month temperature	mwmt	°C	Wang et al., 2012
	Number of frost-free days	nffd	unitless	Wang et al., 2012
	Precipitation as snow	pas	mm	Wang et al., 2012
	Summer precipitation	pptsm	mm	Wang et al., 2012
	Winter precipitation	pptwt	mm	Wang et al., 2012
	Summer heat-to-moisture index	shm	unitless	Wang et al., 2012
	Average summer temperature	tavsm	°C	Wang et al., 2012
	Average winter temperature	tavwt	°C	Wang et al., 2012
	Continentality (MWMT – MCMT)	td	°C	Wang et al., 2012
	Minimum temperature in January	tmn01	°C	Wang et al., 2012
	Maximum temperature in July	tmx07	°C	Wang et al., 2012
Terrain	Elevation	elev	m	digital elevation model
	Compound topographic index	cti	unitless	digital elevation model
	Heat load index	hli	unitless	digital elevation model
	Slope	slope	°degree	digital elevation model
Burn	Time since burn	tsf	years	fire data
	Fire area	area	m^2	fire data
	Distance to burn edge	dbedge	m	derived in ArcGIS
	Burn severity	bsev	index	Parks Canada, 2012
Other	Distance to water	dwater	m	derived in ArcGIS
	Burn (1960-2012)	newburn	category	fire data
	Old burn (1896-1959)	oldburn	category	fire data
	Human use area	hua	category	derived in ArcGIS

Appendix D: List of grizzly bear foods examined in burns, thinned areas, and adjacent controls as well as their percent occurrence and description.

Grizzly bear food Item			Percent (%) of samples with occurrence				
Type	**Common name**	**Scientific name**	**Burned**	**Control**	**Thinned**	**Control**	**Importance**
shrub-fruit	Saskatoon berry	*Amelanchier alnifolia*	5.4	3.9	13.3	17.9	Moderate
	Black twinberry	*Lonicera involucrata*	9.9	8.8	13.3	12.8	Moderate
	Northern gooseberry	*Ribes oxycanthoides*	35.1	15.7	33.3	28.8	Moderate
	† Elderberry	*† Sambucus racemosa*	0.9	0.0	0.0	0.0	Low
	Buffaloberry	*Shepherdia canadensis*	83.8	76.5	88.8	92.3	Critical
	Highbush cranberry	*Viburnum edule*	9.9	6.9	15.5	20.5	Low
herb or	Bearberry	*Arctostaphylos uva-ursi*	63.9	47.1	71.1	69.2	High
dwarf-shrub	† Crowberry	*† Empetrum nigrum*	3.6	3.9	0.0	0.0	Low
fruit	Strawberry	*Fragaria virginiana*	57.7	57.8	73.3	64.4	Low
	Raspberry	*Rubus idaeus*	26.1	1.0	26.6	2.6	Low
	Thimbleberry	*Rubus parviflorus*	9.9	2.9	2.2	5.1	Low
	§ Dwarf bilbery	§ *Vaccinium caespitosum*	2.7	4.9	0.0	2.6	Low
	§ Black huckleberry	§ *Vaccinium membranaceum*	1.8	5.9	2.2	7.7	High
	§ Velvetleaf blueberry	§ *Vaccinium myrilloides*	0.0	2.9	2.2	7.7	Low
	Whortleberry	*Vaccinium myrtillus*	9.0	17.6	8.8	10.3	Moderate
	Grouseberry	*Vaccinium scoparium*	28.8	42.2	20.0	33.3	High
	Ligonberry	*Vaccinium vitis-idaea*	0.0	1.0	4.4	5.1	Low
forb-green	Horsetail	*Equisetum arvense*	7.2	13.7	13.3	7.7	Moderate
	† Cow parsnip	*† Heraculum lanatum*	3.6	1.0	0.0	0.0	High
	Dandelion	*Taraxacum officinale*	17.1	2.9	37.8	7.7	High
	Clover species	*Trifolium* spp.	0.9	1.9	15.5	2.6	Moderate
forb-root	Alpine sweetvetch	*Hedysarum alpinium*	8.1	4.8	13.3	5.1	High
	Yellow sweetvetch	*Hedysarum sulphurescens*	58.6	51.5	55.5	66.6	Critical
protein-insect	Ants	*Formidae* spp.	14.4	3.9	6.6	7.7	High
protein-animal	Ungulates	Ungulate species	35.1	26.5	44.4	38.5	Critical

§ Combined species into *Vaccinium* complex for analyses

† Not analysed because of low occurrence (< 5% of plots)

Appendix E: Description of burn and forest thinned features where grizzly bear food data was collected.

Table E.1: Description of burn features for each sample location (n = 113) where grizzly bear food data was collected within burns.

Burned Plot Details						
Plot ID	Type	Location name	Burn year	Canopy cover (%)	Elevation (m)	Area (ha)
F01	Prescribed fire	Morrison	2003	30.2	1397	3157.6
F02	Prescribed fire	Morrison	2003	43.3	1401	3157.6
F03	Prescribed fire	Fairholm	2003	36.3	1524	595.5
F04	Prescribed fire	Fairholm	2003	19	1493	595.5
F05	Prescribed fire	Sawback	1984	5.3	1467	39.7
F06	Prescribed fire	Sawback	1991	61.5	1520	175.9
F07	Prescribed fire	Sawback	1993	12.9	1576	306.9
F08	Prescribed fire	Minnewanka	2003	40.5	1520	144.2
F09	Prescribed fire	Minnewanka	2003	10	1706	144.2
F10	Prescribed fire	Minnewanka	1993	29.4	1597	147.4
F11	Prescribed fire	Fairholm	2003	42.4	1544	595.5
F12	Prescribed fire	Cascade	2001	0.1	1874	126.6
F13	Prescribed fire	Cascade	2001	1.6	1634	16.8
F14	Prescribed fire	Fairholm	2003	28.1	1720	595.5
F15	Prescribed fire	Fairholm	2003	21.2	1857	595.5
F16	Prescribed fire	Fairholm	2003	53.3	1506	3157.6
F17	Prescribed fire	Fairholm	2003	48	1537	87.5
F18	Prescribed fire	Minnewanka	1994	61.5	1629	137.4
F19	Prescribed fire	Minnewanka	1994	40.5	1553	137.4
F20	Prescribed fire	Hoodoo	2005	2.5	1171	1256.9
F21	Prescribed fire	Hoodoo	2005	53.7	1167	1256.9
F22	Prescribed fire	Hoodoo	2005	8.1	1133	1256.9
F23	Prescribed fire	Castle	1992	108.1	1515	15.9
F24	Prescribed fire	Minnewanka	1988	61.9	1530	35.3
F25	Prescribed fire	Minnewanka	1988	28.1	1470	35.3
F26	Prescribed fire	Reddeer	1994	8.3	1966	14.4
F27	Prescribed fire	Reddeer	1994	0.7	1989	14.4
F28	Prescribed fire	Divide	2005	1.7	2184	99.4
F29	Prescribed fire	Reddeer	2005	0	1904	1221.5
F30	Prescribed fire	Reddeer	1994	15.6	1832	751.5
F31	Prescribed fire	Reddeer	2005	0	1741	66.2
F32	Prescribed fire	Reddeer	1994	35.9	1746	361.0

F33	Prescribed fire	Reddeer	1994	4.6	1764	361.0
F34	Prescribed fire	Reddeer	2005	12.7	1722	121.3
F35	Prescribed fire	Reddeer	1994	45.3	1818	361.0
F36	Prescribed fire	Aylmer	1990	14.2	1544	90.9
F38	Prescribed fire	Stewart Canyon	2003	5.5	1776	313.1
F39	Prescribed fire	Johnson	2003	31.1	1469	3157.6
F40	Prescribed fire	Fairholm	2008	38	1375	174.3
F41	Prescribed fire	Sawback	1993	4.1	1685	13.8
F42	Prescribed fire	Stoney Fire	1990	4.2	2057	336.1
F43	Prescribed fire	Cascade	1990	6.8	1878	336.1
F44	Prescribed fire	Dormer	1990	33.7	1796	336.1
F45	Prescribed fire	Cascade	2001	5.7	1710	126.6
F46	Prescribed fire	Fairholm	2003	33.1	1447	3157.6
F47	Prescribed fire	Fairholm	2003	5.3	1833	3157.6
F48	Prescribed fire	Johnson Lake	2003	36.4	1523	3157.6
F49	Prescribed fire	Spray Lake	2007	63.2	1800	30.8
F50	Prescribed fire	Hoodoo	2005	10.8	1294	1256.9
F51	Prescribed fire	Hoodoo	2005	9.4	1133	1256.9
F52	Prescribed fire	Hoodoo	2005	7.5	1107	1256.9
F53	Prescribed fire	Sask Crossing	2009	0.4	1456	3442.1
F54	Prescribed fire	Sask Crossing	2009	1.4	1421	3442.1
F56	Prescribed fire	Sask Crossing	2009	6.1	1412	3442.1
F57	Prescribed fire	Sask Crossing	2009	0	1411	3442.1
F58	Prescribed fire	Sask Crossing	2009	32.2	1387	3442.1
F59	Prescribed fire	Sask Crossing	2009	4	1705	3442.1
F60	Prescribed fire	Sask Crossing	2009	0.3	1415	3442.1
F61	Prescribed fire	Sask Crossing	2009	33.9	1847	621.6
F62	Prescribed fire	Minnewanka	1988	10.6	1641	449.0
F63	Prescribed fire	Minnewanka	1988	38	1572	449.0
F64	Prescribed fire	Mitchell	2008	14.1	1636	1842.3
F65	Prescribed fire	Mitchell	2008	38.7	1709	1842.3
F66	Prescribed fire	Stewart Canyon	2003	7.6	1672	313.1
F67	Prescribed fire	Sawback	1993	77.4	1434	19.9
F68	Prescribed fire	Cuthead	2001	61.4	1872	685.7
F69	Prescribed fire	Cuthead	2001	63.3	1833	685.7
F70	Prescribed fire	Cuthead	2001	13.1	2095	179.9
F71	Prescribed fire	Cuthead	2001	8.4	2148	134.9
F72	Prescribed fire	Windy	2001	5.6	2016	116.8
F73	Prescribed fire	Windy	2001	8.4	2015	266.7

F74	Prescribed fire	Flints Park	1998	11.7	1907	47.6
F75	Prescribed fire	Flints Park	2007	17.3	1840	4.9
F76	Prescribed fire	Windy	1999	1	2011	2048.9
F77	Prescribed fire	Windy	1999	9.9	1948	2048.9
F78	Prescribed fire	Windy	1999	0	1888	2048.9
F79	Prescribed fire	Windy	2006	9.3	1975	34.0
F80	Prescribed fire	Snow Creek	1989	5.1	2014	225.9
F81	Prescribed fire	Panther	1999	2.5	1802	2048.9
F82	Prescribed fire	Windy	1999	0.8	2109	2048.9
F83	Prescribed fire	Cuthead	2001	19.1	2108	37.9
F84	Prescribed fire	Cascade	2001	19.6	1712	255.1
F85	Wild fire	Dogrib	2001	40.2	1639	10900.4
F86	Wild fire	Dogrib	2001	39	1601	10900.4
F87	Wild fire	Dogrib	2001	49.8	1688	10900.4
F88	Wild fire	Vermillion	1968	80.9	1579	664.9
F89	Wild fire	Vermillion	1968	44.6	1570	664.9
F90	Wild fire	Vermillion	1968	56.9	1628	1579.8
F91	Wild fire	Stanley	2003	4.8	1703	1579.8
F92	Wild fire	Vermillion	1968	87.2	1709	664.9
F93	Wild fire	Tokumn	2003	1.1	1531	16299.8
F94	Wild fire	Tokumn	2003	0	1564	16299.8
F95	Wild fire	Shanks	2001	4.6	1262	3276.3
F96	Wild fire	Vermillion	1968	48.6	1673	1579.8
F97	Wild fire	Floe Lake	2003	0	1508	16299.8
F98	Wild fire	Floe Lake	2003	0	1696	16299.8
F99	Wild fire	Malloch	2009	28.4	1849	133.6
F100	Wild fire	Stanley	2003	10.3	1541	16299.8
F101	Wild fire	Tokum	2003	0.1	1686	16299.8
F102	Wild fire	Vermillion	1968	5.9	1895	1579.8
F103	Wild fire	Floe Lake	2003	0.1	1484	16299.8
F104	Wild fire	Honeymoon	2003	0.6	1809	16299.8
F105	Wild fire	Honeymoon	2003	4.7	1893	16299.8
F106	Wild fire	Hawk Creek	2003	70.9	1534	16299.8
F107	Wild fire	Shanks	2001	27.4	1261	3276.3
F108	Wild fire	Shanks	2001	49.2	1362	3276.3
F109	Wild fire	Vermillion	1968	2.4	2067	1579.8
F110	Wild fire	Tokum	2003	0	1667	16299.8
F111	Wild fire	Kauffman	2003	0.2	2094	16299.8
F112	Wild fire	Kauffman	2003	0	2120	16299.8

F113	Wild fire	Vermillion	1968	68.6	1696	1579.8

Table E.2: Description of forest thinned features for each sample location (n = 44) where grizzly bear food data was collected within thinned areas.

Thinned Area Plot Details						
Plot ID	Type	Location	Thin year	Canopy cover (%)	Elevation (m)	Area (ha)
T01	hand	Cave and Basin	2007	18.9	1427	45.9
T02	machine & hand	Middlesprings	2005	16.5	1443	8.6
T03	machine & hand	Middlesprings	2005	37.2	1443	8.6
T04	machine	Carrot	2007	17.5	1350	21.9
T05	hand	Moose Meadow	2008	47.7	1424	7.0
T06	machine	Harry's Hill	2003	12.4	1560	7.0
T07	hand	Surprise Corner	2006	72.9	1378	13.7
T08	hand	Middlesprings	2006	56.6	1415	9.1
T09	hand	Cave and Basin	2007	22.6	1415	45.9
T10	machine	Rimrock	2005	36.6	1501	9.4
T11	hand	Rimrock	2006	62.2	1412	4.8
T12	machine	Fairholm Guard	2002	4.6	1408	275.0
T13	hand	Fairholm Guard	2010	31.5	1472	275.0
T14	machine & hand	Moose Meadows	2009	49	1423	26.3
T15	machine & hand	Moose Meadows	2009	52.3	1424	26.3
T16	hand	Carrot	2007	53.9	1349	17.2
T17	hand	Cave and Basin	2007	33.1	1427	45.9
T18	machine	Fairholm Guard	2002	29.9	1426	107.6
T19	hand	Castle Junction	1997	38.5	1433	3.6
T20	machine & hand	Rundle	2006	49.2	1400	11.7
T21	machine & hand	Two Jack	1988	0.6	1467	57.6
T22	hand	Tunnel	2009	49.2	1450	2.7
T23	machine	Moraine Lake	2007	29.4	1903	8.6
T24	machine	Hoodoo	2004	0.5	1122	160.0
T25	machine	Emerald Lake	2006	14.4	1289	18.5
T26	machine	Yoho Turnoff	2004	0	1121	160.0
T27	hand	Emerald Lake	2006	9.3	1306	1.9
T28	machine	Sulphur	2005	20.7	1536	11.7

T29	machine	Sulphur	2005	9.5	1751	11.6
T30	machine	Sulphur	2005	43.8	1451	11.7
T31	machine & hand	Sulphur	2005	61.4	1442	8.6
T32	hand	Moose Meadows	2008	63.3	1424	7.0
T33	machine	Moose Meadows	2010	0	1429	63.3
T34	machine	Mitchell Guard	2008	0.9	1216	113.0
T35	hand	Cave and Basin	2008	84.7	1445	4.6
T36	machine	Nordic Center	2003	5.9	1440	213.2
T37	machine	Nordic Center	2003	7.7	1429	213.2
T38	machine	Nordic Center	2003	1	1477	213.2
T39	machine	Harrys Hill	2006	24.7	1562	4.7
T40	hand	Nordic Center	2009	10.1	1424	17.2
T41	machine	Nordic Center	2003	4.5	1604	213.2
T42	machine	Nordic Center	2003	4	1513	213.2
T43	machine	Tunnel	2009	0.1	1460	5.0
T44	machine	HarrysHill	2006	11.2	1586	7.0

Appendix F: Environmental covariates used to model the distribution of grizzly bear foods in burns and thinned areas in Banff area. Variable code, category, unit, and source are presented.

Variable code	Variable description	Variable category	Unit	Source
Tree_cov	Cover of tree canopy (height ≥ 1.3 m)	Disturbance	m	measured on site
Regen_cov	Cover of regenerating tree canopy (height < 1.3 m)	Disturbance	m	measured on site
Age	Time since disturbance	Disturbance	years	derived from fire or thinning data
Area	Area of disturbance	Disturbance	km^2	derived from fire or thinning data
CTI	Compund topographic index	Terrain	unitless	derived from digital elevation model
ELEV	Elevation	Terrain	m	derived from digital elevation model
HLI	Heat-load index	Terrain	unitless	derived from digital elevation model
PPT_WT	Winter precipitation	Winter climate	mm	Wang et al., 2012
TAV_WT	Average winter temperature	Winter climate	ºC	Wang et al., 2012
PPT_SM	Summer precipitation	Summer climate	mm	Wang et al., 2012
TAV_SM	Average summer temperature	Summer climate	ºC	Wang et al., 2012
MAP	Mean annual precipitation	Annual climate	mm	Wang et al., 2012
MAT	Mean annual temperature	Annual climate	ºC	Wang et al., 2012

Appendix G: Name and structure of the five a priori candidate models used for assessing the distribution of grizzly bear foods within burns and thinned areas of Banff area. Disturbance model includes covariates include: tree cover (Tree_cov), regenerating tree cover (Regen_cov), time since disturbance (Age) and disturbance size (Area). The terrain model includes covariates: compound topographic index (CTI), elevation (ELEV) and heat-load index (HLI). The summer climate model includes covariates: average summer precipitation (PPT_SM) and temperature (TAV_SM). The winter climate model includes covariates: average winter precipitation (PPT_WT) and temperature (TAV_WT). The annual climate model includes covariates: mean annual precipitation (MAP) and temperature (MAT).

Model name	Model structure	*K*
Disturbance	Tree_cov + Regen_cov + Age + Area	5
Terrain	CTI + ELEV + HLI	4
Summer climate	PPT_SM + TAV_SM	3
Winter climate	PPT_WT + TAV_WT	3
Annual climate	MAP + MAT	2

Appendix H: Occurrence of grizzly bear foods between burns, thinned areas and adjacent non-disturbed forests.

Table H.6: Percent occurrence for 18 grizzly bear foods in burns (n = 111) and adjacent non-disturbed forests (n = 103). Beta coefficients (± S.E.), significance levels (p), and odds ratios (OR) of finding grizzly bear foods within burns compared to non-disturbed forests are reported from logistic regression models.

Type	**Grizzly bear food item**	**% of burn**	**% of forest**	**β**	**S.E.**	***p***	**OR**
shrub-fruit	*Amelanchier alnifolia*	5.4	3.9	1.489	0.574	0.009	4.431
	Lonicera involucrata	9.9	8.8	0.128	0.472	0.786	1.137
	Ribes oxycanthoides	35.1	15.7	1.069	0.337	0.001	2.912
	Shepherdia canadensis	83.8	76.5	0.464	0.348	0.182	1.590
	Viburnum edule	9.9	6.9	0.401	0.504	0.427	1.493
herb or	*Arctostaphylos uva-ursi*	63.9	47.1	0.692	0.280	0.0135	1.997
dwarf-shrub	*Fragaria virginiana*	57.7	57.8	-0.008	0.278	0.978	0.992
fruit	*Rubus idaeus*	26.1	0.98	3.576	1.028	<0.001	35.720
	Rubus parviflorus	9.9	2.9	1.289	0.667	0.053	3.630
	Vaccinium myrtillus	9	17.6	-0.772	0.421	0.067	0.462
	Vaccinium scoparium	28.8	42.2	-0.223	0.220	0.310	0.800
	Vaccinium spp. complex	7.2	25.5	-0.947	0.373	0.011	0.388
forb	*Equisetum arvense*	7.2	13.7	-0.717	0.466	0.124	0.488
	Hedysarum sulphurescens	58.6	51.5	0.267	0.276	0.334	1.306
	Hedysarum alpinium	8.1	4.8	0.538	0.516	0.350	1.712
	Hedysarum spp. combined	63.1	56.8	0.259	0.280	0.356	1.295
	Taraxacum officinale	17.1	2.9	1.919	0.638	0.00263	6.815
protein	*Formidae* spp.	14.4	3.9	1.417	0.577	0.0141	4.126
	Ungulate spp.	35.1	26.5	0.409	0.300	0.173	1.505

Table H.2: Percent occurrence for 19 grizzly bear foods in thinned areas (n = 45) and adjacent non-disturbed forests (n = 39). Beta coefficients (± S.E.), significance levels (p), and odds ratios (OR) of finding grizzly bear foods within thinned areas compared to non-disturbed forests are reported from logistic regression models.

Type	Grizzly bear food item	% thinned	% of forest	β	S.E.	*p*	OR
shrub-fruit	*Amelanchier alnifolia*	13.3	17.9	-0.352	0.605	0.561	0.703
	Lonicera involucrata	13.3	12.8	0.045	0.649	0.945	1.046
	Ribes oxycanthoides	33.3	28.8	0.241	0.476	0.612	1.273
	Shepherdia canadensis	88.8	92.3	-0.406	0.766	0.596	0.667
herb or	*Viburnum edule*	15.5	20.5	-0.337	-0.571	0.555	0.714
dwarf-shrub	*Arctostaphylos uva-ursi*	71.1	69.2	0.090	0.478	0.851	1.094
fruit	*Fragaria virginiana*	73.3	64.4	0.432	0.474	0.363	1.540
	Rubus idaeus	26.6	2.6	1.473	0.689	0.032	4.364
	Vaccinium myrtillus	8.8	10.3	-0.158	-0.744	0.832	0.854
	Vaccinium scoparium	20.0	33.3	-0.693	-0.504	0.169	0.500
	Vaccinium vitis-idaea	4.4	5.1	-0.150	-1.025	0.883	0.860
	Vaccinium spp. complex	13.3	23.1	-0.668	-0.580	0.250	0.513
forb	*Equisetum arvense*	13.3	7.7	0.613	0.744	0.410	1.846
	Hedysarum alpinium	13.3	5.1	1.405	0.848	0.217	4.074
	Hedysarum sulphurescens	55.5	66.6	-0.470	0.453	0.300	0.625
	Taraxacum officinale	37.8	7.7	1.986	0.675	0.003	7.286
	Trifolium spp.	15.5	2.6	1.946	1.093	0.075	7.001
protein	*Formidae* spp.	6.6	7.7	-0.154	-0.848	0.856	0.857
	Ungulate spp.	44.4	38.5	0.247	0.445	0.579	1.280

Table H.3: Percent occurrence for 18 grizzly bear foods in burns (n = 111) and thinned areas (n = 45). Beta coefficients (± S.E.), significance levels (p), and odds ratios (OR) of finding grizzly bear foods within burns compared to thinned areas are reported from logistic regression models.

	Grizzly bear food item	**% of burn**	**% of thinned**	**β**	**S.E.**	***p***	**OR**
shrub-fruit	*Amelanchier alnifolia*	5.4	13.3	0.162	1.176	0.752	1.176
	Lonicera involucrata	9.9	13.3	-0.336	0.715	0.536	0.715
	Ribes oxycanthoides	35.1	33.3	0.080	1.083	0.830	1.083
	Shepherdia canadensis	83.8	88.8	-0.437	0.646	0.418	0.646
	Viburnum edule	9.9	15.5	-0.516	0.597	0.321	0.597
herb or dwarf-shrub fruit	*Arctostaphylos uva-ursi*	63.9	71.1	-0.327	0.721	0.394	0.721
	Fragaria virginiana	57.7	73.3	-0.703	0.495	0.070	0.495
	Rubus idaeus	26.1	26.6	-0.028	0.973	0.945	0.973
	Vaccinium myrtillus	9.0	8.8	0.015	1.015	0.981	1.015
	Vaccinium scoparium	28.8	20.0	0.134	1.143	0.615	1.143
	Vaccinium spp. complex	7.2	13.3	-0.148	0.862	0.779	0.862
forb	*Equisetum arvense*	7.2	13.3	-0.684	0.505	0.232	0.505
	Hedysarum alpinium	8.1	13.3	-0.556	0.574	0.321	0.574
	Hedysarum sulphurescens	58.6	55.5	0.123	1.130	0.731	1.130
	Taraxacum officinale	17.1	37.8	-1.078	0.340	0.006	0.340
	Trifolium spp.	0.9	15.5	-3.010	1.090	0.006	0.049
protein	*Formidae* spp.	14.4	6.6	0.858	2.358	0.191	2.358
	Ungulate spp.	35.1	44.4	-0.390	0.677	0.279	0.677

Appendix I: Occurrence of fruit on plants in burns and thinned areas.

Of the 12-fruiting species that occurred in >5% of the sample sites, fruit was never observed on *Amelanchier alnifolia*, *Lonicera involucrata, Rubus idaeus* and *Rubus parvifolorus* plants in the unburned forested (controls) paired with the burned plots (Table G.1). Fruit on *Arctostaphylos uva-ursi* and *Ribes oxycanthoides* plants occurred more often in burns than control plots with odds ratios of 3.0 and 2.3 respectively. There was no notable difference in fruit occurrence on the remaining six species (Table G.1). In contrast to burns, there were no notable differences of fruit occurrence between thinned areas and adjacent controls (Table G.2). When comparing burns to thinned areas, only *Arctostaphylos uva-ursi* differed with fruit occurring almost four times more frequently in burns (OR = 3.8; Table G.3).

For the seven-fruiting species that I examined factors contributing to fruit, the disturbance model ranked highest for the occurrence of fruit for four species, while the summer climate model ranked highest for two and the winter climate ranked highest for only one species (Table G.4). Based on likelihood ratio (LR) χ^2 tests, only the disturbance models for *Ribes oxyacanthoides* and *Rubus idaeus* were significant overall. The percent deviance explained was low for all species ranging from 0.94% to 5.36%, whereas, the classification accuracy was good for five species (ranging from 0.73 to 0.94) and poor (0.65) for the remaining two fruiting species (Table G.4).

There was considerable variation among the five, a priori candidate models explaining the occurrence of fruit on 12-fruiting species. The disturbance model explained the occurrence of fruit best for five species, the terrain model was best for four, summer climate was best for two, and winter climate was the top model for only one (Table G.4). Based on likelihood ratio (LR) χ^2

tests, the fit of all fruit models was unlikely due to random variation except that for *Fragaria virginiana*. Consequently, the percent deviance explained was lowest for *Fragaria virginiana* (3.1%) and was highest for *Arctostaphylos uva-ursi* (14.1%). Classification accuracy was good (AUC: 0.7 – 0.9) for all fruiting models except for *Fragaria virginiana* and *Rubus idaeus.*

Table I.1: Percent occurrence of fruit for 13 fruit producing bear foods in burns (n = 111) and adjacent non-disturbed forests (n = 103). Beta coefficients (± S.E.), significance levels (p), and odds ratios (OR) of finding fruit within burns compared to non-disturbed forested controls are reported from logistic regression models.

Type	**Grizzly bear food item**	**% of burn**	**% of forest**	**β**	**S.E.**	***p***	**OR**
shrub-fruit	*Amelanchier alnifolia*	5.4	0				
	Lonicera involucrata	5.4	0				
	Ribes oxycanthoides	18	6.9	1.093	0.463	0.018	2.983
	Shepherdia canadensis	60.3	59.8	0.023	0.280	0.934	1.023
	Viburnum edule	5.4	3.9	0.336	0.661	0.610	1.400
herb or	*Arctostaphylos uva-ursi*	27	13.7	0.845	0.358	0.018	2.328
dwarf-shrub	*Fragaria virginiana*	3.6	0.98	1.329	1.126	0.238	3.776
fruit	*Rubus idaeus*	6.3	0				
	Rubus parviflorus	2.7	0				
	Vaccinium myrtillus	4.5	0.98	1.561	1.104	0.157	4.764
	Vaccinium scoparium	4.5	6.9	-0.446	0.602	0.459	0.640
	Vaccinium spp. complex	7.2	4.9	0.410	0.587	0.485	1.507

Table I.2: Percent occurrence of fruit for 13 fruit producing bear foods in thinned areas (n = 45) and adjacent non-disturbed forests (n = 39). Beta coefficients (± S.E.), significance levels (p), and odds ratio (OR) of finding fruit within thinned areas compared to non-disturbed forested controls are reported from logistic regression models.

Type	**Grizzly bear food**	**% thinned**	**% of forest**	**β**	**S.E.**	***p***	**OR**
shrub-fruit	*Amelanchier alnifolia*	4.3	5.3	-0.150	1.025	-0.147	0.860
	Ribes oxycanthoides	13.0	7.9	0.613	0.744	0.824	1.846
	Shepherdia canadensis	69.6	60.5	0.325	0.460	0.706	1.384
	Viburnum edule	6.5	5.3	0.279	0.940	0.296	1.321
herb or	*Arctostaphylos uva-ursi*	8.7	13.2	-0.410	0.710	-0.578	0.663
dwarf-shrub	*Fragaria virginiana*	8.7	5.3	0.591	0.895	0.660	1.805
fruit	*Rubus idaeus*	6.5	2.6	0.999	1.176	0.849	2.714
	Rubus parviflorus	2.2	0.0				
	Vaccinium myrtillus	8.7	2.6	1.310	1.140	0.251	3.707
	Vaccinium vitis-idaea	6.5	0.0				
	Vaccinium spp. complex	10.9	10.5	0.090	0.710	0.126	1.094

Table I.3: Percent occurrence of fruit for 13 fruit producing bear foods in burns (*n* =111) and thinned areas (*n* = 45). Beta coefficients (± S.E.), significance levels (*p*), and odds ratio (OR) of finding fruit within burns compared to thinned areas are reported from logistic regression models.

Type	**Grizzly bear food item**	**% of burn**	**% of thinned**	**β**	**S.E.**	***p***	**OR**
shrub-fruit	*Amelanchier alnifolia*	5.4	4.3	0.206	0.836	0.806	1.229
	Lonicera involucrata	5.4	0				
	Ribes oxycanthoides	18	13.0	0.357	0.503	0.479	1.429
	Shepherdia canadensis	60.3	69.6	-0.437	0.540	0.418	0.646
	Viburnum edule	5.4	6.5	-0.223	0.730	0.760	0.800
herb or	*Arctostaphylos uva-ursi*	27	8.7	1.334	0.566	0.018	3.796
dwarf-shrub	*Fragaria virginiana*	3.6	8.7	-0.959	0.731	0.189	0.383
fruit	*Rubus idaeus*	6.3	6.5	-0.059	0.714	0.934	0.942
	R. parvifolorus	2.7	2.2	0.201	1.169	0.864	1.222
	Vaccinium myrtillus	2.7	8.7	-0.727	0.696	0.296	0.484
	Vaccinium scoparium	4.5	0				
	Vaccinium vitis-idaea	0	6.5				
	Vaccinium spp. complex	7.2	10.9	-0.476	0.600	0.428	0.621

Table I.4: Akaike's Information Criteria (AIC) top selected model that best describe the occurrence of fruit for 12 species of grizzly bear foods within thinned habitats of Banff area. AIC scores (w_i) for the null model and top ranked model, likelihood ratio (LR) χ^2 tests, and their significance (p), as well as area under the curve (AUC), and percent deviance explained are provided.

Grizzly bear food		**Null model**	**Top selected model**					
Type	**Name**	**AIC (w_i)**	**Model**	**AIC (w_i)**	**LR χ^2**	***p***	**AUC**	**% Dev. Exp.**
shrub-fruit	*Ribes oxycanthoides*	39.34	Disturbance	36.62	10.72	0.029	0.89	5.36
	Shepherdia canadensis	59.79	Disturbance	59.02	8.78	0.067	0.73	4.39
herb or	*Arctostaphylos uva-ursi*	29.05	Summer	30.47	2.58	0.276	0.64	1.29
dwarf-shrub	*Fragaria virginiana*	31.00	Disturbance	29.92	9.08	0.059	0.87	4.54
fruit	*Rubus idaeus*	25.96	Disturbance	24.12	9.84	0.043	0.94	4.92
	Vaccinium myrtillus	31.00	Winter	33.12	1.87	0.392	0.65	0.94
	Vaccinium spp. complex	35.40	Summer	36.67	2.72	0.256	0.75	1.36