Spatial heterogeneity of buffaloberry (*Shepherdia canadensis*) in relation to forest canopy patterns and its importance for grizzly bear (*Ursus arctos*) resource selection

by

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Abstract

Spatial heterogeneity inherent in the environment influences how animals respond to their

surroundings, especially as it relates to the variability of their food resources. Heterogeneity in

specific elements of vegetation, such as the spatial pattern of a single plant species, can be

defined based on patch distribution and abundance. Patterns of plant food resources at the

landscape-scale will be particularly important for wide-ranging wildlife species that perceive

surrounding heterogeneity at a broad spatial extent. Canada buffaloberry

(*Shepherdia canadensis*) is a shrub common to montane and boreal forests of western North

America with its fruit being a primary seasonal resource for birds and mammals, including

grizzly bears (*Ursus arctos*). The objectives of this study were first to relate the spatial

heterogeneity of buffaloberry shrubs to forest canopy patterns, and second to examine how

buffaloberry shrub heterogeneity affected grizzly bear space use (resource selection) during the

fruiting season. Forest canopy and buffaloberry shrub presence were measured in the field with

line-intercept sampling along ten 2-km transects, stratified to different levels of canopy cover

and variability in canopy, in the Rocky Mountain foothills of west-central Alberta, Canada.

Effects of canopy on buffaloberry in the understory were scale-dependent, with shrub presence

negatively related to evergreen canopy cover and positively related to deciduous canopy cover.

The fractal dimensions of both overstory forest canopy and understory buffaloberry shrubs were

estimated using box-counting methods to evaluate spatial heterogeneity based on patch

distribution and abundance. Buffaloberry patch heterogeneity was positively related to evergreen

canopy heterogeneity, but was unrelated to that of deciduous canopy. This demonstrates that

evergreen canopy measurements can be used to scale up buffaloberry patch distribution and

abundance across the landscape at a spatial extent relevant to bears. Grizzly bear GPS radio-

telemetry data for the daytime period were used to estimate resource selection function (RSF) models using predicted abundance and fruit production of buffaloberry at both the patch- and landscape-scales. Measures of surrounding shrub abundance and variability in fruit density were the most important factors explaining habitat selection during the fruiting period. In particular, variability in surrounding fruit density was strongly and positively related to selection of buffaloberry patches by grizzly bears, suggesting the presence of trade-offs between maximizing use of resource patches and the use of complementary resources or cover for day bedding. Clarifying the landscape heterogeneity of food resources and how this influences animal habitat use can provide insight into how consumer-resource interactions may be altered in the future, and can thus inform wildlife conservation and management.

Preface

This thesis is an original work by Catherine Denny. The use of grizzly bear GPS radio-telemetry data as part of this research project received ethics approval from the University of Alberta Research Ethics Board on August 10th, 2015 (REO Reference Number 2015.018Denny). These data were obtained from fRI Research in Hinton, Alberta, who conducted the trapping, collaring, and monitoring of individual grizzly bears following established species-appropriate protocols. I contributed to the concept formation, study design, field data collection, data analysis, and manuscript composition for this thesis. S.E. Nielsen contributed to the concept formation and study design, and provided assistance with data analysis and manuscript edits.

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Chapter 1: General introduction

The spatial heterogeneity inherent in the environment strongly influences how animals interact with and respond to their surroundings (Wiens and Milne, 1989). The study of ecological heterogeneity necessitates attention to the effects of scale, as it involves the variance in a system property in space (Kotliar and Wiens, 1990). However, the appearance of spatial patterns, and thus our conclusions, are dictated by the experimental scale at which they are examined (Wiens, 1989). This scale-dependence emphasizes the difficulty associated with quantifying environmental heterogeneity, although efforts to do so are necessary before the implications of this variability for organisms can be better understood.

A primary aspect of environmental heterogeneity that affects animal behaviour is the spatial variability of their food resources (Heinrich, 1979), which often relates directly or indirectly to plants. Vegetation heterogeneity can be defined based on the distribution and abundance of individual species (Kotliar and Wiens, 1990). These properties may also be applied to the food resources plants provide, such as fruit, the heterogeneity of which does not necessarily equal that of the plant species itself. Fractal analysis is one approach for examining spatial patterns that is practical for describing natural irregularity (Mandelbrot, 1982), such as the arrangement of vegetation patches within a landscape (e.g., Ritchie et al., 1994). It is particularly useful for addressing the challenge of spatial scale (Allen and Starr, 1982; Li, 2000) relevant to evaluating vegetation heterogeneity, and can represent multi-scale patterns with a single metric, the fractal dimension (Mandelbrot, 1982). As field-based methods for estimating fractal dimensions of plant species measure both the distribution and abundance of patches (Ritchie et al., 1994), the value can be considered an indicator of spatial heterogeneity (Richie, 2010).

The identification of relationships between plant species heterogeneity and broader landscape characteristics that are more easily assessed with remote sensing information, such as forest canopy cover, complements field sampling techniques and data. For instance, determining linkages between spatial patterns of understory plants and canopy overstory patterns could facilitate the development of models to estimate understory plant heterogeneity across larger spatial scales (extents).

Knowledge of plant species heterogeneity is especially valuable for those that are key food resources for animal species at risk, as information about food distribution and abundance can inform conservation and management of vulnerable wildlife. Grizzly bears (*Ursus arctos*) are recognized as a threatened species in Alberta (ARSD, 2010) with food resource availability influencing their behaviour and use of habitats (Jonkel and Cowan, 1971; Nielsen et al., 2004a, 2010). Buffaloberry (*Shepherdia canadensis*) is a native shrub common to the understory of boreal and temperate montane forests (Stringer and La Roi, 1970; La Roi and Hnatiuk, 1980) that is one of the primary fruit resources used by grizzly bears in Alberta (Hamer and Herrero, 1987; Hamer et al., 1991; Munro et al., 2006). It is particularly crucial during the summer and early fall (McLellan and Hovey, 1995; Munro et al., 2006), when bears enter hyperphagia and increase food consumption (Nelson, 1980) with shrub occurrence known to significantly predict bear foraging activity (Nielsen et al., 2003, 2010). Although buffaloberry occurrence and fruit density models have been previously developed for the area and used to represent seasonal habitat for grizzly bears (Nielsen et al., 2003, 2010, 2016), more specific details of the spatial heterogeneity of this resource have not been investigated. Grizzly bears in west-central Alberta occupy expansive annual home ranges of hundreds of square-kilometres (Graham and Stenhouse, 2014). Landscape-level estimates of buffaloberry heterogeneity would therefore prove to be valuable in better understanding their utilization of this seasonal resource.

Grizzly bear use of buffaloberry resources in the region has been examined in the context of resource selection function (RSF) models that have incorporated buffaloberry variables measured at the patch-level (Nielsen et al., 2003, 2010). However, grizzly bears likely perceive their surroundings at larger spatial scales corresponding to their environmental "grain" (Levins, 1968). Heterogeneity of buffaloberry within a broader area should therefore be considered as it likely affects foraging behaviour and selection (Searle et al., 2006).

The spatial heterogeneity of buffaloberry and its importance for grizzly bears is not currently well understood. This topic will be explored in the following two thesis chapters.

In Chapter 2, I examine across spatial scales the total and individual effects of evergreen and deciduous forest canopy cover on buffaloberry shrub presence, and apply fractal analysis to estimate relationships between the fractal dimensions of the canopy and buffaloberry using box-counting methods.

In Chapter 3, I use a resource selection approach to evaluate the role of landscape-level food resource heterogeneity in grizzly bear selection for buffaloberry fruit patches both prior to and during the fruit ripening period by comparing a set of foraging hypotheses. The pre-ripening period serves as a control and enables foraging patterns during fruit ripening to be compared with those observed during a timeframe when fruit resources are not available.

Chapter 2: Evaluating the spatial heterogeneity of buffaloberry shrubs in relation to forest canopy patterns using fractal analysis

1.0 Introduction

Spatial heterogeneity is both a product (Urban et al., 1987) and determinant of ecological processes and thus an important landscape property (Kolasa and Rollo, 1991; Li and Reynolds, 1995). Spatial heterogeneity is, however, difficult to quantify (Wiens, 1989; Levin, 1992) as it is scale-dependent (Mandelbrot, 1982; Wiens, 1989; Allen and Hoekstra, 1992). For vegetation, spatial heterogeneity can be defined as the variance in the horizontal distribution of plants determined by both the dispersion of patches and contrast between vegetation types or species (Kotliar and Wiens, 1990). Vegetation patterns are collectively shaped by a series of interactions between climate, terrain, soil, biotic factors and disturbance processes (Watt, 1947; Whittaker, 1975; Levin, 1978; Sousa, 1984).

Spatial patterns in forests are affected by both natural and anthropogenic disturbances, such as timber harvesting, which modify the size and arrangement of tree patches (Franklin and Forman, 1987). Disturbance therefore creates variability in the horizontal structure of the canopy and is an important factor affecting vegetation heterogeneity (Watt, 1947; Levin, 1978; Sousa, 1984). Variation in the forest canopy also exerts strong influences on understory microhabitats through regulation of key resources such as light (Jennings et al., 1999) and soil nutrients (Beatty, 1984; Boettcher and Kalisz, 1990) which control plant growth and survival (Russell, 1961; Smith, 1982). Canopy composition alters resource availability (Macdonald and Fenniak, 2007), suggesting that these "canopy effects" differ between evergreen and deciduous trees (Beatty, 1984; Pelletier et al., 1999; Kembel and Dale, 2006) potentially due to factors such as the lower light transmission of evergreen canopies (Lieffers and Stadt, 1994; Constabel and Lieffers, 1996).

These resource-related interactions between canopy and understory produce linkages between their respective spatial patterns (Beatty, 1984; Palmer, 1988; Spies and Franklin, 1989; Klinka et al., 1996) and, indeed, these vary between evergreen- and deciduous-dominated stands (Kembel

and Dale, 2006). In particular, the presence of evergreen conifers has been identified as a key determinant of understory patterns (Beatty, 1984; Berger and Puettmann, 2000; Svenning and Skov, 2002), the heterogeneity of which may increase with conifer abundance (Kembel and Dale, 2006). Spatial relationships between the canopy and understory may also be more evident in conifer-dominated stands (Kembel and Dale, 2006).

The strength and direction of canopy effects on understory plant presence and canopy-understory spatial relationships are scale-dependent (Tewksbury and Lloyd, 2001; Kembel and Dale, 2006), as the local influence of an individual tree on nearby understory plants is distinct from the collective effect of numerous trees over a larger area (Tewksbury and Lloyd, 2001). However, despite the importance of multi-scale analyses for better understanding spatial dynamics between the canopy and understory, assessments across scales are uncommon.

Fractal analysis is an inherently multi-scale approach for characterizing spatial patterns (Mandelbrot, 1982) and is particularly useful for addressing issues of scale (Allen and Starr, 1982; Li, 2000). Rarely, however, has this been applied to spatial overstory-understory relationships (but see Brosofske et al., 1999 for a multi-scale wavelet approach that related understory plant patterns to ecosystem types which incorporated overstory composition and structure). Unlike exact fractals that are perfectly self-similar, natural fractals demonstrate statistical self-similarity across a limited range of spatial scales (Burrough, 1981; Frontier, 1987) which may amount to several orders of magnitude (Milne, 1992; Milne, 1997). A scaling law will apply within the range of self-similarity, and this type of relationship has been recognized as a tool for clarifying the organization of complex ecological systems given its scale-invariance that can facilitate extrapolation (Brown et al., 2002).Fractal properties of a pattern can be evaluated by calculating the fractal dimension (D) which summarizes complexity and space-filling ability with one succinct non-integer value (Mandelbrot, 1982). A natural pattern is fractal-like over the spatial range where a scaling law holds, characterized by a linear relationship on a log-log plot (Brown et al., 2002), which can be identified through the calculation of D (Sugihara and May, 1990). For a material distributed across a two-dimensional plane, such as an aerial view of a landscape, D will range between 0 and 2; a value of 0 is a single point, 1 suggests high self-similarity and clustering, and 2 denotes a complete random distribution (Milne, 1997). D is affected by the amount and dispersion of a material across the

landscape (Olff and Ritchie, 2002) and indicates pattern homogeneity (Palmer, 1988). Homogeneity can be defined as the randomness of a distribution, which increases as D approaches 2 (Palmer, 1988; Li and Reynolds, 1995), and thus a lower D signifies greater heterogeneity. The value of D may change with experimental scale (Palmer, 1988) and is not an absolute measure of heterogeneity. However, examining measures of forest canopy and understory cover at the same scale facilitates a relative comparison of their patterns (Kenkel and Walker, 1996). Fractal analyses of forest vegetation have mainly assessed attributes such as patch shape (Krummel et al., 1987; Rex and Malanson, 1990; Mladenoff et al., 1993) and canopy height (Drake and Weishampel, 2000; Parker and Russ, 2004) rather than heterogeneity as defined here. Studies often rely on remote sensing data to calculate D and utilize methods such as perimeter-area ratios (Krummel et al., 1987; Rex and Malanson, 1990; Mladenoff et al., 1993), semivariograms (Parker and Russ, 2004), and multifractals (Drake and Weishampel, 2000).

Box-counting is one approach for calculating fractal dimensions (Barnsley, 1988; Milne, 1991; Milne, 1997) that estimates D based on the number of grid segments occupied by a material across different spatial scales. When adapted for one-dimensional vegetation transects (Ritchie et al., 1994), box-counting data represent both patch size and distribution which are pertinent aspects of horizontal vegetation heterogeneity. Field measurements are straightforward, can be obtained at a fine resolution (e.g. centimeters or decimeters), and allow for other attributes, such as species composition, to be collected which are difficult to measure accurately with remote sensing data.

Most applications of box-counting to research on vegetation patterns have focused on individual plant structure (Morse et al., 1985; Gunnarsson, 1992; Escós et al., 1997; Alados et al., 1998) rather than landscape patterns in plant structure or the interactions between different landscape elements. Studies that have employed box-counting to analyze plant distributions have also generally focused on species in non-forested ecosystems such as spatial patterns in crested wheatgrass (*Agropyron desertorum*) in grasslands or big sagebrush (*Artemisia tridentata*) in shrub lands (Ritchie et al., 1994). Rarely has this technique been used in the more vertically complex systems of forests. Evaluating relationships between canopy and understory heterogeneity using fractal metrics such as D can provide important insights into the spatial

dynamics of forest vegetation strata at scales beyond the individual forest stand (i.e., landscape-level). In this study, we compare the spatial patterns of the overstory forest with the spatial patterns of a common shrub in a montane forested ecosystem in the foothills of Alberta, Canada. Canada buffaloberry (*Shepherdia canadensis*) is a shade-intolerant (Humbert et al., 2007) dioecious shrub that occurs in boreal and temperate montane forests (Stringer and La Roi, 1970; La Roi and Hnatiuk, 1980) across Canada and the northern United States (Moss, 1983). Effects of canopy on buffaloberry have been previously examined, but the focus has been on fruit production (Hamer, 1996; Nielsen et al., 2004b), and the individual components of evergreen and deciduous canopy have not been evaluated separately.

Our focus here is to describe spatial patterns and relationships in canopy and buffaloberry to evaluate co-relationships in presence and heterogeneity across multiple spatial scales and landscape forest cover gradients. Specifically, we have two main objectives: first, to determine the total and individual effects of evergreen and deciduous canopy cover on buffaloberry presence across multiple orders of scale, and second, to use fractal box-counting to assess whether there are co-heterogeneity relationships between canopy cover (evergreen vs. deciduous) and buffaloberry patches.

We hypothesize that, given differences in resource regulation, evergreen and deciduous canopy will demonstrate distinct effects on the presence and patterns of buffaloberry that vary with spatial scale due to changes in resource availability in space. Following this, we hypothesize that greater canopy heterogeneity (lower *D*) will be associated with greater buffaloberry heterogeneity, because the patterns in the overstory forest should structure those of understory plants. We expect, however, that evergreen canopy will have a stronger effect on buffaloberry presence and heterogeneity than deciduous canopy due to lower light conditions under evergreen trees that would limit buffaloberry growth.

2.0 Methods

2.1 Study area
The study area covers 2,389 km^2 of managed, conifer-dominated forest southeast of the town of Hinton (53°24'41"N, 117°33'50" W) and north of the town of Robb (53°13'59" N, 116°58'42"

W) in the Rocky Mountain foothills of west-central Alberta (Figure 2.1). The climate is moist and cool (Achuff, 1994), with higher elevation in the west that declines in the east across a range from 950 m to 2500 m. Land cover types include evergreen, deciduous, and mixed forest consisting of dominant tree species such as lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and aspen (*Populus tremuloides*), along with open bogs, meadows, and previously harvested cutblocks (Achuff, 1994; Udell et al., 2013). Active resource extraction and development by the forestry, mining, and energy (oil and gas) industries results in variation in the degree of anthropogenic disturbance.

2.2 Site selection

Field sites were selected using LiDAR-derived canopy cover data (2005-2007) from Coops et al. (2016) scaled at a resolution of 25 m. These data were used to stratify the landscape for sampling into three ordinal canopy cover categories defined by the proportion of the forest floor covered by tree crowns (Jennings et al., 1999): low (0-40% cover), moderate (40-55%), and high (>55%). Each canopy cover category was subsequently divided into low, medium, and high canopy variability levels based on the standard deviation of canopy cover, which was quantile binned in a Geographic Information System (GIS; ArcMap version 10.2.1; ESRI, 2014). To determine transect length for obtaining box-counting measurements in the field, neighbourhood analyses were performed to examine changes in average variability in canopy cover as moving "window" size (scale) was sequentially increased. This process indicated that a transect length of 2 km would both represent a range of canopy conditions and enable sampling efficiency in the field. Ten transect replicates were sited in total using a stratified random sampling design. Replicates were balanced among canopy variability levels with three placed in each of the low and high canopy cover categories and four in the moderate cover category. Mean distance among selected transects was 19.9 km with a maximum and minimum distance of 41.6 km and 4 km, respectively.

2.3 Field methods

The ten 2-km transects were established in the field based on randomized starting locations and orientations. Dominant forest canopy species and land cover type were noted for each transect. This included upland forest, wet forest, and cutblocks at various stages of regeneration. Line-

intercept was used to measure the length of buffaloberry shrub intercepts along the transect tape using a 0.01-m resolution. This resulted in 200,000 recorded segments (binary presence-absence conditions) per transect (Figure 2.2). Intercept length was evaluated per shrub and recorded as the maximum extent of an individual with no differentiation between female and male shrubs.

Canopy intercepts for trees >1.3 m height were also estimated, but at a 0.1-m resolution (20,000 canopy segments per transect) (Figure 2.2), since it was impractical to achieve the same resolution (0.01 m) of buffaloberry shrubs given typical heights of trees above transects. Canopy intercepts were classified as evergreen or deciduous to distinguish their effects on the understory, particularly in terms of shading, which may influence buffaloberry growth. Common evergreen tree species encountered were white spruce (*Picea glauca*), black spruce (*Picea mariana*), and lodgepole pine (*Pinus contorta*), while typical deciduous species were trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and tamarack (*Larix laricina*). Species generally recognized as shrubs but potentially >1.3 m in height, such as green alder (*Alnus viridis*), were not included here. These non-target shrub species did not represent direct overstory canopy for buffaloberry and were thus incorporated within the same vegetation height stratum as buffaloberry shrubs.

2.4 Analysis of effects of canopy type on buffaloberry presence across spatial scales
All analyses were performed in R version 3.1.2 (R Core Team, 2014). The effects of evergreen and deciduous canopy on buffaloberry presence were analyzed separately as well as collectively in a "total canopy" category. This was done to examine whether type of canopy affected the presence of buffaloberry shrubs.

A series of models was built to reflect the influence of canopy at different spatial scales around a given buffaloberry shrub, varying from more immediate local scales to meso-scales that considered larger segments of the transect. We considered the "local" spatial scale range to be from 0 m to 20 m, which we propose represents the scope of influence of an individual tree as this upper limit corresponds to the maximum average height of tree species in Alberta (Huang et al., 1992). Comparatively larger scales between 20 m and 502 m are referred to as "meso-scale" to represent the collective influence of multiple trees at a forest patch-level (note that this term is also applied to broader spatial extents, e.g. Clark et al., 1998).

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Two variants of mixed-effects logistic regression models (Table 2.1) were examined using the "lme4" package (Bates et al., 2015). One model included a total canopy variable, while the second incorporated evergreen and deciduous canopy as individual variables to compare the effects of each component on buffaloberry (Pearson correlation coefficients never exceeded 0.25). Non-linear effects were tested by adding quadratic terms, but these were not supported in an AIC comparison and thus linear responses were subsequently used in all models. A random effect for transect was included in each model to account for non-independence of observations within a transect.

Scales ranged from a minimum of 2 m (average shrub width) to 502 m using a 4-m increment between scales resulting in 125 different scales considered. Beta coefficients of models (total canopy, evergreen, deciduous) were plotted against window size to examine the effects of canopy on buffaloberry presence as a function of spatial scale in canopy cover.

2.5 Analysis of spatial heterogeneity of the forest canopy and buffaloberry
To measure heterogeneity of canopy and buffaloberry, fractal dimensions were calculated for buffaloberry as well as total, evergreen, and deciduous canopy for each transect using an adaptation of the box-counting method (Voss, 1986). Transects provide unbiased estimates of D similar to those obtained by examining a broader spatial extent using computer software (Leduc et al., 1994).

Field intercept measurements for buffaloberry and canopy, recorded at resolutions of 0.01 m and 0.1 m, respectively, were used to evaluate the number of segments occupied (n) for each of the ten transects. Segments was represented with a binary presence-absence values, which were converted to coarser scales (s) of presence-absence (Table 2.2) by increasing the segment or "box" width to a maximum of half the transect length. Appropriate ranges of box widths (scales) for buffaloberry and each of the canopy categories were determined by experimentally increasing the box width until n values generally stabilized, due to a saturation effect (Taylor and Taylor, 1991; Halley et al., 2004) caused by finite sample size (Kenkel, 2013), at which point box width was truncated. Truncation restricts slope estimates to the spatial range across which the scaling law holds and is necessary to ensure representative D values; increasing the box width past this saturation point reduces the slope of the log-log plot and depresses the D value (Kenkel, 2013).

This saturation effect was not an issue for total or evergreen canopy, for which all 13 scales were used, but did occur with buffaloberry and deciduous canopy requiring the number of scales be truncated to nine and three, respectively. Associated values of n and s were produced per scale for buffaloberry and each canopy category.

A generalized linear model (GLM) was used to estimate the slope of a log-log plot of n and s for each transect (Figure 2.4). The slope of the regression of this relationship is equal to 1-D (Voss, 1986) because a transect is a line bisecting a two-dimensional distribution (Ritchie, 2010). These models therefore provided estimates of spatial heterogeneity (D) in buffaloberry and the three canopy categories for each transect. Mean values of D for transects were estimated with confidence intervals calculated based on a t-distribution. Three additional GLMs were fit to assess spatial heterogeneity relationships between the D values of buffaloberry and those of the three canopy categories across all ten transects, thus evaluating whether the fractal dimension of canopy affected the fractal dimension of buffaloberry shrubs (co-heterogeneity patterns).

3.0 Results

3.1 Effects of canopy and scale on buffaloberry presence
Forest canopy of trees >1.3 m in height covered an average of 47% of the landscape sampled by transects (Table 2.3). Evergreen canopy dominated the sites with an average canopy cover of 42%, compared with 8% for deciduous canopy (overlap between these occurred at some sites).

Forest (total) canopy had a positive effect on shrub presence across most spatial scales and in particular was significant ($\alpha = 0.05$) between 170-178 m, 194-202 m, and 234-374 m (Figure 2.3). There was, however, a local negative peak at the 10-m scale and the effect was weakest at the 18-m scale. The effect of total canopy became positive at larger spatial scales of canopy with the strongest relationship at 294 m window size for canopy. Evergreen canopy had a negative effect on the presence of buffaloberry shrubs across all spatial scales and was significant at local scales from 2 m to 42 m. The effect of evergreen canopy was strongest at the 10-m scale, with two additional peaks of negative association at 106 m and 210 m, and was weakest at the 294-m scale. In contrast to evergreen canopy, deciduous canopy had a positive effect on the presence of

buffaloberry shrubs up to a 462-m scale which was significant for nearly all scales ranging between 150 m and 358 m. The effect of deciduous canopy was weakest at the 2-m scale and strongest at 354 m, after which it decreased sharply and became negative at very large scales.

3.2 Spatial heterogeneity of the forest canopy and buffaloberry

Mean fractal dimension (D) of buffaloberry was lower than the mean fractal dimensions of the overstory canopy (Table 2.4), indicating shrub patterns are more heterogeneous. The mean fractal dimension of deciduous canopy was lower than that of evergreen and total canopy, signifying deciduous patterns are the most heterogeneous within the overstory stratum. Deciduous canopy fractal dimensions also had the highest standard deviation, suggesting greater variability in the level of heterogeneity present in deciduous patterns. Buffaloberry fractal dimensions had the lowest standard deviation, implying the level of heterogeneity of shrub patterns is more consistent across the study area. Buffaloberry patterns were fractal-like over approximately 2.7 orders of magnitude from 0.01 m to 5 m as illustrated by the linear relationship of the log-log plot (Figure 2.4), while spatial patterns of evergreen and total canopy cover were fractal-like over four orders of magnitude from 0.1 m to 1000 m (Figure 2.4). In contrast, patterns of deciduous canopy were fractal-like under less than one order of magnitude indicating low self-similarity across spatial scales.

3.3 Relationships between spatial heterogeneity of the forest canopy and buffaloberry

Relationships between fractal dimensions (D) of canopy and buffaloberry were positive for evergreen and total canopy cover (Figure 2.5). Evergreen canopy and buffaloberry fractal dimensions demonstrated the strongest relationship with the greatest slope ($R^2 = 0.46$; $\beta = 0.571$; Table 2.5), while the relationship between total canopy and buffaloberry fractal dimensions was weaker with a lower slope ($R^2 = 0.32$; $\beta = 0.453$; $p = 0.09$). Evergreen canopy fractal dimensions significantly predicted the fractal dimension of buffaloberry shrubs ($p = 0.03$), while the effect of total canopy fractal dimensions was weakly significant ($p = 0.09$) and no relationship was found between deciduous canopy and buffaloberry fractal dimensions ($R^2 = 0.00$; $\beta = -0.009$; $p = 0.96$).

4.0 Discussion

Our results indicate that the effect of forest canopy on buffaloberry presence, as well as relationships between canopy and buffaloberry heterogeneity, differ between evergreen and deciduous components based on intercepts measured along 20 km of transects. These findings support our hypothesis regarding the distinct effects of evergreen and deciduous canopy on buffaloberry patterns, and the variability of these through space.

4.1 Effects of canopy and scale on buffaloberry presence

Evergreen canopy demonstrated a significant negative effect at the local level, suggesting that the reduction in microhabitat light availability by individual evergreen trees could be an important factor for buffaloberry presence given the shade-intolerance of this species. Light variability has been previously identified as a structuring agent of understory shrub patterns at a similar fine spatial scale (Frelich et al., 2003). Evergreen trees may additionally decrease local soil moisture content, pH, and temperature (Nihlgård, 1971; Beatty, 1984; Binkley and Valentine, 1991; Ste-Marie and Paré, 1999; Hobbie et al., 2006). This could reduce buffaloberry growth and contribute to the overall negative effect of evergreen canopy on shrub presence. These results are consistent with those of Kembel and Dale (2006) that indicated understory vascular plant cover was negatively associated with evergreen conifer cover at scales of 5-15 m, but positively associated with broad-leaved deciduous cover over the same spatial range in a boreal mixedwood forest.

We found that the positive effect of deciduous canopy was the strongest and most significant at the meso-scale level, however, implying the cumulative effect of multiple deciduous trees is most relevant for buffaloberry presence. Deciduous trees may promote understory shrub growth by allowing high light penetration during seasonal leaf-off periods (Ross et al., 1986; Constabel and Lieffers, 1996). Canopy light transmission also increases with the basal area of deciduous trees (Lieffers and Stadt, 1994), and thus their influence could be most apparent at broader spatial extents, amounting to a stand-type effect. Stands with a greater proportion of deciduous trees also occur more often at low elevations in the study area that are more favourable for buffaloberry.

The sharp decline in the strength of the deciduous canopy relationship after approximately 360 m implies a spatial limit to the meso-scale effect. This decrease could relate to the dominance of evergreen trees in the study area, such that expanding the spatial scale past this point might not incorporate additional deciduous trees, thereby weakening its effect. The effect of evergreen canopy was also low at similar scales, particularly around 300 and 420 m, which suggests timber harvesting disturbance may begin to moderate the influence of the forest canopy in general as spatial scale increases. Clear-cutting is the primary harvesting method in the study area, and at scales above 300 m most transect replicates would have traversed a cutblock due to their prevalence in the region. Buffaloberry occurred sparsely in cutblocks, but this lack of shrubs was likely caused by removal during harvesting and their slow growth habit (Densmore et al., 2000), rather than a forest canopy effect.

4.2 Relationships between spatial heterogeneity of the forest canopy and buffaloberry

Through fractal analysis, we found a significant positive relationship between evergreen canopy and buffaloberry fractal dimensions (*D*) using the 2-km transects suggesting that heterogeneity in evergreen trees scales with heterogeneity patterns in buffaloberry shrubs. Thus greater canopy heterogeneity is associated with greater buffaloberry heterogeneity, supporting our hypothesis. This relationship was less significant when total canopy, including deciduous trees, was evaluated. These findings suggest that evergreen canopy heterogeneity has a stronger effect on observed buffaloberry patterns, which may be linked to the dominance of evergreen trees within forests in the study area.

Heterogeneity can be an ambiguous term in the ecological literature when the definition is not made explicit (Kolasa and Rollo, 1991; Dutilleul and Legendre, 1993; Li and Reynolds, 1994; Li and Reynolds, 1995). Numerous conceptual interpretations and ecological characteristics that can be measured result in a variety of data types and analytical techniques for examining environmental heterogeneity. Here we use the fractal measure of *D* as a heterogeneity metric, the value of which may change with analysis scale (Palmer, 1988; Leduc et al., 1994); this is not surprising given that it indicates heterogeneity. Measuring vegetation patterns at a common scale, as we have here, enables comparisons of the relative heterogeneity of plant species (Kenkel and Walker, 1996). Calculating the fractal dimension (*D*) as a function of scale can reveal whether vegetation heterogeneity varies in space and identify hierarchical patterns

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(Palmer, 1988). Regions where D remains stable constitute domains of scale between which are transitions that may signify shifts in the processes governing heterogeneity (Mandelbrot, 1982; Wiens, 1989). These dynamics may be of interest for future research of forest spatial patterns and the mechanisms that shape them.

As different calculation methods can produce different D values for identical data (Malinverno, 1989), comparing results among fractal studies with distinct methodologies can be misleading. We are not aware of examples from the literature that utilize a one-dimensional box-counting technique to evaluate horizontal heterogeneity of forest vegetation; this has, however, been applied in grassland systems (Ritchie et al., 1994). Buffaloberry is less heterogeneous and fractal-like over fewer orders of magnitude than big sagebrush (*Artemisia tridentata*), another woody shrub, as measured in a Utah steppe at a similar 1.6 km transect scale (Ritchie et al., 1994). It is worth noting that, despite methodological differences, forest canopies are usually found to be quite homogeneous (Weishampel et al., 2000; Boutet and Weishampel, 2003; Parker and Russ, 2004) and fractal-like over several orders of magnitude (Milne, 1997), which is in line with the findings of this study.

The box-counting technique used here relies on sequential binary observations that are a type of one-dimensional point pattern. This is ideal for line-intercept data, such as those which represent presence of vegetation along a transect. In contrast, point pattern analyses typically assess the distribution of a material over a two-dimensional plane (Wiegand and Moloney, 2014), such as the spatial arrangement of individual trees across a landscape (Moeur, 1993; He et al., 1997). One-dimensional analyses of forest vegetation primarily involve continuous, rather than binary, data and consider heterogeneity in terms of variance as a function of scale (Palmer, 1988; Leduc et al., 1994). Wavelet analysis, for example, is a multi-scale approach (Daubechies, 1988) that can incorporate remote sensing data to identify hierarchical patterns in horizontal attributes like canopy gap structure (Bradshaw and Spies, 1992; Kane et al., 2011) and tree crown diameter (Falkowski et al., 2006; Strand et al., 2006).

4.3 Conclusions

This study highlights the importance of spatial scale and forest canopy composition for characterizing patterns in understory plant presence and relationships between canopy and

understory heterogeneity. Fractal analysis addresses issues of scale-dependence associated with the quantification of environmental heterogeneity, but has been mostly overlooked as a tool for examining forest vegetation patterns and spatial relationships. The box-counting approach used with line-intercept transects is a straightforward and practical technique that enables multi-scale assessments of vegetation heterogeneity, represented by a single metric, D, and can identify fractal-like vegetation patterns.

Indicators of heterogeneity and fractal-like properties for key animal resources like fruiting shrubs (McLellan and Hovey, 1995; Munro et al., 2006) can contribute to studies of foraging strategy, consumer-resource interactions, and animal movement in spatially complex environments (Wiens and Milne, 1989; Ritchie, 1998; Ritchie and Olff, 1999; Haskell et al., 2002; Sims et al., 2008). Fractal-like resource distributions, for example, point to scale-dependence in resource density and consumer foraging behaviour as determined by animal body size, which controls the scale of environmental perception (Ritchie, 1998; Ritchie and Olff, 1999; Haskell et al., 2002) or environmental "grain" (Levins, 1968). The significant relationship identified here between evergreen canopy and buffaloberry heterogeneity indicates the potential for estimating understory plant patterns from canopy patterns, which can be assessed at broad spatial extents with remote sensing, and could contribute to the quantification of buffaloberry fruit resources at a landscape-level.

Table 2.1: Mixed-effects logistic regression model structures developed to evaluate the effects of total forest canopy as well as evergreen and deciduous canopy components on buffaloberry shrub presence, with a random effect for transect.

Model Name	Model Structure
Total Canopy	totalcanopy + (1 | transect)
Evergreen and Deciduous	evergreen + deciduous + (1 | transect)

Table 2.2: Number and width (m) of box-counting segments used for fractal dimension calculations for buffaloberry shrubs and forest canopy.

Intercept Type	Segment or "Box" Width (m) Range	Total Number of Scales
Buffaloberry	0.01, 0.02, 0.05, 0.1, 0.2, 0.5, 1, 2, 5	9
Total Canopy	0.1, 0.2, 0.5, 1, 2, 5, 10, 20, 50, 100, 200, 500, 1000	13
Evergreen Canopy	0.1, 0.2, 0.5, 1, 2, 5, 10, 20, 50, 100, 200, 500, 1000	13
Deciduous Canopy	0.1, 0.2, 0.5	3

Table 2.3: Percentage of each transect covered by total, evergreen, and deciduous canopy as well as buffaloberry shrub intercepts.

Transect Number	Percentage of Transect Covered			
	Total Canopy	Evergreen Canopy	Deciduous Canopy	Buffaloberry Shrubs
1	68.99	49.41	32.47	14.02
2	26.82	24.15	3.35	0.11
3	35.84	34.06	2.69	0.45
4	57.73	49.04	13.74	0.85
5	46.00	41.75	5.39	0.23
6	43.39	37.16	8.98	0.15
7	50.97	46.65	8.27	1.95
8	59.40	59.40	0.02	0.40
9	62.25	62.16	0.12	1.26
10	18.45	18.12	0.56	0.25
Mean	46.98	42.19	7.56	1.97

Table 2.4: Fractal dimensions of buffaloberry shrubs and forest canopy categories for each transect. Fractal dimensions were calculated using an adaptation of the box-counting method (Voss 1986).

Transect Number	Total Canopy	Evergreen Canopy	Deciduous Canopy	Buffaloberry Shrubs
1	1.95	1.91	1.95	1.74
2	1.84	1.83	1.75	1.71
3	1.88	1.87	1.72	1.72
4	1.94	1.91	1.80	1.70
5	1.91	1.90	1.84	1.80
6	1.91	1.88	1.71	1.77
7	1.92	1.91	1.90	1.78
8	1.95	1.95	1.69	1.81
9	1.95	1.95	1.86	1.80
10	1.79	1.78	1.88	1.71
Mean	1.90	1.89	1.81	1.75
Minimum	1.79	1.78	1.69	1.70
Maximum	1.95	1.95	1.95	1.81
Standard Error	0.02	0.02	0.03	0.01
95% Confidence Interval	1.87, 1.94	1.86, 1.92	1.76, 1.87	1.73, 1.78

Table 2.5: Results of generalized linear models describing relationships between fractal dimensions of buffaloberry shrubs and forest canopy categories. Fractal dimensions were calculated using an adaptation of the box-counting method (Voss 1986). Asterisks indicate a significant effect ($\alpha = 0.05$).

Model Name	Beta Coefficient	Intercept	R^2	p	SE	95% C.I.
Total Canopy	0.453	0.892	0.316	0.091	0.236	-0.091, 0.996
Evergreen	0.571	0.674	0.457	0.032 *	0.220	0.064, 1.078
Deciduous	-0.009	1.769	<0.001	0.959	0.170	-0.401, 0.383
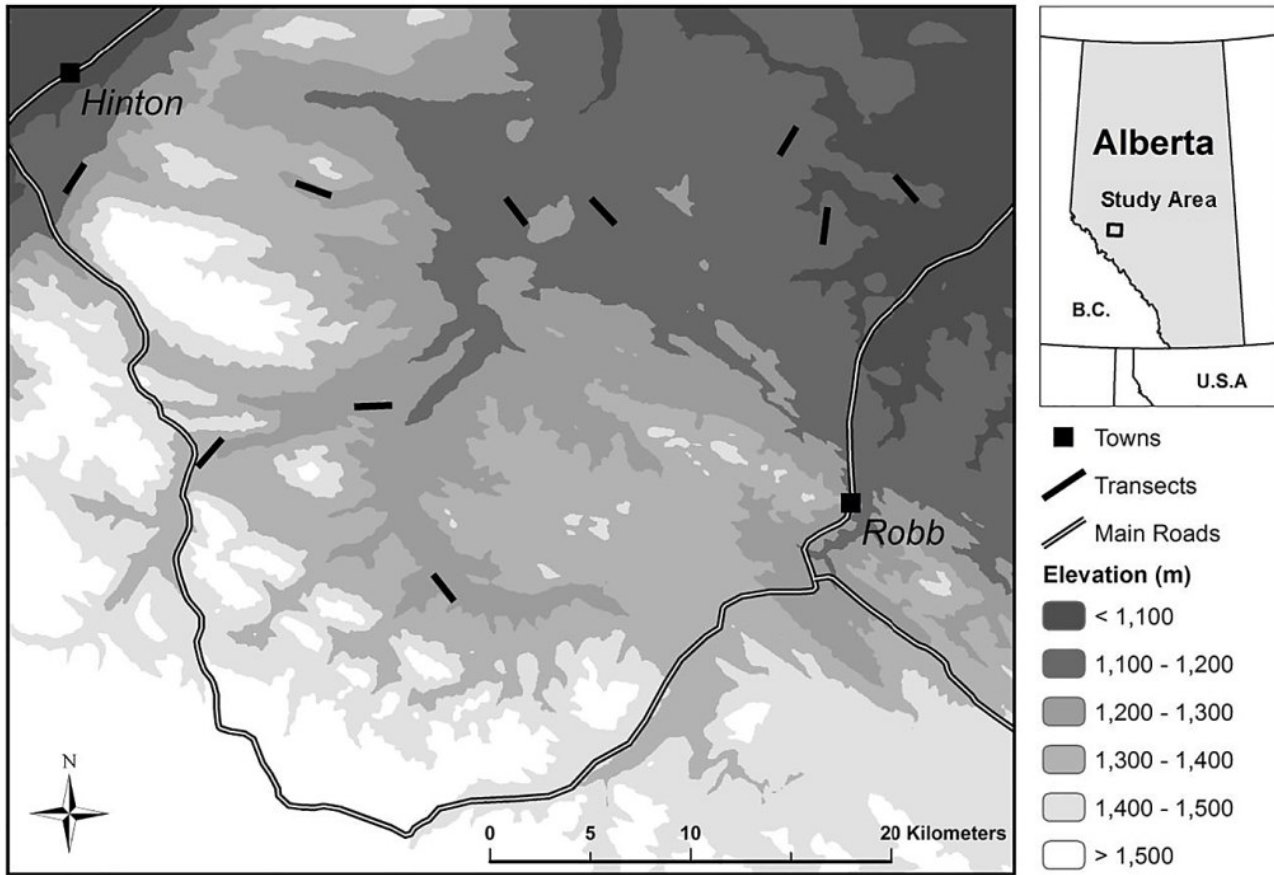
Figure 2.1: Location and elevation of 2-km transects (N=10) established across the study area southeast of Hinton, Alberta (53°24'41"N, 117°33'50" W), in 2015 to measure fractal dimensions of buffaloberry shrubs and forest canopy cover.
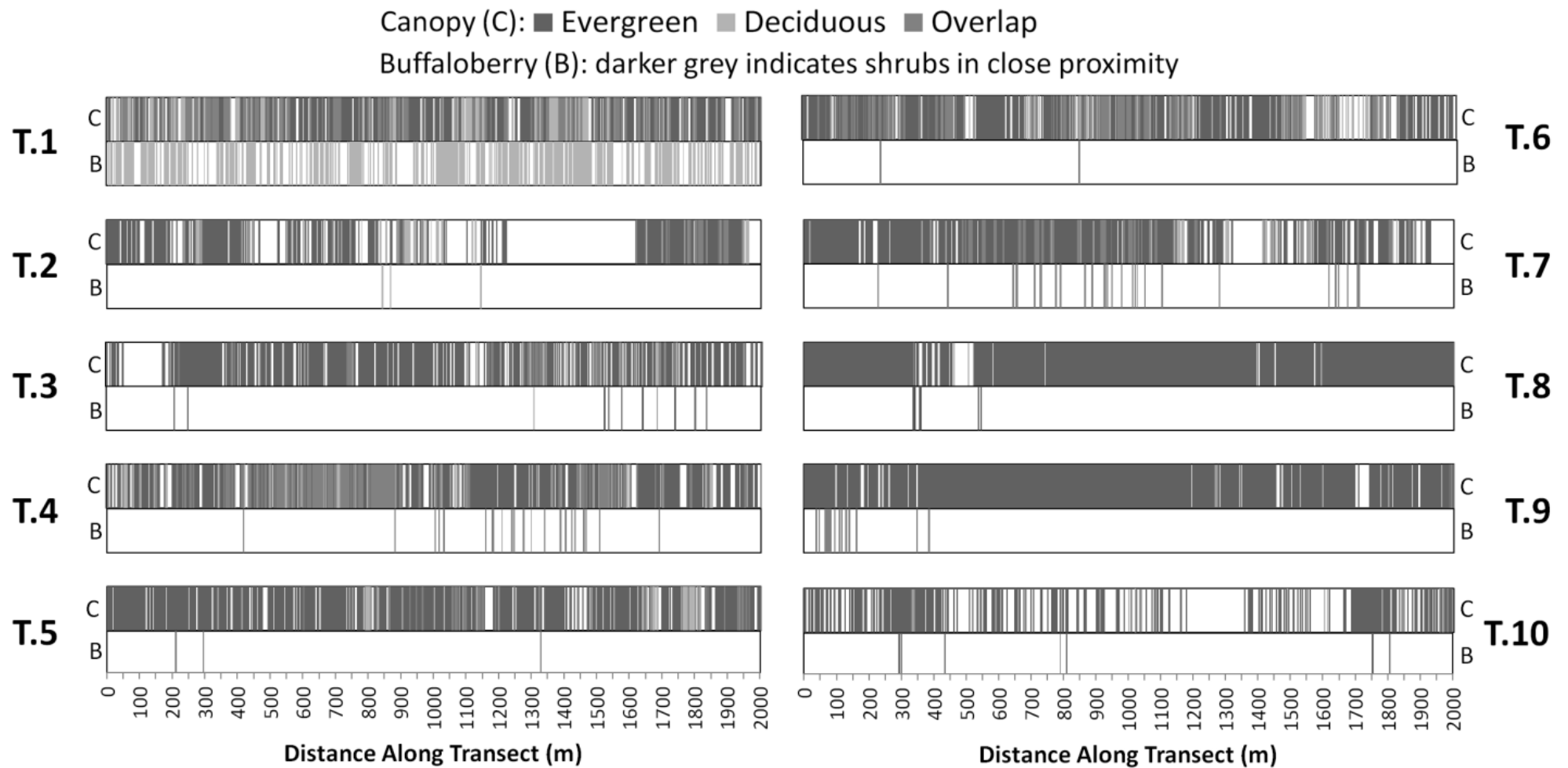
Figure 2.2: Raw intercept data illustrating the distribution of evergreen and deciduous forest canopy (C) and buffaloberry shrub (B) intercepts as measured along 2-km transects (T; N=10) in the area near Hinton, Alberta.
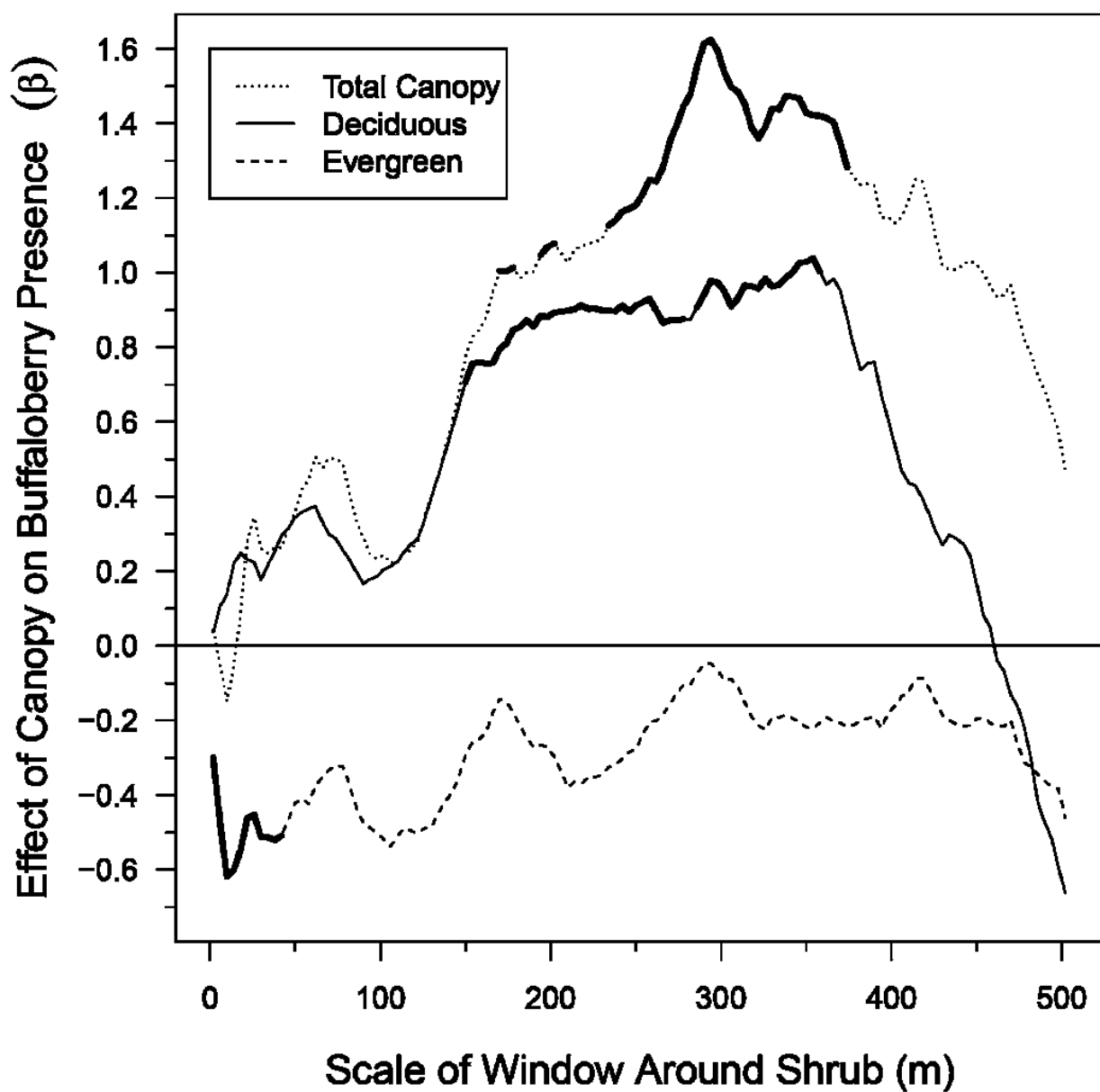
Figure 2.3: Effect of total, evergreen, and deciduous canopy cover on buffaloberry shrub presence across spatial scales from 2-502 m, represented as beta (ß) coefficients of mixed-effects logistic regression models. Bold lines indicate a significant effect ($\alpha = 0.05$) at that scale.
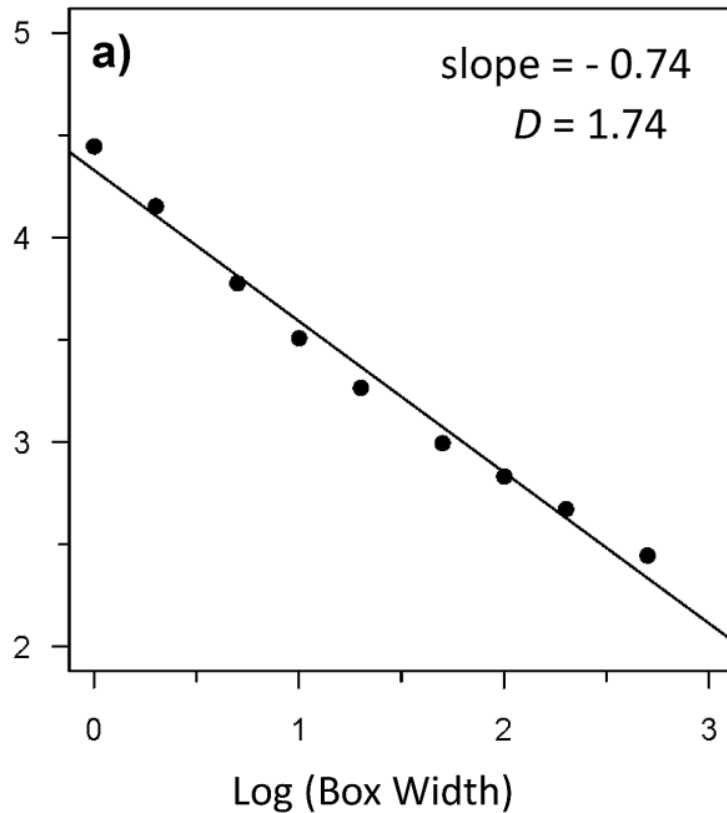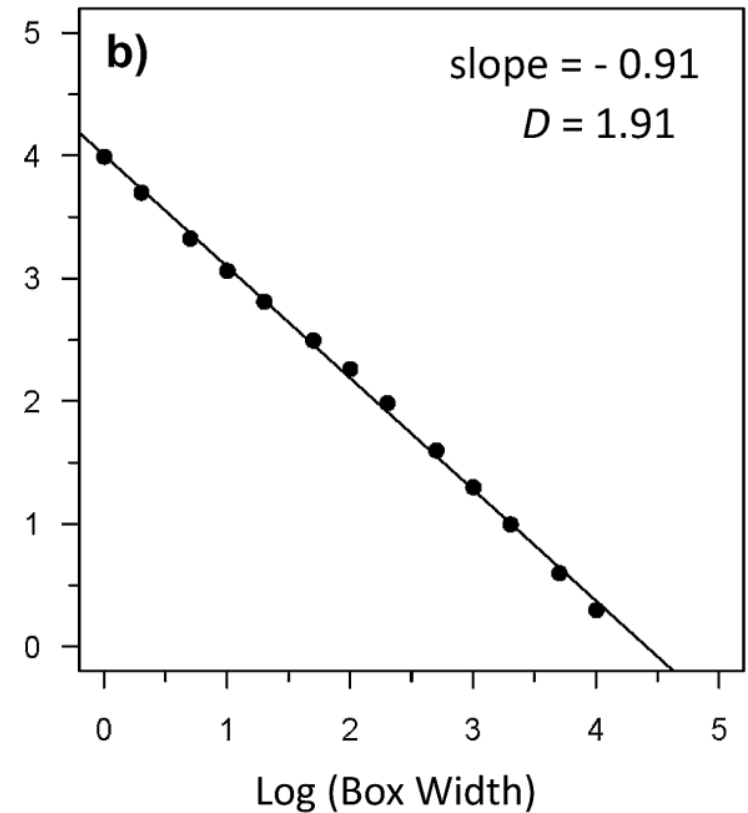
Figure 2.4: Example from Transect 1 of a log-log plot of the relationship between box width (scale) and the number of segments occupied by a) buffaloberry (slope = -0.74), and b) evergreen canopy (slope = -0.91) used to calculate the fractal dimension (D) of each. The slope of the regression line equals 1-D (Voss 1986) for a given transect. The number of orders of magnitude across which the relationship is fractal-like can be determined based on the x-intercept.

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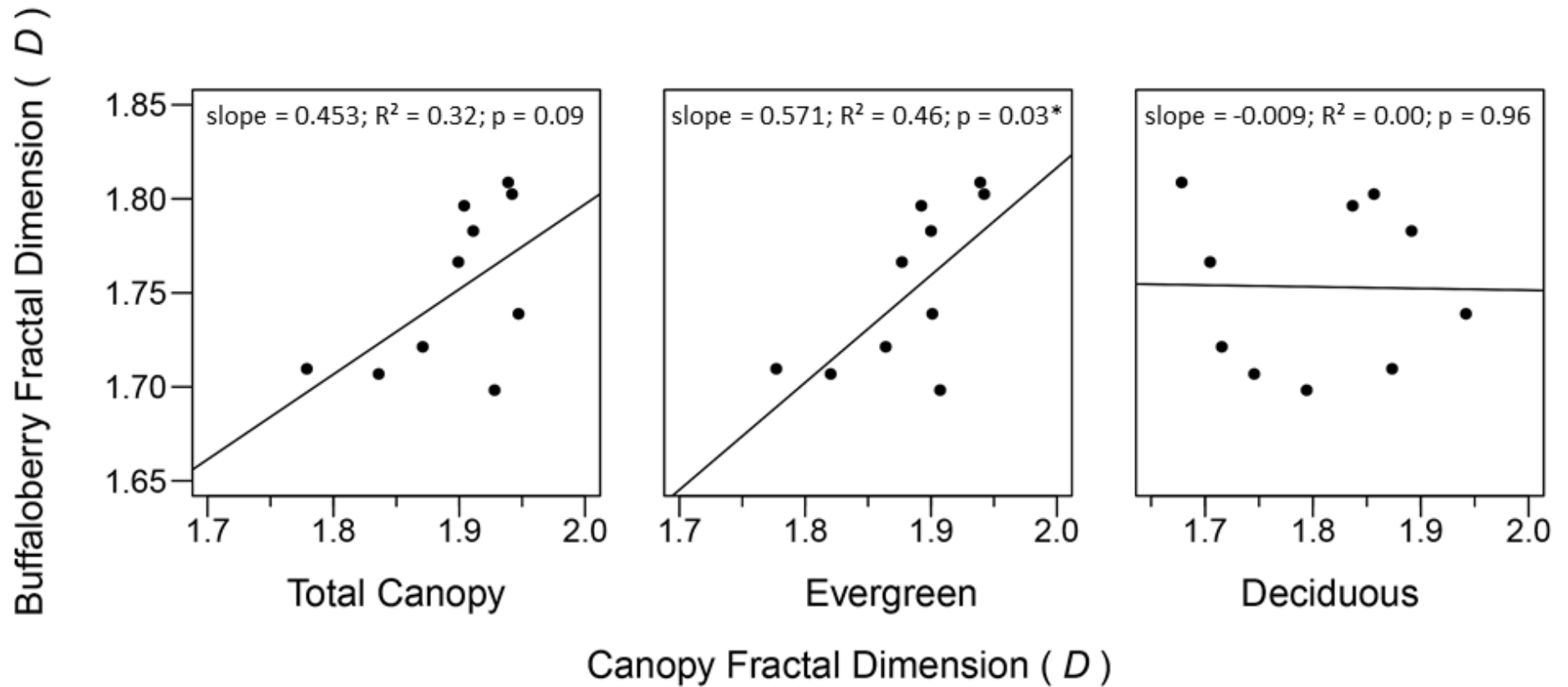
Figure 2.5: Generalized linear models (GLMs) describing relationships between fractal dimensions of buffaloberry shrubs and forest canopy categories. Fractal dimensions were calculated using an adaptation of the box-counting method (Voss 1986). Asterisks indicate a significant effect ($\alpha = 0.05$).

Chapter 3: Assessing the importance of buffaloberry spatial heterogeneity for grizzly bear food resource selection

1.0 Introduction

Environmental heterogeneity influences animal behaviour (Wiens and Milne, 1989; Crist et al., 1992; With, 1994), and selection for food resources likely depends on how the properties of those resources vary in space across the landscape (Heinrich, 1979). The response of an animal to this variation in food quality and abundance is contingent on the amount of resource heterogeneity that it detects in its surroundings, which is consistent with its environmental "grain" (Levins, 1968). Optimal foraging theory proposes that animals will seek to acquire food resources at the lowest energetic cost, thereby maximizing efficiency and fitness (Charnov, 1976), assuming that animals have perfect knowledge of these resources (Rapport, 1991). However, the information available to animals on the heterogeneity of the surrounding resources is not in fact complete (Pyke, 1984), but rather constrained by their grain size, which affects their foraging strategy and selection for food resources. Generally, grain size increases with body size (With, 1994; Ritchie, 1998; Mech and Zollner, 2002), suggesting that large mammals such as grizzly bears (*Ursus arctos*) would perceive their environment at a relatively broad spatial scale beyond that of the local patch. Experimental scales should be dictated by the organism and phenomenon under study (Wiens et al., 1986; Addicott et al., 1987), but if grain size is not considered in analyses of resource selection, then subsequent inferences may not be valid. Examination of grizzly bear food resource selection (e.g. Nielsen et al., 2010) should therefore incorporate landscape-level measures of resource attributes, which would better reflect the amount of resource heterogeneity bears observe and thus provide more valuable insights into the factors relevant for selection.

Resource selection functions (RSFs) are statistical tools for evaluating animal habitat selection and the relative probability of use given particular environmental site characteristics (Manly et al., 2002). RSFs are estimated using a binary response variable representing either presence-absence (used-unused design) or presence-available data types (used-available design) (Boyce et al., 2002). A variety of statistical approaches may be applied to calculate RSFs, although they are

often based on using logistic regression to quantify the selection coefficients (Manly et al., 2002).

The development of GPS radio-telemetry methods in recent decades has facilitated the study of large, vagile mammals (Bergman et al., 2000) such as grizzly bears, and when incorporated in RSF models, these data are compatible with a used-available design as no information is available regarding true absences (Boyce et al., 2002). Though GPS radio-telemetry technology enables substantial amounts of animal movement data to be collected, these data are usually affected by spatio-temporal autocorrelation due to the frequent observation of the same individuals over time (Nielsen et al., 2002; Boyce et al., 2002). The addition of random effects into population-level RSF models has been identified as a method for addressing autocorrelation (Gillies et al., 2006), as well as controlling for differences in the number of GPS locations recorded per individual animal (Bennington and Thayne, 1994). These advantages have contributed to the increased application of mixed-effects logistic models, a type of generalized linear mixed model (GLMM) (Skrondal and Rabe-Hesketh, 2004), in studies of animal resource selection (Gillies et al., 2006; Hebblewhite and Merrill, 2008; Koper and Manseau, 2009).

RSF models that have been developed previously for grizzly bear habitat selection in west-central Alberta (Nielsen et al., 2002, 2003, 2004a; Gillies et al., 2006; Nielsen et al., 2006, 2009, 2010; McKay et al., 2014) have mainly evaluated the effects of environmental variables, such as habitat cover type and elevation (e.g. Nielsen et al., 2002), that are measured at the patch-level. The influence of environmental heterogeneity for resource selection has been investigated for other animals such as large ungulates (Boyce et al., 2003; Anderson et al., 2005), although questions of scale, which are imperative for testing heterogeneity effects, have been largely overlooked in the context of grizzly bear habitat selection. The few studies that have directly considered spatial scale have focused on the extent of the landscape available for bear use (Nielsen et al., 2004a; Ciarniello et al., 2007) rather than the spatial scale at which properties of the resource units themselves were measured. Previous grizzly bear habitat selection models also do not usually incorporate food resource attributes as explanatory variables (but see Nielsen et al., 2003, 2010), despite food-probability models often explaining bear selection more effectively than those which are habitat-oriented (Nielsen et al., 2003). Buffaloberry occurrence in particular, along with that of a few other key food items, significantly predicts bear foraging

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activity (Nielsen et al., 2010). These factors thus indicate that the importance of food resource heterogeneity for grizzly bear selection has not been fully explored, although it has been demonstrated to strongly influence grizzly bear foraging behaviour (Searle et al., 2006).

Canada buffaloberry (*Shepherdia canadensis*) is one of the primary fruit resources for grizzly bears in in the Canadian Rocky Mountains, where it comprises a major component of their summer and early fall diet (Munro et al., 2006). The fruit is particularly crucial during hyperphagia, when bears increase their food consumption to build body fat reserves in preparation for winter denning (Nelson, 1980). Grizzly bear selection for buffaloberry has been assessed using predictions of shrub occurrence (Nielsen et al., 2003; Nielsen et al., 2010), but given the dioecious habit of this species and that only female plants bear fruit, occurrence does not correspond to the availability of the food resource itself. Although local density of grizzly bears is correlated with buffaloberry fruit abundance (Nielsen et al., 2016), selection for buffaloberry fruit resources has not been fully examined. An understanding of seasonal habitat use of this important resource is valuable for informing the conservation and management of grizzly bear populations (Boyce et al., 2002), including the threatened population in Alberta (ASRD, 2010).

The objective of this study is to evaluate the role of landscape-level food resource heterogeneity in grizzly bear selection for buffaloberry fruit patches during the fruit ripening period by comparing responses of bears to different foraging hypotheses. Buffaloberry heterogeneity, as defined here, reflects both shrub distribution and variability in patch quality, represented by fruit density, which are properties that contribute to spatial heterogeneity (Kotilar and Wiens, 1990). Support among different foraging hypotheses will also be compared for the pre-fruiting period (vs. fruiting period) to further highlight the buffaloberry attributes that most affect selection for this resource.

The primary hypothesis is that landscape-level buffaloberry heterogeneity will be important in explaining grizzly bear resource selection during the fruit ripening period because they perceive their environment at spatial scales beyond the patch, in accordance with their environmental grain size, and thus landscape-level food resource patterns affect their foraging behaviours. If patterns during the fruit ripening period affect selection (behaviour), then we would expect less differentiation in the level of support among foraging hypotheses during the pre-ripening period,

since buffaloberry attributes would have a weaker effect on grizzly bear selection before the resource is available (ripe). Although we recognize that patches with buffaloberry may have co-occurring resources and some weak patterns during the pre-ripening period may still be evident, we expect the effects of buffaloberry attributes to be more apparent during the fruit ripening period.

2.0 Methods

2.1 Study Area

The study area was defined by the spatial extent of a buffaloberry fruit density model developed by Nielsen et al. (2016) and is comprised of 19,942 km^2 of managed, conifer-dominated forest located near the town of Hinton (53°24'41"N, 117°33'50" W) in the Rocky Mountains foothills of west-central Alberta (Figure 3.1). The study boundary encompasses the same study area described in the previous chapter but extends further to the south and east, and is contained within the borders of the Yellowhead Population Unit for grizzly bear management as delimited by the provincial government. Elevation ranges from approximately 850–3,200 m, and is higher in the western part where it borders with Jasper National Park.

2.2 Buffaloberry fruit data preparation and spatial analysis

All spatial analyses were performed in a GIS (ArcMap version 10.2.1; ESRI, 2014). The buffaloberry model (Nielsen et al., 2016) provided fruit density estimates for the study area at a 30 m x 30 m (900 m^2) pixel resolution. These density values were divided by 1000 so that model coefficients would reflect the change in bear selection due to a one-unit increase of 1000 berries (~1-3 shrubs depending on annual productivity), which is a scale more relevant to bears. The standard deviation (SD) of fruit density and proportion of the landscape occupied by buffaloberry shrubs were calculated within circular moving "windows" using radius measures of 229 and 457 m. These distances were selected to represent average half-hour and hourly movement rates of grizzly bears, respectively, as determined by analysis of weekly movement path length and step (GPS radio-collar fix) number during the months of July and August for a subsample (5 individuals) of the same bears used here for RSF models (see Appendix 1). Landscape statistics were calculated for both of these spatio-temporal scales to test whether one

was more appropriate for studying fruit foraging behaviour, which may occur at a temporal scale finer than that of hourly GPS radio-collar fixes. Euclidean distance values indicating the proximity to the nearest buffaloberry patch were also calculated for each pixel within the study area, to which a log-plus-one transformation was applied. These steps produced patch- and landscape-level measures of buffaloberry attributes to represent grizzly bear foraging strategies (Table 3.1).

2.3 Grizzly bear GPS radio-telemetry data preparation and spatial analysis

A total of 12,706 GPS radio-telemetry locations (fRI Research; Hinton, AB) were obtained from eleven radio-collared grizzly bears for the period from July 1st – September 15th of the years 2011 to 2015. GPS radio-telemetry locations represented animal "use" locations. The seasonal timeframe used was selected to include the periods prior to and during buffaloberry fruit ripening, based on grizzly bear diet studies in the same study area (Munro et al., 2006). Specifically, Munro et al. (2006) found that fruit resources, primarily buffaloberry and black huckleberry (*Vaccinium membranaceum*), comprised on average 15% of the grizzly bear diet in July, but that this increased to 49.7% during August and early September. As buffaloberry fruiting phenology varies inter-annually with temperature and precipitation (Krebs et al., 2009) and fruit ripening data across the study area (elevation gradients) were not available, increases in bear use of defined buffaloberry patches was thus assumed to coincide with the buffaloberry ripening period when the fruit would be most palatable. Here, the pre-ripening period was defined as July 1st – 31st (Period 1), and the buffaloberry fruit ripening period was defined as August 1st – September 15th (Period 2).

Annual sample size varied between one and four individuals per year due to the limited number of monitored bears and the requirement that summer home ranges largely overlap the geographic extent of the buffaloberry fruit density model. There was no repeated use of the same individual for multiple years even if data were available, in order to reduce potential bias associated with distinctive foraging habits particular to a given bear. The sample of bears consisted of three males and eight females, although it was not known whether females were accompanied by cubs.

GPS coordinates of grizzlies were normally recorded on an hourly basis, although some minor temporal gaps were present due to technical errors. Only crepuscular (twilight) and diurnal

(daylight) locations recorded between 6 am and 10 pm were considered in subsequent analysis as this represents the typical daily foraging period for bears during the summer months (Munro et al., 2006). This hour range was determined by consulting sunrise, sunset, and civil twilight tables for Hinton for the month of August, as a compromise between greater daylight length in July and reduced length in September. Night-time GPS locations recorded between 11 pm and 5 am were thus removed from the analysis.

Separate seasonal home ranges for Periods 1 and 2 were delineated per bear by calculating two Minimum Convex Polygons (MCPs) that effectively encompassed all the GPS locations pertaining to each period. An MCP thereby represented the distinct area of the landscape used by a given bear during one of the timeframes and ensured that resource selection analyses per period were spatially explicit. Random points were generated within each MCP at a density of 10 points/km^2 of home range, resulting in 137,608 random points overall. Random locations were used to define "available" resources for every bear to compare with the aforementioned "used" (GPS locations) resources following a Type III Resource Selection Function (RSF) study design (Manly et al., 2002).

Any "used" or "available" points that fell outside the study area boundary were excluded, since fruit density values for these sites could not be obtained. Patch- or landscape-level buffaloberry attribute values for fruit density, landscape proportion, standard deviation of fruit density, and distance to the nearest resource patch were extracted for all remaining "used" and "available" points.

2.4 Field visits to bear GPS locations

Ground-truth site visits were conducted in the summer of 2015 for a total of 94 grizzly bear GPS radio-collar fix locations. These GPS locations were associated with five individual bears, four of which were later used in RSF models. GPS locations had been recorded between July 1st and August 19th with site visits occurring 1-3 weeks later between July 23rd and August 26th. This timeframe represented the entire pre-ripening period for buffaloberry and part of the ripening period. GPS locations were randomly selected for visitation and were balanced between crepuscular and diurnal sites. Based on field observations, the percentage of sites with buffaloberry shrubs present and the percentage at which fruit was detected were calculated.

2.5 Candidate foraging hypotheses and model development

Ten *a priori* candidate foraging hypotheses (Table 3.2) relating to foraging strategies for patch- and landscape-level buffaloberry (Table 3.1) were developed to describe grizzly bear selection for buffaloberry fruit resources. Patch- and landscape-level buffaloberry measures were also combined to represent trade-offs between foraging strategies represented by each variable. Buffaloberry fruit density at the patch-level represented resource quality and the 'density' hypothesis, which predicted that bears select for higher quality patches while focusing less on patch encounter probability. Distance to the nearest buffaloberry patch represented resource accessibility and the 'proximity' hypothesis, which supposed that bears do not prioritize patch quality or encounter probability, but instead seek to quickly meet their caloric requirements. Buffaloberry landscape proportion represented the broader distribution of the resource and the 'proportion' hypothesis, which suggested that bears do not necessarily discern patch quality but focus instead on encounter probability. Standard deviation of buffaloberry fruit density represented variability in resource quality and the 'variability' hypothesis, which predicted that bears select for areas with greater variability in patch quality because this contrast enables them to more easily identify high quality patches. The proportion and variability hypotheses together comprised the 'heterogeneity' hypothesis, thus representing both resource distribution and abundance, which suggested that bears prioritize patch encounter probability but select for areas with more variable patch quality due to the benefit of landscape contrast for patch assessment.

A set of mixed-effects logistic regression models was built for each of the ten foraging hypotheses (see Appendix 2A–3B). Separate models differed in their inclusion of particular variables and interaction terms (see Table 3.3 for abbreviated codes), as well as the incorporation of local elevation (30-m pixel) as an environmental covariate expected to affect fruiting phenology of buffaloberry which was tested as both a linear and quadratic term. Interactions involving either the standard deviation of fruit density or elevation, in particular, were examined as it was thought that these may alter the effect of several other explanatory variables on grizzly bear selection. Specifically, it was theorized that greater variability in resource quality (standard deviation of fruit density) could increase the effects of both proportion and fruit density on selection, and that higher elevation could potentially decrease the effects of proximity, fruit density, and proportion.

Sets of mixed-effects logistic models corresponding to each foraging hypothesis were fitted to each seasonal period in order to estimate selection coefficients and assess support of hypotheses. As logistic regression assumes a non-linear relationship between the response and explanatory variables and does not require normality or homoscedasticity of the error term (Cox and Snell, 1989), these properties were not evaluated. These models were intended to investigate population-level effects, rather than individual-level, and thus "used" and "available" points for all bears were grouped. Although GPS radio-telemetry data are affected by spatio-temporal autocorrelation, thus violating the assumption of independence, a random intercept term for individual animal was added which addressed these issues by assuming non-independence of observations within an animal, but independence between animals (Gillies et al., 2006).

Each model was fit separately for the 229-m and 457-m radius landscape-level buffaloberry variables to discern which scale was more supported in grizzly bear resource selection. Multicollinearity among explanatory variables was examined using Pearson correlation coefficients (to ensure these did not exceed |0.7|) and variance inflation factors (VIFs) (to confirm these were not greater than 10.0).

2.6 Model selection

Akaike Information Criterion (AIC) (Akaike, 1974) was used to rank the ten most supported models (foraging hypotheses) among models tested within each period thus considering the principles of parsimony (Burnham and Anderson, 2002). Ranking of hypotheses were compared between periods to assess differences in grizzly bear foraging strategies prior to and during the buffaloberry fruiting period.

Coefficients from the top-ranked model for each period were examined to evaluate the relative importance of different buffaloberry measures within the context of each top foraging hypothesis, and the amount of change in bear selection expected per one-unit increase in each explanatory variable. Coefficients were also used to predict individual responses of variables and their interaction terms on the relative probability of grizzly bear use of a site.

2.7 Comparison of foraging hypotheses for field visited bear GPS locations

AIC comparisons were also used to evaluate support for the ten fruiting period models based on field data obtained during the visits to grizzly bear GPS locations, with the goal of further

assessing whether these models could explain buffaloberry shrub presence at sites visited by bears spanning the early to mid-fruit ripening period. Mixed-effects logistic regression was used with a random effect for individual bear to account for differences in the number of sites per bear that were visited. Model structures were mostly consistent with those of the fruiting period, although elevation variables were removed in some cases due to Pearson correlation coefficients that were $\geq|0.7|$. One model (Density + Proximity) also could not be tested due to correlation of the main variables. A temporal variable was added representing the number of days after July 1st that the bear GPS location had been recorded at the site, as it was expected that buffaloberry would be more frequently observed at sites used by bears later in the season.

3.0 Results

3.1 Selection of spatial scale for landscape-level summary of buffaloberry
Neither the 229-m nor the 457-m landscape-level buffaloberry variables consistently ranked higher in model support (AIC comparisons) for explaining habitat selection by grizzly bears (see Appendix 2A–3B). However, because the 457-m variables appeared in the top two models for the primary season of interest of fruit ripening (Period 2), this scale was chosen for assessing and comparing foraging hypotheses for both the pre-fruit ripening period (Period 1) and the fruit ripening period (Period 2).

3.2 Assessing support for foraging hypotheses during the pre-ripening period (Period 1)
During the pre-ripening period, the most supported foraging hypothesis combined the density and proximity hypotheses (Table 3.4). The model exclusively contained patch-level buffaloberry variables including fruit density, distance to buffaloberry, and a quadratic relationship for elevation (Table 3.5).

Distance to buffaloberry patches exhibited a positive effect on selection of habitats thus indicating grizzly bear use of sites further away from buffaloberry patches (Table 3.5). This response was logarithmic in nature, suggesting that changes in selection were substantial even across short linear distances (Figure 3.2). Standardized coefficients demonstrated that distance was the strongest of the fitted explanatory variables, and its effect was over three times greater than that of fruit density, which was the weakest (Table 3.5).

Fruit density was positively related to habitat selection (Table 3.5) with the relative probability of bear use increasing by 30% between sites where no fruit was present and those with a density of 6000 fruit/900 m^2 (Figure 3.3). Elevation negatively affected selection of sites during the pre-ripening period (Table 3.5) with the relative probability of bear use declining by 50% as elevation increased from a low of 800 m to a high of 2800 m (Figure 3.4).

3.3 Assessing support for foraging hypotheses during the fruit ripening period (Period 2)
During the fruit ripening period, the most supported foraging hypothesis was the heterogeneity hypothesis (Table 3.6). The model was composed mainly of landscape-level buffaloberry variables in the form of interactions between the amount of surrounding buffaloberry (proportion) and the variability in resource quality (standard deviation of fruit density), as well as the amount of surrounding buffaloberry and elevation (Table 3.7).

Standardized coefficients demonstrated that variability was positively related to grizzly bear habitat selection during the fruit ripening period (Table 3.7). Amount of surrounding buffaloberry was negatively related to habitat selection, although the interaction between this and variability was positive indicating greater use of areas with more buffaloberry when variability was high (Table 3.7). Indeed, when examining predictions of the relative probability of bear use for these two variables, selection was highest when the amount of surrounding buffaloberry approached 1.0 and variability in resource quality surpassed approximately 4,000 fruit per 900 m^2 (Figure 3.5). However, at similarly high amounts of surrounding buffaloberry, but very low variability, the selection was low thus pointing to the importance of contrast among landscape patches in bear selection for buffaloberry resources. Once variability in resource quality exceeded 800 the probability of bear use was moderate to high across all amounts of surrounding buffaloberry, suggesting that bears are more likely in general to utilize areas of the landscape associated with greater variability.

Elevation was negatively associated with bear habitat selection and was the weakest overall among individual explanatory variables (Table 3.7). The interaction between elevation and amount of surrounding buffaloberry (proportion) was negative and comparable in strength to the first interaction term, albeit opposite in direction (Table 3.7).

3.4 Comparison of foraging hypotheses between the pre-ripening and fruit ripening periods

The elevation and null models received the lowest amount of support in both periods and ranked ninth and tenth, respectively. The pre-ripening period was characterized by lower ΔAIC values compared to the fruit ripening period, with a difference in model support of 611.4 AIC points between the most supported model and the null model (Table 3.4). The fruit ripening period was associated with higher ΔAIC values and therefore greater differences in support among models of up to 985.2 AIC points (Table 3.6). Excluding the null and elevation models, the ΔAIC value between the top and eighth highest-ranked models was 604.4 for the pre-ripening period and 904.0 for the fruit ripening period.

The order of support for foraging hypotheses changed moderately between the pre-ripening and ripening periods. Specifically, the variability hypothesis demonstrated the largest increase in support from the pre-ripening to ripening period, while the largest decrease in support was for the proximity and proportion hypotheses (Table 3.8). The three other models that incorporated the variability hypothesis, including the Heterogeneity, Variability + Proximity, and Variability + Density models, also increased in support between periods, while the Density + Proximity model decreased in support.

3.5 Comparison of patch- and landscape-level variables between the pre-ripening and fruit ripening periods

Neither patch- nor landscape-level models consistently ranked higher in AIC support during either period. Although the most supported model during the pre-ripening period contained patch-level variables, the second-most supported model included landscape-level variables with a ΔAIC of 8.7 points. The most supported model during the fruit ripening period contained landscape-level variables with the second most supported model combining both patch- and landscape-level variables. However, in contrast to the pre-ripening period, these models were separated by 251.1 AIC points indicating that the first model performed considerably better than the second.

3.6 Field visits to bear GPS locations

Of the 94 grizzly bear GPS locations visited in the field, buffaloberry shrubs were present at 30 sites (32%) and fruit was detected on female plants at nine sites (10%). The proportion of sites

with fruit may be underestimated here, as berries may have been present on shrubs when a GPS radio-collar fix was recorded, but could have been depleted by the time of site visit. Additionally, based on field observations, the 2015 fruiting season was characterized by low buffaloberry productivity that was likely well below the inter-annual average.

3.7 Comparison of foraging hypotheses for field visited bear GPS locations

The variability hypothesis was the most supported for explaining buffaloberry shrub presence at sites used by bears, and the combination of this and the density hypothesis ranked lower at a ΔAIC of 0.7, indicating nearly equivalent support (Table 3.9). However, as the second most supported model with greater complexity was ranked lower than the simpler model, this suggests the density variable was an 'uninformative parameter'. Only these two hypotheses received more support than the elevation model. There was a difference of 7.9 AIC points between the most supported model and that which received the lowest amount of support (Proximity). Standardized coefficients from the most supported model (Variability) demonstrated that variability in resource quality (standard deviation of fruit density) was positively related to buffaloberry shrub presence at sites visited by bears, with elevation exhibiting a similarly strong, but negative effect (Table 3.10). The standard error of the temporal coefficient was larger than the value of the coefficient itself, indicating the date of bear use had a weak effect on whether shrubs were present at a site.

4.0 Discussion

These results suggest that grizzly bear selection for buffaloberry is influenced by landscape spatial heterogeneity of fruit resources. Patch-level foraging hypotheses were less meaningful during the buffaloberry fruit ripening period, supporting the importance of broader environmental grain in resource selection by grizzly bears.

Support for the more complicated hypotheses that combine factors for both the pre-ripening and fruit ripening periods implies that grizzly bears utilize multiple foraging strategies when selecting resources (e.g. Senft et al., 1987). This adaptability may be particularly necessary in this study area where anthropogenic disturbance caused by resource extraction and development is prevalent (Gaulton et al., 2011), requiring that bears navigate a dynamic environment.

4.1 Support for foraging hypotheses during the pre-ripening period (Period 1)

Prior to fruit ripening, less differentiation was observed in the level of support for the ten foraging hypotheses, although this was expected as buffaloberry attributes would have less of an effect on bear selection before the food resource is available. The hypothesis representing fruit density and proximity (distance to nearest buffaloberry patch) was most supported, with bears selecting for sites further away from buffaloberry shrubs which may have been associated with other food items such as clover (*Trifolium* spp.) (Roever et al., 2008). The variability hypothesis was represented in both the second and third most supported hypotheses, indicating landscape-level variability in resource quality appears to influence grizzly bear selection prior to fruit becoming ripe (see Appendix 4 for further details regarding the pre-ripening period).

4.2 Support for foraging hypotheses during the fruit ripening period (Period 2)

The heterogeneity foraging hypothesis was the most supported during fruit ripening, demonstrating that both the distribution of a resource and the variability in quality among patches affects resource selection by bears. Foraging strategy thus focuses more on the probability of resource patch encounter (Sims et al., 2008) where greater landscape contrast facilitates the assessment of patch quality and thus enables bears to identify high quality patches more efficiently. Landscape resource heterogeneity therefore acts as a cue for exploitation.

The most supported model tested included an interaction between the amount of surrounding buffaloberry shrubs (landscape proportion) and the variability in resource quality (standard deviation of fruit density), which, together, represented buffaloberry heterogeneity. Selection of habitats was highest when both surrounding buffaloberry and variability in quality were high (Figure 3.5), indicating that landscape contrast promotes use of resource patches.

The second interaction between the amount of surrounding buffaloberry and elevation suggested that when bears used higher elevations there was little to no buffaloberry in the vicinity. Average elevation of sites used by grizzly bears (GPS locations) where buffaloberry was also present was 1502 m (ranged from 838–2508 m), while sites used without buffaloberry averaged 1647 m (ranged from 959–2861 m). It is important to note that buffaloberry presence here represents shrub occurrence and not directly fruit abundance, which declines with elevation based on its positive association with warmer temperatures at lower elevations (Nielsen et al., 2016). These

findings suggest bears were also selecting for higher elevation sites that were less favourable for buffaloberry and more conducive to other bear foods such as black huckleberry (Munro et al., 2006).

During fruit ripening, the heterogeneity hypothesis received considerably more support than the second most supported hypothesis, which was represented by both variability in resource quality and proximity (distance to nearest buffaloberry patch). Support for the heterogeneity hypothesis related most to the interaction between the amount of surrounding buffaloberry and the variability in resource quality. The second-ranked model also incorporated the variability hypothesis, but these had a large discrepancy in AIC value between them.

Overall, the variability hypothesis emerged during the fruit ripening period as the most important element of the foraging hypotheses with an increase in AIC rank of all the models in which it was included. If a bear utilized areas where buffaloberry patches were widespread with high fruit density it would be characterized by lower landscape variability and increased landscape homogeneity. However, the benefit of variability in quality was apparent with the variability and density hypothesis receiving more support than either the variability or density hypotheses alone. Bear use of buffaloberry resources may thus be contingent not only upon locating high quality patches, but also recognizing them as high quality patches.

Aside from clarifying patch quality, the significance of landscape variability in grizzly bear resource selection is likely connected to their generalist nature and ability to utilize a variety of food types (Hamer et al., 1991; Mattson et al., 1991; McLellan and Hovey, 1995; Munro et al., 2006). Both grizzly and black bears (*Ursus americanu*s) adjust their foraging behaviour based on the annual and seasonal availability of food resources (Jonkel and Cowan, 1971; Bunnell and Tait, 1981; Rogers, 1987). Resource distribution and abundance therefore affects habitat selection (Jonkel and Cowan, 1971; Nielsen et al., 2004a, 2010).

Fruit density is a function of environmental and demographic factors that influence shrub growth and fruit production, such as local canopy cover (Hamer, 1996; Nielsen et al., 2004b) and density (Johnson and Nielsen, 2014). Greater variability in fruit density suggests that a broader range of site types provides more potential (high diversity) for other food resources. As environmental heterogeneity promotes plant species richness (Kreft and Jetz, 2007), selecting more

heterogeneous areas of the landscape thus provides animals with the opportunity to substitute food resources more readily because more varieties may be present in the vicinity. This strategy may be in response to environmental stochasticity, whereby if one key food item such as buffaloberry demonstrates poor annual productivity, alternative options are accessible. Greater landscape heterogeneity may thus contribute to grizzly bear foraging success by facilitating dietary flexibility. It also suggests that bears may be optimizing macronutrient diets by foraging on complementary resources (Coogan et al., 2014).

Although the use of GPS radio-telemetry data provides insight into habitat selection, it alone cannot confirm foraging activity unless ground-truthing is performed (Munro et al., 2006). Landscape-level food resource heterogeneity has, however, previously been identified as important to grizzly bear foraging behaviour (Searle et al., 2006). Searle et al. (2006) conducted feeding trial experiments where the spatial arrangement of patches was manipulated and residence times of resource patches examined. The authors demonstrated that residence time within a given patch was affected by the surrounding spatial context in the patch hierarchy with models accounting for this broader heterogeneity 34-times more supported than those that did not consider scales above the local patch-level.

4.3 Field visits to bear GPS locations

Site visits to grizzly bear GPS radio-telemetry locations in summer of 2015 demonstrated that buffaloberry was present at 32% of sites used by bears with fruit observed at 10% of sites. This was lower than expected based on diet and prior site visits by Munro et al. (2006) who found that fruit in general comprised almost 50% of the grizzly bear diet in August and September. No published information is available about buffaloberry productivity in the Alberta foothills during 2001 to 2003 when Munro et al. (2006) obtained scat samples, although the 2015 fruiting season was considered to be below normal. Consequently, in 2015 it is presumed that bears in the study area substituted with other food resources including huckleberry fruit which occurs at higher elevations. Bear GPS locations that were visited had mostly been used by bears in July with the latest date of use being August 19th, so only about 40% of the fruit ripening period was represented. Future site visits conducted in a year of higher productivity that concentrated on August and early September GPS locations may serve as a more suitable indication of the presence of buffaloberry at sites used by bears.

4.4 Comparison of foraging hypotheses for field visited bear GPS locations

The variability hypothesis was also the most-supported model evaluating the presence of buffaloberry shrubs at field visited grizzly bear locations. Bears would be expected to demonstrate weaker selection for buffaloberry resources in years of below average productivity, as was implied by the moderate rank of the null and elevation hypotheses and the low amount of differentiation in support among all hypotheses. These results are consistent with previous habitat selection results described above in that they highlight the role of landscape-level variability in grizzly bear resource selection, with bears more likely to select sites with buffaloberry present if the surrounding area was more variable. This was observed even in a year with lower than normal fruit production.

These findings emphasize the role of landscape resource heterogeneity in animal habitat use and highlight the value of incorporating measures of spatial variability into resource selection frameworks. Consideration of larger spatial scales provides insights into the environmental variables that affect animal space use, and more specifically foraging behaviours, which may be overlooked if the focus is limited to the patch-scale (Morrison et al., 2006). Sampling resources at broader scales is more consistent with the scale at which large animals, including grizzly bears, perceive and respond to their surroundings (Searle et al., 2006) and thus help to clarify the factors that influence their foraging behaviour.

Table 3.1: Buffaloberry attributes and corresponding spatial scales considered as components of candidate foraging hypotheses (model types) for grizzly bear selection of buffaloberry fruit resources prior to and during the fruit ripening period.

Buffaloberry attribute	Spatial scale	Model variable	Variable explanation	Foraging hypothesis	Strategy for maximizing foraging efficiency
Density	Patch (30-m pixel)	fruit density	• local "quality" of resource patch	• bears do perceive local patch quality • less focus on encounter probability • bears will select for higher quality patches	• bears will select for areas of higher patch quality and utilize them until quality is diminished • reduces energy expenditure associated with travelling between patches of lower quality
Proximity	Patch	distance to nearest buffaloberry patch	• immediate potential accessibility of resource	• bears will prioritize satiation and seek to quickly meet caloric requirements • neither patch quality, nor encounter probability are a focus of their strategy	• bears will opportunistically utilize the closest resource patch to their current location • no explicit strategy to increase foraging efficiency

Table 3.1 (extended): Buffaloberry attributes and corresponding spatial scales considered as components of candidate foraging hypotheses (model types) for grizzly bear selection of buffaloberry fruit resources prior to and during the fruit ripening period.

Buffaloberry attribute	Spatial scale	Model variable	Variable explanation	Foraging hypothesis	Strategy for maximizing foraging efficiency
Proportion	Landscape (229-m or 457-m radius)	proportion of buffaloberry present	• broader spatial distribution of resource	• bears do not necessarily perceive local patch quality • more focus on encounter probability • bears will utilize all resource patches they locate	• bears will select for areas where the resource is more widespread • increases probability of encountering a patch of any quality (complementary to proximity)
Variability	Landscape (229-m or 457-m radius)	standard deviation (SD) of fruit density	• degree of differentiation between adjacent resource patches	• bears do perceive patch quality • but with more focus on encounter probability • bears will prioritize high quality patches but still utilize all patches they locate	• bears will select for areas with greater variability in patch quality • higher contrast facilitates assessment of patch quality and ability to identify high quality patches (cue for exploitation)

Table 3.2 Ten candidate foraging hypotheses (models) for grizzly bear selection of buffaloberry fruit resources for which models were developed, tested, and ranked by AIC for both the pre-ripening (Period 1) and fruit ripening periods (Period 2).

Model ID	Model type	Foraging hypothesis
0	Null (bear ID)	• selection for buffaloberry is random as bears move through their environment • bears will utilize resource patches of any quality when they encounter them • no focus on patch quality or encounter probability
1	Elevation	• selection for buffaloberry is influenced by elevation because this affects fruiting phenology • bears will utilize resource patches of any quality when they encounter them • no focus on patch quality or encounter probability
2	Density	• bears will select for higher quality resource patches
3	Proximity	• bears will opportunistically utilize the closest resource patch to their current location
4	Proportion	• bears will select for areas where the resource is more widespread
5	Variability	• bears will select for areas with greater variability in patch quality

Table 3.2 (extended): Ten candidate foraging hypotheses (models) for grizzly bear selection of buffaloberry fruit resources for which models were developed, tested, and ranked by AIC for both the pre-ripening (Period 1) and fruit ripening periods (Period 2).

Model ID	Model type	Foraging hypothesis
6	Density + Proximity	• bears will select for higher quality resource patches from those closest to their current location
7	Variability + Density	• bears will select for higher quality resource patches which become more identifiable in areas of greater variability in patch quality
8	Variability + Proximity	• bears will select for areas with greater variability in patch quality and higher resource accessibility
9	Heterogeneity (both Proportion + Variability)	• bears will select for areas where the resource is more widespread and there is greater variability in patch quality

Table 3.3: Full names of model variables and abbreviated codes used in descriptions of model structure for the ten candidate foraging hypotheses for grizzly bear selection of buffaloberry fruit resources.

Variable name	Related foraging hypotheses	Variable code
Buffaloberry fruit density (fruit/900m^2)	Density	density
Distance to nearest buffaloberry patch (m)	Proximity	distance
Proportion of buffaloberry (229 or 457-m radius)	Proportion; Heterogeneity	proportion
Buffaloberry fruit density standard deviation	Variability; Heterogeneity	SD
Elevation (m)	-	elev

Table 3.4: Name and structure of the ten candidate foraging hypotheses (models) as tested and ranked by AIC for grizzly bear selection of buffaloberry fruit resources during the pre-ripening period from July 1st – 31st (Period 1) with most landscape variables estimated at a 457-m spatial scale[§].

Model ID	Model type	Model name	AIC	ΔAIC	Akaike weight	Model structure
6	Density + Proximity	Density + Proximity + Elevation^2	31167.0	-0.0	0.987	density[§] + distance + elev^2
9	Heterogeneity	Heterogeneity (interaction) + Elevation^2	31175.7	8.7	0.013	proportion[‡] * SD[‡] + elev^2
8	Variability + Proximity	Variability + Proximity	31227.9	60.9	6.02E-14	SD + distance
3	Proximity	Proximity and Elevation (interaction)	31239.6	72.6	1.68E-16	distance * elev
4	Proportion	Proportion + Elevation^2	31295.6	128.6	1.18E-28	proportion + elev^2
7	Variability + Density	Variability and Density (interaction) + Elevation^2	31644.7	477.7	1.86E-104	SD * density + elev^2
2	Density	Density + Elevation^2	31728.9	561.9	9.47E-123	density + elev^2
5	Variability	Variability + Elevation	31771.4	604.4	5.64E-132	SD + elev
1	Elevation	Elevation	31773.8	606.8	1.70E-132	elev + (1|bear ID)
0	Null (bear ID)	Null (bear ID)	31778.4	611.4	1.68E-133	(1|bear ID)

[§]except fruit density which was estimated at a 30-m spatial scale
[‡]estimated at a 457-m spatial scale

Table 3.5: Summary of variables for the most supported model describing grizzly bear selection of buffaloberry fruit resources during the pre-ripening period (Period 1) as tested by AIC.

Fixed effect	Beta coefficient	Standard error	Standardized beta coefficient	Standard error of standardized coefficient
Intercept	-2.422	0.402	-1.745	0.398
Density	0.433	0.044	0.175	0.018
Distance	0.449	0.019	0.555	0.024
Elevation² (scaled)	-0.270	0.030	-0.270	0.030

Table 3.6: Name and structure of the ten candidate foraging hypotheses (models) as tested and ranked by AIC for grizzly bear selection of buffaloberry fruit resources during the fruit ripening period from August 1st – September 15th (Period 2) with most landscape variables estimated at a 457-m spatial scale[§].

Model ID	Model type	Model name	AIC	ΔAIC	Akaike weight	Model structure
9	Heterogeneity	Heterogeneity (interaction) + Proportion and Elevation	42310.4	-0.0	1	proportion[‡] * SD[‡] + proportion * elev
8	Variability + Proximity	Variability + Proximity	42561.6	251.1	2.97E-55	SD + distance
6	Density + Proximity	Density + Proximity + Elevation^2	42827.9	517.5	4.26E-113	density[§] + distance + elev^2
7	Variability + Density	Variability and Density (interaction) + Elevation	42941.9	631.5	7.58E-138	SD * density + elev
5	Variability	Variability + Elevation	42997.0	686.5	8.43E-150	SD + elev
2	Density	Density and Elevation (interaction)	43118.6	808.2	3.17E-176	density * elev
3	Proximity	Proximity	43149.4	839.0	6.62E-183	distance
4	Proportion	Proportion and Elevation (interaction)	43214.5	904.0	4.88E-197	proportion * elev
1	Elevation	Elevation	43283.3	972.9	5.62E-212	elev + (1|bear ID)
0	Null (bear ID)	Null (bear ID)	43295.7	985.2	1.16E-214	(1|bear ID)

[§]except fruit density which was estimated at a 30-m spatial scale
[‡]estimated at a 457-m spatial scale

Table 3.7: Summary of variables for the most supported model describing grizzly bear selection of buffaloberry fruit resources during the fruit ripening period (Period 2) as tested by AIC.

Fixed effect	Beta coefficient	Standard error	Standardized beta coefficient	Standard error of standardized coefficient
Intercept	-1.584	0.340	-1.858	0.337
Proportion	-1.503	0.063	-0.383	0.023
SD	0.003[‡]	0.001[‡]	0.449	0.034
Elevation (scaled)	0.125	0.029	-0.172	0.029
Proportion*SD (interaction)	0.001	0.001[‡]	0.227	0.020
Proportion*Elevation (interaction)	-0.779	0.053	-0.277	0.019

[‡]value reported as 10 times larger than actual for tabular display

Table 3.8: Ranking of support for foraging hypotheses (models) during the pre-ripening (Period 1) and fruit ripening periods (Period 2) as tested by AIC, and changes in rank of each hypothesis from Period 1 to 2.

Model ID	Model type	Rank for Period 1	Rank for Period 2	Change in rank from Period 1 to 2
9	Heterogeneity	2	1	+ 1
8	Variability + Proximity	3	2	+ 1
6	Density + Proximity	1	3	- 2
7	Variability + Density	6	4	+ 2
5	Variability	8	5	+ 3
2	Density	7	6	+ 1
3	Proximity	4	7	- 3
4	Proportion	5	8	- 3
0	Null (bear ID)	9	9	0
1	Null (elevation)	10	10	0

Table 3.9: Name and structure of the ten candidate foraging hypotheses (models) from the buffaloberry fruit ripening period as tested and ranked by AIC to explain buffaloberry shrub presence at grizzly bear GPS locations.

Model ID	Model Type	Model Name	AIC	ΔAIC	Akaike weight	Model Structure
5	Variability	Variability + Elevation + Time	110.0	-0.0	0.355	SD‡ + elev + time
7	Variability + Density	Variability and Density (interaction) + Elevation + Time	110.7	0.7	0.252	SD * density§ + elev + time
1	Elevation	Elevation	111.6	1.6	0.161	elev + (1|bear ID)
9	Heterogeneity	Heterogeneity (interaction) + Time	113.3	3.3	0.067	proportion‡ * SD + time
-	Elevation + Time	Elevation + Time	113.6	3.6	0.060	elev + time + (1|bear ID)
0	Null (bear ID)	Null (bear ID)	114.1	4.1	0.045	(1|bear ID)

Table 3.9 (extended): Name and structure of the ten candidate foraging hypotheses (models) from the buffaloberry fruit ripening period as tested and ranked by AIC to explain buffaloberry shrub presence at grizzly bear GPS locations.

Model ID	Model Type	Model Name	AIC	ΔAIC	Akaike weight	Model Structure
-	Null (bear ID) + Time	Null (bear ID) + Time	116.0	6.0	0.017	(1|bear ID) + time
2	Density	Density and Elevation (interaction) + Time	116.4	6.4	0.014	density * elev + time
8	Variability + Proximity	Variability + Proximity + Time	116.5	6.5	0.014	SD + distance + time
4	Proportion	Proportion + Time	117.6	7.6	0.008	proportion + time
3	Proximity	Proximity + Time	117.9	7.9	0.007	distance + time

[§]estimated at a 30-m spatial scale

[‡]estimated at a 457-m spatial scale

Table 3.10: Summary of variables for the most supported model from the buffaloberry fruit ripening period describing buffaloberry shrub presence at grizzly bear GPS locations as tested by AIC.

Fixed effect	Beta coefficient	Standard error	Standardized beta coefficient	Standard error of standardized beta coefficient
Intercept	1.995	1.347	-0.958	0.265
Time	0.011	0.018	0.165	0.273
SD	0.004	0.001	0.888	0.298
Elevation	-0.003	0.001	-0.769	0.260
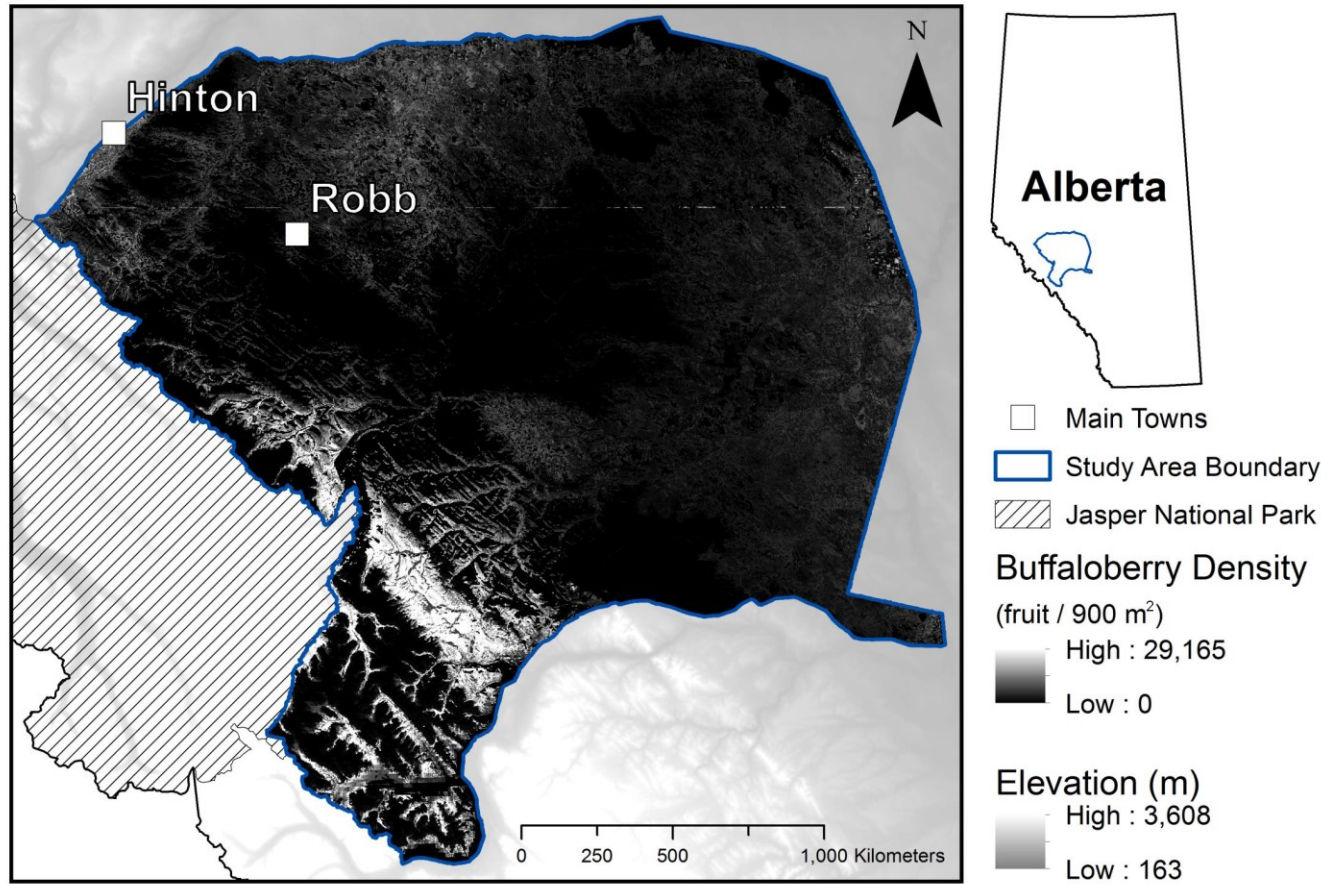
Figure 3.1: Boundary of the study area southeast of Hinton, Alberta (53°24'41"N, 117°33'50" W), as defined by the extent of a buffaloberry fruit density model developed by Nielsen et al. (2016) and predicted fruit density values for the region.
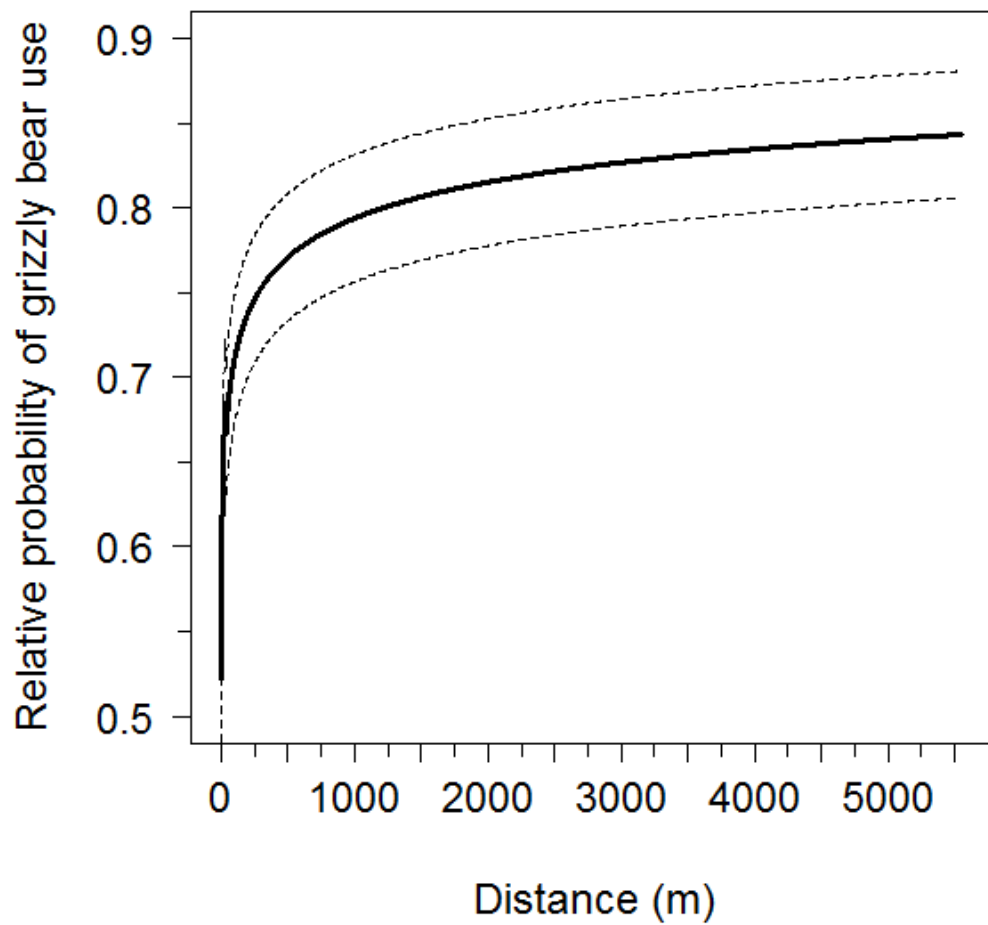
Figure 3.2: Predicted effect of distance to the nearest buffaloberry patch (m) on the relative probability of grizzly bear use (selection) of a site.
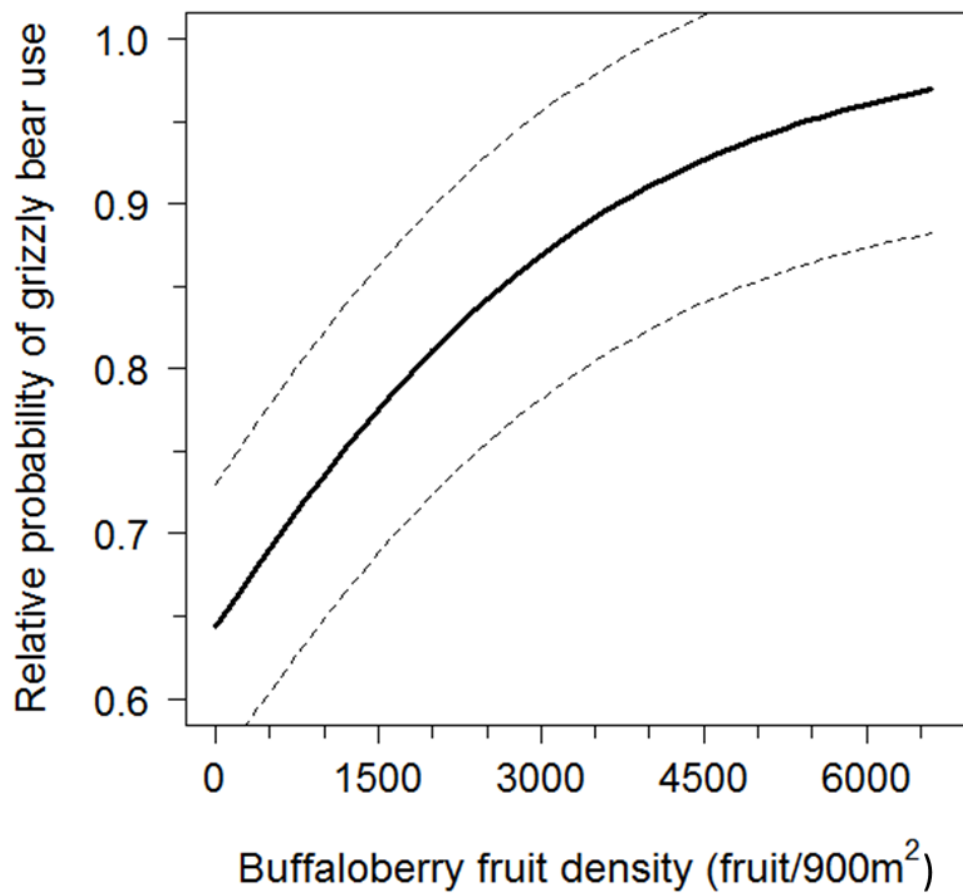
Figure 3.3: Predicted effect of buffaloberry fruit density (fruit/900 m^2) on the relative probability of grizzly bear use (selection) of a site.
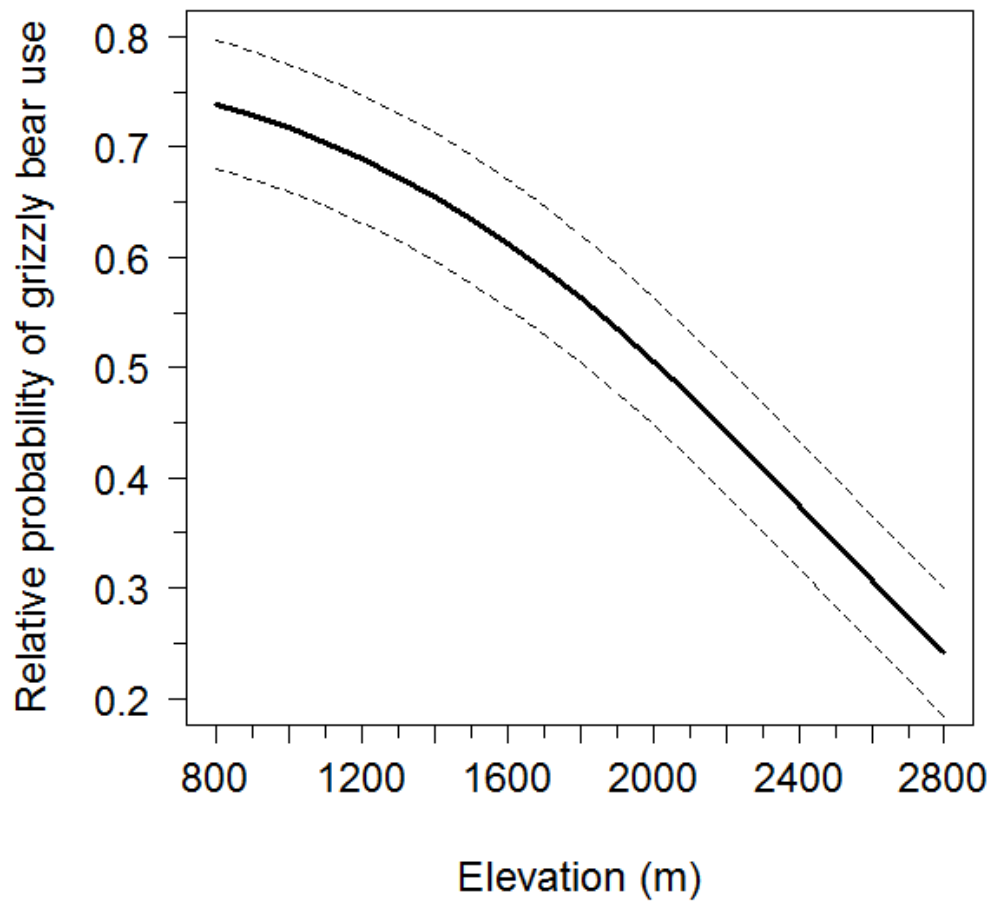
Figure 3.4: Predicted effect of elevation (m) on the relative probability of grizzly bear use (selection) of a site.
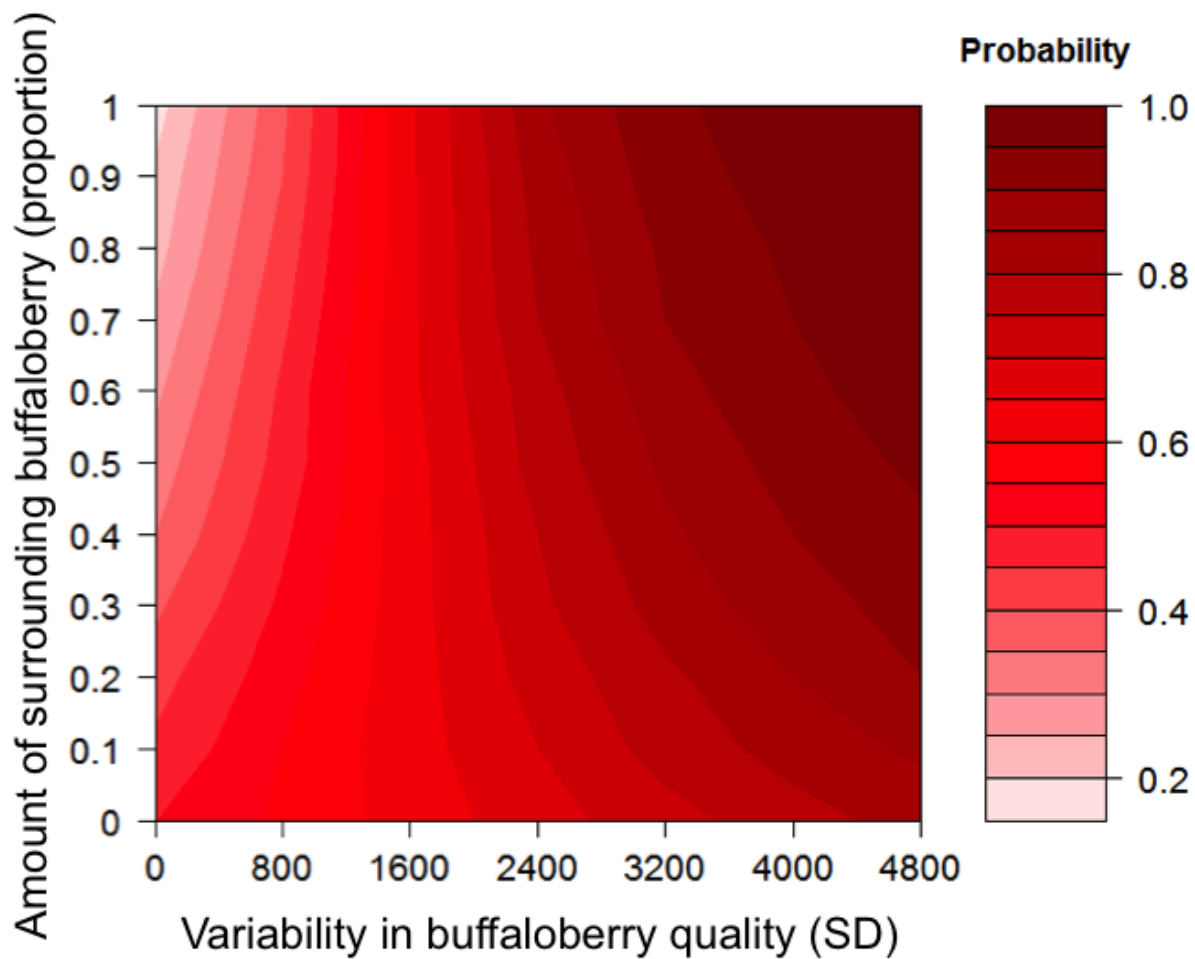
Figure 3.5: Predicted effect of the interaction between the amount of surrounding buffaloberry (proportion) and variability in buffaloberry quality (SD) on the relative probability of grizzly bear use (selection) of a site.

Chapter 4: General conclusion

Spatial heterogeneity remains both a challenge and source of intrigue in ecology (Kolasa and Pickett, 1991). Determining the heterogeneity of plant species that are key food items for consumers, including species at risk, can inform our understanding of consumer-resource interactions. This thesis focused on relating the spatial heterogeneity of buffaloberry shrubs to a broader landscape characteristic, in particular forest canopy patterns, and assessed the importance of this heterogeneity for grizzly bear food resource selection.

Evergreen canopy patterns appear to be significantly more influential than those of deciduous canopy for explaining the presence and spatial heterogeneity of buffaloberry shrubs. This relationship between evergreen canopy and buffaloberry spatial patterns could be used in conjunction with LiDAR data currently available for much of the forested regions in Alberta (Coops et al., 2016) to map buffaloberry heterogeneity at a landscape-level. One challenge is that LiDAR data are typically processed at a coarser spatial resolution than that of field data, although there is steady improvement in instrumental resolving power as remote sensing technology advances. Buffaloberry spatial models, such as the fruit density model used in this study from Nielsen et al. (2016), continue to incorporate a wider range of environmental explanatory variables (Barber et al., 2016) and thus provide more accurate predictions of shrub distribution and fruit abundance. These current models may facilitate the linkage of field data to LiDAR-derived canopy cover measures in order to model buffaloberry heterogeneity across a large spatial extent.

Grizzly bears appear to respond to broader spatial variability in their food resources, as landscape-level buffaloberry heterogeneity was found to be important in explaining bear resource selection by bears. Future work could be directed towards expanding the temporal period analyzed in order to incorporate earlier years of bear GPS radio-telemetry data, which would improve sample size. The awareness of spatial context demonstrated by grizzly bears indicates that studies of resource selection involving other large-bodied animals, such as ungulates, may also benefit from the inclusion of landscape-level heterogeneity measures of resource units of interest. Accounting for landscape perception will more accurately reflect

the factors that affect animal response to the environment, thereby enhancing the realism of RSF models and producing more valid inferences.

Conservation efforts can be enhanced by a more developed understanding of how threatened species interact with their environment, which is particularly crucial given the growing threats to global biodiversity (Parmesan and Yohe, 2003). Vegetation heterogeneity is largely shaped by natural and anthropogenic disturbances expected to become more frequent and severe (Dale et al., 2001), and climate change may additionally cause geographic shifts in suitable habitat for plant species (Kelly and Goulden, 2008). A reduction in the availability of key plant food resources could trigger bottom-up effects that would increase the vulnerability of animal species at higher trophic levels (Roberts et al., 2014), emphasizing the value of knowledge of current plant spatial patterns so that potential changes can be anticipated. Clarifying the heterogeneity of food resources and the importance of this for animal habitat use can thus provide insight into effective future management strategies to support the maintenance and recovery of at-risk wildlife populations.

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Appendix 1: Mean hourly and half-hourly movement rates of grizzly bears near Hinton, AB, during July and early August calculated using a subsample (5 individuals) of the same animals included in the analysis of bear selection for buffaloberry resources.

Week Number	Week Start Date	Mean Step Number (GPS radio-collar fixes)	Mean Path Length (km)	Mean Movement Rate (m/hr)	Mean Movement Rate (m/30 min.)
1	July 3rd	159	52.3	329.6	164.8
2	July 10th	159	78.6	494.2	247.1
3	July 17th	157	77.4	492.4	246.2
4	July 24th	158	78.9	498.8	249.4
5	July 31st	161	83.9	520.6	260.3
6	August 7th	159	64.4	405.9	202.9
Overall Mean		159	73	457	229

Appendix 2A: Model structures considered for the ten candidate foraging hypotheses (models) as tested and ranked by AIC for grizzly bear selection of buffaloberry fruit resources from July 1st – 31st prior to the fruit ripening period, with most landscape variables estimated at a 457-m spatial scale[§].

Model Type	AIC	ΔAIC	Model Structure
Density + Proximity	31167.0	-0.0	density[§] + distance + elev^2
Heterogeneity	31175.7	8.7	proportion[‡] * SD[‡] + elev^2
Heterogeneity	31179.5	12.5	proportion * SD + proportion * elev
Density + Proximity	31197.6	30.6	density * elev + distance
Heterogeneity	31198.4	31.4	proportion + SD + elev^2
Heterogeneity	31204.1	37.1	proportion * SD + elev
Density + Proximity	31208.7	41.7	density + distance + elev
Heterogeneity	31211.2	44.2	proportion * elev + SD
Heterogeneity	31224.2	57.2	proportion + SD + elev
Contrast + Proximity	31227.9	60.9	SD + distance
Proximity	31239.6	72.6	distance * elev
Proximity	31245.3	78.3	distance + elev^2
Density + Proximity	31252.1	85.1	density + distance
Heterogeneity	31252.3	85.3	proportion * SD
Heterogeneity	31260.3	93.3	proportion + SD
Proximity	31284.1	117.1	distance + elev
Proportion	31295.6	128.6	proportion + elev^2
Proximity	31311.0	144.0	distance
Proportion	31328.8	161.8	proportion + elev

Appendix 2A (extended): Model structures considered for the ten candidate foraging hypotheses (models) as tested and ranked by AIC for grizzly bear selection of buffaloberry fruit resources from July 1st – 31st prior to the fruit ripening period, with most landscape variables estimated at a 457-m spatial scale[§].

Model Type	AIC	ΔAIC	Model Structure
Proportion	31330.6	163.6	proportion * elev
Proportion	31355.5	188.5	proportion
Contrast + Density	31644.7	477.7	SD * density + elev^2
Contrast + Density	31654.4	487.4	SD * density
Contrast + Density	31656.4	489.4	SD * density + elev
Density	31728.9	561.9	density + elev^2
Contrast + Density	31729.0	562.0	SD + density + elev
Density	31729.0	562.0	density * elev
Density	31729.1	562.1	density + elev
Contrast + Density	31729.4	562.4	SD + density * elev
Contrast + Density	31729.7	562.7	SD + density + elev^2
Density	31730.2	563.2	density
Contrast + Density	31730.5	563.5	SD + density
Contrast	31771.4	604.4	SD + elev
Contrast	31774.8	607.8	SD
Contrast	31775.0	608.0	SD + elev^2
Null	31778.4	611.4	(1|bear ID)
Elevation	34495.6	3328.6	elev

[§]except fruit density which was estimated at a 30-m spatial scale
[‡]estimated at a 457-m spatial scale

Appendix 2B: Model structures considered for the ten candidate foraging hypotheses (models) as tested and ranked by AIC for grizzly bear selection of buffaloberry fruit resources from July 1st – 31st prior to the fruit ripening period, with most landscape variables estimated at a 229-m spatial scale[§].

Model Type	AIC	ΔAIC	Model Structure
Contrast + Proximity	31140.3	-0.0	SD[‡] + distance
Density + Proximity	31167.0	26.7	density[§] + distance + $elev^2$
Heterogeneity	31177.3	37.0	proportion[‡] * SD + $elev^2$
Density + Proximity	31197.6	57.3	density * elev + distance
Heterogeneity	31199.2	58.9	proportion + SD + $elev^2$
Heterogeneity	31202.7	62.4	proportion * SD + proportion * elev
Heterogeneity	31204.8	64.5	proportion * SD + elev
Density + Proximity	31208.7	68.4	density + distance + elev
Heterogeneity	31223.3	83.1	proportion + SD + elev
Heterogeneity	31224.6	84.3	proportion * elev + SD
Heterogeneity	31235.0	94.7	proportion * SD
Proximity	31239.6	99.3	distance * elev
Heterogeneity	31243.8	103.5	proportion + SD
Proximity	31245.3	105.0	distance + $elev^2$
Density + Proximity	31252.1	111.9	density + distance
Proximity	31284.1	143.8	distance + elev
Proximity	31311.0	170.8	distance
Proportion	31340.0	199.8	proportion + $elev^2$
Proportion	31361.9	221.6	proportion * elev

Appendix 2B (extended): Model structures considered for the ten candidate foraging hypotheses (models) as tested and ranked by AIC for grizzly bear selection of buffaloberry fruit resources from July 1st – 31st prior to the fruit ripening period, with most landscape variables estimated at a 229-m spatial scale[§].

Model Type	AIC	ΔAIC	Model Structure
Proportion	31369.9	229.6	proportion + elev
Proportion	31385.0	244.7	proportion
Contrast + Density	31614.4	474.2	SD * density + elev^2
Contrast + Density	31622.7	482.4	SD * density
Contrast + Density	31624.6	484.3	SD * density + elev
Contrast + Density	31707.9	567.6	SD + density + elev
Contrast + Density	31709.2	568.9	SD + density * elev
Contrast + Density	31710.5	570.2	SD + density
Contrast + Density	31710.6	570.4	SD + density + elev^2
Density	31728.9	588.6	density + elev^2
Density	31729.0	588.7	density * elev
Density	31729.1	588.8	density + elev
Density	31730.2	590.0	density
Contrast	31775.6	635.3	SD + elev
Null	31778.4	638.1	(1|bear ID)
Contrast	31780.4	640.1	SD
Contrast	31781.4	641.1	SD + elev^2
Elevation	34495.6	3355.3	elev

[§]except fruit density which was estimated at a 30-m spatial scale
[‡]estimated at a 229-m spatial scale

Appendix 3A: Model structures considered for the ten candidate foraging hypotheses (models) as tested and ranked by AIC for grizzly bear selection of buffaloberry fruit resources from August 1st – September 15th during the fruit ripening period, with most landscape variables estimated at a 457-m spatial scale[§].

Model Type	AIC	ΔAIC	Model Structure
Heterogeneity	42310.4	-0.0	proportion[‡] * SD[‡] + proportion * elev
Heterogeneity	42450.4	140.0	proportion * elev + SD
Heterogeneity	42523.5	213.0	proportion * SD + elev^2
Heterogeneity	42528.6	218.2	proportion * SD + elev
Heterogeneity	42529.2	218.8	proportion * SD
Contrast + Proximity	42561.6	251.1	SD + distance
Heterogeneity	42607.7	297.2	proportion + SD
Heterogeneity	42607.7	297.3	proportion + SD + elev^2
Heterogeneity	42609.6	299.2	proportion + SD + elev
Density + Proximity	42827.9	517.5	density[§] + distance + elev^2
Density + Proximity	42829.1	518.6	density + distance
Density + Proximity	42829.4	519.0	density * elev + distance
Density + Proximity	42831.1	520.6	density + distance + elev
Contrast + Density	42941.9	631.5	SD * density + elev
Contrast + Density	42953.0	642.6	SD * density + elev^2
Contrast + Density	42954.5	644.1	SD * density
Contrast + Density	42976.0	665.6	SD + density * elev
Contrast + Density	42990.2	679.7	SD + density + elev
Contrast	42997.0	686.5	SD + elev

Appendix 3A (extended): Model structures considered for the ten candidate foraging hypotheses (models) as tested and ranked by AIC for grizzly bear selection of buffaloberry fruit resources from August 1st – September 15th during the fruit ripening period, with most landscape variables estimated at a 457-m spatial scale[§].

Model Type	AIC	ΔAIC	Model Structure
Contrast + Density	43005.6	695.1	SD + density + elev^2
Contrast	43011.9	701.5	SD + elev^2
Contrast + Density	43013.6	703.1	SD + fruit density
Contrast	43019.1	708.6	SD
Density	43118.6	808.2	density * elev
Density	43145.0	834.6	density + elev
Proximity	43149.4	839.0	distance
Proximity	43149.5	839.1	distance + elev^2
Proximity	43150.5	840.1	distance + elev
Proximity	43152.3	841.9	distance * elev
Density	43160.5	850.1	density + elev^2
Density	43164.3	853.9	density
Proportion	43214.5	904.0	proportion * elev
Proportion	43214.7	904.3	proportion + elev
Proportion	43216.0	905.5	proportion
Proportion	43217.7	907.3	proportion + elev^2
Null	43295.7	985.2	(1|bear ID)
Elevation	49456.0	7145.6	elev

[§]except fruit density which was estimated at a 30-m spatial scale
[‡]estimated at a 457-m spatial scale

Appendix 3B: Model structures considered for the ten candidate foraging hypotheses (models) as tested and ranked by AIC for grizzly bear selection of buffaloberry fruit resources from August 1st – September 15th during the fruit ripening period, with most landscape variables estimated at a 229-m spatial scale[§].

Model Type	AIC	ΔAIC	Model Structure
Heterogeneity	42455.6	-0.0	proportion[‡] * SD[‡] + proportion * elev
Contrast + Proximity	42523.8	68.2	SD + distance
Heterogeneity	42556.9	101.3	proportion * elev + SD
Heterogeneity	42575.3	119.7	proportion * SD + elev^2
Heterogeneity	42575.9	120.3	proportion * SD
Heterogeneity	42577.9	122.2	proportion * SD + elev
Heterogeneity	42642.6	187.0	proportion + SD
Heterogeneity	42643.4	187.7	proportion + SD + elev
Heterogeneity	42644.5	188.9	proportion + SD + elev^2
Density + Proximity	42827.9	372.3	density[§] + distance + elev^2
Density + Proximity	42829.1	373.5	density + distance
Density + Proximity	42829.4	373.8	density * elev + distance
Density + Proximity	42831.1	375.5	density + distance + elev
Contrast + Density	42943.5	487.8	SD * density + elev
Contrast + Density	42951.5	495.9	SD + density * elev
Contrast + Density	42957.3	501.7	SD * density + elev^2
Contrast + Density	42961.4	505.8	SD * density
Contrast + Density	42962.1	506.4	SD + density + elev
Contrast	42962.4	506.8	SD + elev

Appendix 3B (extended): Model structures considered for the ten candidate foraging hypotheses (models) as tested and ranked by AIC for grizzly bear selection of buffaloberry fruit resources from August 1st – September 15th during the fruit ripening period, with most landscape variables estimated at a 229-m spatial scale[§].

Model Type	AIC	ΔAIC	Model Structure
Contrast + Density	42978.6	523.0	SD + density + $elev^2$
Contrast	42978.8	523.2	SD + $elev^2$
Contrast	42987.7	532.1	SD
Contrast + Density	42987.8	532.2	SD + density
Density	43118.6	663.0	density * elev
Density	43145.0	689.4	density + elev
Proximity	43149.4	693.8	distance
Proximity	43149.5	693.9	distance + $elev^2$
Proximity	43150.5	694.9	distance + elev
Proximity	43152.3	696.7	distance * elev
Density	43160.5	704.9	density + $elev^2$
Density	43164.3	708.7	density
Proportion	43221.3	765.7	proportion + elev
Proportion	43222.6	767.0	proportion * elev
Proportion	43223.5	767.9	proportion
Proportion	43225.4	769.8	proportion + $elev^2$
Null	43295.7	840.0	(1|bear ID)
Elevation	49456.0	7000.4	elev

[§]except fruit density which was estimated at a 30-m spatial scale
[‡]estimated at a 229-m spatial scale

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Appendix 4: Support for foraging hypotheses during the pre-ripening period (Period 1).

Prior to fruit ripening, less differentiation was observed in the level of support for the ten foraging hypotheses. Increased similarity was expected since buffaloberry attributes would be unlikely to influence bear selection given the lack of fruit, implying the effects of different variables would be comparable as all are less meaningful before fruit ripening.

The hypotheses represented by fruit density (patch-level) and proximity (distance to nearest buffaloberry patch) received the most support during the pre-fruiting period, with proximity demonstrating a strong positive effect on bear selection therefore indicating bears selected for sites further away from buffaloberry shrubs. Munro et al. (2006) found that, during July in the Alberta foothills, grasses and forbs collectively accounted for 54% of the grizzly bear diet on average, suggesting it is likely bears relied on other plant food types in the pre-fruiting period. Some of these alternative food items are associated with site conditions that are unfavourable for buffaloberry, such as disturbed areas like roadsides where clover (*Trifolium* spp.) typically occurs (Roever et al. 2008), and the positive effect of distance possibly reflects bear consumption of these other plant species that have different site requirements from buffaloberry.

The variability hypothesis appeared in both the second and third most supported foraging hypotheses for the pre-fruiting period, with the heterogeneity hypothesis receiving almost as much support as the most supported hypothesis. Interestingly, the individual variability hypothesis ranked the lowest of the non-null models for Period 1 despite appearing in these well-supported combination hypotheses, implying the effect of variability is mainly realized when considered simultaneously with other resource attributes. This opposite result was observed for the fruiting period, where the individual variability hypothesis was the most supported of the four non-combination hypotheses. Landscape-level variability thus appears to determine grizzly bear resource selection to some degree in both periods, but its individual influence over selection is more evident when buffaloberry fruit is ripe.