Effect of Early Seral Forests on Grizzly Bear (*Ursus arctos*) Food Supply, Habitat Selection, and Tradeoffs with Mortality Risk Associated with Roads via an Individual-based Model

by

Christopher Michael Souliere

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Department of Renewable Resources
University of Alberta

Abstract

Large-scale disturbances can shift the distribution, abundance, and quality of animal food resources, which in turn, can influence how habitat is used by individuals. This not only increases competition among conspecifics, but can also lead to lower survival since individuals are more likely to encounter humans in human-dominated landscapes. A key challenge for wildlife managers is therefore to understand how to best minimize the effect of large-scale disturbances – which can be partly anthropogenic in origin – while simultaneously enhancing their positive effect.

In this thesis, I explored the effects of large-scale disturbances and distribution of food resources on grizzly bear (*Ursus arctos*) habitat supply, including the tradeoff between individual health, via body condition, and survival, via mortality risk as it relates to road density, in a human-modified landscape. First, I tested whether harvested areas can act as surrogates to wildfires with respect to grizzly bear food supply by comparing and quantifying key fruit-bearing and herbaceous grizzly bear foods among post-harvest and post-fire disturbance types and at relatively early stages of forest regeneration (5, 20, and 60 years). I found no significant differences between digestible energy available from fruit and forbs when comparing between post-harvest and post-fire stands within any age-class. These results provide evidence that harvested areas can potentially act as surrogates to wildfires in relation to grizzly bear food supply and could thus be used as a means to support ongoing population recovery efforts if human-caused mortality can be controlled. Next, I explored the degree to which grizzly bears may trade off foraging strategies (food resource heterogeneity, defined as both the distribution in digestible energy and variability in digestible energy quality, and homogeneity, defined as digestible energy density) depending on how food resources are spatially allocated and investigated these patterns on seasonal habitat selection for food resources. In general, models that included heterogeneity coupled with homogeneity were most supported and best explained grizzly bear habitat selection across all seasons. Most importantly however, results suggest that bears may alternate between foraging strategies (heterogeneity vs. homogeneity) given they were more likely to use high contrast areas (patchiness) when digestible energy (food) is more widely distributed, and conversely, use resource dense areas when digestible energy distribution is constrained. Finally, I built a novel spatially explicit individual-based model (IBM) that simulates the interaction between grizzly bear agents, a spatiotemporal dynamic landscape of key grizzly bear foods, and differing road density levels for a threatened grizzly bear population in Alberta, Canada. Results suggest that a tradeoff between health and survival may be occurring given the survival rate of bear agents peaked at body condition index values near zero (i.e., when survival was influenced by both road density and low body condition index values). Bear agents that tended to be located in resource poor areas had higher survival rates (areas of low human disturbance) yet were in lower body condition, whereas the opposite pattern occurred in resource rich areas. Lastly, the model showed that the relationship between displacement and body condition index was contingent on whether bear agents foraged in resource rich or poor areas.

Collectively, the findings of this thesis contribute to a growing body of literature showing that by shifting the quality, abundance, and distribution of food resources (via landscape change and large-scale disturbances), such disturbances may benefit a threatened bear population by increasing access to high-quality foods in human-modified areas. In turn, this can influence overall health, and ultimately reproduction and fitness, if mortality risk is lowered. Further, the results of this thesis could be used and expanded upon to inform grizzly bear management practices in Alberta, especially under persistent landscape change.

Preface

This thesis is an original work by Christopher Souliere. Chapter 2 has been published in Forest Ecology and Management along with co-authors S.C.P Coogan, G.B. Stenhouse and S.E. Nielsen as "Harvested forests as a surrogate to wildfires in relation to grizzly bear food-supply in west-central Alberta", *Forest Ecology and Management* 456, 117685. Chapters 3 and 4 are intended for publication along with co-authors C.K. Denny, G.B. Stenhouse, and S.E. Nielsen.

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Chapter 1: General Introduction

1.1. Natural Disturbance Emulation

In general, ecosystem management broadly emphasizes the long-term sustainability of natural resources while meeting ecological, economic, and social needs (Brussard et al, 1998; Lackey, 1998; Szaro et al, 1998). Indeed, one approach to ecosystem management, which has gained increasing popularity in the past three decades, is natural disturbance emulation (NDE) (Hunter, 1993; Bergeron et al., 1999; Long et al., 2009; Kuuluvainen and Grenfell, 2012). The NDE model recognizes the importance, ubiquity, and inherent role of natural disturbances as a driver shaping the complexity and proper function of forest ecosystems (Hunter et al., 1988; Kuuluvainen and Grenfell, 2012). By emulating natural disturbances in managed forests, managers wish to maintain or restore ecological structure and function and thus mitigate the negative effects of forest management practices on biodiversity and other commodities and services (Hunter, 1993; Armstrong et al., 2003). In the boreal forest of western Canada, NDE assumes natural forest ecosystems are mainly structured by fire and are thus populated by fire-adapted species (Stockdale et al., 2016). Because large-scale timber harvesting has become a major disturbance agent in the boreal forest (Andison, 1998), there are concerns that harvesting may not safeguard biodiversity in the same way as fire. Thus, forest and land managers are interested in implementing management actions that mimic the efficacy, structure, and function of fire regimes as a model for sustainable forest management and to maintain comparable levels of biodiversity (Hunter, 1993; Bergeron et al. 1999). Other concepts closely related to NDE include the coarse-filter approach to conservation (Noss et al., 1987) and the natural range variability (NRV) concept (Landres et al, 1999).

1.1.1. Equivalency between Forest Harvest and Wildfire

Although areas disturbed by wildfire and harvest in the boreal forest are dissimilar in important ways, they are also similar in others. Observations show that species occurring in many forest types are also adapted to conditions associated with large-scale wildfire disturbances (Rowe, 1983; Keeley et al., 2017; Pausas and Parr, 2018). Thus, assuming fire regimes are well understood by managers, forest management practices that mimic some macro-characteristics of wildfire might be useful in maintaining biodiversity across the landscape (Stockdale et al, 2016). For example, some macro-characteristics that closely match patterns created by wildfire include the treatment of post-harvest sites, total harvested volume, retention harvesting, size distribution of harvested area, and rotation length (Hunter, 1993; Delong and Tanner, 1996; Bergeron et al., 2002; Schroeder and Perera, 2002). Although harvesting practices can retain patterns similar to wildfire, they cannot fully preserve the habitat conditions and ecological components and processes typical of wildfire (Franklin and Forman, 1987; McRae et al, 2001; Stockdale et al., 2016). Pattern emulation alone cannot be expected to produce the same type of complex forest structures, nor the same types of vegetation communities, nutrient cycling processes, and soil conditions (White, 1979; McRae et al., 2001; Franklin et al., 2002; Certini, 2005). Fine-filter strategies should thus accompany the coarse-filter approach more typical of the NDE model to maintain and manage biodiversity.

1.1.2. Habitat Surrogacy as a Management Tool

Although surrogacy is defined in many ways in the conservation literature (Wiens et al., 2008; Hunter et al., 2016), habitat surrogacy is typically based on site- and landscape-level features such as structure and composition of vegetation, as well as the amount and configuration of vegetative cover (Lindenmayer et al., 2014). In recent decades, disturbance processes that can be more easily emulated have become increasingly important to land managers. For instance, timber management practices have sought to emulate components of natural disturbance and succession regimes, with the goal of managing forest systems while maintaining biodiversity and ecological integrity (Hunter et al., 2016), consistent with the coarse-filter strategy (Noss et al., 1987). In Alberta, increases in timber harvesting coinciding with fire-suppression and a reduction in stand-replacing fires has necessitated management approaches that offer the same types of open canopy habitat that wildfires historically provided. For open habitat species such as grizzly (brown) bears (*Ursus arctos*), the mosaic of open canopy habitat created by harvesting can perhaps act as a surrogate for wildfires. This is not only to maintain comparable features and ecological integrity across the forest landscape, but also to serve as a management tool for maintaining or enhancing preferred vegetation that is critical for a threatened grizzly bear population while limiting mortality risk.

1.2. Heteregeneous (Patchy) Landscapes

Disturbances, whether naturally occurring or human-caused, can alter the distribution of resources across landscapes. Habitats that have been perturbed to some degree can thus have abundance and distribution patterns of food resources – amongst other landscape and habitat features – vary in space and time (Johnson et al., 1992; Devictor et al., 2008a; Devictor et al., 2008b), contributing to spatial heterogeneity in landscapes (Kotliar and Wiens, 1990). Spatial heterogeneity can lead to patchily distributed forage and seasonal variation in food resource abundance and quality (Wiens, 1976), which in turn can influence animal foraging decisions and ultimately individual fitness (MacArthur & Pianka, 1966). Food resource abundance and distribution patterns can mediate the relationship between animal space use and fitness by increasing access to certain food resources while limiting access to others (Kie et al., 2002; Denny et al., 2018; Mangipane et al., 2018). This can not only increase competition among conspecifics and the likelihood of finding mates, but it may also increase the exposure of individuals to humans (e.g., human conflict and human-caused mortality), especially in heavily disturbed landscapes with high levels of human use. For large-bodied generalists with high energetic demands such as the grizzly bear, access to and selection of patchily distributed food resources in human-altered landscapes becomes a focal point of interest, not only to managed extant populations, but also to enhance recovery efforts for populations that are threatened. Indeed, heterogenous (patchy) landscapes can affect such processes as how grizzly bears distribute themselves across a landscape, source-sink dynamics, foraging strategies, and space-use and fitness.

1.2.1. Distribution and Source-Sink Dynamics

Ideal free distribution and ideal despotic distribution models provide a theoretical framework to explore species-habitat relationships (Fretwell and Lucas 1970) and help explain source-sink dynamics (Pulliam, 1988). Heterogeneous (patchy) landscapes contribute to spatiotemporal variation in resources leading to differences in habitat quality, thus providing a basis for higher quality (e.g., sources) and lower quality (e.g., sinks) habitats to emerge (Pulliam, 1988; Dias, 1996). Other habitat characteristics including proximity to patches and patch size can play an influential role in dictating how individuals become distributed on the landscape. Assessing the importance of spatial heterogeneity in structuring habitat selection is key if we wish to understand how animal populations inhabiting human-altered landscapes react to changes in the availability of high-quality and low-quality habitats over time (Pulliam and Danielson, 1991), and how this may influence the viability of populations inhabiting those areas. Indeed, an important challenge in grizzly bear – and large carnivore – conservation is the need to understand and map their habitat requirements as well as associated risks in human-dominated landscapes, with these areas often encompassing the needs of other species (Noss et al., 1996; Cicon, 2019). This is particularly important for grizzly bears in Alberta, whereby some populations select habitats that appear suitable or perhaps confer health and/or reproductive advantages while survival remains low (Nielsen et al., 2006; 2008; 2009). Nielsen (2011) suggested that because of their large energetic (food) and area requirements, vagility, slow life-history characteristics, and sensitivity to overkill, habitat and food resource conditions that identify and preferably map source-sink areas and mortality risk are critical for long-term management and population recovery efforts.

1.2.2. Foraging

Optimal foraging theory assumes that animals will seek to maximized energy gains and fitness while limiting the costs of searching for food (Emlen, 1966; MacArthur and Pianka, 1966; Charnov, 1976). In heterogeneous landscapes, optimal foraging theory predicts that individuals should maximize energy gain in areas of high resource density while minimizing the costs of locating and transitioning between resource locations (MacArthur and Pianka, 1966; Charnov, 1976). This is particularly true for generalists, such as omnivorous grizzly bears, who must track the spatial occurrence, abundance, and quality of patchily distributed food resources while navigating seasonal changes and depletion (Wiens, 1976; Charnov, 1976; Hertel et al., 2016), which can in turn influence foraging decisions and fitness (MacArthur and Pianka, 1966). Indeed, in human-modified areas, there is the added difficultly that bears must track fluctuations in food resources that are highly dynamic while minimizing the risk of human conflict. For threatened grizzly bear populations in Alberta, once management can sufficiently limit conflict and human-caused mortality (top-down approach), the focus on recovery should be on approaches that improve habitat productivity (bottom-up; Braid and Nielsen, 2015; Braid et al., 2016) thereby boosting the recovery of bear populations (Nielsen et al., 2010). A complementary bottom-up approach (Nielsen et al., 2017) that leverages alternative food resources patterns (e.g., patchiness) in a human-modified area could prove beneficial to a threatened grizzly bear population. In the face of continued landscape change, human-dominated areas increasingly challenge the resiliency and persistence of grizzly bear populations. For that reason, bears employing alternative foraging strategies in a landscape with shifting food resources patterns, coupled with phenology and resource depletion (Wiens, 1976), may allow them to optimize dietary flexibility and macronutrient intake (Nielsen et al., 2017; Coogan et al., 2014; Erlenbach et al., 2014), thereby improving reproductive potential and ultimately fitness.

1.2.3. Disturbance and Animal Space Use

Animal space use is often associated with spatiotemporal changes in resource availability, quantity, and quality (van Beest et al., 2011, Van Moorter et al., 2013; Teitelbaum et al., 2015), despite also being linked to body size (McNab, 1963), predation risk (Lima and Dill, 1990), and intraspecific competition (Fahrig, 2007). The ability of animals to meet their resource needs depends on their ability to locate, identify, and use areas of suitable habitat (Schooley and Wiens, 2003). In general, we know little about how animal space use is affected by environments that vary considerably in resources and energy, with research mostly limited to a few taxonomic groups or geographic ranges. It is therefore important to know how expanding or shrinking habitat influences whether individuals have enough resources and space to persist indefinitely (Hirt et al., 2021), especially in areas repeatedly and heavily disturbed by humans. For example, studies have observed reductions in mammalian space use (i.e., home-range size, movement, and migration) in resource rich areas (van Beest et al., 2011; Morellet et al., 2013; Teitelbaum et al., 2015; Tucker et al., 2018). This could conceivably support higher population densities despite these areas having higher rates of disturbance related to habitat fragmentation (Devictor et al., 2008b), human barriers (e.g., human-caused mortality via roads; Boulanger and Stenhouse, 2014), and exploitation (e.g., hunting; Brodie et al., 2015). Although some species, especially carnivores, are sensitive to anthropogenic structures and can often exhibit avoidance behavior as a result (Fedriani et al., 2001), omnivores, on the other hand, may be attracted to human-modified areas with accessible food resources (Martin et al., 2010), thus potentially supporting higher densities. In addition to favorable biophysical conditions and food resources in areas disturbed by humans, omnivores may exhibit greater life history adaptations and behavioral and diet plasticity while being less constrained by morphology, making them effectively winners in human-modified areas (Šálek et al., 2015; Tucker et al., 2021). A way to quantify the cost and benefits of disturbance on foraging, fitness, and survival (Ciuti et al., 2012) is probably needed if human-modified areas are to facilitate human-wildlife coexistence in the future.

1.3. The Boreal and Foothills Forest

Among the world's four major biomes, the boreal zone is the most northerly and represents one of the largest biogeoclimatic areas. The boreal forest – which is part of boreal zone – encompasses approximately 30% of the global forest area and is characterized by large tracts of cold-tolerant tree species in mostly high-latitude regions of Canada, Russia, and Alaska (Brandt et al., 2013; Gauthier et al., 2015). Forests within this zone consist of tree species predominantly within the genera *Abies*, *Betula*, *Picea*, *Pinus*, *Populus*, and *Larix*. This zone also contains naturally treeless areas which include alpine, heathland, and grassland areas, while also including many lakes, rivers, and wetlands (Brandt 2009; Brandt et al., 2013). In addition, these forests regulate regional and global climates, sequester carbon, maintain high rates of biological and genetic diversity, and provide various socio-economic and cultural benefits to communities and global populations (Brandt, 2009; Brandt et al., 2013; Gauthier et al., 2015).

The cordilleran systems of western North America contain a diversity of ecosystems that range from forested valley bottoms to treeless alpine areas dominated by tundra, rocks, and ice. In western Canada, the foothills regions adjacent to the Rocky Mountains act as a transition zone between the mountainous ecosystems further west and the predominantly closed canopy forests of the boreal zone further east. This transition area contains tree species and understory vegetation similar to that found within the boreal forest, but in this case, better adapted to the sub-alpine and montane climates of the Rocky Mountains (Downing and Pettapiece, 2006). For instance, in west-central Alberta, subalpine fir (*Abies lasiocarpa*) as well as Engelmann spruce (*Picea engelmannii*) are generally found at higher elevations just below the treeline ecotone, whereas lodgepole pine (*Pinus contorta*) is more likely found at lower elevations, with this species readily hybridizing with the closely related jack pine (*Pinus banksiana*) – a widely distributed tree species of the boreal forest (Eckert and Hall, 2006). In addition, the Canadian Rocky Mountains region as well as the adjacent foothills contain large contiguous areas with high levels of ecological diversity supporting significant populations of carnivores and ungulates, while also providing habitat for numerous species of conservation concern (Laliberte and Ripple, 2004).

1.3.1. Forestry and Wildfire Disturbance

Disturbances in the boreal forest are important drivers of ecosystem processes as they can alter forest structure (Weber and Flannigan, 1997), contribute to landscape heterogeneity (Kumar et al., 2017), and increase biodiversity (Turner, 2010; Fedrowitz et al., 2014). Although natural and anthropogenic disturbances can affect biodiversity and the structure and function of forests in different ways (McRae et al. 2001), disturbances in general can help drive ecosystem processes that support an array of organisms, partly through the creation of habitat heterogeneity (Attiwill, 1994). In the boreal forest of Canada, the most important natural drivers of forest ecosystem dynamics are fire, insect outbreaks, diseases, and interannual variation in climate (Brandt et al., 2013), with fire being the primary disturbance agent, especially in western regions (Weber and Flannigan, 1997). Today forest harvesting is considered one of the main anthropogenic disturbance agents in the boreal forest of Canada, providing important economic benefits, although leading to different landscape patterns and vegetation dynamics compared to areas disturbed by fire (Schroeder et al., 2011).

Natural disturbances can range from frequent, low-severity, small-scale disturbances (e.g., gap dynamics) to infrequent, high-severity, large-scale stand-replacing disturbance events. Wildfire, and to a lesser extent, insect outbreaks, are considered the most dominant stand-replacing disturbance events in the boreal forest (De Grandpré et al., 2018), especially in Western Canada. In the Canadian Rocky Mountains region fire regimes tend to be dominated by high-intensity stand-replacing fires (Johnson and Fryer, 1987; Johnson and Larsen, 1991), whereas in the adjacent foothills of west-central Alberta, mixed-fire regimes are becoming increasingly more common leading to less frequent stand-replacing fires (Amoroso et al., 2011; Stockdale et al., 2016). The extent, frequency, and severity of wildfire can affect forest ecosystem dynamics in different ways. For instance, the successional stage of a forest landscape can be reset to some condition depending mostly on the time since, and severity (e.g., low-severity and high-severity) of, the most recent wildfire event, leading to a mosaic of different age class distributions, tree species composition, and regeneration patterns (Stockdale et al., 2016). Wildfires can also affect the shape of burn patches, which tend to leave ragged edges and either unburnt patches of residual trees or a single live tree, contributing to structural, biological, and landscape diversity. Residuals are critical habitat for nesting birds and denning mammals, act as thermal refuges for many species, and are especially important for old-growth specialists (McRae et al., 2001). Wildfires also influence the consumption of buried propagules (Rowe, 1983), soil nutrient cycling, and thins the organic layer promoting seedling regeneration (Greene et al., 2007). This has important implications for understory plant community composition, in which a variety of organisms depend on, leading to favorable habitat for many faunae (McRae et al., 2001).

As forest harvesting levels have steadily increased over recent decades, harvesting is now considered to be one of the main disturbance agents in the boreal forest of Canada (Schindler and Lee, 2010; Schroeder et al., 2011). The impacts of forest harvesting can differ from wildfire in important ways. For instance, the patch sizes created by forest harvesting are only a small subset of those created by wildfire and contemporary forest harvesting does not maintain the natural age-class distributions associated with wildfire. Additionally, wildfire leaves large amounts of snags and coarse woody debris, with harvesting typically leaving fewer standing trees and lower quantities of debris (McRae et al., 2001). Harvesting also affects overstory and understory plant communities, often by changing structure, composition, and diversity, especially with increasing treatment severity (Haeussler et al., 1999; Haeussler et al., 2002). Clearcut harvesting continues to be more frequently used over selection harvesting across the boreal forest of Canada because it is generally considered the most appropriate for the emulation of natural processes (Wulder et al., 2007). Moreover, canopy closure appears to recover more quickly following a harvesting event (White et al., 2017), although recovery rates of early seral vegetation are comparable when considering wildfires that occur in productive areas (Madoui et al., 2015). The removal of canopy from harvesting affects wildlife in different ways, but in general, is similar to wildfire disturbances. For instance, moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and grizzly bears (*Ursus arctos*) use early seral forests for foraging, whereas, old-growth specialists, such as caribou (*Rangifer tarandus*), marten (*Martes americana*), and fishers (*Martes pennanti*) have greater abundance in largely undisturbed old-growth forests (Fisher et al., 2005).

1.3.2. Grizzly Bears

Grizzly (brown) bears are a large, wide-ranging, omnivorous carnivore with high metabolic demands occupying a diverse range of habitats distributed throughout the Palearctic and Nearctic faunal regions. Prior to European settlement, grizzly bears were more widely distributed throughout western North America, with their range extended eastward into the prairies and southward into the grassland and chaparral ecoregions of California and Northern Mexico (Schwartz et al., 2003). In the absence of human interference, grizzly bear body size, reproductive rates, and population density are largely determined by the abundance of high-quality foods (i.e., habitat productivity) (Schwartz et al., 2003). However, human impacts on the landscape are a major conservation concern and threatened the viability of grizzly bear populations in North America, especially in human-dominated areas on the southern fringe of their distribution, where bear populations are often fragmented and isolated contributing to lower densities and lower genetic diversity (McLellan et al., 1998; Proctor et al., 2012). These conditions increase the risk of human conflict leading to increased levels of human-caused mortality, and this coupled with habitat degradation (e.g., loss and displacement), affects the continued persistence and viability of grizzly bear populations. Recovering and sustaining grizzly bear populations, particularly in human-dominated areas, requires stemming habitat degradation, enhancing productive habitats in secure locations where human conflict is minimal, and limiting human-caused mortality.

Prior to European settlement, grizzly bears maintained a continuous distribution, except perhaps in hot desert areas (Mattson and Merrill, 2002), from the Arctic Ocean to northern Mexico and from the Pacific Ocean into the riparian bottoms of the Great Plains (Herrero, 1972; Schwartz et al., 2003). After European settlement, the distribution of grizzly bears in North America was drastically reduced coinciding with increasing human density, leading to habitat degradation and human-caused mortality. In fact, grizzly bears were extirpated throughout much of their historical range (~98%) within the contiguous United States (Servheen, 1999). In Canada, grizzly bears were extirpated from part of their historical range in Manitoba, Saskatchewan, and Alberta, primarily in the prairies and boreal plains. Today local grizzly bear populations are considered vulnerable in southern portions of Canada, especially in British Columbia and Alberta. COSEWIC (2012) estimated 26,000 bears occupy portions of western Alberta, British Columbia, and the Yukon, Northwest, and Nunavut territories.

Grizzly bears are listed as a Species of Special Concern under federal legislation but have not received federal protection under the Species at Risk Act (COSEWIC, 2012). Provincially, grizzly bears were classified as Threatened by the Government of Alberta in 2010, largely due to low reproductive rates, low population size, human-caused mortality, and undetermined habitat quality (Alberta Sustainable Resource Development and Alberta Conservation Association, 2010). Recovering and sustaining viable grizzly bear populations in Alberta can be particulary challenging because habitat degradation, habitat fragmentation, and human-caused mortality and conflict associated with increasing human density contributes to isolated bear populations with lower genetic diversity and lower population density than healthier populations (McLellan et al., 1998; Proctor et al., 2012). To minimize the negative effects of increasing human density on grizzly bears, especially in the context of resource development, much attention in Alberta has focused on using the distribution and density of roads as proxies for mortality risk coupled with the identification of core habitat, where habitat quality is high and road density and access are limited (Nielsen et al., 2006; Nielsen et al., 2009; McLoughlin and Stenhouse, 2021). More recently, bear population recovery efforts in Alberta have expanded and become more focused on modelling and mapping the nutrional and energetic value of bear foods (Nielsen et al., 2010 2017; Coogan et al., 2012, 2014; López-Alfaro et al., 2013, 2014) as well using spatially explicit capture recpature approaches to determine the abundance and distribution of bears (Boulanger et al., 2018).

Grizzly bear habitat in Alberta typically consists of a mosaic of open- and closed-canopy forests (Herrero, 1972) that have been predominantly maintained by large, stand-replacing fires, and increasingly, by mixed-fire regimes, especially in the foothills (Amoroso et al., 2011). Yet large-scale timber harvesting has become increasingly more common in the Alberta foothills (Andison, 1998), and this coupled with ongoing fire suppression, has led to reductions in early seral habitat and landscape heterogeneity (Tande, 1979; Andison, 1998; Rhemtulla et al., 2002; Rogeau et al., 2016), has contributed to post-harvest stands becoming increasingly important habitat for grizzly bears in the foothills (Nielsen et al., 2004b, Nielsen et al., 2008; Kearney et al., 2019). Alpine meadows and avalanche chutes are also considered important bear habitat in the Rocky Mountains (Hamer and Herrero, 1987a; McLellan and Hovey, 2001) adjacent to the foothills. In general, these patchily distributed open habitats are favoured by grizzly bears because they provide early seral vegetation (Martin, 1983; Hamer and Herrero, 1987a; McLellan and Hovey, 1995; Nielsen et al., 2004c; Munro et al., 2006), contributing to an abundance of seasonally important bear foods such as energy-rich fruits, forbs, roots, and graminoids, with these foods also supporting higher densities of ungulate prey (Fisher and Wilkinson, 2005). Conversely, adjacent stands of mature forest provide cover that is used by bears for bedding, security with proximity to foraging areas, and to avoid thermal stress (Blanchard, 1983; Waller and Mace, 1997; Munro et al., 2006; Cristescu et al., 2015; Pigeon et al., 2016).

Grizzly bears select for a variety of open vegetation and early seral habitats such as those disturbed by forest harvesting and wildfire (Herrero, 1972; Hamer and Herrero, 1987a; Hamer and Herrero, 1987b; Nielsen et al., 2004a; Kearney et al., 2019). These open canopy habitats and habitat edges of post-harvest and post-fire stands encourage the growth of seasonally important bear foods (Nielsen et al., 2004c; Nielsen et al., 2008; Larsen et al., 2019; Souliere et al., 2020). Early seral species such as forbs, roots, graminoids, and certain fruits can respond positively to harvesting and wildfire disturbance and may proliferate as limiting resources (e.g., sunlight, favorable temperatures) become increasingly available under open canopy conditions (Zager et al., 1983; Nielsen et al., 2004c; Souliere et al., 2020). Other food sources such as *Vaccinium* spp., however, are sensitive to mechanical disturbance and/or scarification and are thus more negatively affected by such disturbance events (Martin, 1983; Zager et al., 1983; Knight, 1999, Larsen et al., 2019). As succession proceeds and the canopy closes, early seral species that grizzly bears favor are replaced by mid-to-late seral species, leading to reduced biomass of important bear foods (Martin, 1983; Visscher and Merrill, 2009; Souliere et al., 2020).

In Alberta, grizzly bears may select roads (Gibeau et al., 2002; Roever et al., 2008), agricultural lands (Northrup et al., 2012), mining areas (Cristescu et al., 2016), oil and gas sites (Mckay et al., 2014), railways (Pollock et al., 2017), seismic lines (Finnegan et al., 2018), and near town sites (Gibeau et al, 2002). Although these types of disturbances increase the supply of important bear foods, they can sometimes be located near densely populated areas, thus increasing the risk of human-caused mortality (Benn and Herrero, 2002; Nielsen et al., 2004b; Lamb et al., 2018). As attractive habitat becomes a sink, bears in these areas become more susceptible to ecological traps (Nielsen et al., 2006; Northrup et al., 2012; Lamb et al., 2016), where habitat quality and mortality risk (i.e., low survival) are high. Because of novel conditions created by such disturbances, bears may not be able to identify cues in a changing landscape as habitat quality becomes decoupled from fitness, leading to maladaptive habitat selection (Delibes et al., 2001). These attractive sinks can therefore limit the growth of grizzly bear populations. Thus, some researchers and wildlife managers have suggested that population recovery efforts should focus on enhancing and/or securing high-quality habitat in secure areas with low-road and human density and strengthened access management (Nielsen et al., 2006; Lamb et al., 2018), preferably in proximity or adjacent to wilderness areas with low human presence (Lamb et al., 2020).

1.4. Research Objectives

This thesis explores the effects of landscape change, large-scale disturbances, and food resources on grizzly bear food and habitat supply, as well as how such disturbances, and the spatial distribution of food resources, influence habitat selection, individual health (body condition), and survival (mortality risk as it relates to road density) of grizzly bears. This thesis also has the objective of broadening the scientific foundation upon which grizzly bears trade off access to food and high-quality habitat while navigating human-modified areas and patchily distributed food resources against increasing mortality risk. Moreover, the thesis aims to inform management practices (via spatial mapping) to effectively enhance food and habitat supply (*sensu* health), when constrained by elevated mortality risk and the need for high-quality and secure locations in human-modified areas – and how management scenarios can be tested and explored via individual-based modeling (IBM).

Each of the following chapters consider the effects of landscape change, disturbances, and food resources on grizzly bear food supply, habitat supply, and overall health in a human-modified area. In chapter 2, I investigated whether forest harvest areas can act as surrogates to natural wildfire disturbances with respect to grizzly bear food supply (occurrence, abundance, and digestible energy) by comparing and quantifying fruit-bearing and herbaceous grizzly bear foods among post-harvest, post-fire, and mature forests disturbance types, and across very young (~5 yrs), young (~20 yrs), and mid (~60 yrs) age-classes for post-harvest and post-fire disturbances. In chapter 3, I examined how food resource heterogeneity and homogeneity influence grizzly bear habitat selection patterns across hypophagia, mesophagia, and hyperphagia to determine to what degree do grizzly bears trade off foraging strategies (heterogeneity vs. homogeneity), depending on how food resources are spatially allocated when navigating a human-modified area. In chapter 4, I presented a novel spatially explicit individual-based model that simulates the interaction between grizzly bear agents, a spatiotemporal dynamic landscape with key grizzly bear foods, and differing road density levels for a threatened grizzly bear population in Alberta, Canada. The study aims to decouple and understand how the quality and distribution of food resources and road density influence individual health (body condition) and survival (mortality risk as it relates to roads). In chapter 5, I summarize the findings, highlight potential areas of future research, and discuss management implications in the context of the thesis.

This thesis is organized into three data chapters and follows the formatting style of *Forest Ecology and Management*.

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Chapter 2: Harvested Forests as a Surrogate to Wildfires in Relation to Grizzly Bear Food supply in west-central Alberta

2.1. Abstract

Grizzly bear (*Ursus arctos*) populations residing in interior ecosystems of North America are known to frequent harvested areas and areas burnt by wildfires, as both disturbances encourage growth of early seral vegetation preferred by them. This is especially evident in places where there is a paucity of large natural openings and areas with a long history of wildfire suppression, such as the foothill forests of west-central Alberta. Little has been done, however, to directly quantify and compare grizzly bear food supply in both disturbance types and at early stages of forest regeneration. In this paper, I explore whether harvested areas can act as surrogates to wildfires for grizzly bear food supply in west-central Alberta, Canada. I sampled known fruit-bearing and herbaceous grizzly bear foods for their occurrence, productivity, and digestible energy supply among post-harvest, post-fire, and mature forests disturbance types, and across very young (~5 yrs), young (~20 yrs), and mid (~60 yrs) age-classes for post-harvest and post-fire disturbances. A variety of foods occurred at greater frequency in post-harvest stands, with the occurrence of most foods explained by the main effects of disturbance and age-class, or in combination with one environmental covariate. Overall, fruit productivity and digestible energy from fruits were highest in the young age-class, whereas forb productivity and digestible energy from forbs were highest in the very young age-class. There were no significant differences in total available digestible energy (fruit + forb) between post-harvest and post-fire stands within any age-class, but significant differences were evident between age-classes. These results suggest that harvested areas can potentially act as a surrogate to wildfires in relation to grizzly bear food supply, but human access remains a key challenge for harvests given their

association with roads. I suggest that harvested areas could be used as management tool to maintain or enhance grizzly bear food supply and thus contribute to population recovery efforts, especially in areas of wildfire suppression.

2.2. Introduction

The role of disturbances in influencing ecosystems, species compositions, and populations are well recognized by ecologists and conservation biologists (Sousa, 1984; Petraitis et al., 1989). Disturbances are important drivers of ecosystem dynamics as they alter forest structure (Weber and Flannigan, 1997), increase species richness and diversity (Thom and Seidl, 2016), and change the rate of succession (Attiwill, 1994). Wildfires and forestry are common disturbances in boreal and cordilleran ecosystems that alter the availability of suitable habitat for species that are well adapted to disturbance, with the potential to increase overall biodiversity at local scales (Brawn et al., 2002; Turner, 2010; Fedrowitz et al., 2014).

The grizzly bear (*Ursus arctos* L., 1758) is a large omnivorous carnivore, which forages on a wide variety of plant and animal foods that vary in availability both seasonally and spatially (López-Alfaro et al., 2015; Stenset et al., 2016; Coogan et al., 2018). Diets of grizzly bear populations residing in interior ecosystems of North American typically contain high proportions of roots and ungulates during the pre-green-up period, and high proportions of herbaceous vegetation in the spring and early summer, with late-summer and early-autumn diets dominated by fruit (Mattson et al., 1991; McLellan and Hovey, 1995; Munro et al., 2006; López-Alfaro et al., 2015). Importantly, grizzly bears have been shown to have varied dietary preferences consisting primarily of lipids, carbohydrates, and proteins (Erlenbach et al., 2014), and mix their diet to consume food resources with complementary nutritional properties (Robbins et al., 2007; Coogan et al., 2014; Coogan et al., 2018). Fruit is an especially critical high-carbohydrate food resource of grizzly bears in many interior ecosystems of North America (McLellan and Hovey, 1995; Munro et al., 2006), because it allows bears to optimize their diet in a way to maximize weight gain (Coogan et al., 2014; Hertel et al., 2018). Accumulating mass (both fat and lean) is critical for over-winter survival, and is particularly important to hibernating females that produce altricial cubs in the den (Hilderbrand et al., 2000; McLellan, 2011; López-Alfaro et al., 2013). In fact, McLellan (2011) showed that grizzly bears residing in interior North America – and in particular females – with no dietary access to salmon consumed high amounts of fruits (~85%) and had higher densities than those populations that relied more heavily on meat of terrestrial species. Likewise, local grizzly bear densities in west-central Alberta were higher in areas with higher amounts of both fruit and ungulates, as opposed to either food resource on its own (Nielsen et al., 2017).

Importantly, areas disturbed by wildfire and forest harvest are frequented by foraging grizzly bears. Grizzly bear populations of interior North America are known to select for a variety of open vegetation and early seral habitats (Herrero, 1972; Hamer and Herrero, 1987). The open-canopy habitats of post-harvest and post-fire stands encourage early seral vegetation, which provides seasonally important foods that include abundant fruit-bearing species (Hamer and Herrero, 1987; McLellan and Hovey, 1995; Nielsen et al., 2004c; Munro et al., 2006). For example, grizzly bears likely benefit from foraging in early seral post-fire stands due to increases in graminoids, forbs, roots, ants, and fruiting shrubs that emerge post disturbance (Martin, 1983; Hamer and Herrero, 1987; McLellan and Hovey, 1995). Likewise, these open-canopy habitats sustain higher ungulate densities (Fisher and Wilkinson, 2005), which are a key dietary component of grizzly bears during the hypophagic period (McLellan and Hovey, 1995; Mattson, 1997; Munro et al., 2006; Stenset et al., 2016). This coupled with the fact that grizzly bear body size and condition are positively related to forestry disturbance (Zedrosser et al., 2006; Nielsen et al., 2013; Bourbonnais et al., 2014) and food resource abundance (Waller and Mace, 1997; Nielsen et al., 2004c) suggest early seral forests are important components shaping grizzly bear condition.

Fire regimes in the Canadian Rocky mountain system tend to be dominated by high-intensity stand-replacing fires (Johnson and Fryer, 1987; Johnson and Larsen, 1991). In contrast, the foothills of west-central Alberta have more mixed-severity fire regimes and less frequent stand-replacing fires (Amoroso et al., 2011). Moreover, widespread fire suppression in the area has reduced the frequency of stand-replacing fires (Andison, 1998; Rogeau et al., 2016). Consequently, this has restricted the availability of open-canopy habitats and early seral forests important to foraging grizzly bears. Thus, grizzly bears inhabiting the foothills have relatively limited access to large natural openings and fewer opportunities to forage for foods important to their diet compared to bears inhabiting mountainous areas (e.g., Canadian Rocky Mountain Parks).

Previous research, however, has shown that grizzly bears inhabiting the foothills frequent harvested areas (Nielsen et al., 2004a), as canopy removal encourages regeneration of early seral vegetation preferred by them (Martin, 1983; Nielsen et al., 2004c). Likewise, ungulates occur at higher densities in landscapes associated with post-harvest stands (Fisher and Wilkinson, 2005). Furthermore, grizzly bear body size and local abundance was noted to be highest in locations with the longest history of forest management, as favorable food supply and habitat diversity are at a greater availability to grizzly bears (Nielsen et al., 2013, 2017). In contrast to the foothills, studies in the Rocky Mountains have documented bears avoiding harvested areas in favor of naturally occurring openings and early seral habitats (Zager et al., 1983; Waller, 1992; McLellan and Hovey, 2001; Apps et al., 2004). A potential explanation for this discrepancy is that grizzly bears inhabiting the foothills have limited access to the same kind of open habitats (e.g., burns, alpine meadows) that characterize more mountainous populations. Therefore, there may be benefits in exploring whether harvested areas in the foothills can act as surrogates to relatively infrequent stand-replacing fires.

The purpose of this study was to investigate whether harvested areas can act as surrogates to natural wildfire disturbances with respect to grizzly bear food supply (occurrence, abundance, and digestible energy). Specifically, my objectives were two-fold: (1) quantify differences in food occurrence, overall productivity, and digestible energy of known grizzly bear foods between post-harvest and post-fire stands of three different age-classes; and (2) develop models to evaluate which additional variables, other than disturbance type and age-class contribute to the occurrence of local grizzly bear foods. With respect to quantifying differences in digestible energy, I hypothesized that if harvested areas represent surrogates to wildfires: 1) digestible energy from fruits, digestible energy from forbs, and total (fruit + forb) available digestible energy will not vary between post-harvest and post-fire stands; 2) whereas digestible energy from fruits, digestible energy from forbs, and total available digestible energy will vary between age-classes. I explore these questions in the foothills of west-central Alberta, Canada.

2.3. Methods

2.3.1. *Study area*

The study area (Fig. 2.1) is located in west-central Alberta, Canada (approximate location 53°24′N, 117°33′W) and includes portions of the eastern slopes of the Rocky Mountains and Foothills, with the western and eastern areas characterized by mountainous terrain and foothills, respectively. I chose this area because wildfire and forestry have been the primary disturbance agents since the 1950s (Andison, 1998). Furthermore, I focused the sampling entirely within the upper foothills subregion because concurrently sampling both the upper and lower foothills subregions was not logistically feasible, and the grizzly bear population density is higher in the upper foothills, with estimates of 5–10 bears per 1000 km^2 (Boulanger et al., 2018). The upper foothills are distinguished from the lower foothills by higher precipitation and a lower average temperature, and the climate is continental with a mean annual temperature of 1.3 °C and a mean annual precipitation of 632 mm (Natural Regions Committee, 2006). Most of the area is public land managed by the province and zoned for multiples uses, with forestry and development from the energy sector (oil and gas, coal mining) being the primary human activity. The foothills are dominated by forests and support a range of habitats with lodgepole pine (*Pinus contorta*) being the most common tree species. Mesic upland sites at higher elevation are composed of mix stands of lodgepole pine, white spruce (*Picea glauca*), and trembling aspen (*Populus tremuloides*), whereas wet lowland sites at lower elevation are composed of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) bogs.

2.3.2. Wildfire and forestry

Historically, the eastern slopes of the Rocky Mountains and Foothills were characterized as a mixed-fire severity regime, with frequent low severity fires overlapping infrequent high-severity fires (Amoroso et al., 2011; Davis et al., 2016; Rogeau et al., 2016). This past century, however, has seen an increase in fire suppression and departure from historical fire regimes leading to less stand-replacing fires and consequently a longer fire cycle (Tande, 1979; Andison, 1998; Davis et al., 2016; Rogeau et al., 2016). With the foothills being dominated by productive forests (Andison, 1998), large-scale timber harvesting has become the main disturbance agent replacing natural wildfire in this region.

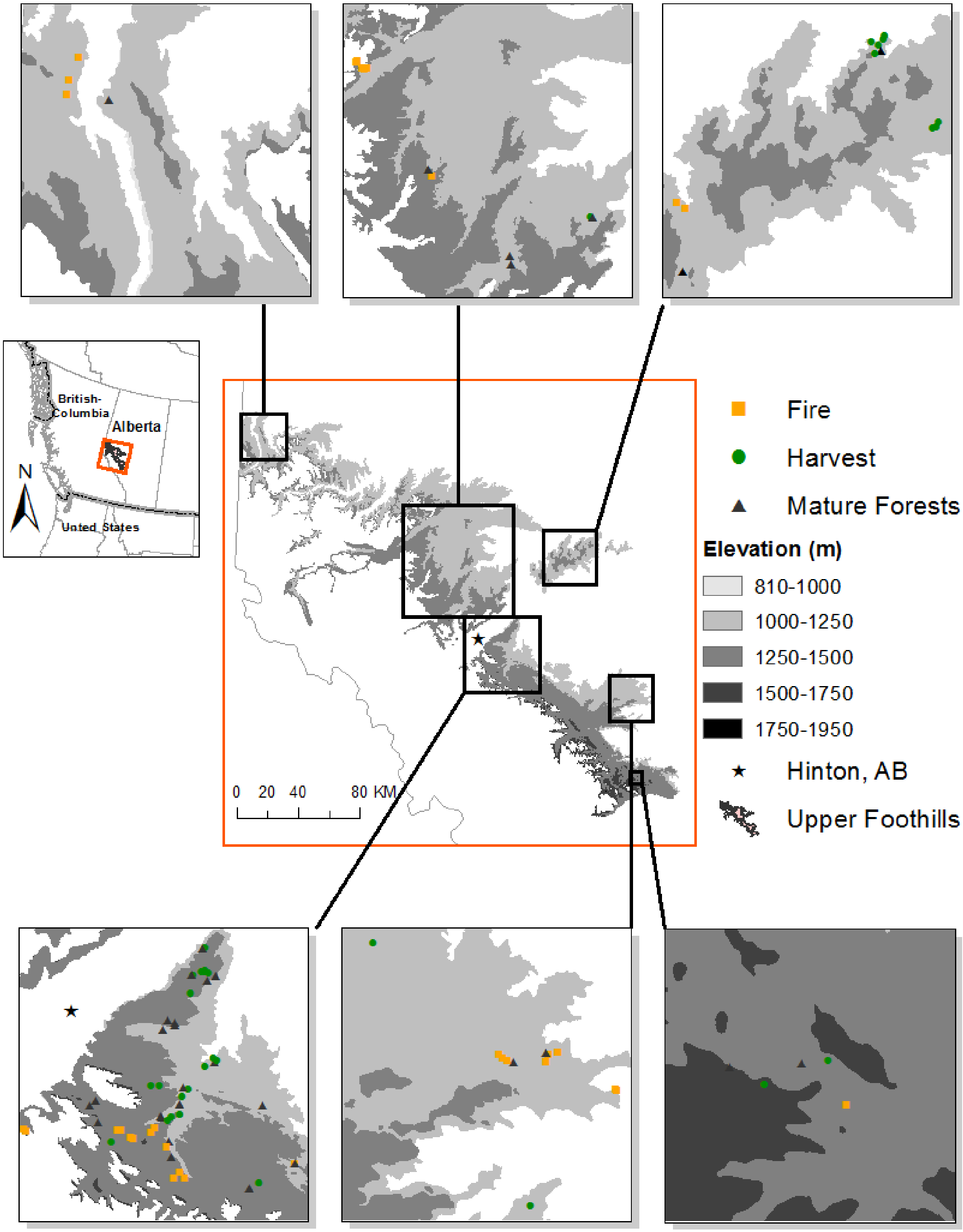


Fig. 2.1. Study area depicting sampling sites located within the upper foothills subregion of Alberta, Canada. The extent and elevational gradients of the upper foothills are shown, including the location of Hinton, AB. The middle panel shows the full sampling extent and inset boundaries of the upper and lower panels.

2.3.3. Field plots and data recording

In the summer of 2017 (late June – late August) I sampled 33 sites in each of the three disturbance types: post-harvest stands, post-fire stands, and reference mature forests. All mature forest stands were largely undisturbed by human activities and dominated by coniferous species, which represents older forests (> 80 years old) in the area (Andison, 1998). The same sampling procedure was used among the three disturbance types. I used a combination of previously sampled sites (Nielsen et al., 2004c) and a 25-m Landsat-derived wildlife habitat classification product (approximately 90% of sampled sites; Nijland et al., 2015) to identify random plot coordinates based on forest harvests data (ABMI Human Footprint Inventory, 2016) and wildfire spatial inventory data (Alberta Wildfire, 2017). I randomly stratified plot locations between both post-harvest and post-fire disturbances according to different age-classes, to ensure proportionality of three successional stages (very young: ~5 yrs; young: ~20 yrs; and mid: ~60 yrs). I choose the very young and young age-classes because they are characterized by early seral vegetation, which provides a diverse array of seasonally important foods critical to bear diets (Hamer and Herrero, 1987; McLellan and Hovey, 1995; Nielsen et al., 2004c; Munro et al., 2006), whereas the mid age-class lacks early seral vegetation because of canopy closure related to forest succession (Kneeshaw and Bergeron, 1998). However, I did sample the mid age-class because the occurrence of some species has been shown to increase with canopy cover (e.g., cow parsnip, *Heracleum lanatum*; Nielsen et al., 2004c). Forest age (age-class) was not considered among mature forests because stands are considered to be > 80 years old (Andison, 1998).

At each field-sampling site, I first quantified plant and ant (Formicidae spp.) occurrence within a 50 × 20 m belt transect (0.1 ha) that ran south-to-north. I then estimated the abundance of thirteen berry-producing shrubs and four herbaceous plants (three forbs and one green vegetation) in a 50 × 2 m belt transect (0.01 ha) located within the 0.1 ha belt transect. These bear food items are considered important to the diet of grizzly bears in west-central Alberta (Hamer and Herrero, 1987; Hamer, 1996; Hamer, 1999; McLellan and Hovey, 1995; Nielsen et al., 2004c; Munro et al., 2006). Sweetvetch (*Hedysarum* spp.) roots and ungulate species, as indicated by pellet counts, were recorded, but not further analyzed here because of low prevalence. For ground dwelling shrubs (< 0.5 m in height) and herbaceous plants, ten herbaceous quadrats (0.5 m^2) were established at 5-m intervals along the midline of the belt transect to record percent cover, number of berries, and number of herbaceous plants. Within each quadrat I recorded seven ground-dwelling shrubs and four herbaceous plants. The shrubs include: bearberry (*Arctostaphylos uva-ursi*), strawberry (*Fragaria virginiana*), raspberry (*Rubus idaeus*), dwarf bilberry (*Vaccinium caespitosum*), huckleberry (*Vaccinium membranaceum*), blueberry (*Vaccinium myrtilloides*), and lingonberry (*Vaccinium vitis-idaea*). The herbaceous plants include: horsetail (*Equisetum* spp.), cow parsnip (*Heracleum lanatum*), dandelion (*Taraxacum officinale*), and clover (*Trifolium* spp.). For large shrubs (≥ 0.5 m in height), I not only counted the number of shrubs (density), but also the number of berries that fell within the 2-m belt transect. The shrubs include: black twinberry (*Lonicera involucrata*), currant and gooseberry (*Ribes* spp.), buffaloberry (*Shepherdia canadensis*), western mountain-ash (*Sorbus scopulina*), and lowbursh cranberry (*Viburnum edule*). The recorded presence of ant colonies that occurred in logs, stumps, or mounds were pooled together within the 0.1 ha belt transect. Finally, within each belt transect, canopy cover was measured with a spherical densiometer, as canopy is considered a good predictor of occurrence and abundance of bear food items (Nielsen et al., 2004c). Four measurements from each cardinal direction were taken at 5-m intervals along the midline of the belt transect and averaged within each interval and across the entire transect.

2.3.4. Statistical analyses

2.3.4.1. Food occurrence and distribution

I used logistic regression to contrast the occurrence of 18 grizzly bear food items for target (T) and reference (R) categories, that being: post-harvest (T) vs. post-fire (R), post-harvest (T) vs. mature forests (R), and post-fire (T) vs. mature forests (R). Logistic regression results are reported with beta coefficients and odds ratios, with the reference category being post-fire stands when compared to post-harvest stands, and mature forests otherwise. I interpret the odds ratio as the odds that a grizzly bear food item occurred in the target category compared with that of the reference category for each age-class. An odds ratio > 1 can be interpreted as higher occurrence in the target category, whereas an odds ratio < 1 can be interpreted as higher occurrence in the reference category. I grouped species into three broad categories, which include shrub-fruit (plant height ≥ 50 cm), dwarf shrub-fruit (plant height < 50 cm), and forb (including horsetail) and ants.

Table 2.1. Model structure of eight *a priori* candidate models used to assess the occurrence of grizzly bear food items in post-harvest and post-fire stands. The covariates include: combined disturbance and age-class (DIST_AGE), elevation (ELEV), canopy cover (CAN), and compound topographic index (CTI).

Model Structure	K
DIST_AGE	2
DIST_AGE + ELEV	3
DIST_AGE + ELEV + CAN	4
DIST_AGE + ELEV + CTI	4
DIST_AGE + CAN	3
DIST_AGE + CTI	3
DIST_AGE + CAN + CTI	4
DIST_AGE + ELEV + CAN + CTI	5

I also examined the distribution (occurrence) of 18 grizzly bear food items against predictor variables previously used to predict bear food occurrence (Nielsen et al., 2004c; Braid and Nielsen, 2015) in foothills of Alberta. The predictor variables include: combined disturbance and age-class (DIST_AGE), elevation (ELEV), a soil wetness index referred to as the compound topographic index (CTI) that is used as a proxy for soil conditions, and a field-based measure of canopy cover (CAN). I used these predictor variables in combination to develop 8 *a priori* candidate models (Table 2.1) and evaluated which model best predicted the occurrence of each food item using Akaike information criteria with a small sample size correction (AICc; Burnham and Anderson, 2002). Collinearity among predictor variables was assessed with Pearson's Correlation (r) with all variables assumed to be uncorrelated $r < |0.7|$ (Swets, 1988). I used area under the curve (AUC) of the receiver operating characteristic (ROC) to assess model accuracy (Fawcett, 2006), with AUC values < 0.7 and ≥ 0.7 representing poor model accuracy and good model accuracy, respectively (Swets, 1988).

Finally, I created separate models to estimate and plot the probability of occurrence of each food item in relation to canopy cover using a global model structure with quadratic terms (DIST + AGE + AGE^2 + CAN + CAN^2 + ELEV + ELEV^2 + CTI + CTI^2), while holding all other variables in the global model at their mean level. Here, age was treated as continuous variable in order to provide a visual interpretation of the predicted nonlinear responses for both post-harvest and post-fire disturbances.

2.3.4.2. Food productivity and energy

I assessed fruit (berry) and forb productivity for 17 grizzly bear foods using Mann-Whitney *U*-tests. For each bear food item, I estimated average density on a per hectare basis between post-harvest, post-fire, and mature forests, and among the three age-classes. I did not assess ant density because ant abundance was not recorded in this study.

I estimated the digestible energy from fruit on a per hectare basis by converting the total number of berries for 12 fruiting species into a measure of digestible energy using the following equations:

$$\text{dig\_ene}_\text{i} = \text{fruit count } \left(\frac{\text{berry}}{\text{ha}}\right) \text{X fruit DM}_\text{i} \left(\frac{\text{gram DM}}{\text{berry}}\right) \text{X digestible energy } \left(\frac{\text{kcal}}{\text{gram DM}}\right)$$

$$\text{digestible energy} = \sum_{\text{i}=1}^{\text{n}} \text{dig\_ene}_\text{i}$$

DM = Dry Mass

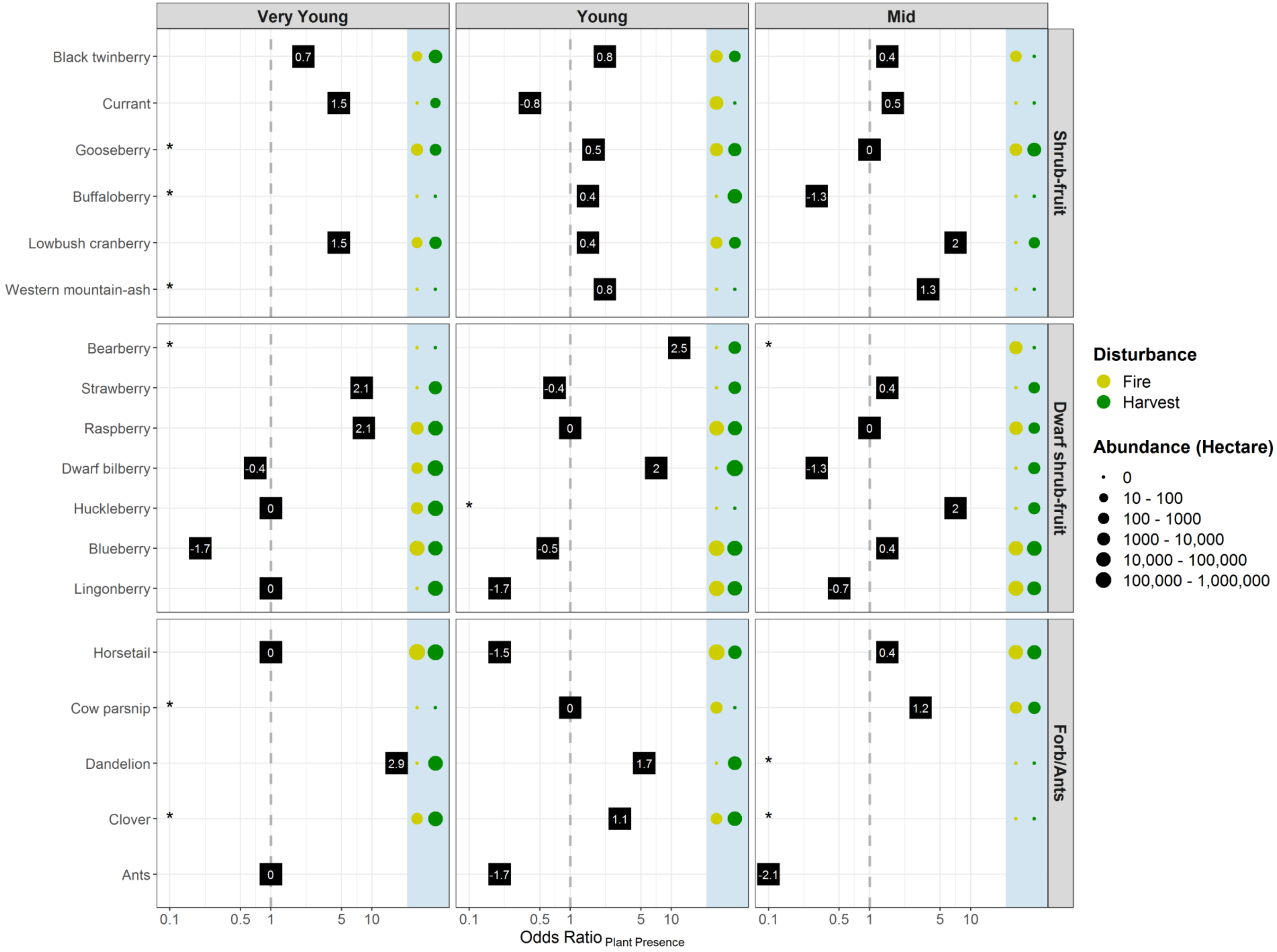
Digestible energy conversions were obtained from López-Alfaro et al. (2015), and fruit dry weights (mass in g) were estimated using data from the literature (Appendix 2.1). I also estimated the digestible energy of four herbaceous plants on a per hectare basis by converting percent cover into biomass (g dry weight) using allometric conversion equations (Nielsen et al., 2015), with this further converted into digestible energy following López-Alfaro et al. (2015). I summed digestible energy from fruits and forbs to estimate the total digestible energy available from these foods. Finally, I estimated total available digestible energy in the upper foothills by multiplying the average energy per hectare by the area disturbed by forestry and fire in the study area, respectively. I did not have access to reliable data needed to estimate average digestible energy per hectare for mature forests.

To evaluate whether digestible energy varied as a function of disturbance and age-class, I conducted three separate two-way ANOVAs that examined the effect of disturbance, age-class, and the interaction between disturbance and age-class (model: $(\text{digestible energy})^{0.5}$ = disturbance + age-class + disturbance * age-class) on digestible energy from fruits, digestible energy from forbs, and total available digestible energy, respectively. All digestible energy variations were square root transformed. I used a post hoc Tukey HSD test following a significant ANOVA, where all tests were considered significant at $\alpha \leq 0.05$. I conducted all analyses in R v3.5.0 (R Core Team, 2018).

2.4. Results

2.4.1. Food occurrence in harvest and fire

Among the very young age-class, six species had greater presence in post-harvest stands compared to post-fire stands (Fig. 2.2). These species included black twinberry, currant, lowbush cranberry, strawberry, raspberry, and dandelion. Among both the young and mid age-classes, each had nine species with greater presence in post-harvest stands compared to post-fire stands. For the young age-class, these included: black twinberry, gooseberry, buffaloberry, lowbush cranberry, western mountain-ash, bearberry, dwarf bilberry, dandelion, and clover. For the mid age-class, these included: black twinberry, currant, lowbush cranberry, western mountain-ash, strawberry, huckleberry, blueberry, horsetail, and cow parsnip. Overall, only two species had greater presence in post-harvest stands for all three age-classes, which included black twinberry and lowbush cranberry. In general, most species within the shrub-fruit category (plant height ≥50 cm) were more likely to occur in post-harvest stands, whereas no clear pattern of presence was evident for species within the dwarf-shrub fruit (plant height < 50 cm) and forb and ants categories, respectively (Fig. 2.2). As a general pattern, however, and apart from a few exceptions, *Vaccinium* spp. and ants were more likely to occur in post-fire stands compared with post-harvest stands. The average odds ratio for *Vaccinium* spp. (apart from dwarf bilberry in the young age-class and huckleberry the mid age-class) was 0.65 with 95% CIs ranging from a low of 0.1 to a high of 2.6. For ants, the average odds ratio was 0.44 with 95% CIs ranging from a low of 0.1 to a high of 1.8.



Very Young
Young
Mid
Shrub-fruit
Dwarf shrub-fruit
Forb/Ants
Black twinberry
Currant
Gooseberry
Buffaloberry
Lowbush cranberry
Western mountain-ash
Bearberry
Strawberry
Raspberry
Dwarf bilberry
Huckleberry
Blueberry
Lingonberry
Horsetail
Cow parsnip
Dandelion
Clover
Ants
0.7
1.5
*
*
1.5
*
*
2.1
2.1
-0.4
0
-1.7
0
0
*
2.9
*
0
0.8
-0.8
0.5
0.4
0.4
0.8
2.5
-0.4
0
2
*
-0.5
-1.7
-1.5
0
1.7
1.1
-1.7
0.4
0.5
0
-1.3
2
1.3
*
0.4
0
-1.3
2
0.4
-0.7
0.4
1.2
*
*
-2.1
0.1
0.5
1
5
10
Odds Ratio Plant Presence
Disturbance
Fire
Harvest
Abundance (Hectare)
0
10 - 100
100 - 1000
1000 - 10,000
10,000 - 100,000
100,000 - 1,000,000

Fig. 2.2. Estimated odds ratios (black squares) and beta coefficients (white text embedded in black squares) from logistic regression models describing the occurrence of 18 grizzly bear food items between post-harvest and post-fire stands by age-class. Odds ratios represent the odds of finding bear foods items in post-harvest stands compared to post-fire stands within each age-class. Positive beta coefficients indicate a greater occurrence of bear food items in post-harvest stands, whereas negative coefficients indicate greater occurrence in post-fire stands. Colored circles within the shaded section represent the average berry density for shrub-fruit (plant height ≥ 50 cm) and dwarf-shrub fruit (plant height < 50 cm) categories, and the average stem density for the forb and ants category, on a per hectare basis for 17 grizzly bear food items in post-harvest and post-fire stands. Abundance estimates for ants are absent as this was not recorded in this study. Asterisks indicate bear food items with models that failed to converge.

2.4.2. Distribution of foods

Based on AICc rankings in Table 2.2, there was moderate variation in support of the eight *a priori* candidate models listed in Table 2.1. Model DIST_AGE ranked highest for five of the eighteen grizzly bear food species, including buffaloberry and huckleberry which are critical bear foods. In contrast, model DIST_AGE + CAN ranked highest for bearberry and ants. Apart from huckleberry, the top ranked models for *Vaccinium* spp. included at least one environmental covariate other than DIST_AGE. Using likelihood ratio (χ^2) tests, I found 12 AICc-selected models (Table 2.2) to be significant ($\alpha < 0.05$), while six were not found to be significant including: black twinberry, currant, lowbush cranberry, western mountain-ash, raspberry, and horsetail. The percent deviance explained varied from a low of 4.9% for black twinberry to a high of 50.8% for dandelion. Overall, *Vaccinium* spp. and forbs (other than horsetail) generally had higher values of percent deviance explained. Classification accuracy (AUC) proved poor (< 0.7) for 7 of the 18 grizzly bear food species and good (≥ 0.7) for the remaining 11 species.

Overall, nonlinear responses in occurrence against canopy cover (Fig. 2.4) were similar between post-harvest and post-fire stands for most food items. Buffaloberry peaked at intermediate levels of canopy, while most species categorized as dwarf-shrub fruit (plant height < 50 cm) peaked at lower levels and dropped precipitously at higher levels, except for huckleberry, blueberry, and strawberry. Ants also peaked at lower levels of canopy cover and decreased as canopy increased, while cow parsnip increased with increasing canopy.

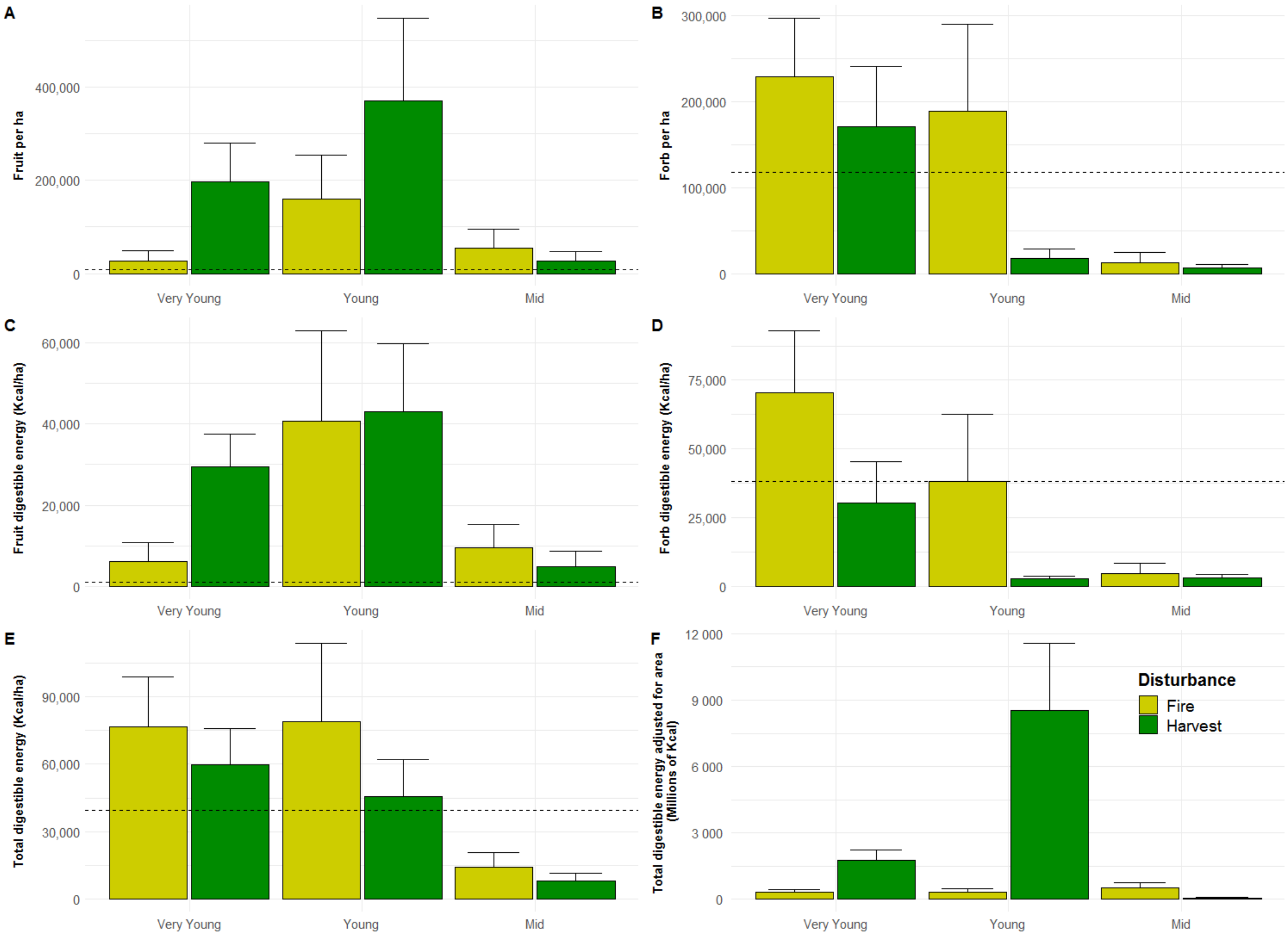
2.4.3. Fruit productivity and digestible energy in harvest and fire

Among all age-classes (Fig. 2.2), *Vaccinium* spp. and raspberry were often the most productive food items in terms of berry productivity in both post-harvest and post-fire stands, whereas species within the shrub-fruit (plant height ≥ 50 cm) category were not as productive overall. Important grizzly bear foods such as huckleberry and buffaloberry showed contrasting results, with huckleberry being more productive overall. In each age-class, the food items with the highest berry productivity always occurred in post-harvest stands (Fig. 2.2). Average fruit production peaked in the young age-class for both post-harvest and post-fire stands (Fig. 2.3; Panel A). When comparing between post-harvest and post-fire stands, berry productivity was highest in the very young and young age-classes of post-harvest stands, whereas the opposite pattern occurred in the mid age-class (Fig. 2.3; Panel A). Mann-Whitney *U*-tests ($\alpha < 0.05$) revealed that only one species significantly differed in fruit production when comparing between disturbances and among the same age-class. In this case, dwarf bilberry in post-harvest stands of the young age-class differed from post-fire stands of the same age-class ($U = 88$, $P = 0.016$).

Overall, patterns of digestible energy from fruits were similar to fruit productivity, with digestible energy peaking in the young age-class (Fig. 2.3; Panel C). When comparing between post-harvest and post-fire stands, digestible energy was highest in very young and young age-classes of post-harvest stands, albeit only marginally for the young age-class. When looking at digestible energy from fruits, the main effect of age-class was significant ($F(2, 60) = 3.693$, $p = 0.031$, $\eta_p^2 = 0.110$), whereas the main effect of disturbance was not significant ($F(1, 60) = 1.928$, $p = 0.170$, $\eta_p^2 = 0.031$). The interaction effect between disturbance and age-class was likewise not significant ($F(2,60 = 1.598$, $p = 0.211$, $\eta_p^2 = 0.051$). A *post hoc* Tukey HSD test revealed that the mid age-class significantly differed from the young age-class ($p = 0.023$).

Table 2.2. AICc top-selected models that best describe the occurrence of 18 grizzly bear food items in post-harvest stands, post-fire stands, and mature forests of west-central Alberta. For each species, an AICc score is provided for both the null and top ranked model, as well as, likelihood ratio (χ^2) tests, statistical significance values (*p*), area under the curve (AUC), and percent deviance explained. List of model structures can be found in Table 2.1.

Grizzly bear food item		Null model	AICc-selected model					
Category	Species Name	AIC_c	Model Structure	AIC_c	LR χ^2	*p*	AUC	% Dev. Explained
Shrub-fruit	Black twinberry	139.03	DIST_AGE + ELEV	148.15	6.74	0.456	0.66	4.92
	Currant	123.50	DIST_AGE + CTI	126.40	12.66	0.081	0.71	10.42
	Gooseberry	128.07	DIST_AGE	127.29	13.97	0.03	0.69	11.09
	Buffaloberry	101.67	DIST_AGE	98.51	16.35	0.012	0.75	16.41
	Lowbush cranberry	137.57	DIST_AGE + CAN	139.74	13.40	0.063	0.68	9.88
	Western mountain-ash	92.84	DIST_AGE	96.46	9.58	0.144	0.69	10.55
Dwarf shrub-fruit	Bearberry	82.73	DIST_AGE + CAN	68.24	30.05	<0.001	0.90	37.24
	Strawberry	139.27	DIST_AGE	139.69	12.77	0.047	0.69	9.31
	Raspberry	136.35	DIST_AGE	138.91	10.63	0.1	0.66	7.92
	Dwarf bilberry	128.07	DIST_AGE + CAN + CTI	122.06	23.99	0.002	0.80	19.04
	Huckleberry	113.93	DIST_AGE	108.52	18.6	0.005	0.73	16.62
	Blueberry	126.64	DIST_AGE + ELEV	107.83	34.37	<0.001	0.84	27.58
	Lingonberry	137.57	DIST_AGE + ELEV + CAN	134.40	21.15	0.007	0.77	15.60
Forb/Ants	Horsetail	135.62	DIST_AGE	139.91	8.89	0.180	0.66	6.66
	Cow parsnip	89.62	DIST_AGE	87.76	15.05	0.020	0.76	17.19
	Dandelion	109.37	DIST_AGE + CTI	70.45	54.48	<0.001	0.93	50.76
	Clover	111.71	DIST_AGE	81.31	43.58	<0.001	0.86	39.74
	Ants	125.11	DIST_AGE + CAN	106.32	34.35	<0.001	0.84	27.91



A
Fruit per ha
400,000
200,000
0
Very Young
Young
Mid
B
Forb per ha
300,000
200,000
100,000
0
Very Young
Young
Mid
C
Fruit digestible energy (Kcal/ha)
60,000
40,000
20,000
0
Very Young
Young
Mid
D
Forb digestible energy (Kcal/ha)
75,000
50,000
25,000
0
Very Young
Young
Mid
E
Total digestible energy (Kcal/ha)
90,000
60,000
30,000
0
Very Young
Young
Mid
F
Total digestible energy adjusted for area (Millions of Kcal)
12 000
9 000
6 000
3 000
0
Very Young
Young
Mid
Disturbance
Fire
Harvest

Fig. 2.3. Productivity and digestible energy differences (+SE) between post-harvest and post-fire stands for each age-class. Panel A depicts fruit (berry) density from 12 fruiting species, excluding western mountain-ash. Panel B depicts forb density from four species (horsetail, cow parsnip, dandelion, and clover). Panel C depicts digestible energy from fruits with the same 12 species used in panel A. Panel D depicts digestible energy from forbs with the same four species used in panel B. Panel E depicts the combined total available digestible energy from fruits and forbs. Panel F depicts total available digestible energy adjusted for actual area of disturbance on the landscape of the upper foothills of this study area. The black dotted lines refer to mature forests; this line is absent from panel F because I did not have access to reliable data needed to estimate this value.

2.4.4. Forb productivity and digestible energy in harvest and fire

Among the forb and ants category (Fig. 2.2), horsetail was productive among both disturbances and all age-classes, albeit slightly more productive in post-fire stands. Dandelion and clover were more productive in the very young and young age-classes, whereas cow parsnip was productive in the mid age-class. For both post-harvest and post-fire stands (Fig. 2.3; Panel B), forb density peaked in the very young age-class. In the young age-class, density dropped precipitously in post-harvest stands and only slightly in post-fire stands. Mann-Whitney U-tests ($\alpha < 0.05$) revealed that two species differed in forb productivity between disturbances and among age-classes, including horsetail in the young age-class ($U = 22.5$, $P = 0.001$), and dandelion in the very young age-class ($U = 82.5$, $P = 0.036$).

Overall, patterns of digestible energy from forbs were similar to forb density, with digestible energy peaking in the very young age-class of both disturbances, and digestible energy levels highest in post-fire stands across all age classes (Fig. 2.3; Panel D). When looking at digestible energy from forbs, both age-class ($F(2, 60) = 8.966$, $p < 0.001$, $\eta_p^2 = 0.230$) and disturbance ($F(1, 60) = 4.906$, $p = 0.031$, $\eta_p^2 = 0.076$) were significant, whereas the interaction between disturbance and age-class was not significant ($F(2, 60) = 1.426$, $p = 0.248$, $\eta_p^2 = 0.045$). A *post hoc* Tukey HSD test revealed that the very young age-class significantly differed from both the young age-class ($p = 0.028$) and mid age-class ($p < 0.001$), while the young age-class did not significantly differ from the mid age-class ($p = 0.278$).

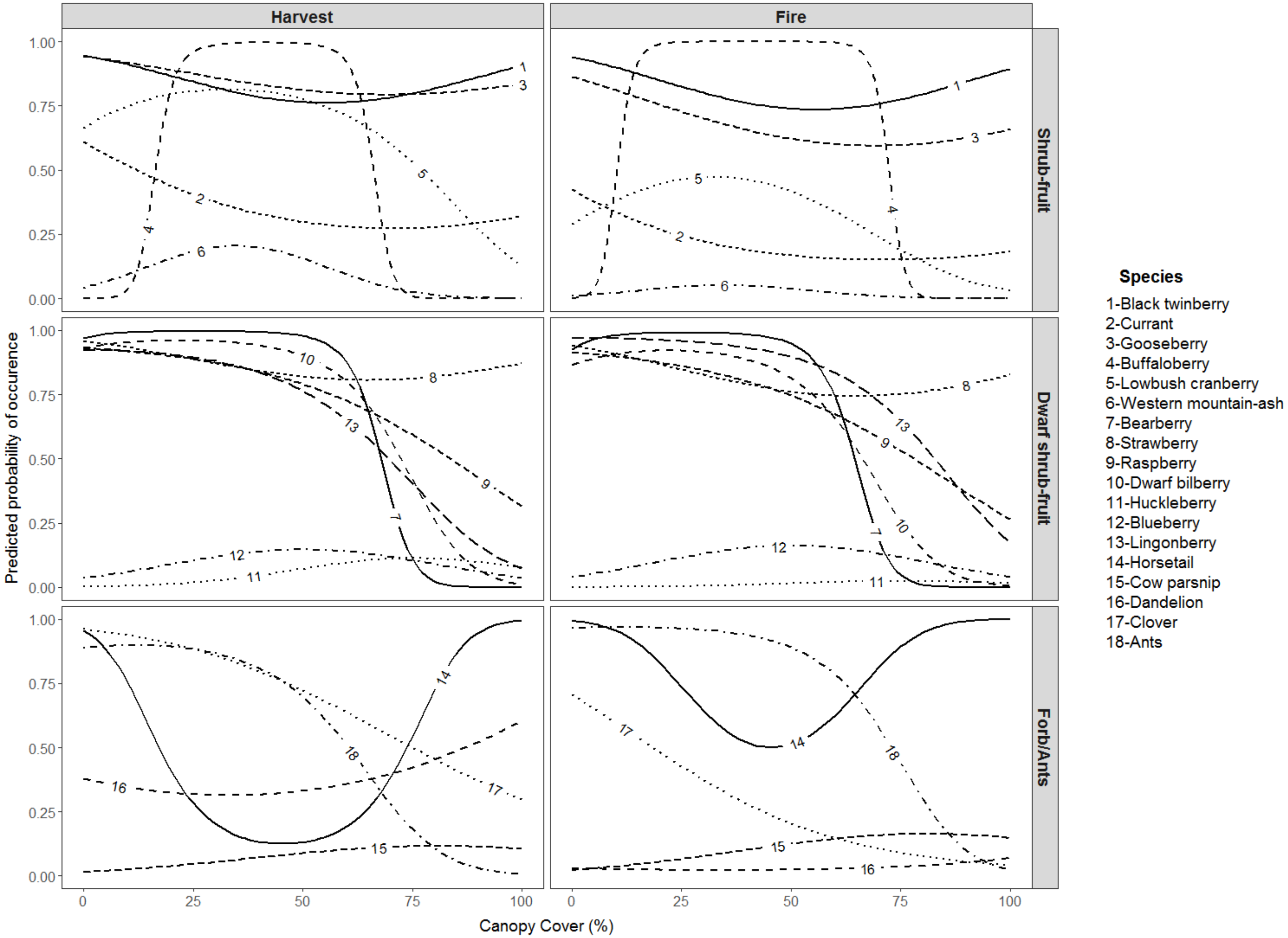


Fig. 2.4. Predicted probability of occurrence of bear food items as a function of canopy cover in post-harvest and post-fire stands. Environmental covariates in the global model were held at their mean level. Numbers embedded within each line correspond to the associated bear food item located within the legend.

2.4.5. Total available digestible energy in harvest and fire

Overall, patterns of total available digestible energy were highest in post-fire stands across all age-classes, with the highest digestible energy levels in the very young and young age-classes for both disturbances (Fig. 2.3; Panel E). Results indicated that the main effect of age-class was significant ($F(2, 60) = 7.446$, $p = 0.001$, $\eta_p^2 = 0.199$), whereas the main effect of disturbance was not significant ($F(1, 60) = 0.300$, $p = 0.586$, $\eta_p^2 = 0.005$). The interaction between disturbance and age-class was also not significant ($F(2, 60) = 0.003$, $p = 0.997$, $\eta_p^2 = 0$). A *post hoc* Tukey HSD test revealed that the mid age-class significantly differed from both the very young ($p = 0.021$) and young age-classes ($p = 0.001$). When adjusting total available digestible energy in each disturbance and age-class for actual area disturbed in the upper foothills of the study area, I found that the amount of total available digestible energy was approximately 5× greater in the very young age-class and 26 × greater in young age-class of post-harvest stands. In contrast, total available digestible energy was approximately 9 × greater in the mid age-class of post-fire stands (Fig. 2.3; Panel F).

Table 2.3. Odds ratios describing the occurrence of important grizzly bear food items in post-fire and post-harvest stands compared to mature forests alone, with 95% confidence intervals in parentheses. Asterisks indicate no recorded presence.

Species	Very Young		Young		Mid	
	Fire	Harvest	Fire	Harvest	Fire	Harvest
Buffaloberry	*	*	2.1 (1.1, 4.0)	3 (1.6, 5.7)	1.4 (0.7, 2.7)	0.4 (0.2, 0.9)
Huckleberry	1.7(0.9, 3.3)	1.7 (0.9, 3.3)	*	1 (0.5, 2.0)	1.7(0.9, 3.3)	12 (6.1, 23.4)
Horsetail	1.3 (0.7, 2.4)	1.3 (0.7, 2.4)	1.3 (0.7, 2.4)	0.3 (0.2, 0.5)	0.3 (0.2, 0.5)	0.4 (0.2, 0.7)
Cow parsnip	0.7 (0.3, 1.8)	*	0.7 (0.3, 1.8)	0.7 (0.3, 1.8)	2.7 (1.3, 5.7)	8.7 (4.2, 17.8)
Clover	*	45 (19, 105)	5.7 (2.6, 12.6)	17.5 (7.9, 38.6)	1 (0.4, 2.6)	*
Ants	5.7 (2.6, 12.6)	5.7 (2.6, 12.6)	45 (19.1, 105)	8.3 (3.8, 18.3)	8.3 (3.8, 18.3)	1 (0.4, 2.6)

2.5. Discussion

These results suggest that harvested areas can potentially act as a surrogate to wildfire disturbances for grizzly bears inhabiting west-central Alberta. Grizzly bears in the study area have been shown to select for harvested areas (Nielsen et al., 2004a) – similar to bears in other parts of interior of North America (Ciarniello et al., 2007) and Scandinavia (Moe et al., 2007) – which provide a diverse range of food resources (Martin, 1983; Nielsen et al., 2004c) needed for optimal dietary intake (Robbins et al., 2007; Coogan et al., 2014), with this complementary diet being positively associated with local population density (Nielsen et al., 2017) and fitness (McLellan, 2011; Erlenbach et al., 2014). Because west-central Alberta generally lacks large naturally occurring open-canopy habitats, harvested areas may be an attractive alternative to bears on a fire-suppressed landscape. Indeed, sites disturbed by humans may allow bears to exploit preferred foods on habitats that are functionally similar to large natural openings and early seral fire-regenerated habitats (Nielsen et al., 2004a). For instance, in Yellowstone National Park, declines in cutthroat trout has paralleled an increase in predation rates on elk neonates (Middleton et al., 2013), suggesting a shift in grizzly bear foraging behavior as a consequence of human actions. Even so, any benefits that bears derive from foraging in harvested areas may be offset by an elevated mortality risk due to increased human access, primarily via roads (Nielsen et al., 2004b; Boulanger and Stenhouse, 2014).

When comparing the occurrence of food items in post-harvest and post-fire stands, only black twinberry and lowbush cranberry occurred at higher frequencies in post-harvest stands for all three age-classes. Harvesting appeared to benefit these large shrub species, suggesting that rhizome disturbance and canopy removal may help explain deviation from post-fires stands. Overall, a greater number of species occurred at higher frequencies in the young and mid age-classes compared to the very young age-class, suggesting canopy cover is positively related to the occurrence of a greater number of species overall (Nielsen et al., 2004c). In contrast, blueberry and lingonberry were more likely to occur in post-fire stands, suggesting that harvesting negatively affected their occurrence, especially among the very young and young age-classes. This result is consistent with previous studies which found blueberry and lingonberry to be sensitive to recent harvesting events (Haeussler et al., 1999; Roberts and Zhu, 2002, Nielsen et al., 2004c), likely resulting in destroyed rhizomes (Zager et al., 1983). Clover and dandelion of the young age-class were more likely to occur in post-harvest stands, similar to previous studies showing favorable responses of these exotic species to harvesting (Haeussler et al., 1999; Roberts and Zhu, 2002; Nielsen et al., 2004c). Among critical foods consumed by grizzly bears (McLellan and Hovey, 1995; Nielsen et al., 2004c; Munro et al., 2006), buffaloberry and huckleberry had greater occurrence in the mid age-class of post-fire and post-harvest stands, respectively. Soil scarification has been suggested to negatively affect the occurrence and abundance of buffaloberry (Knight, 1999; Nielsen et al., 2004c), which may partially account for the absence in the very young age-class of post-harvest stands and the greater occurrence in the mid age-class of post-fire stands; although Hamer (1996) showed that fruit production was negatively associated with forest canopy cover in 50-year old burns. Soil scarification is also speculated to destroy the rhizomes of huckleberry and thus prevent vegetative propagation, especially for recent (< 25 years) harvesting events (Martin, 1983). I suspect, however, that the effect of soil scarification on huckleberry in post-harvest stands may be negligible following sufficient forest recovery (e.g., 60 years), as can be seen when comparing post-harvest stands to mature forests alone (Table 2.3). Overall, ants had higher frequency of occurrence in post-fire stands in each of the three age-classes, and similarly, in post-harvest stands of the very young and young age-classes when compared to mature forests alone (Table 2.3). This is consistent with previous studies showing the favorable response of ants to fire and harvesting in temperate forests (Punttila et al., 1991; Nielsen et al., 2004c; Palladini et al., 2007).

Among both post-harvest and post-fire disturbances, fruit productivity was often highest among *Vaccinium* spp. Previous studies, looking at fruit productivity in coniferous stands, have also reported high productivity levels of *Vaccinium* spp. (Noyce and Coy, 1990; Nielsen et al., 2004c; Larsen et al., 2019). When comparing between disturbances, fruit production was highest in the very young and young age-classes of post-harvest stands, whereas for the mid age-class, productivity was highest in post-fire stands. The general pattern among both disturbances saw productivity peak in the young age-class, while falling sharply in the mid age-class. Although, differences in digestible energy from fruits between the two disturbances were less noticeable in the young age-class; this may be due in part to post-fire stands sampled in this study having a higher proportion of fruit from relatively energy-rich species compared to post-harvest stands. The digestible energy results from fruits support my hypothesis that post-harvest and post-fire stands are not different from one another when considering fruit species important to grizzly bears. However, differences between age-classes were evident, with the mid age-class being significantly different from the young age-class, thus supporting my age-class hypothesis here. Finally, fruit productivity and digestible energy in the very young age-class is comparatively smaller in the post-fire stands. This may be influenced by fire severity, where plant succession can be hindered following a severe fire. However, I was unable to account for fire severity in this analysis as reliable data were not available.

In contrast to fruit productivity, forb productivity was highest among the very young age-class, which indicated the proliferation of exotic (clover and dandelion) and early-successional (horsetail) species following a disturbance. Among all three age-classes, forb productivity was highest in post-fire stands, with large differences in productivity between disturbances in the young age-class. The proliferation of early-successional species is typical following a disturbance, as increased exposure to sunlight and extreme temperatures favor plant communities dominated by annual and shade-intolerant herbaceous species (Swanson et al., 2011). Low forb productivity in the young age-class of post-harvest stands may stem from a combination of canopy closure following succession and herbicide application frequently used in the timber industry to encourage growth of economically valuable coniferous species (Thompson and Pitt, 2011). The digestible energy results from forbs do not support my hypothesis that post-harvest and post-fire stands are not different from one another, whereas my results do support that there were differences between age-classes, thus only supporting my age-class hypothesis here. Differences between age-classes were evident, with most of the variation in age-class covariate explained by the mid age-class.

When considering total available digestible energy, the results support my hypotheses that there were no differences between post-harvest and post-fire stands and that there were differences between age-classes, with most variation in the age-class covariate explained by the mid age-class. When adjusting total available digestible energy in the upper foothills of this study area, there was considerably more total energy available in very young and young age-classes of post-harvest stands, while the opposite pattern was observed in the mid age-class of post-fire stands. This can have important implications for grizzly bear conservation as grizzly bears are known to frequent relatively recent disturbances (Nielsen et al., 2004a; Kearney et al., 2019). In this study area, the amount of total available digestible energy in post-harvest stands, and comparatively little in post-fire stands, suggests some form of continued disturbance from forestry practices may benefit grizzly bears if access management can be controlled. I further suspect that this pattern would hold even when considering digestible energy derived from meat sources, as ungulates are known to make extensive use of areas recently (< 25 yrs) disturbed by forestry and/or wildfire (Fisher and Wilkinson, 2005). This suggests that harvested areas could be used as a management tool to boost population recovery efforts and increase population sizes, by enhancing food- and habitat-supply for a threatened grizzly bear population in a fire-suppressed landscape, so long as human access (source of mortality) is managed.

Differences in energy between harvested areas and areas disturbed by fire may be inflated, especially for the very young and young age-classes. The lack of relatively young post-fire stands suggests that the occurrence and distribution of forest fires in this study area may not be entirely natural, in the sense that recent wildfires are more likely to be suppressed (Johnson et al., 2001; Cumming, 2005). This conceivably results in an overrepresentation of relatively young post-fire stands moderated by fire suppression, relative to stands in which wildfire is allowed to burn largely in the absence of human influence. Furthermore, because of fire suppression, changing fire regimes in the region has contributed towards forest stands dominated by coniferous species (Rhemtulla et al., 2002), which are of high timber value. As such, fire-suppressed areas that historically would have produced productive early seral burns following a natural wildfire disturbance are now favored by the timber industry for harvesting. This leaves natural wildfires to occur more frequently in areas not historically predisposed to fire disturbance, thus further contributing to an overrepresentation of relatively young post-fire stands of lower habitat quality, specifically as it relates to plant foods consumed by grizzly bears. I speculate that this may contribute to how differences in digestible energy between both disturbances are interpreted in this study, as field observations indicated that some post-fire plots sampled in this study occurred in areas of fire suppression. Further studies may consider comparing harvested areas to areas disturbed by natural wildfire alone (i.e., not fire-suppressed) to better understand differences between disturbance types.

Both recent forest harvests and fire disturbances in the foothills of west-central Alberta increase the availability of grizzly bear foods. I suggest that current and future forestry disturbances may act as a surrogate for wildfires in a fire-suppressed landscape, and thus serve as a management tool for maintaining or enhancing grizzly bear food supply. This may therefore contribute to population recovery efforts, especially in fire-suppressed areas. However, control of human access is still needed, as productive bear habitats in areas of increased road access can be associated with increases in human-caused mortality (Nielsen et al., 2004b; Boulanger and Stenhouse, 2014), which could create trap-like conditions as an attractive habitat becomes a sink (Nielsen et al., 2006; Northrup et al., 2012; Lamb et al., 2016). Fire activity in the boreal forest is anticipated to increase under climate change (Flannigan et al., 2009). Under these conditions, persistent fire management and response will likely lead to continued fire suppression. Thus, a future fire-suppressed landscape denuded of relatively young post-fire stands may favor some form of continued disturbance (e.g., forest harvesting) that is similar to wildfire disturbance, especially as it relates to grizzly bear food supply. However, wildfire suppression is already reaching its peak effectiveness, and small increases in wildfire occurrence can lead to a disproportionate increase in wildfires (Podur and Wotton, 2010). Furthermore, there has been a move towards allowing more wildfires to burn on the landscape to maintain ecological processes (Coogan et al., 2019). Thus, forestry harvest practices to maintain grizzly bear food- and habitat-supply may not be as necessary under more active future fire regimes.

2.6. References

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Appendix 2.1. Literature sources of fruit dry mass and digestible energy for various species and food categories.

Species	Fruit Dry Mass (gram)	Source
Black twinberry	0.042	Ehrlén and Eriksson, 1991; White et al., 2005
Currant	0.053	Piper, 1986; López-Alfaro et al., 2015
Gooseberry	0.053	Piper, 1986; López-Alfaro et al., 2015
Buffaloberry	0.024	Coogan et al., 2014, Supporting Information Table 11
Lowbush cranberry	0.04	Travaset et al., 2004
Bearberry	0.08	Travaset et al., 2004
Strawberry	0.023	Revegetation Species Profiles 2013
Raspberry	0.357	Jolliffee 1975a,b (fresh weight); Ehrlén and Eriksson, 1991
Dwarf bilberry	0.035	Nielsen et al., 2004
Huckleberry	0.035	Nielsen et al., 2004
Blueberry	0.039	Coogan 2012, Table A3
Lingonberry	0.035	Coogan 2012, Table A3; Ehrlén and Eriksson, 1991
Food Category	**Digestible Energy (Kcal/gram_dry mass)**	**Source**
Fruit	2.6	López-Alfaro et al., 2015, Table 2.
Vegetation Summer	1.6	López-Alfaro et al., 2015, Table 2.

Appendix 2.2. Estimated odds ratios and 95% confidence intervals describing the occurrence of 18 grizzly bear food items between post-harvest and post-fire stands by age-class. Refer to Fig. 2.2 for visual representation.

Grizzly bear food item		Age-class		
Category	Species Name	Very Young	Young	Mid
Shrub-fruit	Black twinberry	2.1 (1.2, 3.7)	2.22 (1.2, 4.0)	1.46 (0.8, 2.6)
	Currant	4.67 (2.6, 8.5)	0.45 (0.2, 0.8)	1.68 (0.9, 3.3)
	Gooseberry	NA	1.68 (0.9, 3.3)	1 (0.6, 1.7)
	Buffaloberry	NA	1.46 (0.8, 2.6)	0.27 (0.1, 0.6)
	Lowbush cranberry	4.67 (2.6, 8.5),	1.46 (0.8, 2.6)	7.11 (3.8, 13.2)
	Western mountain-ash	NA	2.22 (0.9, 5.2)	3.75 (2, 7.1)
Dwarf shrub-fruit	Bearberry	NA	12 (5.4, 26.3)	NA
	Strawberry	7.89 (4.1, 15.1)	0.66 (0.4, 1.2)	1.52 (0.8, 2.8)
	Raspberry	8.33 (3.8, 18.3)	1 (0.5, 1.9)	1 (0.6, 1.7)
	Dwarf bilberry	0.69 (0.4, 1.2)	7.11(3.8, 13.2)	0.27 (0.1, 0.5)
	Huckleberry	1 (0.5, 1.9)	NA	7.11(3.8, 13.2)
	Blueberry	0.19 (0.1, 0.4)	0.59 (0.3, 1.2)	1.46 (0.8, 2.6)
	Lingonberry	1 (0.6, 1.8)	0.18 (0.1, 0.4)	0.48 (0.3, 0.8)
	Horsetail	1 (0.5, 1.9)	0.21 (0.1, 0.4)	1.46 (0.8, 2.6)
	Cow parsnip	NA	1 (0.4, 2.6)	3.18 (1.8, 5.8)
Forb/Ants	Dandelion	17.45 (7.9, 38.6)	5.38 (2.8, 10.2)	NA
	Clover	NA	3.06 (1.7, 5.4)	NA
	Ants	1 (0.6, 1.8)	0.19 (0.1, 0.4)	0.12 (0.1, 0.3)

Appendix 2.3. The average berry density of shrub-fruit (plant height ≥ 50 cm) and dwarf-shrub fruit (plant height < 50 cm) categories, and the average stem density of forbs, on a per hectare basis for 17 grizzly bear food items in post-harvest, post-fire, and mature forests. Abundance estimates for ants are absent as this was not recorded in this study. Age-class categories are as follows: Very Young (VY); Young (Y); and Mid (M).

Category	Species Name	Age-class	Harvest	SE	Fire	SE	Mature forests	SE
Shrub-fruit	Black twinberry	VY	3327	2000	46	NA[a]	136	66
		Y	182	100	846	606		
		M	0	NA	136	92		
	Currant	VY	46	NA[a]	0	NA	0	NA
		Y	0	NA	3864	2842		
		M	0	NA	0	NA		
	Gooseberry	VY	191	130	364	247	1406	643
		Y	1664	646	1782	993		
		M	3482	3199	800	667		
	Buffaloberry	VY	0	NA	0	NA	1012	520
		Y	9673	8801	0	NA		
		M	0	NA	0	NA		
	Lowbush cranberry	VY	527	302	82	59	221	97
		Y	255	116	327	186		
		M	109	63	0	NA		
	Western mountain-ash	VY	0	NA	0	NA	0	NA
		Y	0	NA	0	NA		
		M	0	NA	0	NA		
Dwarf shrub-fruit	Bearberry	VY	0	NA	0	NA	0	NA
		Y	909	NA[a]	0	NA		
		M	0	NA	1636	NA[a]		
	Strawberry	VY	2000	NA[a]	0	NA	0	NA
		Y	727	NA[a]	0	NA		

		M	182	NA[a]	0	NA		
	Raspberry	VY	15273	8015	1091	NA[a]	121	84
		Y	6182	5041	18546	16794		
		M	182	NA[a]	3273	2340		
	Dwarf bilberry	VY	89273	50705	182	NA[a]	0	NA
		Y	306909	182208	0	NA		
		M	364	NA	0	NA		
	Huckleberry	VY	51455	NA[a]	364	NA[a]	1091	NA[a]
		Y	0	NA	0	NA		
		M	364	244	0	NA		
	Blueberry	VY	9636	6533	25273	21796	788	564
		Y	31455	NA[a]	84182	82202		
		M	18909	16478	12000	NA[a]		
	Lingonberry	VY	26000	25603	0	NA	4364	2328
		Y	12000	11413	50182	40951		
		M	3637	NA[a]	36182	30513		
Forb	Horsetail	VY	133455	60954	228727	68825	118121	27952
		Y	2727	1690	188546	101012		
		M	6546	3659	12546	11559		
	Cow parsnip	VY	0	NA	0	NA	61	NA[a]
		Y	0	NA	364	NA[a]		
		M	546	390	364	NA[a]		
	Dandelion	VY	18727	9939	0	NA	0	NA
		Y	4182	3308	0	NA		
		M	0	NA	0	NA	0	NA
	Clover	VY	18364	15276	182	NA[a]		
		Y	11091	10498	182	NA[a]		
		M	0	NA	0	NA		

[a] – recorded only single observation

Chapter 3: Grizzly Bear Habitat Selection Linked to Food Resource Heterogeneity and Homogeneity

3.1. Abstract

Disturbed habitats can alter the abundance and distribution of food resources, structuring animal space use and foraging decisions. Indeed, we know little about how grizzly (brown) bears (*Ursus acrtos*) are influenced by the heterogeneity (and homogeneity) of food resource properties and how this affects habitat selection and foraging decisions in human-modified areas. I examined how heterogeneity, defined as both the distribution in digestible energy and variability in digestible energy quality, and homogeneity, defined as digestible energy density, influenced seasonal habitat selection in grizzly bears. I sought to understand how grizzly bears balance tradeoffs between alternative foraging strategies (heterogeneity vs. homogeneity) when navigating a human-modified area. I combined food resource variables (digestible energy) from 19 plant food items adjusted for phenology and GPS telemetry data from ten bears in hypophagia, eight in mesophagia, and six in hyperphagia using third-order resource selection functions (RSFs) in west-central Alberta, Canada. In general, models that included heterogeneity coupled with homogeneity were most supported and best explained grizzly bear habitat (food resource) selection across all seasons. Bears selected for greater variability in digestible energy quality (patchiness), widespread distribution in digestible energy, and resource dense areas during mesophagia and hyperphagia. Across all seasons, a positive interaction between variability in digestible energy quality and the proportion of the landscape with digestible energy (distribution) suggest bears increasingly select for high contrast areas in digestible energy quality when coupled with a more widespread distribution in digestible energy. For mesophagia and hyperphagia, the interaction between resource density and the proportion of the landscape with

digestible energy (distribution) was negative, indicating a tradeoff, where selection of resource density increased in areas with a more constrained distribution in digestible energy. These results suggest that bears may alternate between foraging strategies (heterogeneity vs. homogeneity) since bears will use high contrast areas (patchiness) when digestible energy is more widely distributed, and conversely, use resource dense areas when digestible energy distribution is constrained. Forest harvesting has largely replaced natural wildfire as the main disturbance agent in this study area, and hence, disproportionally contributes to the early seral habitat (e.g., < 30 years) available on the landscape. Forest harvesting, combined with the results herein, could increase the probability of grizzly bears encountering and exploiting high-quality patches – preferably in secure locations with low mortality risk – which should promote mass gain and ultimately higher fitness.

3.2. Introduction

Disturbed habitats, whether naturally occurring or anthropogenically driven, provide an array of niches and foraging opportunities for a variety of species (Turner et al., 2010; Thom and Seidl, 2016). These conditions are especially relevant to habitat generalists who may tolerate a wider range of habitat disturbances and should be able to exploit heterogenous environments (Devictor et al., 2008a, b) as they have the capacity to consume a diverse range of foods (Machovsky-Capuska et al., 2016). As such, disturbed habitats alter the abundance and distribution of food resources influencing how such properties vary spatiotemporally both annually and seasonally, which itself contributes to patchy landscapes where generalists must successfully navigate to survive (Wiens et al., 1976). Generalist, therefore, have the challenge of not only tracking the abundance, distribution, and quality of different food resources, but also the flux of various food items stemming from phenology and resource depletion (Wiens et al., 1976;

Charnov et al., 1976). Thus, animal resource selection can be partly explained by the spatial and temporal heterogeneity of food resources (Martin et al., 2010; Nielsen et al., 2010; Denny et al., 2018).

In forested environments managed by humans, silvicultural practices offer a way to alter food resource heterogeneity patterns, which can be an effective management strategy for species that are habitat generalists. Grizzly bears are a large and widely distributed omnivorous carnivore that partly depend on disturbed habitat to meet their food resource needs, which can vary both annually and seasonally (Zager et al., 1983; Hamer and Herrero, 1987; McLellan and Hovey, 1995; Nielsen et al., 2004a; Kearney et al., 2019; Larsen et al., 2019). Food resource abundance and distribution can affect grizzly bear body condition (Zedrosser et al., 2006; Nielsen et al., 2013; Bourbonnais et al., 2014), habitat use (Nielsen et al., 2004a; Nielsen et al., 2010; Denny et al., 2018), and population abundance (Nielsen et al., 2017). In addition, forested environments managed by humans can shift the abundance and distribution patterns of grizzly bear foods (Nielsen et al., 2004c; Souliere et al., 2020). Thus, understanding how food resource heterogeneity (and homogeneity) patterns influence grizzly bear habitat (food resource) selection becomes an important priority for management, especially considering the elevated human-caused morality risk of bears in silvicultural areas (Nielsen et al., 2004b; Boulanger and Stenhouse, 2014).

Food resource properties are seldom used as explanatory variables in grizzly bear habitat selection studies, even though studies that include such attributes are often more effective at explaining habitat selection than those that focus on habitat-centric metrics (Nielsen et al., 2003). Those studies that have used food attributes as explanatory variables often focus on a narrow set of key food resource properties (typically a fruiting shrub species, e.g., buffaloberry (*Shepherdia* *canadensis*)) or focus on a single season, especially hyperphagia (Nielsen et al., 2010; Hertel et al., 2016; Nielsen et al., 2017; Denny et al., 2018). Although selection of berries important to grizzly bear mass gain has been previously studied during hyperphagia (see Hertel et al., 2016 and Denny et al., 2018), selection of digestible energy based on major food groupings (e.g., horsetail (*Equisetum* spp.), sweetvetch (*Hedysarum* spp.) roots, ants (Formicidae spp.), forbs, and fruit) adjusted for phenology (i.e., season) has not been fully examined across hypophagia, mesophagia, and hyperphagia. Understanding how grizzly bears respond to spatial and seasonal variation in food resources is valuable for informing the conservation and management of grizzly bears in general, but also populations listed as Threatened, such as those in Alberta, Canada (ASRD, 2010) that inhabit a landscape where timber harvesting has become the main disturbance agent.

Although a few studies have explored the response of grizzly bears to spatial and temporal variation of key food resources (see Hertel et al., 2016 and Denny et al., 2018), examination of food resource heterogeneity relative to homogeneity based on a suite of major food groupings has receive less attention. Studies examining such responses, however, have found that as a landscape becomes more heterogenous (i.e., increasing patchiness), grizzly bears will use smaller areas assuming constant resource quality (Mangipane et al., 2018). Similarly, broader food resource heterogeneity appears to influence grizzly bear foraging behavior at finer spatial scales (Searle et al., 2006). Buffaloberry spatial heterogeneity can influence habitat use by providing a higher probability of encountering shrubs and greater contrast between resource patches (Denny et al., 2018). Likewise, recent work examining the effects of human-induced prey depletion on tiger (*Panthera tigris*) populations in an agent-based model setting, indicated that spatially heterogenous prey resources resulted in smaller territory size, which in turn altered landscape carrying capacity (Carter et al., 2019). Hence the spatial distribution and abundance of food resources can mediate animal space use and ultimately affect fitness. Thus these spatial distribution and food abundance patterns are important given that human-modified areas can lead to attractive sink dynamics in grizzly bear populations (Nielsen et al., 2006; Northrup et al., 2012; Lamb et al., 2016).

Here, I seek to understand how spatial heterogeneity and spatial homogeneity in food resources influence grizzly bear selection patterns across hypophagia, mesophagia, and hyperphagia. Specifically, I focus this study on investigating how spatial homogeneity, defined as resource density in digestible energy, and spatial heterogeneity, defined as the both the distribution in digestible energy and variability in digestible energy quality (Kotliar and Wiens, 1990; Denny et al., 2018) affect bear food resource selection patterns. I explore the degree to which grizzly bears may trade off foraging strategies (heterogeneity vs. homogeneity) depending on how food resources are spatially allocated and investigate these patterns within annual and seasonal home ranges (hypophagia, mesophagia, and hyperphagia). Food resources are described via distribution, variability, and resource density (abundance), and are represented by digestible energy. In general, I hypothesize that across all seasons, both heterogeneity and homogeneity will best explain grizzly bear habitat (food resource) selection. Specifically, I expect bears to select for high contrast in patch (digestible energy) quality when digestible energy is more widely distributed (prediction 1). In contrast, I expect bears to select for resource density regardless of the distribution pattern (constrained or widespread) in digestible energy (prediction 2). I expect these patterns to hold across hypophagia, mesophagia, and hyperphagia (prediction 3).

3.3. Methods

3.3.1. Study area

The study area was located in the eastern foothills of the Canadian Rocky Mountains in west-central Alberta, Canada (~ 53°24′N, 117°33′W). The area includes two natural subregions (lower foothills and upper foothills) and the elevation ranges from 706 to 3676 m, with the western portion characterized by mountainous terrain and the eastern portion transitioning from mountainous to low rolling terrain (Fig. 3.1). The climate is continental with a mean annual temperature of 1.3 ºC and a mean annual precipitation of 632 mm, with snow cover generally lasting from late October to early May (Natural Regions Committee, 2006). The area is dominated by conifer forests with lodgepole pine (*Pinus contorta*) being the most common tree species. White and Engelmann spruce (*Picea glauca*, *P. engelmannii*) are generally found at higher elevations and in the southern parts of the study, whereas black spruce (*P. mariana*) and tamarack (*Larix laricina*) are more common in wet lowland areas. Deciduous stands of trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) are more common in upland sites at lower elevations. In addition to grizzly bears, other predators include black bears (*Ursus americanus*), wolves (*Canis lupus*), cougars (*Felis concolor*), wolverines (*Gulo gulo*), lynx (*Lynx canadensis*), and coyotes (*Canis latrans*). Ungulates in the area include whitetail deer (*Odocoileus virginianus*) and mule deer (*O. humionus*), moose (*Alces alces*), elk (*Cervus elaphus*), and caribou (*Rangifer tarandus*). Ongoing natural resource extraction related primarily to forestry, oil and gas, and mining industries, as well as a half-century of forest harvesting and fire suppression (Andison et al., 1998; Rogeau et al., 2016) have produce a landscape mosaic of early seral forests and human disturbances in the region.

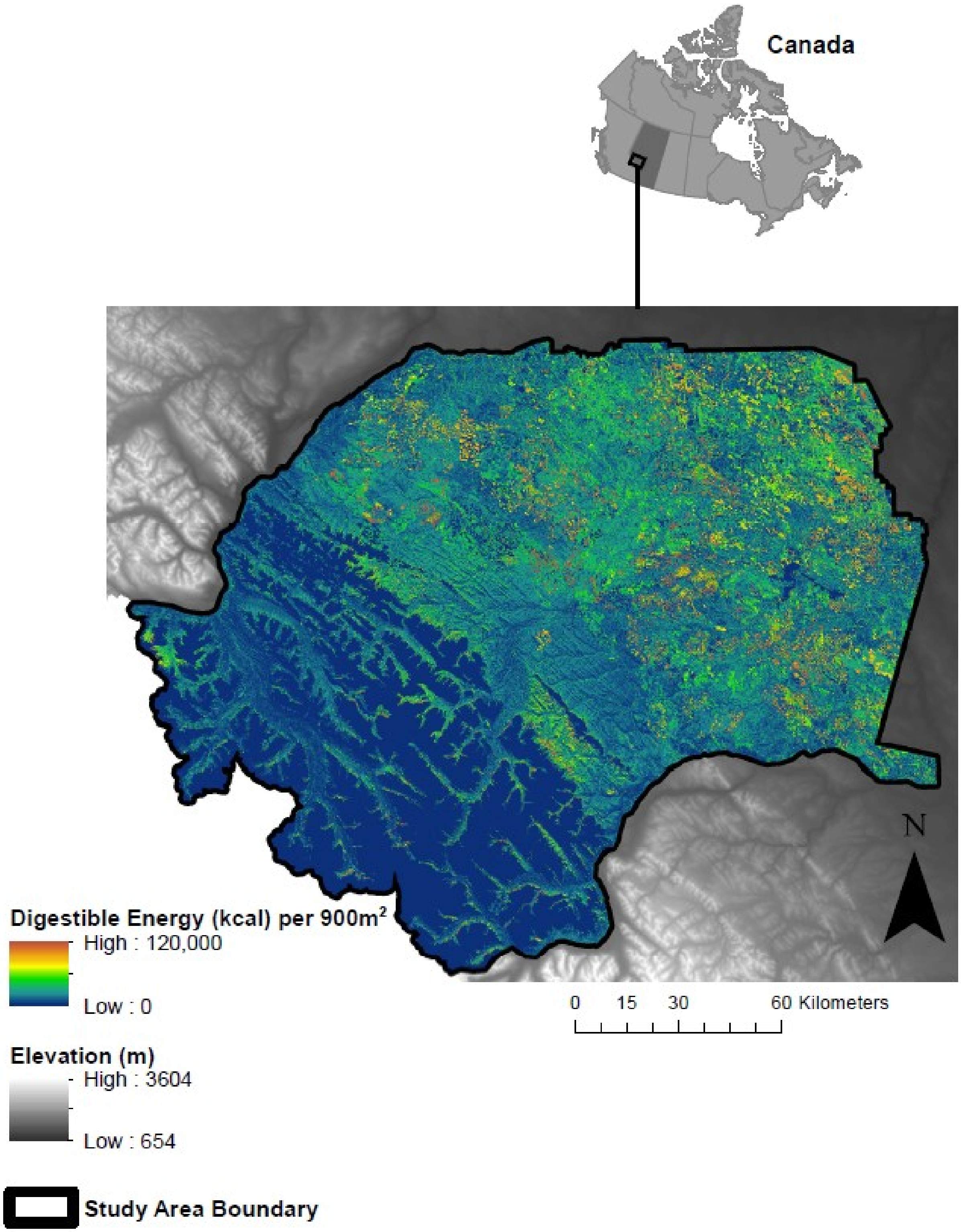

Fig. 3.1. Location of the study area in west-central Alberta, Canada, illustrating digestible energy (kcal) per 900m^2 summed across all seasons in 2014 for 19 bear food items. Inset map shows the study location within the province of Alberta.

3.3.2. Telemetry data

I investigated how food resource heterogeneity influenced the habitat selection of grizzly bears using 2004 and 2014 GPS telemetry data collected from collared bears. Grizzly bear GPS data were collected as part of a long-term research project by fRI (Hinton, Alberta) using either leg snares, aerial darting, or culvert traps (Cattet et al., 2003). Capture and handling protocols were approved and conducted in accordance with Animal Care Committees by both the University of Saskatchewan and the University of Alberta, and by the Alberta Environment and Sustainable Resource Development. Bears were fitted with one of three collar types: Televilt GPS-Simplex (Lindesberg, Sweden), Followit (Lindesberg, Sweden), or Advanced Telemetry Systems (ATS, Isanti, MN, USA) and programmed to acquire locations at intervals ranging from < 30 min to 4 h. I gathered GPS telemetry information on 16 unique bears totaling 3276 relocation events in 2004 and 22 unique bears totaling 24,915 relocation events in 2014. To account for seasonal variation in habitat selection and diet within the region, I separated telemetry data into three seasons: hypophagia (den emergence to 15 June), mesophagia (16 June to August 15), and hyperphagia (16 August to late October) (Nielsen et al., 2004a; Munro et al., 2006; Kearney et al., 2019). During hypophagia, bears typically feed on sweetvetch roots and winter-killed ungulates. During mesophagia, bears will broaden their diet to include ants (myrmecophagy), forbs, graminoids, early-season fruit, and ungulate calves. Lastly, during hyperphagia, frugivory becomes important as bears seek out berries (e.g., *Vaccinium* spp., *buffaloberry*), followed by late-season return to digging for sweetvetch roots. I discarded individuals with < 50 locations per season, resulting in ten collared bears in hypophagia, eight in mesophagia, and six in hyperphagia for analyses. In total, I had GPS telemetry information on 14 unique bears when accounting for bears that had seasonal home ranges across two or more seasons.

3.3.3. Spatial analysis

The goal was to investigate the importance of food resource heterogeneity and homogeneity in influencing habitat (food resource) selection across three seasons, where food resource attributes differ in their phenology. To do this, I evaluated resource selection functions (RSFs) using third-order selection based on a use-available design (Boyce et al., 2002; Manly et al., 2002). I used GPS telemetry locations to delineate individual home ranges per season per year by calculating 100% minimum convex polygons (MCPs), within which I generated 10 'available' points for each used location (Northrup et al., 2013). To improve model convergence, I standardized all continuous variables. To account for the typical daily foraging period of bears in west-central Alberta (Munro et al., 2006), I only considered diurnal and crepuscular locations based on local sunrise and sunset times corresponding to the GPS coordinates and day of year of each location. I derived environmental variables from 19 plant food items that are important to grizzly bear diet in this study area (Hamer and Herrero, 1987; Hamer, 1996; Hamer, 1999; McLellan and Hovey, 1995; Nielsen et al., 2004c; Munro et al., 2006). I divided food types into 5 major food groups to calculate seasonal food weights based on plant phenology (Munro et al., 2006). I divided groups as follows: horsetail; sweetvetch roots; ants; forbs which included cow parsnip (*Heracleum lanatum*), dandelion (*Taraxacum officinale*), clover (*Trifolium* spp.); and fruit which included saskatoon berry (*Amelanchier alnifolia*), bearberry (*Arctostaphylos uva-ursi*), strawberry (*Fragaria virginiana*), black twinberry (*Lonicera involucrata*), currant and gooseberry (*Ribes* spp.), raspberry (*Rubus idaeus*), thimbleberry (*Rubus parviflorus*), buffaloberry, lowbush cranberry (*Viburnum edule*), huckleberry (*Vaccinium membranaceum*), blueberry (*V. myrtilloides*), grouseberry (*V. scoparium*), and lingonberry (*V. vitis-idaea*). I derived environmental variables from 2004 and 2014 field plot data that were used to model plant occurrence and abundance and subsequently mapped at a 30 m resolution using a Geographic Information System (GIS) (Nielsen et al., 2015). I then converted these layers into density estimates using methods derived from Nielsen et al. (2015) and Nielsen et al. (2017), and subsequently converted these estimates into a measure of digestible energy following methods outlined in López-Alfaro et al. (2015) and Souliere et al. (2020). Seasonal weights were applied to each major food group based on seasonal food items reported in Munro et al. (2006), a study conducted in west-central Alberta. I subsequently grouped major food groups into a single layer of digestible energy for both 2004 and 2014, from which I extracted covariates of interest within a 300 m buffer. This buffer corresponds to the approximate average hourly movement rate of grizzly bears in this study area (Graham and Stenhouse, 2014) and a flight-response scale representing exposure to direct human activity (Archibald et al., 1987; Nielsen et al., 2013). For each of the 2004 and 2014 digestible energy layers, I calculated mean digestible energy, total (sum) digestible energy, coefficient of variation in digestible energy, standard deviation in digestible energy, and proportion of the landscape with digestible energy. I conducted all spatial analyses in ArcGIS 10.3 (ESRI, 2014) and R v3.6.3 (R Core Team, 2020).

3.3.4. Statistical analysis

I used a mixed-effects logistic regression model to evaluate selection of food resource properties within each season and estimated this with the bbmle package (Bolker et al., 2020). Random intercepts and random coefficients have been recommended in RSF models as they can account for unequal sample sizes among individuals and individual-specific differences in selection, respectively (Gillies et al., 2006; Hebblewhite and Merrill, 2008; Muff et al., 2020).

This methodological development has led to increased adoption of generalized linear mixed-effects models in studies of animal resource selection (Muff et al., 2020). I first evaluated RSF models by developing nine *a priori* candidate models and associated hypotheses that describe grizzly bear selection of food resources across three seasons (Table 3.1). These hypotheses were put forward to evaluate the role of heterogeneity coupled with homogeneity in influencing habitat (food resource) selection patterns in grizzly bears. Specific to the heterogeneity hypothesis, I considered an interaction between distribution in digestible energy and variability in digestible energy quality across all seasons as I hypothesized that bears would select for areas with a wider distribution in digestible energy and greater contrast in digestible energy quality (Denny et al., 2018). I suspected that this offered bears a greater probability of encountering resources while also assisting bears in differentiating between patch (digestible energy) quality.

Table 3.1. *A priori* seasonal candidate models and associated hypotheses describing grizzly bear selection for food resources (digestible energy) over three seasonal periods. All models are tested with bearYear nested within bearID as a random intercept.

Model ID	Hypothesis	Model
M0	Null	~
M1	Resource density	~ density
M2	Distribution	~ proportion
M3	Variability	~ coefficient of variation
M4	Heterogeneity (additive)	~ coefficient of variation + proportion
M5	Heterogeneity (interaction)	~ coefficient of variation * proportion
M6	Resource density and heterogeneity (additive)	~ density + coefficient of variation + proportion
M7	Resource density and heterogeneity (interaction between variability and distribution)	~ density + coefficient of variation * proportion
M8	Resource density and heterogeneity (interaction between resource density and variability, and variability and distribution)	~ density * coefficient of variation + coefficient of variation * proportion
M9	Resource density and heterogeneity (interaction between resource density and distribution, and variability and distribution)	~ density * proportion + coefficient of variation * proportion

I fit a mixed-effects logistic regression model with a random intercept for bear identity. Each model represented an individual hypothesis. For each season, I further tested random structures of the most parsimonious model by comparing it to a model fitted with the proportion of the landscape with digestible energy as a random coefficient. If supported by AIC and R^2_{GLMM}, I report population-level beta coefficients (β) with models fitted with both a random intercept and random coefficient. Before statistical analyses, I tested for multicollinearity among covariates with variance inflation factor (VIF < 5, Dormann et al., 2013). Based on this, I excluded total digestible energy from the analyses as it was highly correlated with mean digestible energy. Likewise, because of high correlation, I excluded standard deviation in lieu of coefficient of variation as I was more interested in the latter. To facilitate model convergence, I centered and scaled all continuous variables to have a mean of 0 and SD of 1. I performed model selection on eight *a priori* candidate models using Akaike Information Criterion (AIC) (Burnham and Anderson, 2002). I conducted all statistical analyses in R v3.6.3 (R Core Team, 2020).

3.4. Results

The models that included homogeneity (resource density in digestible energy) and heterogeneity (distribution in digestible energy and variability in digestible energy quality) were the most supported models across all seasons (Table 3.2). M9 (interaction between resource density and distribution, and variability and distribution) was most supported in mesophagia and hyperphagia, whereas M8 (interaction between resource density and variability, and variability and distribution) was most supported in hypophagia. Yet in hypophagia, M9 was within ΔAIC score of 3.2 from M8, the most supported model during that season (Table 3.2). Excluding hypophagia, resource density, distribution (proportion of the landscape with digestible energy), and variability in digestible energy quality (coefficient of variation) had a strong positive effect on grizzly bear habitat selection when considering M9.

Table 3.2. Seasonal AIC selected models describing habitat selection in hypophagia, mesophagia, and hyperphagia. I report the number of parameters (k_i), log likelihood (LL), change in AIC from the lowest model, Akaike weights (w_i), and conditional R^2 for generalized linear mixed-effect models (see Nakagawa and Schielzeth, 2013). Dashes indicate the model failed to converge.

Season	Model ID	k_i	LL	ΔAIC	w_i	Conditional R^2_{GLMM}
Hypophagia	M8	7	-63,687.6	0.0	0.62	0.254
	M7	6	-63,689.5	1.8	0.25	0.251
	M9	7	-63,689.2	3.2	0.13	0.235
	M5	5	-63,696.0	12.9	<0.001	0.245
	M6	5	-63,788.0	196.9	<0.001	0.041
	M4	4	-63,799.1	217.0	<0.001	0.038
	M3	3	-63,802.0	220.9	<0.001	0.032
	M2	3	-64,056.6	730.2	<0.001	0.034
	M1	3	-64,195.0	1006.8	<0.001	-
	M0	2	-64,202.9	1020.7	<0.001	-
Mesophagia	M9	7	-37,245.2	0.0	1	0.067
	M8	7	-37,283.9	77.4	<0.001	0.073
	M7	6	-37,295.6	98.9	<0.001	0.075
	M5	5	-37,296.9	99.4	<0.001	0.074
	M4	4	-37,460.8	425.3	<0.001	0.031
	M6	5	-37,460.6	426.9	<0.001	0.032
	M3	3	-37,463.5	428.7	<0.001	0.032
	M2	3	-39,424.9	4351.4	<0.001	0.057
	M1	3	-39,551.6	4604.9	<0.001	0.020
	M0	2	-39,646.9	4793.5	<0.001	-
Hyperphagia	M9	7	-26,203.5	0.0	1	0.109
	M8	7	-26,235.1	63.3	<0.001	0.093
	M7	6	-26,238.0	67.0	<0.001	0.093
	M5	5	-26,272.5	134.0	<0.001	0.098
	M6	5	-26,358.7	306.4	<0.001	0.069

M4	4	-26,394.5	376.0	<0.001	0.062
M3	3	-26,477.0	539.0	<0.001	0.042
M2	3	-30,589.4	8763.9	<0.001	0.085
M1	3	-30,863.1	9311.3	<0.001	0.008
M0	2	-30,896.6	9376.3	<0.001	-

Table 3.3. Random structures tested for the most parsimonious model describing habitat selection in hypophagia, mesophagia, and hyperphagia. Dashes indicate random coefficient was absent in model structure.

Season	Model ID	Random intercept	Random coefficient	LL	ΔAIC	w_i	Conditional R^2_{GLMM}
Hypophagia	M9: A	bearID	-	-63,689.2	769.4	<0.001	0.235
	M9: B	bearID	proportion	-63,303.5	0.0	1	0.395
Mesophagia	M9: A	bearID	-	-37,245.2	576.0	<0.001	0.067
	M9: B	bearID	proportion	-36956.2	0.0	1	0.097
Hyperphagia	M9: A	bearID	-	-26,203.5	387.6	<0.001	0.109
	M9: B	bearID	proportion	-26,008.6	0.0	1	0.181

Table 3.4. Standardized beta coefficients values of the fixed effect covariates of the most parsimonious model describing third-order resource selection functions of grizzly bears during hypophagia, mesophagia, and hyperphagia. Beta coefficients (*β*) are provided with standard errors and significance values.

Variable Name	M9: B Hypophagia			M9: B Mesophagia			M9: B Hyperphagia		
	β	SE	*p*-value	*β*	SE	*p*-value	*β*	SE	*p*-value
Intercept	-8.990	0.124	<0.001	-8.684	0.082	<0.001	-8.980	0.181	<0.001
Density	-0.132	0.026	<0.001	0.437	0.046	<0.001	0.783	0.095	<0.001
CV[a]	-0.022	0.071	0.757	0.822	0.061	<0.001	0.632	0.056	<0.001
Proportion	0.276	0.243	0.255	0.267	0.183	0.145	0.797	0.221	0.003
Density * Proportion	0.130	0.051	0.011	-0.659	0.052	<0.001	-0.893	0.072	<0.001
CV[a] * Proportion	0.474	0.051	<0.001	0.613	0.042	<0.001	0.610	0.047	<0.001

[a] – coefficient of variation

Resource density and distribution had the strongest effect on bear habitat selection in hyperphagia, whereas variability in digestible energy quality had the strongest effect on bear habitat selection in mesophagia (Table 3.4).

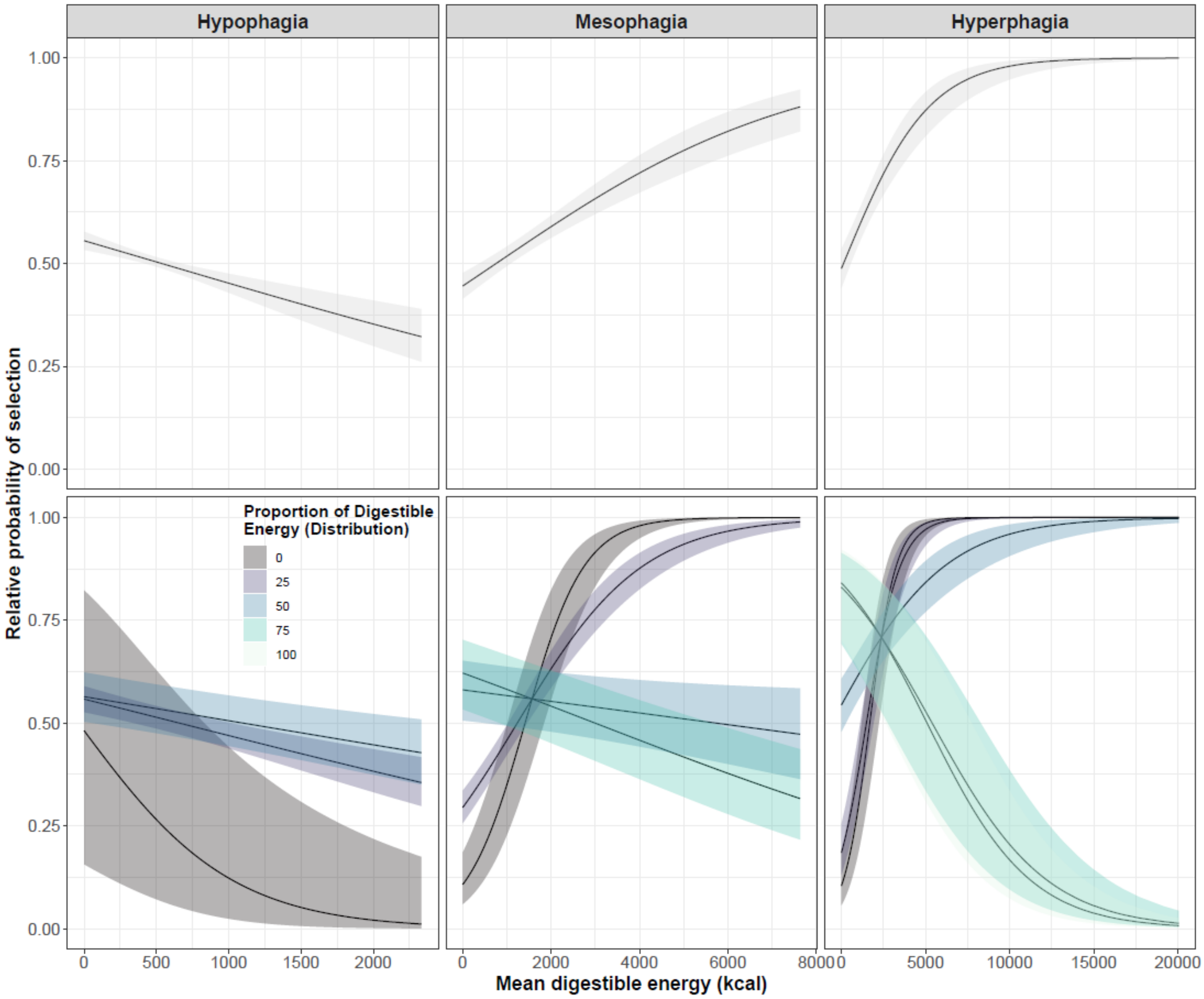

Fig. 3.2. Relative probability of selection from the most supported model showing the predicted effect of mean digestible energy (resource density) across seasons for both the upper and lower panels. Proportion of digestible energy (distribution) is binned into categories based on quantiles in the lower panels, allowing for visual representation of interaction. Shaded areas represent 95% confidence intervals. Mean digestible energy is plotted within its predicted range and all other variables are held at their mean level.

Not accounting for interactions between covariates of interest, the relative probability of selection was predicted to increase ~2X between areas of low and high resource density (homogeneity) for both mesophagia and hyperphagia (Fig. 3.2; upper panels). Likewise, the relative probability of selection was predicted to increase ~1.3X and ~2.5X between constrained and widespread distribution in digestible energy for mesophagia and hyperphagia, respectively (Fig. 3.3; upper panels).

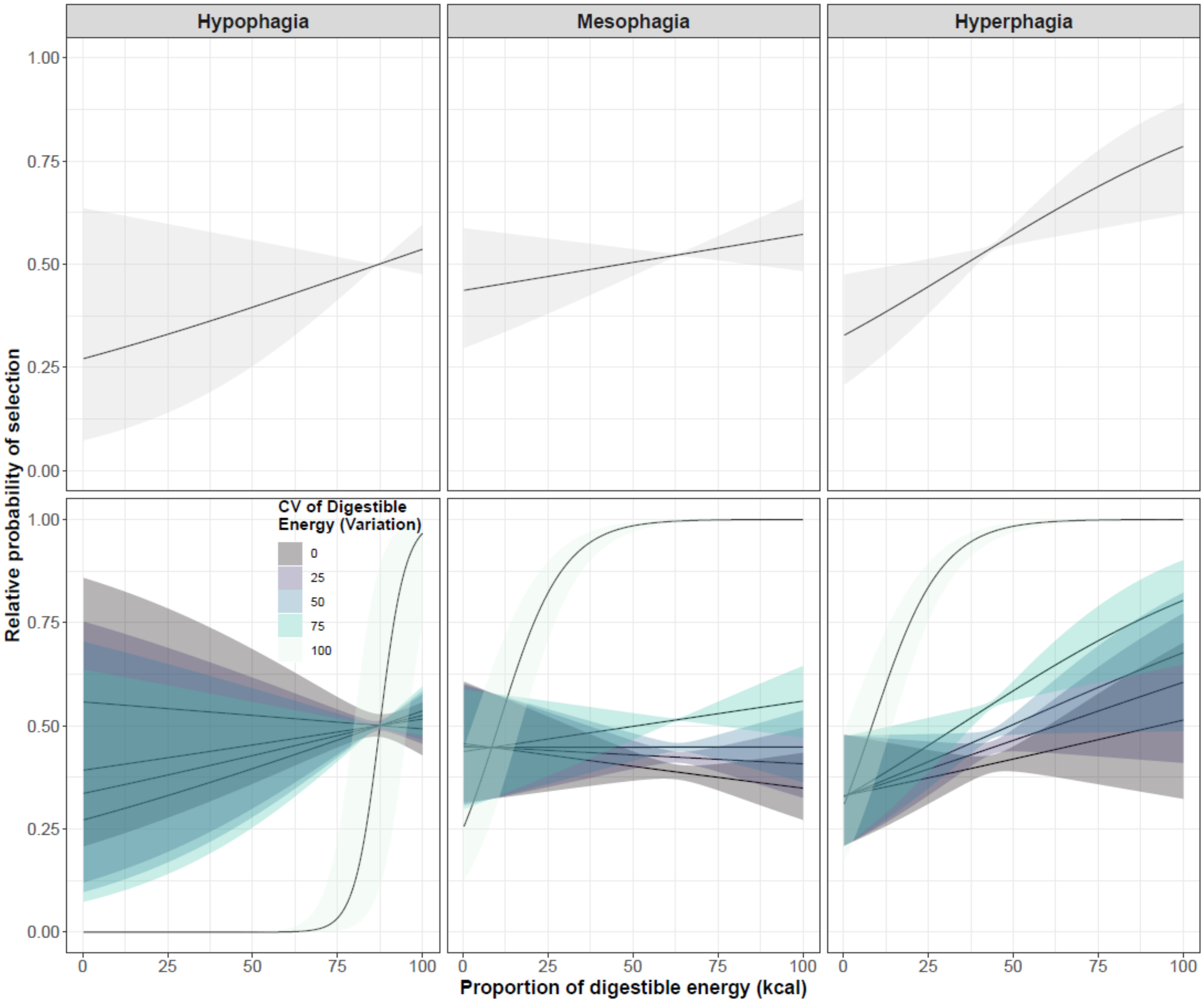

Fig. 3.3. Relative probability of selection from the most supported model showing the predicted effect of the proportion of the landscape with digestible energy (distribution) across seasons for both the upper and lower panels. The coefficient of variation of digestible energy (variation) is binned into categories based on quantiles in the lower panels, allowing for visual representation of interaction. Shaded areas represent 95% confidence intervals. The proportion of the landscape with digestible energy is plotted within its predicted range and all other variables are held at their mean level.

Similarly, the relative probability of selection was predicted to increase ~2.7X and ~2.3X between low and high contrast areas in variability in digestible energy quality for mesophagia and hyperphagia, respectively (Fig. 3.4; upper panels). Although both resource density and distribution (proportion of the landscape with digestible energy) had a strong positive effect on habitat selection in mesophagia and hyperphagia, the interaction between both covariates was negative, indicating a tradeoff, where selection of resource density increased in areas with a constrained distribution in digestible energy (Table 3.4). For both mesophagia and hyperphagia, the relative probability of selection in resource dense areas increased as the probability of encountering a more widespread distribution in digestible energy decreased (Fig. 3.2; lower panels). In contrast, the interaction between variability in digestible energy quality and distribution was positive, where selection of high contrast areas increased in areas with a widespread distribution in digestible energy (Table 3.4). For mesophagia and hyperphagia, the relative probability of selection in variability in digestible energy quality (i.e., patchiness) increased as the probability of encountering a more widespread distribution in digestible energy increased (Fig. 3.4; lower panels).

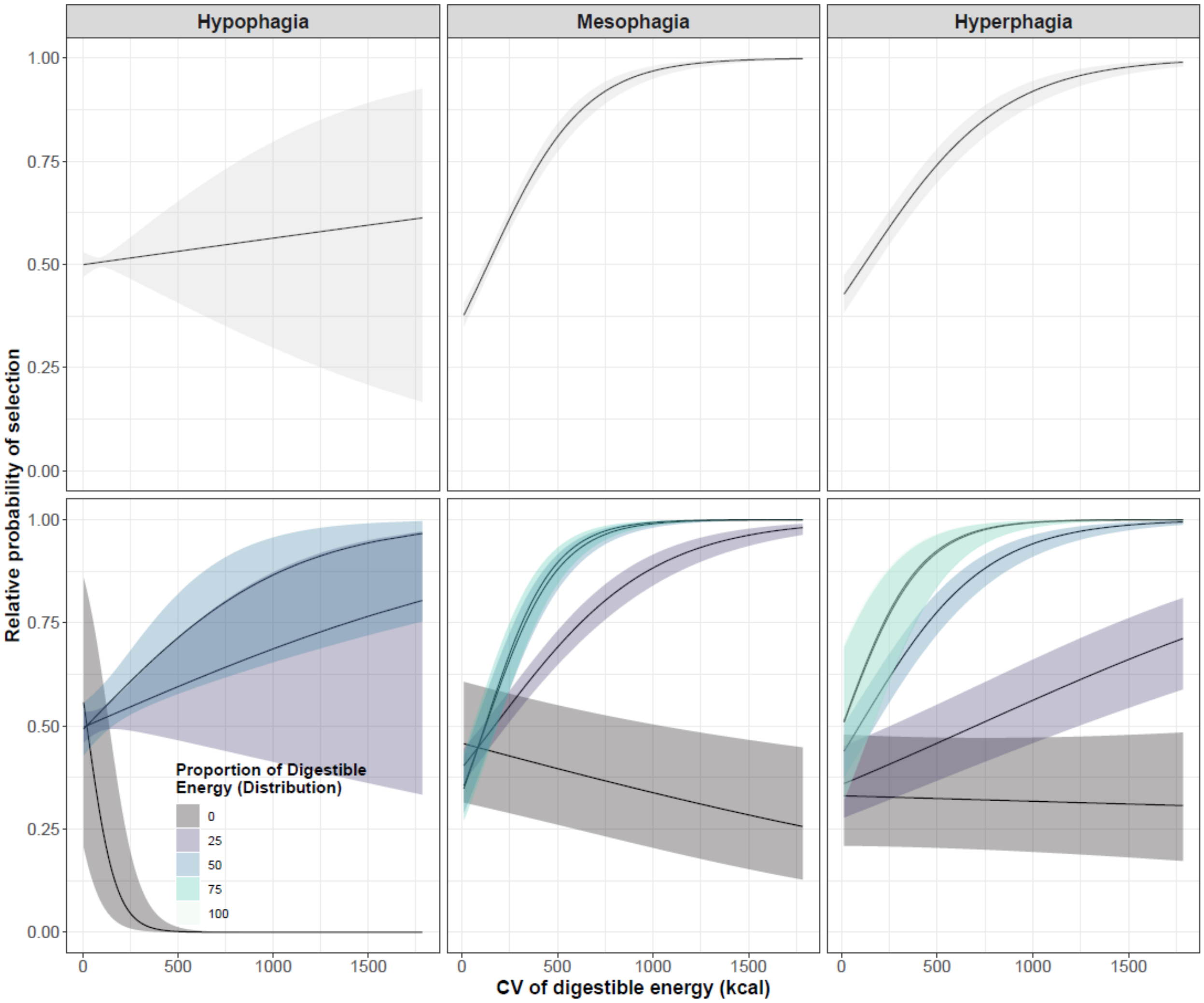

Fig. 3.4. Relative probability of selection from the most supported model showing the predicted effect of the coefficient of variation in digestible energy (variation) across seasons for both the upper and lower panels. Proportion of the landscape with digestible energy (distribution) is binned into categories based on quantiles, allowing for visual representation of interaction. Shaded areas represent 95% confidence intervals. The coefficient of variation in digestible energy is plotted within its predicted range and all other variables are held at their mean level.

3.5. Discussion

Food resource patterns are critical components in structuring foraging behavior and habitat selection of species, which can be especially important in landscapes with ongoing human disturbance. I sought to understand how food resource heterogeneity (distribution in digestible energy and variability in digestible energy quality) and homogeneity (resource density in digestible energy) influenced grizzly bear food resource selection patterns across hypophagia, mesophagia, and hyperphagia and explored whether bears trade off foraging strategies depending on how food resources are spatially allocated in a landscape primarily disturbed by humans. I found that grizzly bear selection of food resources was best explained by heterogeneity and homogeneity across all seasons. For mesophagia and hyperphagia, bears selected for wider distribution (proportion of landscape with digestible energy), greater variability (coefficient of variation) in digestible energy quality, and greater resource density (in digestible energy). In hypophagia, however, bears selected for lower variability and lower resource density yet a wider distribution in digestible energy. Related to my first prediction, I observed a positive interaction between distribution and variability in digestible energy across all seasons. This indicates that bears are selecting for areas with a wider distribution in digestible energy as well as a greater variability in digestible energy quality. Contrary to my second prediction, I observed a negative interaction between resource density and distribution in mesophagia and hyperphagia, indicating a tradeoff, where bears are selecting for higher average resource density when distribution in digestible energy is constrained. Related to my third prediction, patterns in homogeneity and heterogeneity differed among seasons. My findings, therefore, underscore that bears simultaneously respond to both homogeneity and heterogeneity in food resources, implying that bears alternate between foraging strategies contingent on how resources are spatially allocated, likely to optimize macronutrient intake and mass gain (Coogan et al., 2014; Erlenbach et al., 2014).

The interaction between distribution and variability was an especially meaningful finding, as the inclusion of both factors in M9 (interaction between resource density and distribution, and variability and distribution) had considerably more support compared to all other hypotheses. This implies that bears seek out high contrast areas in digestible energy and areas with a wide distribution in digestible energy. High contrast areas increase the probability of bears locating high-quality patches, and recognizing said patches as such, may act as a cue for exploitation (Denny et al., 2018). Considering a wider distribution in digestible energy increases the probability of encountering high-quality patches, a wider distribution in and of itself (i.e., as a property), may further promote contrast between patches, and hence further increased the probability of bears both locating and recognizing high-quality patches and thus exploiting them. Although Denny et al. (2018) found buffaloberry spatial heterogeneity best explained grizzly bear selection for fruit, a negative interaction between buffaloberry distribution and variability was observed, contrary to the positive interaction observed in my study between distribution and variability. The effect of terrain may partly explain the result found in Denny et al. (2018). Given I assessed 19 different food items, the effect of terrain may be of less importance. Other studies, for instance, Mangipane et al. (2018), have shown landscape heterogeneity influencing grizzly bear space use, where bears used smaller areas when landscape heterogeneity increased. Searle et al. (2006) investigating patch residence time of grizzly bears showed that models that accounted for broader heterogeneity were vastly more supported over models that failed to consider the surrounding spatial context, suggesting foraging decisions in grizzly bears are influenced by heterogeneity at larger scales. Similarly, increasing spatial heterogeneity in prey resources via agent-based modeling can reduce tiger territory size thus resulting in larger population sizes, suggesting that energetic requirements are more easily met in landscapes characterized by patchier distributions in prey resources (Carter et al., 2019).

Hypotheses that include the interaction between resource density and heterogeneity showed considerably more support than hypotheses that did not include such interactions. In particular, M9 was most supported in mesophagia and hyperphagia. Contrary to my expectations, however, bears did not seek resource dense areas regardless of the distribution pattern in mesophagia and hyperphagia, but instead showed a negative interaction between factors, where bears selected for higher average resource density in areas with a constrained distribution in digestible energy. This negative interaction suggests that bears are selecting for homogeneity when the probability of encountering a resource is low and avoiding homogeneity (or selecting for heterogeneity) when the probability of encountering a resource is high. Presumably, the selection for heterogeneity is because areas with a wider distribution in digestible energy allow bears to distinguish areas of high quality more easily from areas of low quality. By contrast, in areas with a constrained distribution in digestible energy, the cue to distinguish high-quality areas from low-quality areas is less recognizable, which may instead promote bears to alternatively seek out resource dense areas. This alternating selection pattern suggests that bears may adapt their foraging strategy contingent on the patchiness of the area – assuming resource quality is constant across the landscape – and the risk-to-reward ratio is beneficial. Foragers can recognize patchiness at smaller scales that enables them to concentrate foraging efforts when responding to heterogeneity in resource abundance, thereby biasing them towards areas with richer foods (Schmidt and Brown, 1996).

Alternating between homogeneous and heterogeneous foraging strategies may benefit bears in several ways. First, it may allow bears to buffer against inter-annual fluctuation in the properties of key food resources, with a large portion of that variation resulting from changes in fruit production (Hamer and Herrero, 1987; McLellan and Hovey, 1995; Stenset et al., 2016; Hertel et al., 2018). Second, in landscapes with ongoing and pervasive resource extraction, food abundance and distribution patterns have likely shifted and will likely continue to do so (Nielsen et al., 2004c; Kearney et al., 2019; Souliere et al., 2020). In such cases, bears employing alternative foraging strategies in the face of fluctuating and spatially disparate food resources may help them buffer against the effects of such disturbances. Third, alternative foraging strategies may allow bears to exercise dietary flexibility in choice and abundance (Nielsen et al., 2017), as well as optimize macronutrient intake and mass gain, thereby influencing fitness (Coogan et al., 2014; Erlenbach et al., 2014).

In general, patterns observed in hypophagia diverged from those observed in mesophagia and hyperphagia. One reason may be that during hypophagia bears are limited by seasonally specific and spatially wide-ranging food sources which require large movement bouts to increase the opportunity of encountering key foods. For instance, bears in west-central Alberta rely heavily on sweetvetch roots and winter-starved ungulates after den emergence (Schwartz et al., 2003; Munro et al., 2006), each of which evidently require different habitat needs. Large foraging movements that increase the probability of encountering ungulate winter kills and/or sweetvetch roots may help explain the diverging patterns observed in hypophagia here. An alternative or possibly complementary reason is that late hypophagia coincides with bears actively hunting neonate calves and the mating season (Hamer and Herrero, 1991; Green et al., 1997; Mattson, 1997; Schwartz et al., 2003). Both behaviors could promote larger movement bouts and alternative habitat use that may only weakly overlap with spatial food patterns found during hypophagia, thus contributing to the diverging patterns observed here.

My results suggest that human disturbed landscapes have shifted the distribution and abundance of important grizzly bears foods, which may stimulate the simultaneous use of alternative foraging strategies and tradeoffs depending on how food resources are spatially allocated. For example, both forest harvest areas and wildfire areas (although with ongoing fire suppression measures) in Alberta foster the growth of various bear plant foods (Nielsen et al., 2004c; Munro et al., 2006; Souliere et al., 2020) and increase habitat use (Nielsen et al., 2002; Nielsen et al., 2004a; Kearney et al., 2019). Forestry practices in Sweden have a large effect on berry occurrence and abundance, and brown bears have been shown to use areas of higher average berry abundance, suggesting successful navigation of human-modified areas (Hertel et al., 2016). Furthermore, implications of climate change may further alter the distribution and abundance of key grizzly bears foods via shifting plant phenology, thereby increasing the risk of trophic asynchrony (Deacy et al., 2017; Laskin et al., 2019). For instance, Laskin et al. (2019) noted that a three-week advance in buffaloberry fruit ripening could create a temporal mismatch between the availability of buffaloberry – a critical food resource of grizzly bears in Alberta – and pre-hibernation fat deposition in grizzly bears, with the latter closely linked to female fecundity (Robbins et al., 2012; López-Alfaro et al., 2013).

A disturbed landscape, whether from forest harvesting or natural wildfire alters landscape patterns, stand composition, and forest structure, thus providing niches for many species, albeit in varying ways (Kuuluvainen and Grenfell 2012; Thom and Seidl, 2016). Such changes in forest attributes could contribute to a wider distribution and greater variation (patchiness) of key grizzly bear foods. A fire disturbed landscape might drive greater habitat complexity when compared to an equally sized landscape disturbed by forest harvesting alone. Thus, a fire disturbed landscape could promote a wider distribution and greater variation of key grizzly bear foods on account of greater habitat complexity. In contrast, contemporary forest harvesting in the boreal forest is often designed to emulate the structure and patterns of a fire disturbance (e.g., natural disturbance emulation; Kuuluvainen and Grenfell, 2012) yet can fall short of that objective in such cases where harvesting leads to simplified forest structure and patterns, and thus habitat simplification (i.e., lower habitat complexity) (Petraitis et al., 1989; Long, 2009). Nonetheless, since forest harvesting has become the main disturbance agent in my study area, and neighboring wildfires are largely fire suppressed, relatively young open-canopy habitats that are preferred by grizzly bears, by and large, now occur in harvested areas (i.e., the surface area disturbed by recent harvesting is larger than that disturbed by recent wildfire). These open-canopy habitats occurring in harvested areas could promote, in absolute terms, a more widespread distribution of key food resources, thus increasing the probability of bears encountering and distinguishing between low- and high-quality areas (patchiness). Hence, forest harvesting in general may promote a higher probability of bears encountering key foods, and thus ease the ability of bears to recognize and exploit high-quality patches when compared to natural wildfire alone. This poses well for grizzly bears as increased access to high-quality patches can promote mass gain and ultimately higher fitness (McLellan, 2011; Nielsen et al., 2013), and may contribute to population recovery efforts. However, canopy closure appears to be occurring more quickly in harvested areas compared to wildfire areas in this study area, largely because of silvicultural management practices, limiting the spatiotemporal window that bears have access to key foods (Kearney et al., 2019). Moreover, control of human access to roads is still needed in harvested areas since roads are associated with an increased risk of bears to human-caused mortality (Nielsen et al., 2004b; Boulanger and Stenhouse, 2014). Additionally, a landscape disturbed by both natural wildfire and forest harvesting (*sensu* natural disturbance emulation) may produce a complex forest state, with increased complexity across multiple scales, over and above either disturbance type in isolation, which could benefit grizzly bears in some further capacity.

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Chapter 4: Disentangling the Effects of Food Resources and Road Density on Grizzly Bear Body Condition and Mortality Risk via an Individual-based Model

4.1. Abstract

As ongoing land-use change continues to be a threat to wildlife populations, management and recovery of wide-ranging omnivorous species in human-dominated landscapes requires us to understand how tradeoffs between food resources (health) and mortality risk (survival) change as a function of landscape change. Understanding how anthropogenic activity and habitat productivity influence grizzly bear (*Ursus arctos*) health and survival can aid population recovery goals and prioritize areas for conservation. In this study, I present a novel spatially explicit individual-based model (IBM) that simulates the interaction between grizzly bear agents, a spatiotemporal dynamic landscape of key grizzly bear foods, and differing road density levels for a threatened grizzly bear population in Alberta, Canada. Movement and decision heuristics of grizzly bear agents in this model were primarily derived from literature and field data on grizzly bear biology, bioenergetics, and behavioral ecology principles. I mainly sought to understand how the quality and distribution of food resources and road density influence individual health (body condition) and survival (mortality risk as it relates to roads). This model showed that survival rate of grizzly bear agents peaked at body condition index values near zero when survival was influenced by both road density and low body condition index values, suggesting a tradeoff between health and survival. I also found that grizzly bear agents that tended to be located in resource poor areas had higher survival rates yet were in lower body condition, whereas the opposite pattern occurred in resource rich areas. I also provide spatial maps of areas where bear agents of various sex-and-age classes have the highest probability of increasing their body condition (health) in contrast to areas where bear agents have the highest risk of mortality

(survival), and how these areas overlap with gradients of anthropogenic activity and habitat productivity. Finally, this model showed that the relationship between displacement and body condition index was contingent on whether grizzly bear agents foraged in resource rich or poor areas. Taken together, these findings in combination with this model provide a useful planning tool that could help support grizzly bear population recovery efforts and prioritize areas for conservation.

4.2. Introduction

In many areas of the world, intensified human use of landscapes continues to be a threat to animal populations affecting their distribution and abundance (Estes et al., 2011; Ripple et al., 2014). These land-use changes can mediate how wildlife populations respond to ‘bottom-up’ and ‘top-down’ processes, thereby influencing which factors limit and regulate populations (Sinclair and Krebs, 2002; Terborgh et al., 2001). The availability and quality of food resources as well as human-caused mortality are two such factors that can affect individual health and survival (Nielsen et al., 2013; 2017; Boulanger and Stenhouse, 2014). Indeed, wide-ranging and conflict prone species, such as large-bodied carnivores with high metabolic demands, must increasingly adapt to dynamic landscapes in human-dominated areas to meet energetic requirements whilst minimizing mortality risk (Carter and Linnell, 2016; Lamb et al., 2020). In the face of intensified and ongoing land-use changes, management of such species in human-dominated landscapes requires us to understand how tradeoffs between food resources (health) and mortality risk (survival) change as a function of landscape change, and how such findings can be used to enhance population recovery goals.

Monitoring and obtaining population criteria on elusive, large-bodied, wide-ranging, and conflict prone species such as the grizzly bear (*Ursus arctos*) is often cost-prohibitive and time consuming (Gompper et al., 2006; Steenweg et al., 2016). Moreover, human-caused mortality (top-down) is often considered a critical component shaping mortality rates in grizzly bear populations (Boyce et al., 2001) yet requires managing human behavior. Given these challenges, however, some have focused on 'bottom-up' regulation, whereby food resources and habitat supply are acknowledged as components that also shape grizzly bear populations (Nielsen et al., 2010; Nielsen et al., 2017; Souliere et al., 2020), yet can be more easily managed. Indeed, increases in grizzly (brown) bear body size and condition, as well as reproductive success, have been associated with food resource abundance and access to regenerating habitat (Nielsen et al., 2013; Boulanger et al., 2013; Bourbonnais et al., 2014; Hertel et al., 2018). Yet high-quality grizzly bear habitat often overlaps with areas that have higher road densities (Boulanger and Stenhouse, 2014; Proctor et al., 2019), which suggest a tradeoff between food resources (health) and human-caused mortality (survival) as it relates to roads. This in turn has implications on how wildlife managers establish population recovery goals. For instance, setting recovery targets for grizzly bears in Alberta requires knowing how gradients of anthropogenic activity and habitat productivity influence grizzly bear health, while at the same time, mitigating increased exposure of bears to roads. This tradeoff coupled with the fact that grizzly bear populations in Alberta may expand eastwards following a gradient in habitat productivity that increasingly overlaps with human-modified areas (McClelland et al., 2021) warrants tools that can provide guidance on recovery objectives.

Simulation modelling offers a flexible way to examine how decision-making, foraging, and bioenergetic processes influence tradeoff decisions made by animals when constrained by natural and anthropogenic features in dynamic landscapes. With individual-based models (IBM) in particular, individual animals can be thought as autonomous agents that have the capacity to interact with one another and with the environment over space and time (McLane et al., 2011; Railsback and Grimm, 2019). Although studies have used individual-based approaches to advance grizzly bear research (e.g., Zubiria Perez et al., 2021), or other bear species native to North America (e.g., Dey et al., 2017; Marley et al., 2017; 2019), the examination of how grizzly bears trade off food resources and mortality risk when navigating gradients of anthropogenic activity and habitat productivity has received much less attention. The interactions between fluxes in food resources, mortality risk in relation to road density, and bear decision-making and bioenergetics (Nielsen et al., 2010; Boulanger et al., 2013; Boulanger and Stenhouse, 2014; López-Alfaro et al., 2015) are complex, which necessitates tools for disentangling their interactions and informing the recovery of a provincially threatened species in a landscape increasingly modified by humans. Furthermore, identifying key areas where bears have the highest probability of increasing their body condition (health) in contrast to areas where bears have the highest risk of mortality (survival), and how this is linked to gradients in anthropogenic activity and habitat productivity, can help guide managers to focus recovery efforts and limited public resources more effectively and prioritize areas for conservation action.

Here, I simulate the interaction between grizzly bear agents, a spatiotemporal dynamic landscape of key grizzly bear foods, and differing road density levels using individual-based modeling, which focuses on modeling individual components (agents) that behave according to specified behavioral rules (Railsback and Grimm, 2019). IBMs are increasingly used in ecology and conservation biology as a means of representing structurally realistic ecological systems, where autonomous agents, each possessing heterogeneous characteristics and adaptive behaviors, can interact with one another and with the environment (McLane et al., 2011; Railsback and Grimm, 2019). IBMs can be thought as a bottom-up approach that focuses on understanding how a system's properties emerge from, and are linked to, the characteristics, interactions, and behaviors of its individual components (Grimm, 1999; McLane et al., 2011; Railsback and Grimm, 2019). IBMs provide an ideal framework to examine human-wildlife interactions, especially when investigated in a dynamic landscape, as complexity can be readily incorporated to generate emergent properties that improve our understanding of spatially structured populations (McLane et al., 2011). The IBM used in this study is composed of grizzly bear agents whose movements and decision-making are derived from a combination of literature and field data on grizzly bear biology, bioenergetics, and behavioral ecology principles.

4.3. Methods

4.3.1. Model overview

I built an IBM to evaluate how the quality and distribution of digestible energy and road density influence grizzly bear body condition (health) and survival (human-caused mortality as it relates to movements of bears in areas of high risk) for grizzly bears residing in an interior system of North America. I implemented the model in NetLogo 6.2.0 (Wilensky, 1999) and have included a comprehensive description of the model as well as the relevant code in the Supporting Information. This includes a TRACE document ("TRAnsparent and Comprehensive model Evaludation"; Schmolke et al., 2010; Grimm et al., 2014; Augusiak et al., 2014) containing a complete description of the model using the standard Overview, Design concepts, and Details (ODD) protocol (Grimm et al., 2006, 2010), and the methods used to parameterize, verify, calibrate, analyze, and corroborate the model (see Appendix S1). Apart from two model parameters determined via calibration, all other parameters were parameterized from previously published studies, long-term datasets of grizzly bear ecology, and field data. I used pattern-oriented modeling (POM; Grimm et al., 2005) via visual inspection to determine whether model outputs (e.g., mass gain pattern, bioenergetics, body condition index, and displacement (distance traveled, km/y); consult section 8 in TRACE for further details) closely matched observed patterns of grizzly bear populations of interior North America. The IBM aims to address three primary questions: (i) investigate whether grizzly bears can gain sufficient body mass needed to meet energetic requirements in a landscape where food resources vary both spatially and temporally, especially regarding adult females, (ii) determine how the quality and distribution of food resources and road density influence individual health (body condition) and survival (mortality risk), and (iii) show whether sex and age-class influence how grizzly bears navigate gradients of food resources and road density. I provide a brief outline here of the major components of the model, however, details are available in the TRACE document along with the model code (Appendix S2).

4.3.2. Landscape components

The IBM simulated grizzly bear agents navigating a landscape in west-central Alberta, Canada, that represented a real landscape with digestible energy values derived from real-world data collected from field plots, and the physical location of real-world roads. The two-dimensional landscape consisted of 60 by 60 m square cells (patches), with a total landscape area of 11,162 km^2 (see Figure S1 in TRACE). Each patch was assigned a value representing digestible energy unless the patch was considered a road. Digestible energy values varied spatiotemporally corresponding to field food resource models representing key grizzly bear foods and plant phenology, which influenced the energy acquisition of grizzly bear agents, and thus their body condition and overall movement. Road density varied spatially and influenced the survival rate of grizzly bear agents. Although the same landscape was generated for each model run and populated with the same digestible energy values that fluctuated based on location and phenology, grizzly bear agents were distributed at random locations instead and allowed to move based on the landscape and their internal state. Consult sections 2.5, 3.1, and 3.2 in TRACE for further details. During each hourly time-step (i.e., 24 time-steps per day), grizzly bear agents behaved according to general rules. Each model run began on April 15th and ended on October 15th, representing den exit and den entry, respectively. See section 2.3 in TRACE for further details.

4.3.3. Digestible energy agents

Digestible energy values (patch agents) representing empirical digestible energy were estimated from field data collected in west-central, Alberta, Canada. These empirically derived food models (biomass) were grouped into major grizzly bear food groupings based on Munro et al. (2006) and were converted into digestible energy following methods outlined in the literature (López-Alfaro et al., 2015; Nielsen et al., 2015; Nielsen et al., 2017; Souliere et al., 2020; McClelland et al., 2021). The major food groupings include fruit, forb, horsetail, sweetvetch roots, ant, and ungulate. All pixels were assigned digestible energy values based on major food groupings and a total digestible energy value, which represented the sum value of all major digestible energy layers (food groupings). The total digestible energy value was the only value selected by grizzly bear agents when interacting with patches. For further details, see section 2.5 in TRACE.

Grizzly bears adjust their foraging behavior and diet based on seasonality and phenology of important food items (Munro et al., 2006; Nielsen et al., 2010). To model this process, I weighted digestible energy values based on the changing phenology of major food groupings so that grizzly bear agents had access to spatiotemporally realistic digestible energy values from den exit to den entry. I weighted each major food grouping value based on biweekly food weights extracted from Munro et al. (2006) and subsequently summed these values into a total digestible energy value, which was updated biweekly. That way, the total digestible energy value of every patch was distributed throughout the active period according to food resource phenology. For further details, see section 3.1 in TRACE.

4.3.4. Grizzly bear agents

Grizzly bear agents were able to move around the landscape to acquire digestible energy to meet their energetic needs. This behavior was contingent on their internal state (resting, foraging, or moving), energetic state (body condition index [BCI]; Cattet et al., 2002), and their ability to sense the quality of digestible energy (dependent on spatial location and food resource phenology) in their surrounding environment. Grizzly bear agents that were in poor BCI were more likely to actively forage to increase their BCI, which restricted their opportunity to encounter high-quality areas compared to bear agents in good BCI. Those in good BCI were more likely to forage in high-quality areas they encountered opportunistically, as they could risk briefly lowering their BCI. Grizzly bear agents could sense the mean digestible energy in 5 surrounding patches every hour, which included the patch they currently occupy, and incorporate this information into their decision-making process, with each patch equivalent to 60 m (Gibeau et al., 2002; Nielsen et al., 2017; Denny et al., 2018). The survival of grizzly bear agents was solely influenced by road density and calculated before den entry. I did, however, adjust the survival rate of grizzly bear agents during statistical analysis to understand model findings (see *Model analysis*). Movement rates (m/h) and energetic demands were influenced by the sex-and-age-class of bear agents. Furthermore, adult female agents with offspring (i.e., a single cub-of-the-year or single yearling) had reduced movement rates and increased energetic demands since offspring could be thought as an energetic “anchor” (López-Alfaro, 2014; Graham and Stenhouse, 2014). See sections 2.4, 2.5, 2.7, 3.1, and 3.3 of TRACE for further details.

4.3.5. Road crossing frequency and survival

I used simple road crossing decision rules that dictated how grizzly bear agents navigated roads when encountering them while in a foraging or moving state. The intent of the model was not to simulate complex road crossing decision rules. For instance, once a road was encountered, grizzly bear agents could only ‘cross’ the road and could not (immediately) turn around nor move parallel to it. This rule applied to all bear agents. To estimate the relationship between survival and road crossing frequency, I first needed an intermediary step that established the relationship between road density and road crossing frequency. I did so by building a small separate IBM that simulated agents navigating the same landscape as the main IBM (see Figure S1) yet with agents constrained within the boundaries of individual watersheds, each of which with different road densities and a single agent moving in a random walk (see Appendix S3). I used the results from this simulation to build a linear model showing the relationship between road density and road crossing frequency and used the parameters from this linear model to parameterize the main IBM. Using data from Boulanger and Stenhouse (2014), I then established a relationship between survival and road density and used these reconstructed models to parameterize the main IBM as well. These steps allowed me to link survival to road crossing frequency via the relationship between road density and road crossing frequency. In other words, I linked survival of grizzly bear agents to road crossing frequency via the parameters describing the relationship between road density and road crossing frequency. The newly predicted (effective) road density would then be used to predict survival using the models reconstructed from Boulanger and Stenhouse (2014). Consult Appendix S3 and section 3.4 in TRACE for further details.

4.3.6. Model parameterization

I parameterized this model using a combination of literature and field data on grizzly bear ecology, behavioral ecology principles, bioenergetics, and field food resource and road density layers (GIS). I included a list of model parameters in Table S1 and sections 2 and 3 of the TRACE document. Furthermore, I calibrated two model parameters (coefficient for the proportion of day active and minimum hourly energy consumed by agents) using inverse determination via calibration as these parameter values could influence various model processes and overall results and could not be properly derived from literature sources. Further details on inverse calibration of model parameters can be found in section 6 of the TRACE document. As this study area was centered in west-central Alberta and grizzly bears are listed as threatened in Alberta, a large portion of the model was parameterized with literature sources and/or data originating from Alberta, which provided good background data on grizzly bear ecology. When data was not available from Alberta, I prioritized data from adjacent areas (e.g., literature sources from interior populations of grizzly bears in western Canada and the contiguous U.S.).

4.3.7. Sensitivity analysis

To understand how uncertainty in parameter values influenced model outputs, I performed a sensitivity analysis that is detailed in section 7 of the TRACE document. In short, I selected seven key parameters that were associated with some uncertainty and that I considered to have an important influence on model outputs. I then randomly varied each parameter within intervals of uncertainty (range) and used regression-based techniques to understand how each parameter of interest contributed to variance in model outputs. In general, BCI and survival rates for both male and female grizzly bear agents were insensitive to changes in parameters values. Uncertainty in most parameter values explained < 2% of variation in model outputs across model runs (Table S4). Varying some parameters, however, had moderate effects on some model outputs. For instance, forage probability when BCI < BCI threshold (-2 to +2) explained 5.5% and 9% of the variance in female survival rate and male survival rate, respectively. Likewise, forage probability when BCI >= BCI threshold (-2 to +2) explained between 5.8% and 10.6% of the variance when considering all model outputs (Table S4).

4.3.8. Model validation via POM

To validate (corroborate) this model, I used pattern-oriented modeling (POM; Grimm et al., 2005). The idea here is to have the model reproduce patterns observed in real systems that were not included, or preferably not known, during model design to understand the model's internal organization. Thus, the model's emergent (reproduced) patterns act as indicators of the model's underlying structure and processes, effectively reassuring users that the model contains the correct mechanisms to address the problem and makes useful predictions that can be trusted to some degree (Grimm et al., 2005; Grimm and Railsback, 2012; Grimm et al., 2014; Railsback and Grimm, 2019). Furthermore, a model that reproduces patterns of a real system at multiple levels (both agent and system level) and at different scales reduces the risk that the model is completely unrealistic (Grimm et al., 2014), thus reassuring users of the model's utility. To that end, this model reproduced empirical results of grizzly bear bioenergetics which included similar yearly mass gain and loss patterns (Kingsley et al., 1988; Blanchard, 1987; Schwartz et al., 2003; McLellan, 2011), rates of mass gain per day (Pearson, 1975; Nagy and Russell, 1978; Bunnell and Hamilton, 1983; Kingsley et al., 1983; Blanchard, 1987; Hilderbrand et al., 1999; Rode et al., 2001), changes and patterns in BCI (McLellan, 2011), mean BCI during spring (McLellan, 2011; Bourbonnais et al., 2014), and yearly movement rates (Boulanger et al., 2013; Graham and Stenhouse, 2014) observed in wild grizzly bear populations. Similar to observations in Boulanger et al. (2013), grizzly bear agents in the model had similar geographic patterns in BCI change relative to gradients of forested areas. In other words, BCI gains of grizzly bear agents were associated with regenerating forest habitats, whereas reductions in BCI were associated with older forest. Furthermore, grizzly bear agents tended to have higher BCI values in areas with high amounts of digestible energy, large variation in digestible energy, and areas with higher proportions of early seral forests (≤ 30 years). Consult section 8 of TRACE for further details.

4.3.9. Model analysis

To understand general model findings and account for variation due to stochasticity in the model, I ran 100 replications (model runs) in BehaviorSpace (Wilensky and Shargel, 2002) and exported results to R for statistical analysis. To analyze the relationship between survival rate and BCI, I fitted generalized linear models (GLMs) and generalized additive models (GAMs) with thin-plate regression splines to results from 100 model runs (Table 4.1). These models were fitted with a beta distribution with a logit-link as the observations were limited to the open interval (0, 1) (Ferrari and Cribari-Neto, 2004; Smithson and Verkuilen, 2006). Recognizing that the response variable contained observations of zero, I transformed the response variable according to suggestions outlined in Smithson & Verkuilen (2006) and Douma and Weedon (2019). I estimated statistical models with the *mgcv* package (Wood, 2017) in R using maximum-likelihood methods and compared the fit of these models with Akaike information criterion (AIC) (lower AIC values indicating better model fit; Akaike 1974). I accounted for shared variance among model runs by fitting a random intercept in each model, however, the inclusion of a random intercept did not improve model fit and so I report models fitted with fixed effects only. I used the survival rate of each grizzly bear agent at the end of the active period as the response variable. I modeled survival rate in two ways: 1) solely influenced by road density, and 2) influenced by road density and low BCI (bear agents with BCI ≤ -1 were considered dead and so were assigned a survival rate of zero) (Table 4.1). I chose a threshold BCI value ≤ -1 because BCI values reported in wild populations rarely fall below this threshold (McLellan, 2011; Bourbonnais et al., 2014). The fixed effects included in the model were the sex-and-age-class (adult female, adult female with offspring, sub-adult female, adult male, and sub-adult male) and end-of-active-period BCI of grizzly bear agents. I plotted trends in survival rate against BCI for each sex-and-age-class. I also visually display the spatial relationship between relative density and survival rate, and relative density and BCI across a real landscape.

To evaluate how displacement varied as a function of BCI and resource quality in adult male and adult female grizzly bear agents, I fit two separate (adult male and adult female) multiple linear regressions that examine the effect of resource quality, BCI, and the interaction between resource quality and BCI on displacement (model: displacement = resource quality + spring body mass + BCI + resource quality * BCI). For simplicity, I delineated whether bears were located in resource rich or poor areas (i.e., resource quality) based on the mean latitude and longitude of individual bear locations throughout the active period. I considered multicollinearity in covariates by using variance inflation factor (VIF) to assess linear terms did not exceed a threshold value of 5 (Dormann et al., 2013). I considered all tests significant at $\alpha \leq 0.05$ and used R v4.0.3 to perform all statistical analyses (R Core Team, 2020).

Table 4.1. Summary of model fits for survival rate modeled in two ways: 1) solely influenced by road density, and 2) influenced by road density and low BCI (bear agents with BCI <= -1 were considered dead and so were assigned a survival rate of zero). The models depict the relationship between survival rate as a function of BCI and were fit by the gam function in *mgcv* (Wood, 2017). Statistical models consider the results from 100 model runs. I report AIC, generalized cross-validation score, and adjusted R^2.

	AIC	GCV	Adjusted R^2
$\text{GLM}_{\text{Survival}}$	-82 327	-41 154	0.19
$\text{GAM}_{\text{Survival}}$	-82 877	-41 421	0.26
$\text{GLM}_{\text{Survival\_BCI}}$	-85 474	-42 727	0.07
$\text{GAM}_{\text{Survival\_BCI}}$	-85 796	-42 876	0.13

4.4. Results

4.4.1. Relationship between BCI and survival

When solely accounting for the influence of road density, the relationship between survival rate and body condition was sigmoid and was best fit by a GAM (Table 4.1), where survival rate was high for low BCI values and dropped precipitously through mid and high BCI values across all sex-and-age-classes (Fig. 4.1A). This GAM fitted with a beta distribution explained 26% of the variance in survival rate (Table 4.1). In contrast, when accounting for the influence of road density and low BCI (i.e., bear agents with BCI $\leq$ -1 were considered dead and so were assigned a survival rate of zero), the relationship between survival rate and body condition peaked at BCI values just below zero across all sex-and-age-classes (Fig. 4.1B), indicating that grizzly bear agents with the highest survival rate had neither very low nor very high BCI values, suggesting a tradeoff between road density and food resources. Again, a GAM fitted with a beta distribution explained 13% of the variance in survival rate (Table 4.1). When considering road density and low BCI, peak survival rate of adult females was comparatively higher than other sex-and-age classes (Fig. 4.1B).

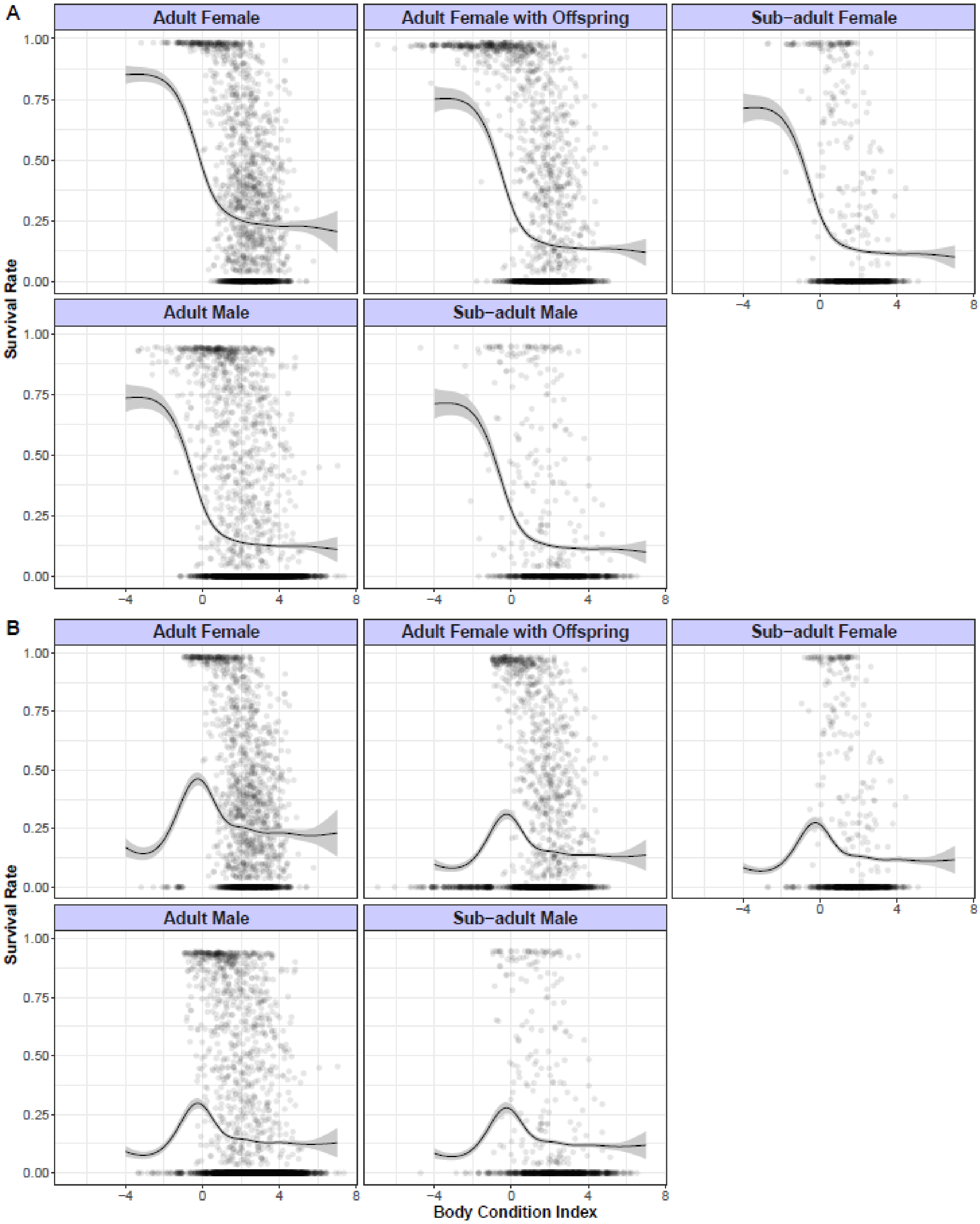
A
Adult Female
Adult Female with Offspring
Sub−adult Female
Adult Male
Sub−adult Male
Survival Rate
1.00
0.75
0.50
0.25
0.00
−4
0
4
8
B
Adult Female
Adult Female with Offspring
Sub−adult Female
Adult Male
Sub−adult Male
Survival Rate
Body Condition Index

Fig 4.1. Predicted survival rate influenced solely by road density (A) and predicted survival rate influenced by road density and low BCI (B), of grizzly bear agents among five sex-and-age classes as a function of BCI. Points show end-of-simulation survival rates. Curves represent the predictions from the most supported model, which here is the model $\mathrm{GAM}_{\mathrm{Survival}}$ for Panel A and model $\mathrm{GAM}_{\mathrm{Survival\_BCI}}$ for Panel B (Table 4.1).

4.4.2. Spatial patterns of survival across environmental gradients

Across all sex-and-age-classes, grizzly bear agents tended to have low survival rates in areas with high road density and conversely, high survival rates in areas with low road density (Fig. 4.4; Fig. 4.2B). Distribution patterns were slightly different among sex for grizzly bear agents with survival rates ≥ 0.25 & < 0.75, where female locations, and in particular adult females and adult females with offspring, tended to span areas with intermediate levels of road density (Fig. 4.4; Fig. 4.2B), whereas adult males and sub-adult males tended to be located in areas with low road densities (Fig. 4.4; Fig. 4.2B).

4.4.3. Spatial patterns of BCI across environmental gradients

Across all sex-and-age-classes, grizzly bear agents tended to have low BCI values in areas (Fig. 4.5) with low digestible energy (Fig. 4.3A), low variance in digestible energy (Fig. 4.3B), in areas with little forestry disturbance (Fig. 4.2A). Conversely, grizzly bear agents with moderate and high BCI tended to be located in areas (Fig. 4.5) with high digestible energy (Fig. 4.3A), high variance in digestible energy (Fig. 4.3B), and in areas with higher rates of forestry disturbance (Fig. 4.2A). In general, male grizzly bear agents with high BCI values (Fig. 4.5) tended to occupy a larger portion of the landscape than females (Fig. 4.5), which overlapped areas with high digestible energy (Fig. 4.3A), high variance in digestible energy (Fig. 4.3B), and areas with early seral forests (Fig. 4.2A). BCI gains were associated with early seral forests, which coincided with areas that had higher amounts and larger variance in digestible energy, whereas reductions in BCI were associated with areas lacking early seral forests, which coincided with areas that had lower amounts and smaller variance in digestible energy.

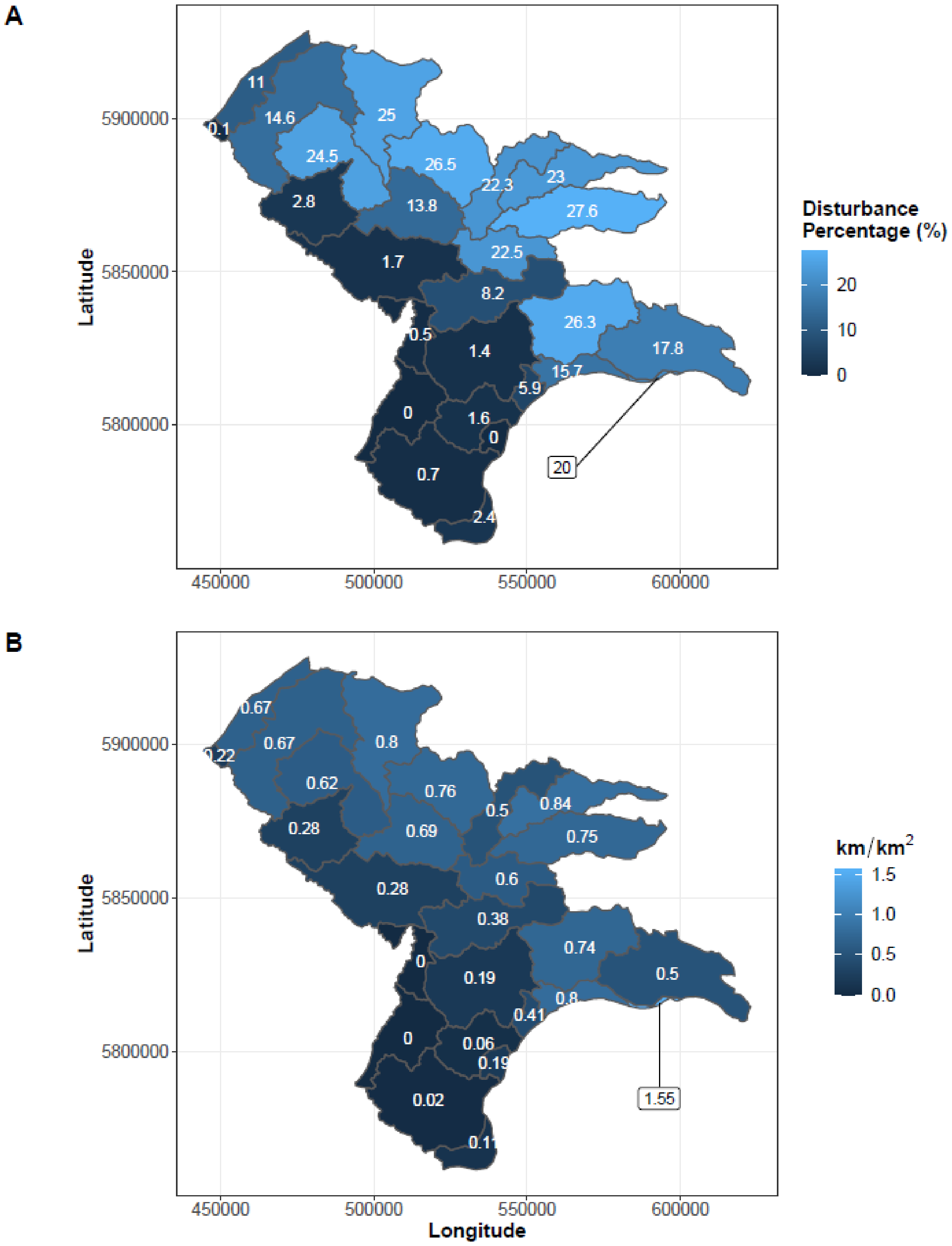

Fig 4.2. A) The percentage of surface area disturbed by early seral forests (≤ 30 years) in each Alberta watershed. B) Empirical road density values recorded in Alberta and mapped within watersheds. Road density values are derived from road GIS layers which were used within the simulation itself.

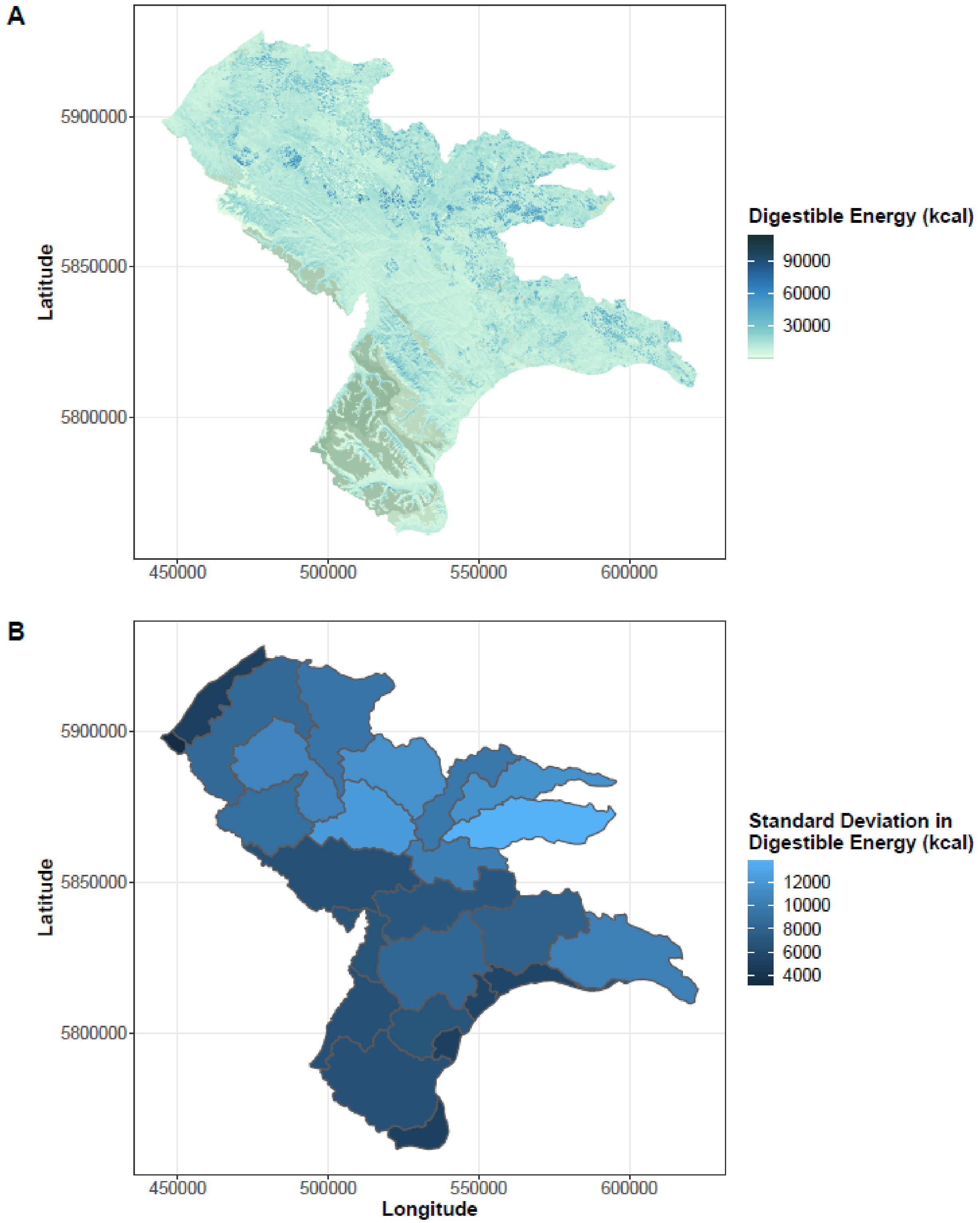

Fig 4.3. A) The total amount of digestible energy (kcal) and B) standard deviation in the total amount of digestible energy (kcal) available on the landscape summarized from individual food groupings (fruit, forb, horsetail, sweetvetch roots, ant, and ungulate). Panel B is summarized within Alberta watersheds.

4.4.4. Spatial patterns of survival and BCI across environmental gradients

Spatial patterns in survival rate (Fig. 4.6) when adjusted for road density and low BCI (i.e., bear agents with BCI ≤ -1 were considered dead and so were assigned a survival rate of zero) did not, in general, differ all that much from spatial patterns in survival rate solely influenced by road density (Fig. 4.4). I suspect this is the case because too few grizzly bear agents had BCI ≤ -1 to drastically change the spatial patterns in survival rate. However, adult females and adult females with offspring had survival patterns that noticeably differed from that of males, whether looking at survival rate solely influenced by road density (Fig. 4.4) or adjusted for road density and low BCI (Fig. 4.6), specifically when considering intermediate survival rate values ranging from ≥ 0.25 to < 0.75. The location of females with intermediate levels of survival overlapped more so with areas of high digestible energy, high variance in digestible energy, early seral forests, and higher road densities (Fig. 4.2 and Fig. 4.3), compared to males.

4.4.5. Synthesis of environmental factors influencing survival and BCI

Grizzly bear agents that tended to be located in areas with lower road densities (Fig. 4.2B) had a higher probability of survival (Fig. 4.4), yet those areas overlapped with areas that had low amounts of digestible energy (Fig. 4.3A), low variance in digestible energy (Fig. 4.3B), and little early seral forests (Fig. 4.2A). Hence, bear agents in those areas had a lower probability of increasing their body condition, but also had a lower risk of mortality (higher survival). In contrast, bear agents that tended to be located in areas with higher road densities (Fig. 4.2B) had a lower probability of survival (Fig. 4.4), yet those areas overlapped areas with high digestible energy (Fig. 4.3A), high variance in digestible energy (Fig. 4.3B), and areas with more early seral forests (Fig. 4.2A). Hence, bear agents in those areas had a higher probability of increasing their body condition (Fig. 4.5), but also had a higher risk of mortality (lower survival).

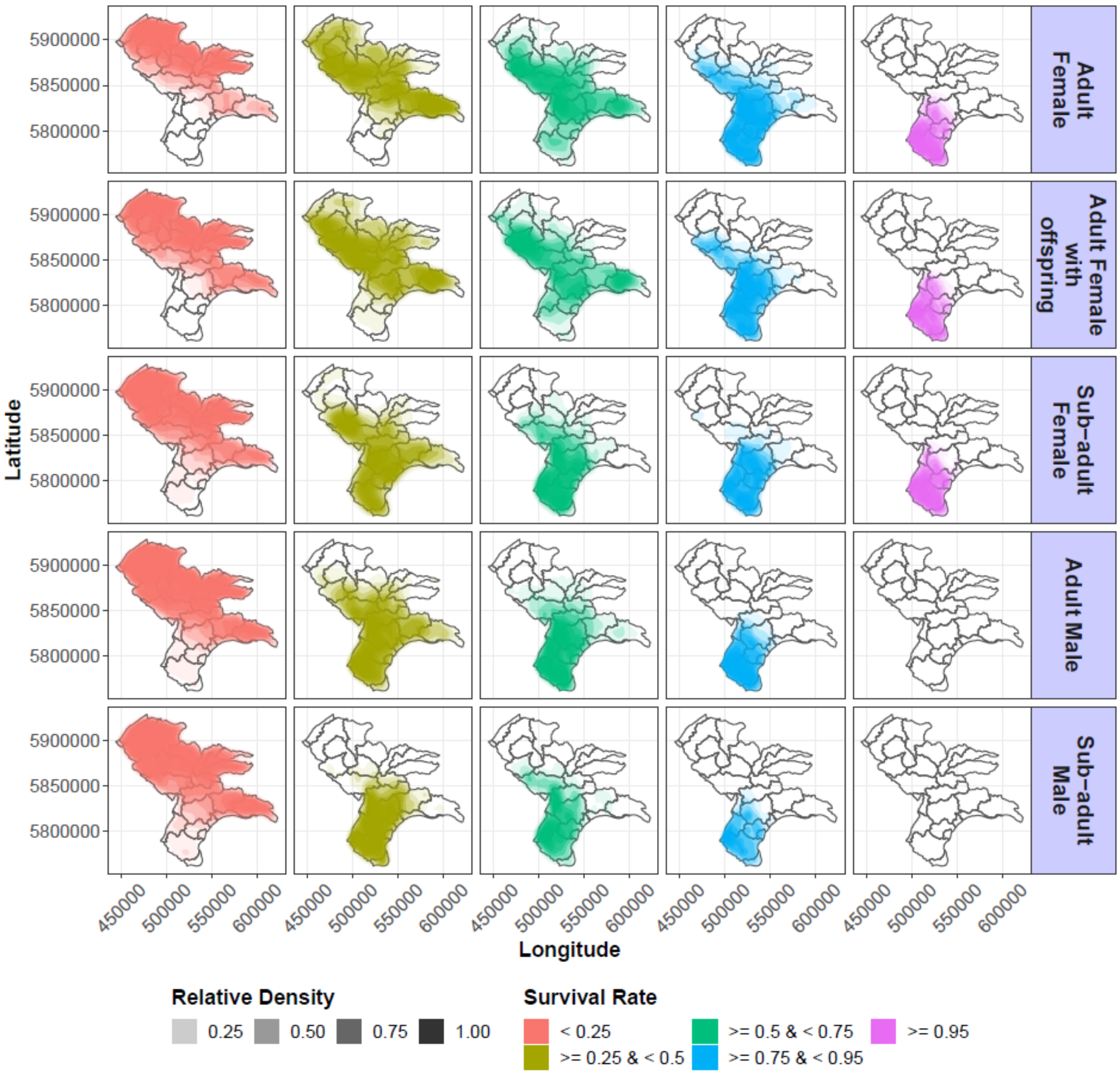

Fig 4.4. Spatial relationship illustrating the relative location density contrasted against survival rate of grizzly bear agents among five different sex-and-age-classes. Spatial locations are recorded once per day (at the beginning of each day) throughout the simulation and contrasted, for visualization purposes, against end-of-simulation survival rate values. Data is not summarized within each model run, rather it is pooled here across 100 model runs. In contrast to female agents, the model did not record male agents with end-of-simulation survival rates >= 0.95.

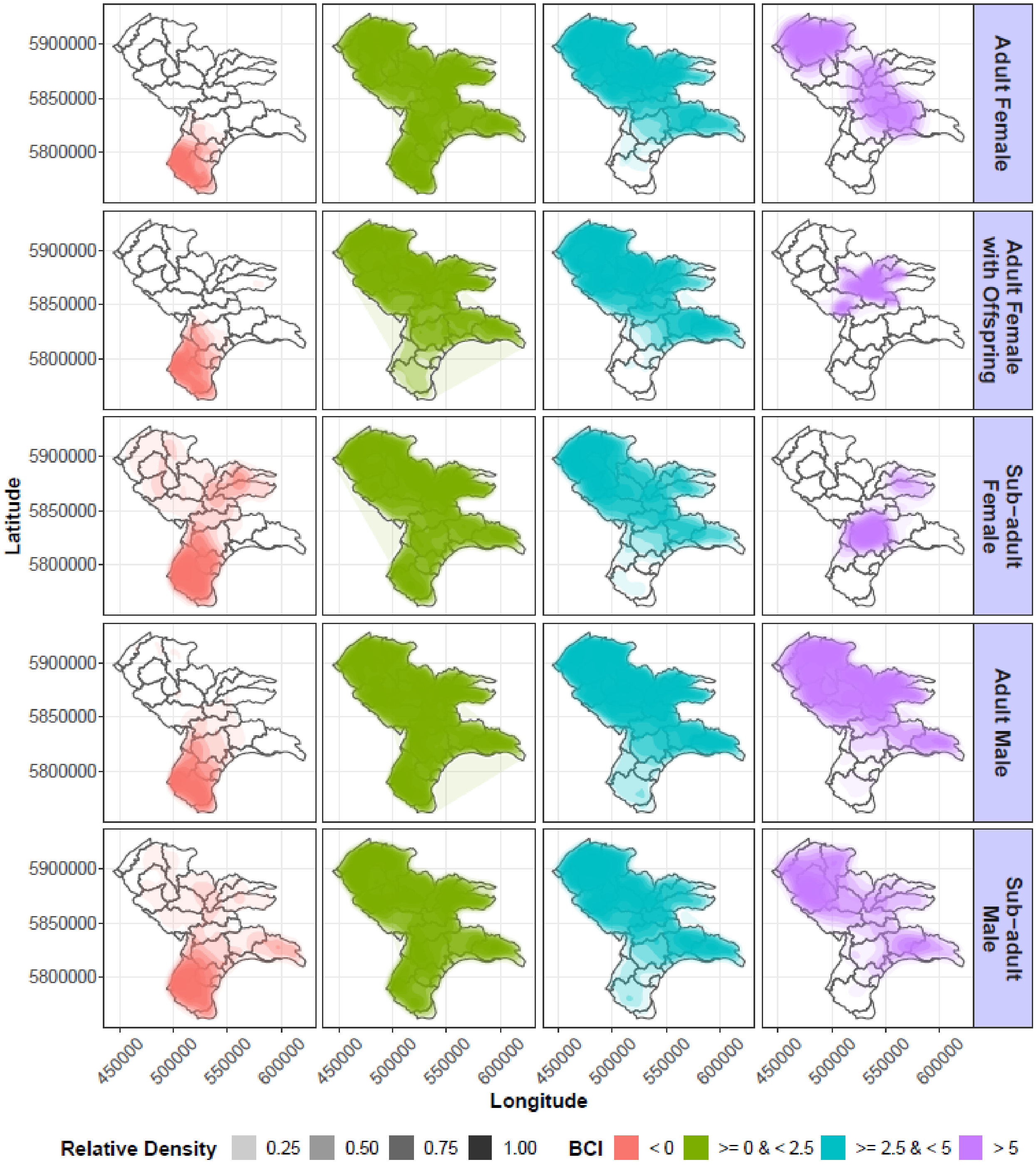

Fig 4.5. Spatial relationship illustrating the relative location density contrasted against BCI of grizzly bear agents among five different sex-and-age-classes. Spatial locations are recorded once per day (at the beginning of each day) throughout the simulation and contrasted, for visualization purposes, against end-of-simulation BCI values. Data is not summarized within each model run, rather it is pooled here across 100 model runs.

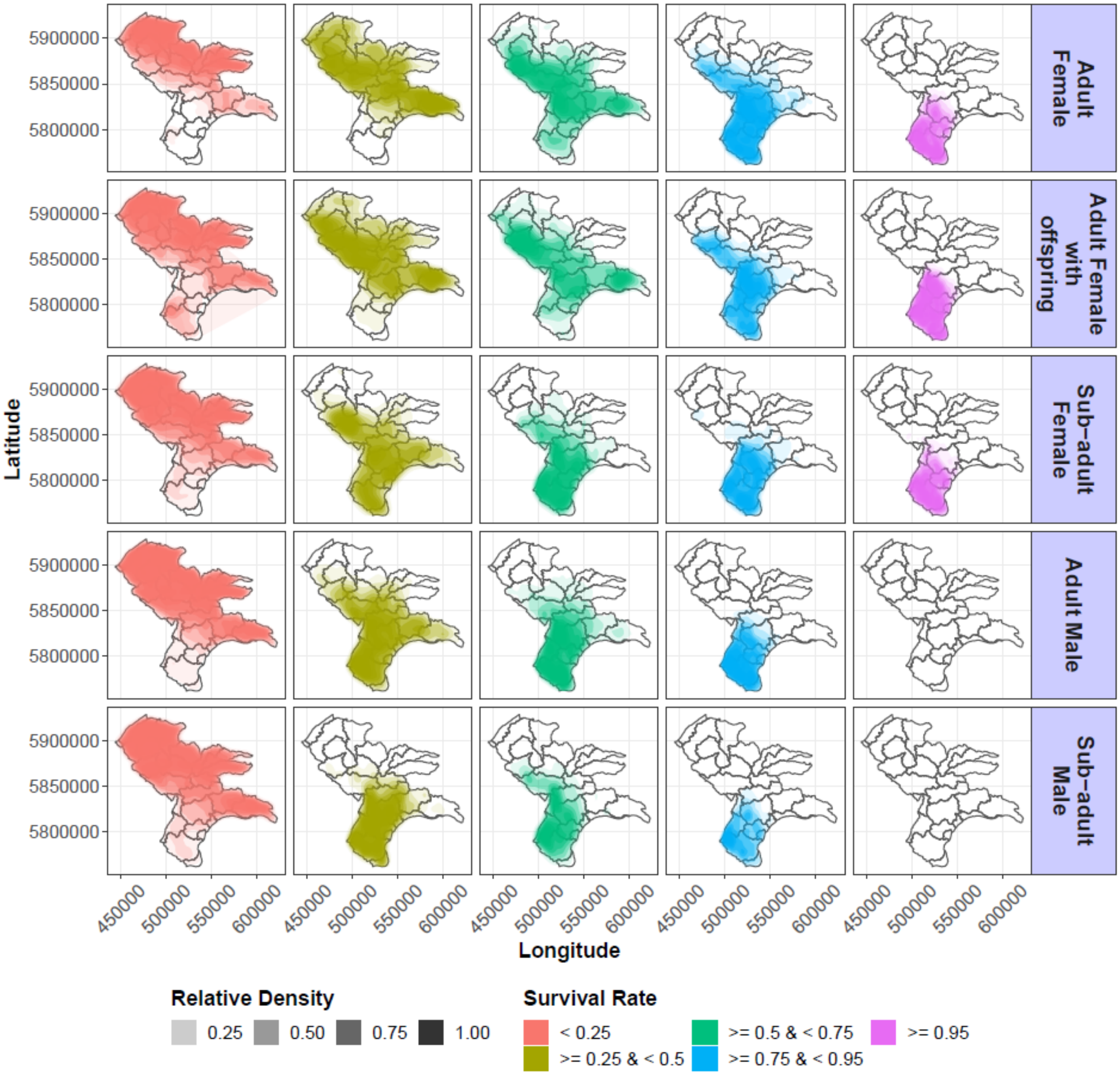

Fig 4.6. Spatial relationship illustrating the relative location density contrasted against survival rate of grizzly bear agents among five different sex-and-age classes. Here survival rate is based on the influence of both road density and low BCI (i.e., bear agents with BCI <= -1 were considered dead and so were assigned a survival rate of zero). Spatial locations are recorded once per day (at the beginning of each day) throughout the simulation and contrasted, for visualization purposes, against end-of-simulation survival rate values adjusted for low BCI. Data is not summarized within each model run, rather it is pooled here across 100 model runs. In contrast to female agents, the model did not record male agents with end-of-simulation survival rates >= 0.95 when adjusting for low BCI.

4.4.6. Relationship between displacement (distance traveled) and BCI

For adult males, displacement increased significantly as BCI increased ($F(1, 3973) = 79.682$, $p = < 0.001$, $\eta_p^2 = 0.02$; Table 4.2 and Fig. 4.7), with an R^2adj of 0.05; this pattern was similar between resource rich and resource poor areas ($F(1, 3973) = 0.016$, $p = 0.901$, $\eta_p^2 = 0$; Table 4.2 and Fig. 4.7). However, across BCI, grizzly bear agents in resource poor areas tended to have larger displacement compared to bear agents in resource rich areas ($F(1, 3973) = 55.537$, $p < 0.001$, $\eta_p^2 = 0.014$; Table 4.2 and Fig. 4.7). For adult females, the relationship between displacement and BCI significantly depended on whether grizzly bear agents foraged in resource poor or rich areas ($F(2, 1670) = 11.572$, $p < 0.001$, $\eta_p^2 = 0.007$; Table 4.2 and Fig. 4.7), with an R^2adj of 0.18 . Similar to males, female grizzly bear agents in resource poor areas tended to have larger displacement compared to bear agents in resource rich areas ($F(1, 1670) = 263.314$, $p < 0.001$, $\eta_p^2 = 0.136$; Table 4.2 and Fig. 4.7).

Table 4.2. Standardized parameter estimates, standard errors, and *p* values predicting displacement (traveled distance in km per year) among adult male and lone adult female (i.e., no offspring) grizzly bear agents. Separate models were used for each sex.

	Female			Male		
Variable	*β*	SE	*p*	*β*	SE	*p*
Intercept/Resource Quality (rich)	-0.183	0.025	< 0.001	-0.065	0.017	< 0.001
Resource Quality (poor)	0.916	0.097	< 0.001	0.474	0.057	< 0.001
Spring Body Mass	-0.234	0.023	< 0.001	0.061	0.018	< 0.001
BCI	0.122	0.029	< 0.001	0.167	0.020	< 0.001
Resource Quality * BCI (poor = 1, rich = 0)	-0.226	0.067	<0.001	-0.006	0.046	0.901

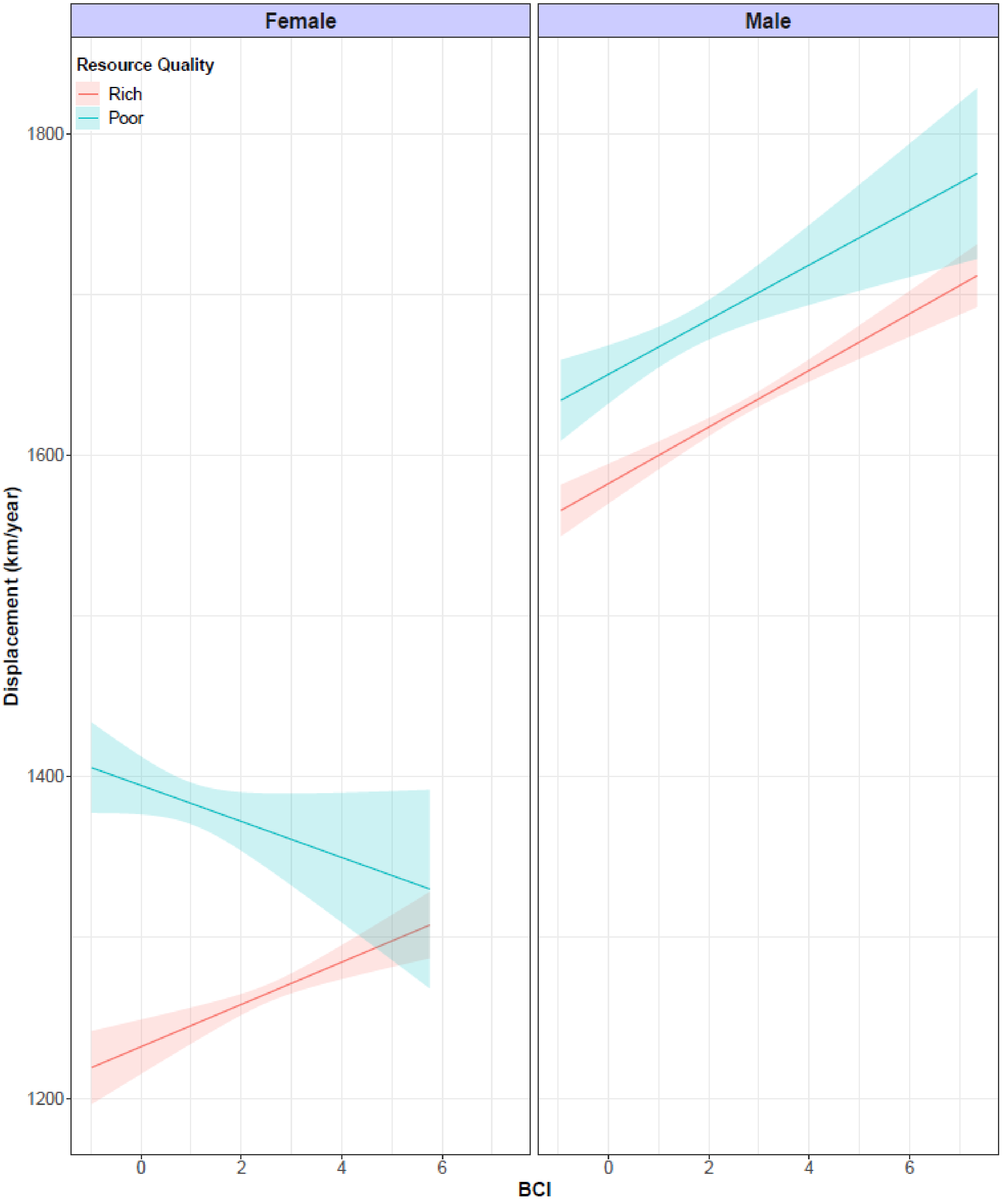

Fig 4.7. Predicted displacement (km/year) for lone adult female (i.e., no offspring) and adult male grizzly bear agents as a function of BCI in resource rich and poor areas (i.e., resource quality). Lines represent prediction estimates and shaded regions represent 95% confidence intervals of prediction estimates. Separate models were used for each sex.

4.4.7. Model Validation Results

This model produced results consistent with previous findings in the grizzly bear literature (further details and other patterns not described here can be found in section 8 of TRACE). Specifically, spring BCI values showed similarities to BCI values recorded from grizzly bears captured in spring residing in interior North America (McLellan 2011, Bourbonnais et al., 2014; Table S6), providing some credibility to patterns of BCI change throughout the active period (Figure S7) and BCI recordings before denning (Figure S8). Furthermore, I provided measurements on daily mass gain for different sex-and-age classes (Table S6), which is often reported for captive bears, yet has not been recorded in this study area. I also provided estimates on the minimum hourly energy consumed by grizzly bear agents for different sex-and-age-classes to reproduce patterns as described here, which to my knowledge, has not been recorded in the literature (see section 6.2 of TRACE for values and details). The validation (corroboration) of the results confirms that this model can accurately reproduce patterns that emerge from the interaction between real-world environments, grizzly bear biology, and decisions made by real grizzly bears.

4.5. Discussion

The model presented here provides insights into how a spatiotemporal dynamic landscape informed by empirically derived food resources and road density metrics influence grizzly bear body condition and survival (human-caused mortality as it relates to movements of bears in areas of high risk) for grizzly bears residing in an interior system of North America using individual-based modeling. I found that survival rate of grizzly bear agents peaked at BCI values near zero when survival was influenced by both road density and low BCI values (i.e., bear agents with BCI $\leq$ -1 were considered dead and so were assigned a survival rate of zero), suggesting a tradeoff between food resources and road density. I also found that grizzly bear agents that tended to be located in resource poor areas had higher survival rates, yet lower body condition. Bear agents that tended to be located in resource rich areas had lower survival rates, yet higher body condition. The findings also provide spatial maps of areas where bear agents of various sex-and-age classes have the highest probability of increasing their body condition (health) in contrast to areas where bear agents have the highest risk of mortality (survival), and how these areas overlap with gradients of anthropogenic activity and habitat productivity. I also demonstrated that the linear association between displacement and BCI for lone adult females (i.e., no offspring) and adult males was contingent on whether grizzly bear agents foraged in resource rich or poor areas.

When accounting for the influence of road density and low BCI (Fig. 4.1B), I found survival rate for all sex-and-age classes peaked at BCI values near zero, indicating that bear agents with the highest probability of survival had neither very low nor very high BCI values, suggesting a tradeoff between road density and food resources whereby bears occupying habitats of marginal productivity (*sensu* food resources) had the highest probability of survival. Furthermore, since the areas in which bear agents had higher BCI were more likely to overlap with areas that had more early seral forests, larger amounts of digestible energy, and larger variance in digestible energy, bears occupying similar real-world areas may be able to increase their overall body condition (health). Those same areas, however, overlapped with areas that had higher road densities, thus increasing the mortality risk (lower survival) of bear agents as it relates to roads. My findings demonstrate anthropogenic activity, through the creation of regenerative forest habitat, potentially increases body condition (health) in real-world bears via increased access to high-quality food resources and habitat. In constrast, potential gains in body condition (health) are offset by increases in mortality risk (lower survival) since areas with regenerative forest habitat often contain higher road densities, thus creating sink habitats and dampening the beneficial effect of regenerative forest habitat on grizzly bear overall survival via direct increases in health. These patterns suggest that bears using early seral forests – which provide a diverse range of food resources (Martin, 1983; Nielsen et al., 2004b; Souliere et al., 2020) and are associated with increases in local population density (Nielsen et al., 2017) and fitness (McLellan, 2011; Erlenbach et al., 2014) – may be experiencing a tradeoff between health and survival, whereby bears are caught in an ecological trap or attractive sink where food resources are abundant and varied enough to sustain health yet occur in areas with high road densities leading to low survival (Nielsen et al., 2006; Northrup et al., 2012; Boulanger et al., 2013; Lamb et al., 2016). Thus, to avert extirpation in sink habitats, an influx of bears dispersing from adjacent wilderness areas (low human presence) may be needed to sustain stable population growth in an actively managed landscape (Lamb et al., 2020), such as is the case in Alberta.

The spatial maps not only describe where grizzly bear agents have the highest probability of increasing their body condition in contrast to areas where bear agents have the highest risk of mortality, but they also help link how gradients of anthropogenic activity and habitat productivity potentially shape grizzly bear health and survival, thus delineating source and sink habitats and how this can be effectively used to focus conservation efforts. For instance, grizzly bear agents in this model increased their body condition in areas that overlapped with early seral forests and high amounts and large variance in digestible energy, suggesting bears in this study area are not only benefiting from early seral forests disturbed primarily by forest harvesting, but they may also be benefiting from heterogeneity in food resources created by such disturbances. Heterogeneity (i.e., broader distribution of food resources and larger contrast between food resource patches), may in fact, facilitate the probability of encountering and identifying high-quality food resources (Denny et al., 2018), thus enabling bears to optimize macronutrient intake, and increase body condition and mass gain (Bourbonnais et al., 2014; Coogan et al., 2014; Erlenbach et al., 2014). Notwithstanding the increased mortality risk in harvested areas because of higher road densities, a mosaic of early seral forests in proximity to secure forest stands provides bears with both high-quality forage as well as bedding and hiding cover (Nielsen et al., 2004a). Moreover, grizzly bear agents with high BCI values tended to be located more often in areas that corresponded with a general gradient of increasing habitat productivity, suggesting the foothills may be able to sustain higher bear densities. This correspondence pattern is consistent with recent findings in the foothills, whereby grizzly bear carrying capacity (density) estimates increased eastward, coinciding with a general gradient of increasing habitat productivity (McClelland et al., 2021).

Overall, adult females and adult females with offspring had different patterns than other sex-and-age classes, especially compared to males. For instance, when considering road density and low BCI, peak survival rate of adult females was comparatively higher than adult males. Likewise, adult females and adult females with offspring that had survival rates values ranging from ≥ 0.25 to < 0.75 tended to be located more often in areas that overlapped with high amounts of digestible energy, high variance in digestible energy, early seral forests, and higher road densities, compared to males. However, adult males could sustain higher BCI values across a broader breadth of the landscape than adult females. Nonetheless, these patterns suggest that adult females, whether alone or with offspring, can navigate and sustain higher survival rates at higher road densities, and thereby benefit from increasing their BCI in those high productive areas that overlap with early seral forests, relative to males, which is an important attribute considering body condition in adult females is a predictor of reproductive success (López-Alfaro et al., 2015). I suspect that these patterns are due to adult females having lower energetic requirements, lower movement rates, and the presence of offspring, which increase the energetic costs of females with a yearling or nursing females with an attendant cub. Presumably, this also explains why lone adult females can sustain BCI values > 0 across a larger breadth of the landscape (Fig. 4.5) or why their BCI values are higher before denning (section 8 of TRACE), compared to adult females with offspring. Regardless of the mechanism, this is concerning given female reproductive success is contingent on lean mass during spring (López-Alfaro et al., 2015), and in particular, fat mass reserves acquired before denning (Hilderbrand et al., 1999; McLellan, 2011), with successful reproduction in adult females not possible if fat reserves are below 20% (López-Alfaro et al., 2013).

Interestingly, the relationship between movement rate and BCI was dependent on resource quality as well as sex. First, my findings indicate that bears, regardless of sex or across BCI, will expand their movement rates in resource poor areas to meet energetic demands since the probability of encountering high-quality areas is lower compared to bears in resource rich areas, thus increasing their exposure to roads relative to bears in resource rich areas who have reduced movement rates. Second, adult females have inherently lower energetic requirements and can thus adopt a more sedentary foraging strategy with increasing BCI in resource poor areas, as the absolute probability of encountering high-quality areas is lower compared to resource rich areas. This therefore lowers their exposure to roads with increasing BCI. In contrast, adult males in resource poor areas may adopt a more active foraging strategy that increases their probability of encountering high-quality areas to meet their larger energetic demands, even though the absolute probability of encountering high-quality areas is lower compared to resource rich areas. Hence this increases their exposure to roads with increasing BCI. Third, in resource rich areas, bears of either sex in good BCI may adopt a foraging strategy that increases their opportunity to encounter high-quality areas as they are not constrained by energetic expenditure as much; although this type of strategy increases their exposure to roads as it requires greater movements relative to bears in poorer BCI. I feel, however, that modifying the simulation so that bear agents in very good condition maintain their BCI level (e.g., via resting), rather than expanding upon it, would reduce their relative exposure to roads while retaining good health. I suspect that the type of foraging strategies adopted in resource rich areas are not only a reflection of the amount of food resources available to bears, but also because of the increase probability of encountering and identifying high-quality food resources in patchy (heterogeneous) environments (Denny et al., 2018). This appears to be the case in Alaska, where grizzly bears used smaller areas as landscape heterogeneity (patchiness) increased (Mangipane et al., 2018). My findings suggests that higher amounts and variability in food resources within resource rich areas, which coincides with areas of early seral forests disturbed primarily by forestry, may promote increasing health in bears, although with greater exposure to roads.

While the methodology used here can be used to prioritize areas for conservation and contribute to population recovery efforts, it is important to recognize the limitations of the model and areas of further research to expand on the existing model framework. I did not incorporate denning behavior and bioenergetics as this was beyond the scope of this study, although the inclusion of such factors within future studies, especially regarding adult females, could further inform on grizzly bear management and population recovery efforts (López-Alfaro et al., 2013; Pigeon et al., 2016). Although consumption rates of wild (free-ranging) grizzly bears are largely lacking (though see for example Welch et al., 1997, Rode et al., 2001, and Erlenbach et al., 2014 for captive bears), I did provide estimates on the range of hourly digestible energy needed to reproduce, among other things, body mass and body condition patterns found in empirical grizzly bear studies (see sections 2.7, 6.2 and 8 of TRACE). This could be used to estimate consumption rates as well as energy expenditure of wild bears for different sex-and-age classes. Indeed, future iterations of the model could build off the consumption and energetic rates provide here to estimate carrying capacity (McLelland et al., 2021) under alternative management, population recovery, and land-use change scenarios. This type of approach coupled with a multi-year simulation, year-round bear behavior and bioenergetics (i.e., active and denning periods), and forest succession could be used to project high-quality habitat and high-risk areas (i.e., source-sink habitats) and serve as a prototype for a spatial planning tool (Carter et al., 2019). Future studies could also create a more robust road model that considers bear decision-making near roads, motorized access management, and variations in vehicular traffic volume (Proctor et al., 2019).

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Appendix 4.1. A TRACE document containing a complete description of the model using the standard Overview, Design concepts, and Details protocol, and the methods used to parameterize, verify, calibrate, analyze, and corroborate the model.

TRACE document

This is a TRACE document ("TRAnsparent and Comprehensive model Evaludation") which provides supporting evidence that this model presented in:

> **Souliere, C.M., Denny, C.K., Stenhouse, G.B., Nielsen, S.E. 2023. Disentangling the effects of food resources and road density on grizzly bear body condition and mortality risk via an individual-based model**

was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

The rationale of this document follows:

> Schmolke A, Thorbek P, DeAngelis DL, Grimm V. 2010. Ecological modelling supporting environmental decision making: a strategy for the future. *Trends in Ecology and Evolution* 25: 479-486.

and uses the updated standard terminology and document structure in:

> Grimm V, Augusiak J, Focks A, Frank B, Gabsi F, Johnston ASA, Kułakowska K, Liu C, Martin BT, Meli M, Radchuk V, Schmolke A, Thorbek P, Railsback SF. 2014. Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. *Ecological Modelling*

and

> Augusiak J, Van den Brink PJ, Grimm V. 2014. Merging validation and evaluation of ecological models to 'evaludation': a review of terminology and a practical approach. *Ecological Modelling*.

If this document includes **hyperlinks**, navigation back and forth along previously chosen links works via "ALT" + "←" or "ALT" + "→".

1 Problem formulation

Summary:

Few studies have used individual-based models (IBM) to investigate grizzly bear ecology, especially in the context of bottom-up (BU) and top-down (TP) approaches. Grizzly bear populations in Alberta, Canada are listed as threatened due to low reproductive rates, small population size, and a reduction in habitat quality linked to landscape change. TP approaches, such as managing roads to limit human-caused mortality, which have been well-studied and are of high priority for grizzly bear management, could be complemented further by the inclusion of BU factors as there is evidence that such factors affect the behavior and population density of grizzly bears in Alberta. Yet, little has been done to explore how BU factors influence individual health, population, and habitat characteristics, specifically when interacting or being modulated by TP factors. Here I investigate how the quality and availability of digestible energy and road density influence grizzly bears by using an IBM to simulate aspects of grizzly bear ecology, behavioral ecology, and bioenergetics in a simulated landscape primarily derived from empirical data. The IBM aims to understand how grizzly bears trade off the quality and availability of food resources against human-caused mortality related to roads.

The IBM is designed to explore (disentangle) how empirically derived digestible energy and road-density metrics (GIS layers) influence grizzly bear body condition (health) and mortality risk (survival). The IBM uses a combination of literature and field data on grizzly bear ecology, behavioral ecology principles, bioenergetics, and field food resource layers (GIS) to simulate how grizzly bears gain energy by searching for food resources (digestible energy) while being exposed to differential road density via displacement during the active period from mid-April to mid-

October. The broader aim of the IBM is to assess the relative influence of BU (food resources) and TP (human-caused mortality in relation to road density) factors on grizzly bear individual health and survival, and to identify which of the factors have a greater (if any) contribution in regulating grizzly bear populations in Alberta. Collectively, results from this research may direct future management actions on prioritization of habitat that can enhance the recovery of a provincially threatened species. Thus, the IBM will be most useful to wildlife managers and decision makers who must consider how to manage, conserve, and set possible recovery targets for threatened grizzly bear populations in multi-use landscapes.

Specific questions addressed by the model are: (i) Investigate whether grizzly bears can gain sufficient body mass needed to meet energetic requirements in a landscape where food resources vary both spatially and temporally, especially regarding adult females, (ii) determine how the quality and distribution of food resources and road density influence individual health (body condition) and survival (mortality risk), and (iii) show whether sex and age-class influence how grizzly bears navigate gradients of food resources and road density. Further, the IBM provides an opportunity to perhaps reconcile or disentangle the differences posed by BU and TP approaches, and contribute to a greater understanding of how grizzly bear populations are shaped by such factors in a humand-modified landscape. Although the landscape and grizzly bear variables are partially parameterized for grizzly bears residing in interior ecosystems of North America (e.g., west-central Alberta), the IBM and results should be generalizable to other grizzly/brown bear systems where food resource metrics (e.g., digestible energy layers) are readily accessible and human-caused mortality related to road density are a management concern.

2 Model description

Summary:

Here I were present a complete model description following the ODD (Overview, Design concepts and Details) protocol for describing individual-based models, as outlined in Grimm et al. (2006, 2010).

The model was implemented in NetLogo 6.2.0 (Wilensky, 1999), an open source and freely available individual-based modeling platform. The NetLogo code has been made available in the Supplementary Material associated with this article: Souliere et al. (2023).

2.1 Purpose

The purpose of the model is to simulate how the spatial and temporal variation in digestible energy influences grizzly bear body condition (health). It is also intended to investigate how road density influences survival, and how this is related to quality and distribution of digestible energy on the landscape. The model also considers how sex-and-age-class influence the way grizzly bears navigate the gradients of digestible energy and road density, and ultimately the tradeoff associated with decreasing mortality risk (survival) and increasing overall body condition (health).

2.2 Entities, state variables and scales

Agents in the IBM are represented by individual grizzly bears. The state variables of each agent include sex, age, age-class, body mass, body length, body condition index, survival rate, distance traveled, active state, movement state, hours resting, road crossing frequency, location, energy reserves, watershed identifier, and a unique identification number.

The population size of grizzly bear agents does not change throughout the simulation. However, survival rates of individual grizzly bear agents are adjusted at the end of the simulation (active period) based on displacement (movement) and body condition (health), which influences which individuals survive at the end of the simulation.

The landscape is composed of square cells representing an area of 60 m by 60 m (Figure S1), with a total landscape area of 11,162 km^2 (excluding black cells in Figure S1, which are considered out-of-bounds). The irregular shaped landscape area is a representation of a real landscape within west-central Alberta, Canada. The cells belong to one of three categories: digestible energy cells, road cells, and out-of-bound cells. Each landscape patch is characterized by the amount of total available digestible energy which fluctuates according to the phenology of grizzly bear food groupings (e.g., fruit-energy, ungulate-energy, ant-energy), the cell type, and how much digestible energy is consumed by bears.

The model proceeds in discrete time-steps representing 1 hour intervals, equating to 24 time-steps per day over a 6 month period. The model begins on April 15 and runs until October 15 – the approximate dates of den emergence and entry, respectively. A new model run can be initiated once the previous model run ends.

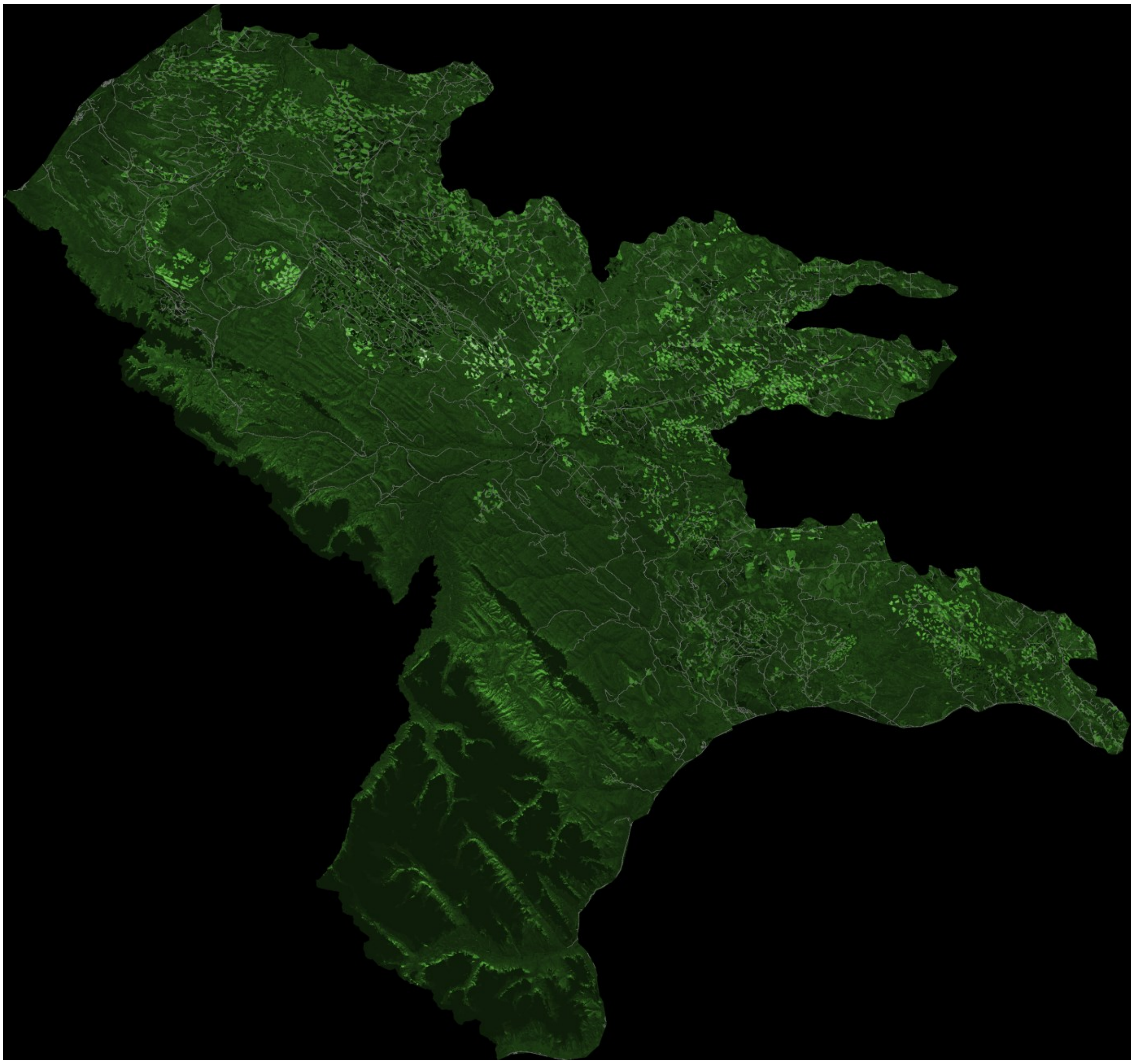

Figure S1. Depiction of the landscape used in the IBM. Each cell represents a 60 m x 60 m area. Green cells indicate areas in which grizzly bear agents can acquire digestible energy, grey cell indicate roads, and black cells indicate areas that grizzly bear agents cannot access (i.e., out-of-bounds) as these cells lack empirically derived digestible energy data for this simulation. This landscape is used in each model run as described in section 2.5.

2.3 Process overview and scheduling

The model simulates grizzly bear agents moving through the landscape to acquire sufficient digestible energy while encountering varying road density levels. First, empirically derived digestible energy data and the spatial location of roads are loaded and assigned to patches. On the first day of the simulation, body mass and body length are calculated for each grizzly bear agent, as well as their age and parental status. Movement rate is assigned for each grizzly bear agent based on age-class. Patch digestible energy values are updated biweekly based on the phenology of grizzly bear food groupings (fruit, forb, horsetail, sweetvetch roots, ant, and ungulate) over the course of the simulation following details outlined in Munro et al. (2006).

All grizzly bear agents are activated on the first time step of the simulation at a random location (excluding roads or out-of-bound patches) to simulate den emergence. From this first time step onwards, grizzly bear agents assess their state and energy level, update their behavior, movement step distance, body condition, location, and personal information.

To ensure the model can run without significant computational delays, the digestible energy value of each patch is only updated once a grizzly bear agent comes within a radius of 1 patch from the target patch. This is done continuously throughout the simulation. Further, the digestible energy value of each target patch is updated based on the time step (i.e., time of year) which is directly related to the phenology of individual food groupings.

2.4 Design concepts

2.4.1 Basic Principles

The premise of this model is based on how wildlife trade off foraging decisions against mortality risk when navigating human disturbed landscapes. The focus here is how grizzly bears navigate a human disturbed landscape to improve body condition via energy acquisition while reducing the risk of mortality via roads (Boulanger et al., 2013). How grizzly bears navigate such a landscape and the decisions they make can be related to basic principles such as resource requirements and risk management (Houston et al., 1993). In Alberta, grizzly bears have increased access to disturbed habitat because of ongoing forest harvesting and natural wildfire which creates opportunities for bears to access key food resources (Nielsen et al., 2004, Kearney et al., 2019; Souliere et al., 2020). Forest harvesting, however, has become the main disturbance agent in the region, largely replacing natural wildfire, with recent fires now largely fire suppressed. Yet, forest harvesting inevitably creates higher road density, which requires bears to trade off foraging decisions (i.e., digestible energy acquisition and body condition) against increased mortality risk associated with navigating landscapes with higher road densities (Boulanger et al., 2013). Roads increase the risk of human-caused mortality in grizzly bears and thus are of a concern for grizzly bear management (Boulanger and Stenhouse, 2014). Therefore, managing the landscape to increase grizzly bear populations requires understanding the tradeoff between access to and acquisition of key food resources and increased mortality risk in areas where both elements overlap.

I simulated the behavior of grizzly bears from den exit to den entry in a landscape that varied spatiotemporally in both digestible energy and road density. Bear behavior was based on bioenergetics, bear ecology, foraging ecology, and expert opinion. In general, grizzly bear agents try to maximize their energy gain (i.e., improve their body condition index) by following the phenology of key grizzly bear foods while crossing roads to reach this objective. If their body condition index falls below a threshold, grizzly bear agents will likely stop to actively forage rather than continue searching for food. However, if their body condition index surpasses a certain threshold, grizzly bear agents will likely forage only in areas where the surrounding energy is greater than the active energy cost, else they will continue searching for food.

If a grizzly bear agent encounters a road while searching for food (foraging or moving), it will cross the road until it hits a patch of digestible energy (i.e., fully crosses the road), where it will continue searching and following the food resource gradient to maximize its energy gain. Crossing a road while actively foraging or actively moving was recorded as a road crossing event.

2.4.2 Emergence

(i) **Fluctuations in digestible energy values over space and time and bear agent foraging decisions.** The spatial location and phenology of grizzly bear food resources influences the relative time bear agents will spend actively moving or actively foraging for food. This itself not only influences the ability of bear agents to gain mass but also indirectly influences the frequency at which bear agents cross roads, and hence their survival rate related to road density.

(ii) **The maximum and minimum amount of energy a bear agents can consume per hour**. Bear agents can consume a maximum and minimum amount of digestible energy per hour, with the maximum energy based on the sex-and-age-class of individual bear agents at the beginning the simulation after den emergence (i.e., spring body mass) and the minimum energy based on parameter calibration. This condition, therefore, influences foraging decisions and movement patterns.

(iii) **Differences in road density across the landscape and bear agent crossing rate.** The density of roads across the landscape is non-uniform since road density is based on real-world values (i.e., digital road maps). This being the case, bear agents will encounter and cross roads at a higher frequency in areas with higher road densities and vice versa in areas with lower road densities. Therefore, survival rate (i.e., road crossing frequency) is not only based on movement patterns when searching for food resources but also on the density of roads in a given area.

(iv) **The influence of sex-and-age-class on foraging decisions and movement patterns.** The sex-and-age-class of individual bears influence their size, which itself controls the amount of energy a bear agent can consume at rest, while moving, and its movement range. All these factors influence how bear agents choose to actively forage or actively move when searching for food and their mortality rate via exposure to different road densities.

(v) **Previously consumed energy patches and bear agent foraging decisions.** Albeit largely a minor emergence, the consumption of energy patches by bear agents reduces the amount of energy available for any bear agent visiting the patch in the future. This can influence the visitation rate of certain high traffic areas and influence the costs and benefits of foraging in those areas.

2.4.3 Adaptation

Grizzly bear agents adapt their behavior based on meeting their energetic demands when foraging and moving across the landscape between den exit and den entry. This adaptive behavior is based on rules primarily outlined in *grizzly bear foraging decision and movement*, *grizzly bear bioenergetics*, and *landscape energetics*. In brief, these rules determine when grizzly bear agents should forage, move, or rest, and consequently updates their body condition. Grizzly bear agents sense the energetic value of surrounding patches to optimize foraging decisions. Digestible energy values of individual patches are not only determined by their spatial location and phenology but also by whether the patch was consumed by grizzly bear agents.

2.4.4 Objectives

The main objective of grizzly bear agents is to consume as much energy as possible to improve overall body condition before denning while navigating areas with differential road density in an effort to reduce mortality risk (i.e., increase survival). Digestible energy values are based on two components: (1) the spatial location of digestible energy values is based on real-world data collected from field plots; (2) fluctuations in digestible energy values from den exit to den entry are based on the phenology of grizzly bear food groupings (see section 2.3). This objective can be met by (a) maximizing energy acquisition while (b) reducing road crossing frequency rate.

1.1.1 *Learning*

Learning was not considered in this simulation.

1.1.2 *Prediction*

Prediction was not considered in this simulation.

2.4.7 *Sensing*

Grizzly bear agent foraging decisions were partly based on the search (i.e., sensing) radius of digestible energy in the surrounding area. Given the computational limitation of a simulating a large sensing radius and the lack of information in the literature on the link between grizzly bear foraging decisions and sensing radius, I chose a sensing radius of 60 m, the pixel size of each patch on the landscape. This also approximates the hourly feeding radius of an adult female grizzly bear in Alberta (Gibeau et al., 2002). A bear agent on any given patch can sense the mean digestible energy in 5 surrounding patches, including the patch it is currently occupying, and incorporate this information into its decision making. Daily energy gains and losses are converted into body mass gains and losses at the end of each day. More information can be found in sections 2.7, 3.3 and 7**.**

2.4.8 *Interaction*

Grizzly bear agents do not interact with one another in this simulation. Grizzly bear agents do, however, change the digestible energy value of patches that they have consumed. In brief, if a bear consumes digestible energy from a patch, then that patch will have a digestible energy value adjusted for the amount of digestible energy consumed by the bear agent. Depending on the amount of digestible energy available throughout the entire year (i.e., following phenology) and the density of bear agents in the surrounding area, a single patch may be consumed multiple times by an individual bear or by multiple bears on separate occasions.

2.4.9 *Stochasticity*

Several model processes were influenced by stochasticity. Some model processes, such as spring body mass, sex age distribution, distance traveled per hour, as well as foraging processes had stochastic elements. Furthermore, sex age distribution and distance traveled per hour were each determine from a gaussian distribution, with random values determine by drawing from that distribution.

2.4.10 *Collectives*

Collectives were not considered in this simulation.

2.4.11 *Observation*

I collected data at the end of each model run to support the three main questions posed in Section 1 – Problem Formulation. For each model run, I recorded age, sex, and class information, spring and fall body mass, survival rates, whether an individual bear agent survived, road crossing frequency, road density, distance traveled, end of run body condition index. Furthermore, throughout each model run I recorded mean body mass, mean distance traveled, mean road crossing frequency, percentage of bears that survive each day, mean survival rates, and the physical location of bear agents on an hourly basis.

2.5 Initialization

Landscape generation

The landscape was generated using digestible energy (kcal) datasets that was read into NetLogo using the GIS extension. GIS layers represented empirical digestible energy values that were estimated from field data collected in west-central Alberta, Canada. Field data were used to model plant occurrence and abundance which was subsequently mapped to GIS layers (Nielsen et al., 2015). These layers were first converted into density estimates using methods derived from Nielsen et al. (2015) and Nielsen et al. (2017), and then subsequently converted into digestible energy values following the methods outlined in López-Alfaro et al. (2015) and Souliere et al. (2020). Individual plant layers were then grouped into major grizzly bear food groupings based on Munro et al. (2006). The major food groupings used in this model include fruit, forb, horsetail, sweetvetch roots, ant, and ungulate. Ungulate digestible energy values were calculated from methods outlined in Nielsen et al. (2017). All cells were assigned digestible energy values based on major food groupings and a total digestible energy value, which represented the sum value of all major digestible energy layers (food groupings) discussed above. Each cell (patch) represented 60 by 60 m area.

A GIS dataset describing the physical location of roads in west-central Alberta was also read into NetLogo using the GIS extension. Cells that were initialized as a road were not assigned a digestible energy value. The landscape initialized in this model represents a real-world landscape with empirically derived digestible energy values and road locations. See section 3.1 for more details on parameters used to initialize the landscape.

Initial sex, age, body mass of bear agents

I simulated sex and age distribution of grizzly bear agents. To do so I simulated 10000 agents and assigned a random sex and age drawn from a uniform distribution between 1 and 25. I then allowed this population to age and die for 1000 years to ensure that the sex and age distribution remained unchanged. The probability of a bear agent dying was informed from a sex-specific survival probability. This sex and age distribution closely matched the sex and age distribution of captured bears in Montana and British-Columbia (Mace and Waller, 1998; McLellan, 2005). I then randomly sampled from this distribution to assign sex and age to sub-adult and adult grizzly bear agents. I initialized female grizzly bear agents with a 1/3 probability of either having an attendant cub-of-the-year, attendant yearling, or no offspring (Dey et al., 2017).

Number of agents

I used 50 males and 50 female grizzly bear agents in all model runs. See section 3.2 for additional details.

2.6 Input data

Parameter values used in the model are listed in Table S1.

Table S1: Parameters used in the model with associated definitions, values, and references

Symbol	Definition	Value	Units	References	Notes
SR	M:F adult sex ratio in west-central Alberta	52:48		Stenhouse et al., 2015	Table 20, p. 45
S_{sa}	Survival rates of senescent adult (≥	0.75	%	Knight and Eberhardt, 1985	Table 6, p. 332 Mean of survival rate of

	20) in Yellowstone				ages 20 and 22 onwards
S_{am}	Survival rates of adult males (≥ 5 and < 20) in Alberta	0.84	%	Boulanger and Stenhouse, 2009	Table 10, p. 20 Estimated rate includes bears > 20
S_{af}	Survival rates of adult females (≥ 5 and < 20) in Alberta	0.95	%	Boulanger and Stenhouse, 2009	Table 10, p. 20 Estimated rate includes bears > 20
$S_{\mathrm{sub\text{-}m}}$	Survival rates of sub-adult males (2 -4) in Alberta	0.67	%	Boulanger and Stenhouse, 2009	Table 10, p. 20 Estimated rate includes yearlings
$S_{\mathrm{sub\text{-}f}}$	Survival rates of sub-adult females (≥ 2 - 4) in Alberta	0.74	%	Boulanger and Stenhouse, 2009	Table 10, p. 20 Estimated rate includes yearlings
S_{year}	Survival rates of yearlings (1 - 2) in Flathead River, BC	0.88	%	McLellan, 1989	Table 1, p.1862
$\mathrm{S}_{\mathrm{coy}}$	Survival rates of cubs-of-the-year in Alberta	0.56	%	Boulanger and Stenhouse, 2009	Table 10, p. 20
L_m	Asymptotic body length of males	180	cm	GB Stenhouse, *unpublished data*	Empirically estimated with von Bertalanffy regression
L_f	Asymptotic body length of females	158	cm	GB Stenhouse, *unpublished data*	Empirically estimated with von Bertalanffy regression
K_{mL}	von Bertalanffy growth rate for male body length	0.402	years^{-1}	GB Stenhouse, *unpublished data*	Empirically estimated with von Bertalanffy regression
K_{fL}	von Bertalanffy growth rate for	0.647	years^{-1}	GB Stenhouse, *unpublished data*	Empirically estimated with

	female body length				von Bertalanffy regression
A_{mL}	Extrapolated age at 0 size for male body length	-1.420	years	GB Stenhouse, *unpublished data*	Empirically estimated with von Bertalanffy regression
A_{fL}	Extrapolated age at 0 size for female body length	-1.190	years	GB Stenhouse, *unpublished data*	Empirically estimated with von Bertalanffy regression
W_m	Asymptotic body mass of males	231	kg	GB Stenhouse, *unpublished data*	Empirically estimated with von Bertalanffy regression
W_f	Asymptotic body mass of female	106	kg	GB Stenhouse, *unpublished data*	Empirically estimated with von Bertalanffy regression
K_{mM}	von Bertalanffy growth rate for male body mass	0.297	years^{-1}	GB Stenhouse, *unpublished data*	Empirically estimated with von Bertalanffy regression
K_{fM}	von Bertalanffy growth rate for female body length	0.582	years^{-1}	GB Stenhouse, *unpublished data*	Empirically estimated with von Bertalanffy regression
A_{mM}	Extrapolated age at 0 size for male body mass	-1.518	years	GB Stenhouse, *unpublished data*	Empirically estimated with von Bertalanffy regression
A_{fM}	Extrapolated age at 0 size for female body mass	-1.578	years	GB Stenhouse, *unpublished data*	Empirically estimated with von Bertalanffy regression
M_{am}	Max step length per hour for adult males	34	patch	Graham and Stenhouse, 2014	Calculated from values in Table 6 and IBM patch size

M_{af}	Max step length per hour for adult females	24	patch	Graham and Stenhouse, 2014	Calculated from values in Table 6 and IBM patch size
$M_{sub\text{-}m}$	Max step length per hour for sub-adult males	27	patch	Graham and Stenhouse, 2014	Calculated from values in Table 6 and IBM patch size
$M_{sub\text{-}f}$	Max step length per hour for sub-adult females	27	patch	Graham and Stenhouse, 2014	Calculated from values in Table 6 and IBM patch size
$M_{f\text{-}w\text{-}year}$	Max step length per hour for females with yearlings	24	patch	Graham and Stenhouse, 2014	Calculated from values in Table 6 and IBM patch size
$M_{f\text{-}w\text{-}coy}$	Max step length per hour for females with cubs-of-the-year	16	patch	Graham and Stenhouse, 2014	Calculated from values in Table 6 and IBM patch size

2.7 Submodels

Landscape Energetics

At the start of each model run, I defined the digestible energy value of a cell based on major food groupings important to grizzly bears (fruit, forb, horsetail, sweetvetch roots, ant, and ungulate) (Munro et al., 2006). First, I initialized a total digestible energy layer (kcal) which was the sum of all major food groupings (individual GIS layers). I then weighted each major food grouping (GIS layer) biweekly to match changing phenology using the following equations:

$$PeakDigEng_k = \frac{TotalDigEng_k}{\sum_{i=1}^{12} M_i}$$

where M_i represents the biweekly weights from mid-April (den exit) until mid-October (den entry) and $TotalDigEng_k$ represents the total amount of digestible energy in a cell.

$$TotalDigEngWeighted_k = PeakDigEng_k + \left(\sum_{j=1}^{11} M_j * PeakDigEng_k \right)$$

where M_j represents biweekly weights excluding the two-week period of *PeakDigEng*. $TotalDigEngWeighted_k$ represents the total amount of energy a cell will have from mid-April to mid-October.

Note that the simulation updates biweekly values throughout the simulation, so bear agents only have access to a 'slotted' digestible energy value over a two-week period following plant phenology, such that:

$$BiweeklyDigEng_k = M_j * PeakDigEng_k$$

where M_j represents individual biweekly weights applied to individual food groupings for *k* cell. Hence weighted individual food groupings are summed into a biweekly 'slotted' digestible energy value, such that:

$$BiweeklyDigEng_{kp} = \sum_{p=1}^{6} BiweeklyDigEng_{kp}$$

where *p* represents individual food groupings and *k* is an individual cell. See section 3.1 for further details on parameterization.

Grizzly bear length and mass

Spring body length and mass were estimated at the beginning of every run and dependent on the age and sex assigned to each grizzly bear agent. I estimated grizzly bear body length using von

Bertalanffy growth curves for the population unit in west-central Alberta (GB Stenhouse, *unpublished data*). Body length was estimated using the following equation:

$$L(B) = L_{\infty} * \left(1 - e^{-K(A-A_0)}\right)$$

where B is the grizzly bear agent's age in years, L_{∞} is the asymptotic body length, K is the von Bertalanffy growth rate, and A_0 represents the extrapolated age at zero size. The values for L_{∞}, K, and A_0 are sex-specific and are presented in Table S1. I introduced intra-variation in body length by allowing body length to be drawn from a normal distribution with a mean equal to the expected body length value from the von Bertalanffy curve and a standard deviation of 11 cm for males and 8.1 cm for females.

Body mass was also estimated using von Bertalanffy growth curves using data from the population unit in west-central Alberta. I also introduced intra-variation in body mass by allowing body mass to be drawn from a normal distribution with a mean equal to the expected body mass value from the von Bertalanffy curve and standard deviation of 43.2 kg for males and 17.6 kg for females. See section 3.3 for further details on these values.

Grizzly decision-making and movement

In this model, foraging decisions and movement decisions of grizzly bear agents are primarily dependent on their individual state at any given time, which is influenced by bioenergetics rules and physiological constraints (i.e., need to forage and rest). This is to ensure that the grizzly bear agents adhere to realistic time constraints.

Grizzly bears will spend a larger proportion of their time inactive during early spring and late fall. In between these two periods, grizzly bears will increasingly spend a larger proportion of their time active (foraging and moving), which will peak during summer (mesophagia and early hyperphagia) coinciding with berry productivity in the northern hemisphere (MacHutchon, 2001; McLellan and McLellan, 2015). I used the values from McLellan and McLellan (2015), which I adjusted via calibration (see section 6.1 for further details) for my purposes here, to assign activity rates to grizzly bear agents. Grizzly bear agents rested for (1 – (A_i * 24 h)) time steps, with A_i representing the proportion of time a grizzly bear agent was active during a given month. If a grizzly bear agent was awake, then it was active (foraging or moving) for (A_i * 24 h) time steps, again adjusted for monthly periods.

If grizzly bear agents were in an active (foraging or moving) state, they would assess whether it was worthwhile to stop and forage or continue moving based on their BCI. Once in an active state, grizzly bear agents in good BCI could estimate whether foraging in a local area would likely lead to a net energetic gain instead of moving on, whereas bear agents in poor BCI were obligated to forage regardless of the energetic gain from the local area. Note that the degree to which grizzly bear agents stayed in a foraging state or moving state was partially influenced by probability values (see section 7 for sensitivity analysis). These behaviors were influenced by the phenomenon of risk sensitivity in foraging animals (Bateson, 2002). It may be optimal for animals (*sensu* grizzly bears) in good body condition to select behaviors supporting energy conservation (i.e., risk-averse), whereas it may be optimal for animals in poor body condition to opt for risky behaviors (i.e., risk-prone) in an attempt to maximize net energy gain. If bear agents were in a foraging state, they could sense the quality of digestible energy in the local area and move to the cell with the likely highest value and reevaluate the local area once again, influencing whether to continue foraging or to move on. Grizzly bear agents entering a moving state moved a random distance sampled from their maximum step distance value (Table S1) which was based on their sex-and-age-class (see *Grizzly bear foraging* below and section 3.3 for further details).

Grizzly bear bioenergetics

During both active and inactive periods, grizzly bear agents lose energy at every time step, yet do so at different rates. If a grizzly bear agent was resting, the amount of energy lost E_r was determined by the hourly basal metabolic rate (kcal):

$$Er = \frac{61.9m^{0.77}}{24}$$

where m is the body mass (kg) of a grizzly bear agent (Robbins et al., 2012).

If a grizzly bear agent was active, the amount of energy lost E_a was determined by the hourly active metabolic rate (kcal), such that:

$$Ea = ((2.57 * m) - 0.316) * 0.341$$

where m is the body mass (kg) of a grizzly bear agent (Shine et al., 2015; Whiteman et al., 2015; Pagano et al., 2018). See section 3.3 for details on parameterization.

Furthermore, I also added the energetic cost of attendant offspring to adult female agents with cub-of-the-year and yearlings. For yearlings, I inputted an age-appropriate mass into E_a, and added the energetic cost to adult female agents who had an attendant yearling. For cub-of-the-year, I added the energetic cost of milk production based on the month (Figure 4-2a; López-Alfaro, 2014) to adult female agents with an attendent cub-of-the-year.

Grizzly bear agents could only increase their energy gains by foraging and consuming digestible energy available to them on the landscape. See section 2.7 and 3.3 for additional details.

At the end of each day, daily energy gains and losses were converted into body mass gains and losses (kg) using the following equations:

$$DailyEnergy_{Gains/Losses} = (0.106 * \left(\frac{hourly\ energy}{m^{0.75}}\right) - 10.8)$$

$$BodyMass_{Gains/Losses} = \frac{DailyEnergy_{Gains/Losses} * m^{0.75}}{1000}$$

where m is the body mass (kg) of a grizzly bear agent (Robbins et al., 2007). Daily energy was reset to zero at the end of each day.

The maximum amount of energy a grizzly bear agent could consume per hour was estimated using the following:

$$Max_{Eng} = \frac{240 * SpringBodyMass}{13}$$

where spring body mass represents mass assigned at den exit (Erlenbach, 2014).

I chose to use spring body mass instead of cumulative body mass, since body length is fixed throughout the year, under the assumption that stomach capacity is related to overall body size (length) rather than mass gain throughout the year. I also assumed that bears had a mean foraging time of 13 hours per day to simplify calculations (MacHutchon, 2001; McLellan and McLellan, 2015).

I used inverse determination via calibration to determine parameter values for the minimum amount of energy that a grizzly bear agent could consume per hour, as I could not derived appropriate values from literature sources. See section 6.2 for further details on parameterization.

Grizzly bear foraging

I used body condition index (BCI) for ursids developed by Cattet et al. (2002) to determine the condition of grizzly bear agents at the end of each day. BCI was developed to offer a reliable index of true body condition and allow individual bears to be compared regardless of age, sex, reproductive status, geographical location, or date of capture. The following equation is specifically developed for grizzly bears:

$$BCI = \frac{\ln TBM - 3.21 * \ln SLBL + 11.64}{0.29 - 0.017 * \ln SLBL}$$

where TBM is the total body mass and SLBL represents the straight-line body length. Grizzly bear agents update their body condition by calculating their body condition index at the end of each day. They then compare their previous day BCI_p (t – 1) to their current day BCI_c (t) to obtain a relative difference in BCI between days. Grizzly bear agents will be more likely to stop moving and assess whether to forage in a given area if the difference between their BCI_c and BCI_p falls below 0, defined as:

$$0 < BCI_c - BCI_p$$

If the above inequality is true, then grizzly bear agents will assess whether to forage or not and will have a higher probability of entering a foraging state rather than a moving state. Grizzly bear agents in good BCI (above inequality is false) can also enter a foraging state but with a lower probability than those bears in poor BCI; though they will only do so when the mean digestible energy measured within their sensing radius is greater than their active energy cost. Once bear agents enter a foraging state, they will consume the cell they currently occupy and move to a neighboring cell with the highest digestible energy value and will continue to do so until they enter a resting or moving state. Bear agents will either consume the entirety of digestible energy available to them in a particular cell or up to a maximum if the amount of digestible energy available to them in a cell exceeds their maximum energy consumption per hour, which is dictated by sex-and-age-class.

Grizzly bear agents' foraging decisions were partly based on the search (i.e., sensing) radius of digestible energy in the surrounding area. Given the computational limitation of a simulating a large sensing radius and the lack of information in the literature on the link between grizzly bear foraging decisions and sensing radius, I chose a sensing radius of 60 m, the pixel size of each patch on the landscape. This also approximates the hourly feeding radius of an adult female grizzly bear in Alberta (Gibeau et al., 2002). A bear agent on any given patch can sense the mean digestible energy in 5 surrounding patches, which includes the patch it is currently occupying, and incorporate this information into decision making. Sensing radii of 2 or more patches (i.e., 120 m; 13 patches in total) decreased mass gain and body condition index of bear agents, and so was not deemed an appropriate sensing hourly radius for this study. See sections 3.3 and 7 for further details.

Road crossing decision-making and road survival

If a bear agent was in a foraging state and encountered a road (i.e., bear agent occupied a patch considered a road), then it crossed the road until it encountered a patch that was not considered a road (i.e., digestible energy patches). If a bear agent encountered a road in a moving state, it calculated (detected) the number of roads ahead based on the step distance assigned to it for that tick. It then 'crossed' the roads detected ahead of it (based on the step distance) until it reached a patch considered digestible energy. These crossing events counted as a road crossing 'hit' and were incorporated and tabulated into a bear agent's personal information. In this way, grizzly bear agents could count the frequency at which they encountered and crossed roads while navigating the landscape. See section 3.4 for further details.

Survival rate related to roads was reported by first estimating the relationship between road crossing frequency and road density using the following equation:

$$Road\ Density = 0.04268 + 0.005212 * Road\ Crossing\ Frequency$$

Following this, I used the road density value to estimate survival rate of various sex-and-age-classes, defined using the following equations:

$$Survival_{AdultMale} = 0.946014 - (0.042284 * Road\ Density) - (0.031795 * Road\ Density^2) - (0.006340 * Road\ Density^3)$$

$$Survival_{LoneAdultFemale} = 0.984809 - (0.009914 * Road\ Density) - (0.042663 * Road\ Density^2)$$

$$Survival_{SubAdultMale} = 0.942445 - (0.080035 * Road\ Density) - (0.353526 * Road\ Density^2) - (0.075524 * Road\ Density^3)$$

$$Survival_{SubAdultFemale} = 0.96643 - (0.11602 * Road\ Density) - (0.21249 * Road\ Density^2) - (0.02300 * Road\ Density^3)$$

$$Survival_{AdultFemaleWithCubs/Yearlings} = 0.97954 - (0.11163 * Road\ Density) - (0.14217 * Road\ Density^2) - (0.14685 * Road\ Density^3)$$

If road density fell below a certain threshold based on the sex-and-age-class, then survival related to road crossings was deemed zero. See section 3.4 for further details on parameterization.

3 Data evaluation

Summary:

Most of the data used to fit this model was derived directly from literature sources or field data, which are listed in Table S1 and expanded on in sections 2 and 3. However, some calculations where needed to derive novel values from literature sources and/or field data. I provide detailed information and reasoning on parameterization, and whether values are derived from direct or indirect sources.

3.1 Digestible energy generation parameters

Grizzly bears are known to adjust their foraging behavior and diet based on seasonality and phenology of important food items (Munro et al., 2006; Nielsen et al., 2010). To model this process, I weighted digestible energy values based on the changing phenology of major food groupings, so that grizzly bear agents had access to spatiotemporally realistic digestible energy values from den exit to den entry. Following Munro et al. (2006), I weighted major food groupings biweekly to match changing phenology of important grizzly bear foods and summed those weighted values into a total digestible energy value, from which grizzly bear agents could select when navigating the simulated landscape. I grouped individual GIS food layers (kcal) into major food groupings which included fruit, forb, horsetail, sweetvetch roots, ant, and ungulate. First, I assigned to each patch (cell) values from every major food group. From here, I weighted each major food group value based on biweekly food weights extracted from Munro et al. (2006). These biweekly values – weighted major food groupings – were subsequently summed into a total digestible energy value for a 2-week period. These values were then updated biweekly throughout the simulation, with all available digestible energy from every patch being exhausted by den entry, i.e., distributed throughout the year according to biweekly weights (phenology) and total digestible energy calculated from major food groups.

3.2 Agent initialization parameters

Number of bear agents

I used 100 bears in the model with a 50:50 sex ratio. This number is calculated using a density of 10 bears/1000km^2, which is the approximate density of the grizzly bear population in west-central Alberta (Boulanger et al., 2018). With a simulated landscape of 11,162 km^2, this density equates to approximately using 100 bear agents. This value was subjected to sensitivity analysis (see section 7 for further details).

Distribution of bear agents

Since grizzly bear agents can move large distances over the course of the simulation, largely owing to the spatial quality of digestible energy and advancing phenology as well as assigned movement steps based on sex-and-age class, I randomly initiated the location of grizzly bear agents throughout the landscape.

Proportion of time active

Grizzly bears are known to spend a portion of their day (24 h period) actively searching for food, primarily by foraging/feeding and/or moving. Because of the type of food consumed, advancing phenology, temperature changes, and changing day light hours, grizzly bear activity levels fluctuate throughout the season, with activity bouts highest during the summer, coinciding with hyperphagia, and lowest in early spring and fall, coinciding with den exit and den entry (MacHutchon, 2001; Schwartz et al., 2010; Fortin et al., 2013; McLellan and McLellan, 2015). Hence, the proportion of time a grizzly bear is active per day can change based on the season and/or month. I parameterized the proportion of day a grizzly bear agent is active based on monthly values derived from McLellan and McLellan (2015). In brief, the parameter controlling monthly activity influences the amount of time per day a bear agent can forage or move when searching for food, and conversely, the amount of time at rest. I used inverse determination via calibration to adjust this model parameter (see section 6.1).

3.3 Grizzly bear agent parameters

Spring body length and mass estimation

I estimated the variance in spring body length and mass using an empirical dataset of length, mass, and age from 246 grizzly bears captured in west-central Alberta from 2000-2017. Apart from a few bears, the dataset consisted mostly of bears 3 years of age or older. All bears used in this dataset were captured in the spring to ensure accurate estimation of spring body length and mass. From here, I fitted von Bertalanffy regressions on both male and female grizzly bears using the FSA package in R (Ogle et al., 2021), and first calculated the values for L_∞, K, and A_0 which were subsequently used to parameterize the estimation of spring body length and mass of grizzly bear agents (see Table S1). I also used these von Bertalanffy models to estimate the variance in body length and mass of the grizzly bear agents. Occasionally, due to the stochastic nature of introducing random variation when calculating body length and mass of bear agents, agents were assigned unrealistic body length and/or mass values. To compensate for this, I truncated body length and mass of both male and female bear agents to approximately match the minimum and maximum body length and mass of bears from the empirical dataset. See Figure S2 for estimation of von Bertalanffy growth curves.

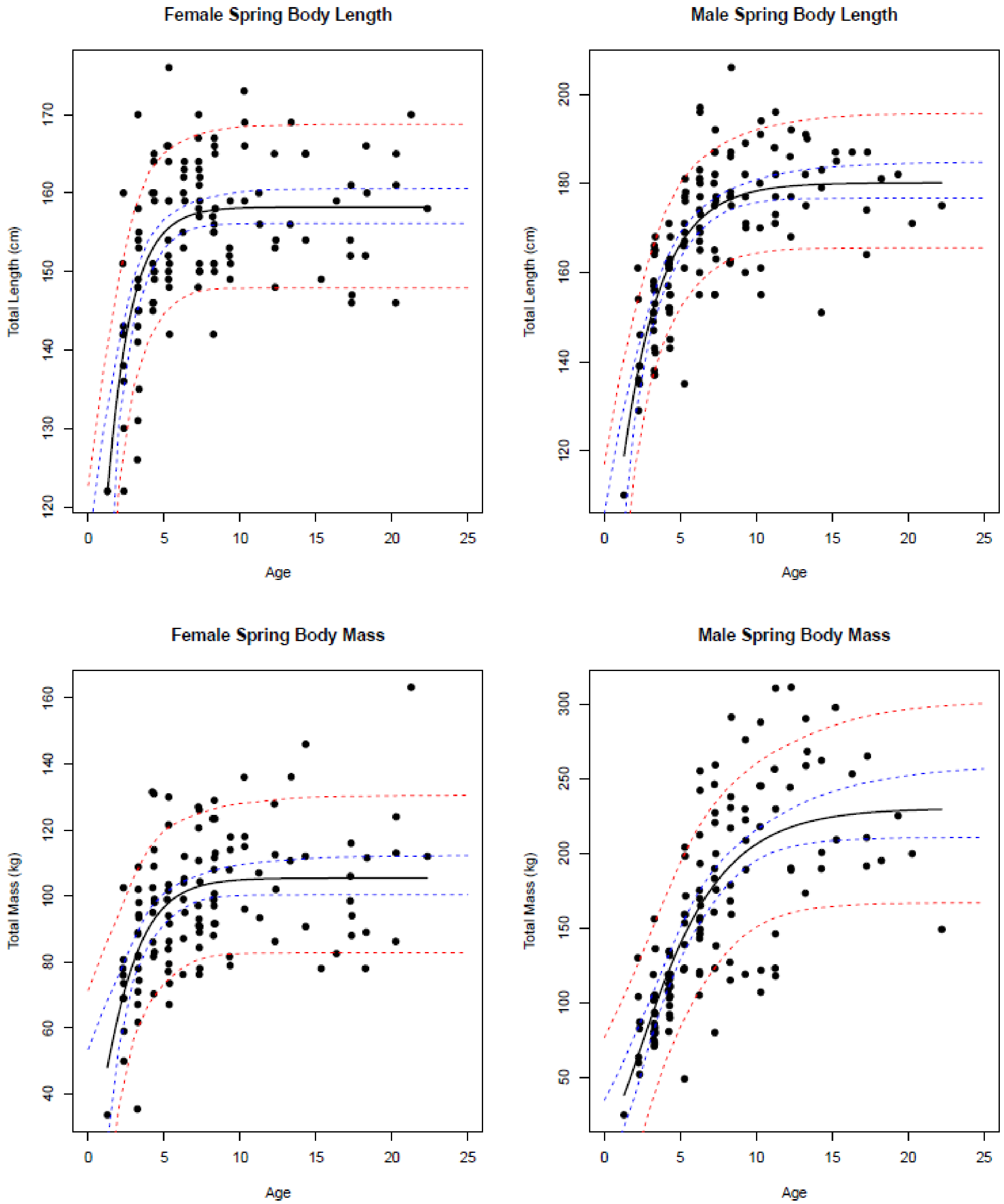

Figure S2: Spring body length and mass estimated with von Bertalanffy growth curves for female and male grizzly bears from west-central Alberta. The blue dotted line represents 95% bootstrap confidence intervals, whereas the red dotted line represents 95% bootstrap prediction intervals.

Movement parameters

There are a considerable number of studies on grizzly bear movement patterns, with much of this focus on landscape level movement patterns over larger scales. Yet a few studies, such as Graham and Stenhouse (2014), have documented the movement patterns of grizzly bears over small scales in west-central Alberta. Here, I use simple movement rules that dictate how grizzly bear agents navigate the simulated landscape when not foraging or resting. The mean hourly movement distances (steps) used in the model (see Table S1 for further details) were calculated from the mean movement rates (m/h) for grizzly bears with different sex, ages, and reproductive classes in west-central Alberta (Graham and Stenhouse, 2014). These patterns reveal that males move more quickly than females and sub-adults, females with attendant offspring (cub-of-the year or yearling) move more slowly than lone females, and sub-adults move more quickly than females regardless of reproductive status.

If grizzly bear agents are not foraging or resting, they will be in a move state and will make relatively larger movement bouts (see Table S1). In such cases, step lengths (distance traveled per hour) values are drawn from a normal distribution with a mean for each sex-and-age class determined from Graham and Stenhouse (2014) and a standard deviation of 100 m. Although mean values are adjusted for average walking speeds of approximately 1.2 m/s assuming bears are traversing areas with various levels of undulation and landscape impediments (e.g., dense forests/shrublands); rather than 1.5 m/s assuming bears are traversing flat and unimpeded areas, for instance, when captive bears walk along a runway (Shine et al., 2015). Depending on their BCI and sensing the quality of surrounding cells, grizzly bear agents will alternate between large movement bouts and foraging while active. These movement rules follow realistic animal movement properties (Benhamou et al., 2007), where grizzly bear agents will, in general, alternate between large and relatively straight movement bouts (move state) in resource poor areas, and shorter and relatively more tortuous movements (foraging state) in resource rich areas. These movement properties are not imposed artificially and instead emerge from the interaction between the agents and the simulated environment.

During each time step, grizzly bear agents will expend energy by either foraging, moving, or resting, each of which is dependent on BCI, sensing of the surrounding environment, and the number of hours awake. While grizzly bear agents are in foraging or moving state, road crossing frequency is also computed.

Body condition index

Body condition influences grizzly bear habitat use, foraging decisions, and reproductive performance (Cattet et al., 2002.; Bourbonnais et al., 2013; Nielsen et al., 2013; Bourbonnais et al. 2014). Grizzly bear body condition can be represented by using a body condition index (BCI; Cattet et al., 2002), which itself can be used as a threshold to determine whether a bear is energetically stressed. BCI was developed based on standardized residuals from the log-transformed linear regression of total body mass (TBM) and straight-line body length (SLBL) using grizzly bear capture data (Cattet et al., 2002). Higher BCI values indicate bears are in better condition. BCI values typically range from -3 to +3, but those values can be exceeded. This parameter value was subjected to sensitivity analysis (see section 7 for further details).

Active and inactive energetic costs

Metabolic cost in grizzly bears is dependent on whether a bear is considered active (i.e., foraging or moving) or inactive (i.e., resting) (Robbins et al., 2012; Pagano et al., 2018). For simplicity, I assumed that bear agents expended the same amount of energy while active in either a foraging or moving state. I assumed that bear agents had an average movement rate of 1.5 m/s (Pagano et al., 2018; Shine et al., 2015) assuming added energy cost from traversing undulated areas and landscape impediments, which is associated with a mass specific metabolic rate E_a calculated from Whiteman et al. (2015) and Pagano et al. (2018). While it is expected that foraging grizzly bears will likely move slower than the average movement rate and thus expend less energy, there are additional energetic costs associated with searching and handling food. Hence, for modeling purposes I assumed that the energetic cost of foraging was analogous to moving. Females with attendant offspring had reduced movement rates and increased energetic demands (López-Alfaro, 2014). Bear agents at rest were assigned a basal metabolic rate E_r which was extracted from Robbins et al. (2012). See section 2.7 for further details.

Foraging

Relevant information on grizzly bear foraging behavior while consuming digestible energy in a 60 x 60 m cell was not available. I assumed that grizzly bear agents had perfect knowledge of the amount of digestible energy available to them within a sensing radius of 60 m from the cell in which they occupied at every time step. I refrained from using Holling's disc equation (type II functional response; Holling, 1959) because I did not have available information on grizzly bear searching and handling time during consumption of digestible energy units. Instead, I used a simplified submodel that checked whether grizzly bear agents should forage based on them meeting a BCI threshold. Grizzly bear agents with poor BCI were more likely to forage than bears in good BCI. See section 2.7 for further details. I tested the sensitivity of foraging parameter values in section 7.

Sensing radius

While there is limited information available on the link between grizzly bear foraging decisions and sensing radius, previous studies on habitat selection have used sensing radii and/or moving windows that range from 1.5-2 km. For instance, Gibeau et al. (2002) used a 1.5 km radius which corresponds to the daily feeding radius of adult females in Alberta. Nielsen et al. (2017) and Denny et al. (2018) used 1.6-1.8 km radii when considering selection of buffaloberry fruit, a critical food of grizzly bears in Alberta. Moreover, I encountered computational limitations when simulating a large sensing radius in the model. For these reasons, I choose a sensing radius of 60 m, which is the width of 1 patch (cell) in the model and approximates the hourly scale of the above-mentioned studies (60-75 m). I tested the sensitivity of this parameter value in section 7.

3.4 Road decision-making, road density, crossing frequency, and survival

Road decision-making

I used simple road crossing decision rules that dictated how grizzly bear agents navigate roads when encountering them while in a foraging or moving state. I did so because previous studies examining the use of roads have varied results. Some studies have found that males were near roads more frequently than females, while other have found the opposite pattern, or that subadults use them more often. Use of roads is also determined by adjacent habitat, traffic volume, sex, season, time of day, and protection status (Graham et al., 2010). For these reasons and because the intent of the model was not to simulate complex road crossing decision-making, I kept road crossing rules to a minimum. For instance, once a road was encountered, grizzly bear agents could only 'cross' the road and could not (immediately) turn around nor move in parallel to it. This rule applied to all bear agents. See section 2.7 for further details.

Relationship between road density and road crossing frequency

To estimate the relationship between survival and road crossing frequency, I first needed to establish a relationship between road density and road crossing frequency. To do so, I built a small separate IBM (Appendix S3) that simulated agents navigating the same landscape as the main IBM (see Figure S1) yet with agents constrained within watersheds that had different road densities. To delineate watershed boundaries, major watershed units were divided by the approximate home range size of an adult female grizzly bear in Alberta (see Boulanger and Stenhouse, 2014; McLelland et al., 2021). In brief, a single agent was initialized within each watershed and the simulation could run for 4415 ticks, the same number of ticks as the main IBM. I simulated each agent moving in a random walk (Codling et al., 2008) and counted the number of times the agent encountered a road using the same road crossing rules mentioned above. I ran (replicate) this simulation 1000 times and subsequently used the data to build a linear model showing the relationship between road density and road crossing frequency (Figure S3) and used the linear model's parameters within the main IBM.

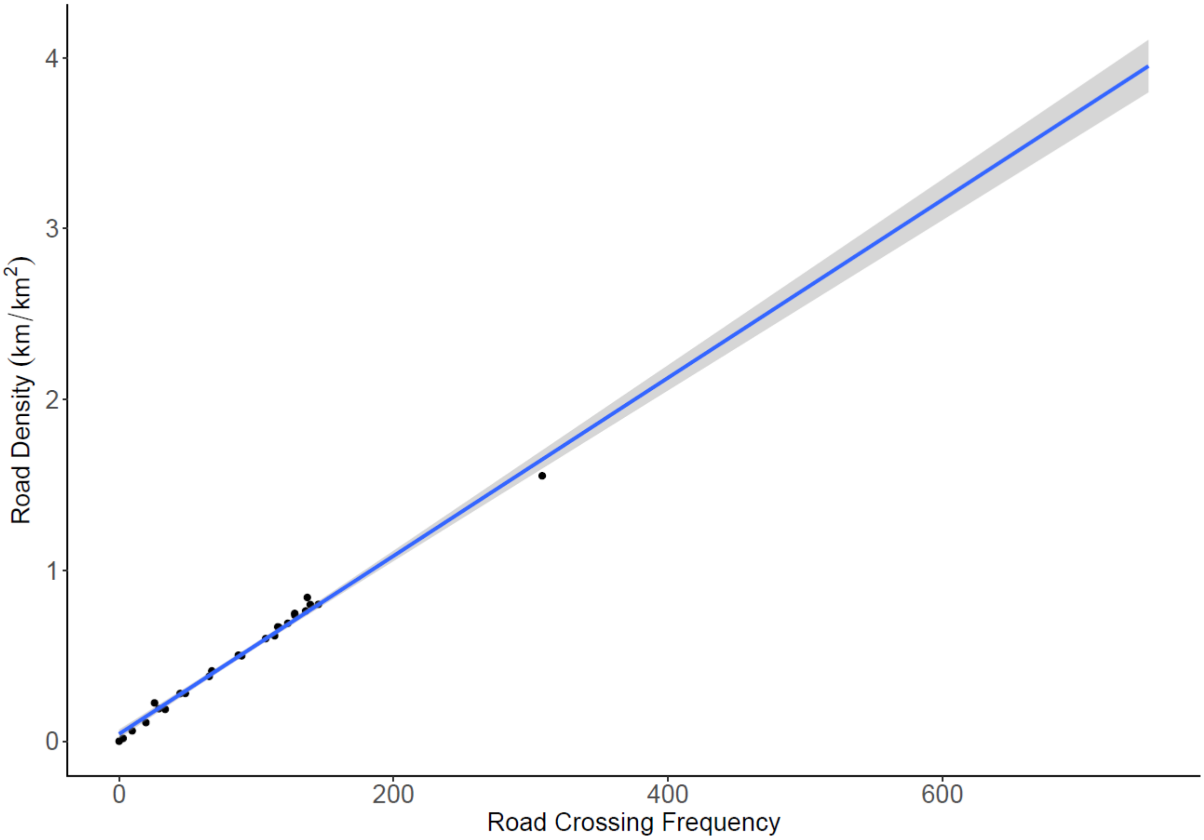

Figure S3: The relationship between road density and road crossing frequency used within the IBM. Individual points represent the mean value of 1000 replicates.

Relationship between survival and road density

To establish a relationship between survival and road density I extracted data on the impact of roads in terms of survival and reproductive class from Boulanger and Stenhouse (2014). For each sex-and-age-class (adult male, adult female, females with cubs/yearlings, subadult male, and subadult female) I reconstructed the relationship between survival rate and road density using data points from Figure 2 in Boulanger and Stenhouse (2014) and fitted second or third order polynomial regressions (Figure S4). I subsequently used these reconstructed models to parameterize the IBM to establish a relationship between survival, road density, and sex-and-age-class. That way I could estimate survival throughout the year and just before denning by linking survival rates to road crossing frequency of individual bear agents via the linear model describing road crossing frequency against road density.

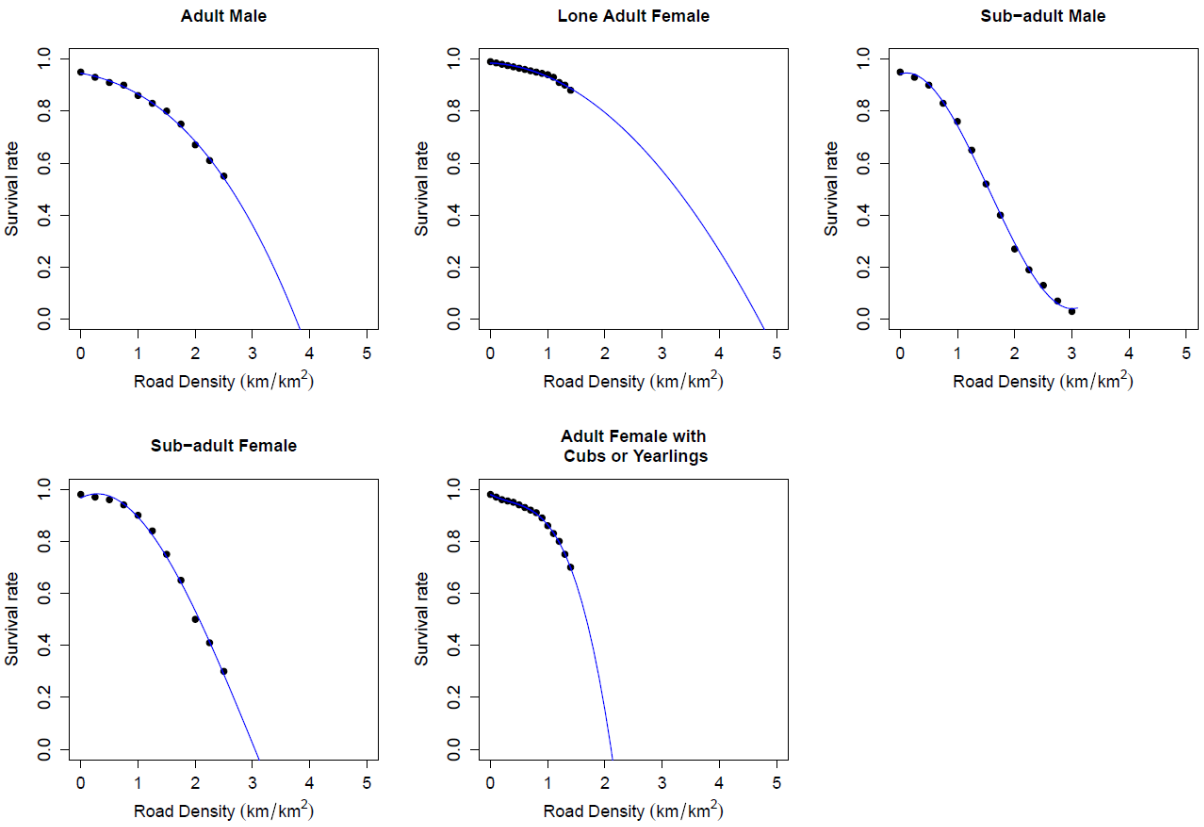

Figure S4: Models establishing the relationship between survival rate and road density and subsequently used to parameterize the IBM. Models are derived from Boulanger and Stenhouse (2014).

4 Conceptual model evaluation

Summary:

The simplifying assumptions underlying the model's design are outlined in section 1 – Problem Formulation and section 2.2 – Entities, state variables and scales. Additional information underlying the simplifying assumptions and model design concepts can be found in Section 2 – Model description, section 3 – Data Evaluation, and the methods section of the main paper.

5 Implementation verification

Summary:

To test whether the computer code has been thoroughly tested for errors and worked as intended according to the specifications outlined in Section 2 and in the conceptual model, I performed a range of tests and debugging techniques during model development and on the final model. The techniques included, syntax checking, parameter monitoring via plots and monitors using the 'Interface' tab, qualitatively and quantitatively comparing changes in the model to results expected from the conceptual model and by comparing results to statistical distributions in R, and using error statements, conditional statements and writing submodels in isolation before full implementation.

5.1 Software

The model was implemented in NetLogo 6.2.0 (Wilensky, 1999), which can be freely downloaded from https://ccl.northwestern.edu/netlogo/index.shtml and is available on all major operating systems. NetLogo is a cross-platform, open source, and freely available agent-based modeling platform intended to be a programmable multi-agent modeling environment primarily designed for simulating natural and social phenomena. It is well suited for modeling complex systems that change over time. Modelers can give instructions to individual agents that have the possibility of operating independently. This feature allows the modeler to connect micro-level behavior of individuals to macro-level system patterns that emerge from their interaction. NetLogo has an active user community that contributes to identifying, fixing, and updating software bugs. NetLogo developers allow multiple older versions to be installed on a system, which allow users to access models built in previous versions of NetLogo. The complete model program (computer code and associated graphical user interface) is available in the supplementary material. If desired, the model program can be run (using the graphical user interface or BehaviorSpace) and modified by the user. NetLogo's BehaviorSpace (Wilensky and

Shargel, 2002) tool, which is integrated within NetLogo, allows users to perform multiple simulation experiments by systematically varying the model's settings and recording results. BehaviorSpace was used in this simulation to perform multiple runs and assess model sensitivity and calibration.

5.2 Computer Code Verification

I tested the program by following the standards outlined in Railsback and Grimm (2019). I built the model incrementally by verifying whether each new line or section of code produced the expected results through an assortment of testing and debugging techniques. I used NetLogo's inbuilt software testing tools to check for run-time errors, faulty syntax via the 'Check' button tool, and implemented plots and monitors within the 'Interface' tab. By updating plots and monitors, I tracked bear variables (i.e., mean body mass and distanced traveled), road crossing frequency, survival rates (i.e., mean survival rate and percentage of bear agents that survive each day), and age distribution of bear agents according to age-class categories. I qualitatively compared changes from monitors and reporters (e.g., body condition index) to those expected from the conceptual model. I also compared quantitative results with expected results via R (R Core Team, 2020). When using stochastic processes to generate some model processes (e.g., spring body length and mass and age distribution), I compared the distribution of a large number of samples (i.e., 1000 or 10000) generated from such random processes to similar distributions created using R (R Core Team, 2020). I further used visual testing in the 'Interface' tab to check for unexpected results and implemented spot tests to monitor agents via the 'watch' and 'inspect' commands during model runs to ensure agents were behaving as expected and that agent-specific parameters did not have unreasonable values. I used print statements to write information to the display and/or to file to identify anomalies and for future analysis. I tested each submodel by writing a short program and tested the chunk of code in isolation before implementing it in the full model. I used conditional statements and errors messages to check for parameters that had unrealistic values (e.g., outside of theoretical ranges). Each bear agent was labeled with their current behavioral state and traced with the 'pen' command found in the NetLogo. Lastly, agent-specific parameters that were programmed to fluctuate throughout the simulation were updated and stored by each individual agent (turtle).

6 Model output verification

Summary:

In this section I provide details on inverse determination of two model parameters via calibration. The model parameters used with this method include minimum hourly energy of bear agents and proportion of day bear agents are active.

I used inverse determination via calibration on two model variables to determine parameter values that could not be properly derived from literature sources or had multiple (conflicting) values from literature sources. Because these values could influence various model processes and overall results, I calibrated them by searching for parameter values that most closely matched similar empirical values found in the literature.

I first ran exploratory analyses and visually checked whether each parameter value generated results and general patterns that broadly matched a parameter value from literature sources. I did this to generate an interval of reasonable parameter values to input into the simulation runs (replicates). From this, I selected a range of values for each parameter and replicated the simulation many times by varying each parameter value based on the interval determined during exploratory analyses. For each parameter, I then chose a value by comparing the percentile value from the simulated data to a similar percentile value found in empirical datasets. Here, I chose the relative (percentile) change in body mass between den exit (spring) and den entry (fall) to decide on final parameter values.

6.1 The coefficient for the proportion of day active, *active-coeff*

Grizzly bears spend a proportion of their day (24 h period) either in an active state (i.e., foraging/feeding and moving) or in an inactive state (i.e., resting) (MacHutchon, 2001; McLellan and McLellan, 2015). Moreover, the proportion of time a grizzly bear is active per day can change based on the season (McLellan and McLellan, 2015). I assigned the proportion of day a grizzly bear agent was active based on monthly values obtained from McLellan and McLellan (2015) (see section 3.2 for further details). I used the model parameter *active-coeff*, the coefficient that varies the proportion of day a grizzly bear agent is active, to determine the proportion of time a grizzly bear agent is active based on the month it is currently in. I adjusted the proportion of time grizzly bear agents were active (i.e., I did not solely rely on empirical values) because the study area is slightly further North than that found in McLellan and McLellan (2015) and bear agents in the area do not have access to salmon, which are typically clustered. Furthermore, exploratory analyses indicated that this model variable, the proportion of day a grizzly bear agent is active, could influence model results, and hence should be calibrated for this study area. To calculate the most appropriate value for *active-coeff*, I chose a range of parameter values and conducted multiple (replicate) simulations for each parameter value. Because *minimum-hourly-energy-coeff* (see section 6.2) also influences model results and interacts with *active-coeff*, I varied *active-coeff* in conjunction with *minimum-hourly-energy-coeff*. In total, I had 330 model runs (each parameter combination was replicated five times). Hence, each *active-coeff* value is summarized based on *minimum-hourly-energy-coeff* values ranging from 2000-3000 kcal. To choose the final *active-*

coeff value, I determined the relative change in body mass between den exit and den entry, when considering *minimum-hourly-energy-coeff* values ranging from 2000-3000 kcal.

Table S2: The inverse determination of the proportion of day active coefficient, *active-coeff*. I report the mean and standard error of the mean in the relative change in body mass between den exit and den entry (i.e., fall body mass relative to spring body mass) for adult female and adult male agents. The value of 1.2 is used in the final model because it produced results that most closely matched empirical mass gain values, when considering minimum energy values ranging from 2000-3000 kcal (see section 6.2 and Table S3 for details).

Proportion of Day Active Coefficient	Sex	Relative Change in Body Mass (SE)
0.6	Adult Female	-16.38% (0.55%)
0.8	Adult Female	1.97% (0.70%)
1.0	Adult Female	15.53% (0.81%)
1.2	Adult Female	31.40% (0.92%)
1.4	Adult Female	46.39% (1.07%)
1.6	Adult Female	63.96% (1.18%)
0.6	Adult Male	-18.29% (0.33%)
0.8	Adult Male	-5.74% (0.44%)
1.0	Adult Male	6.27% (0.50%)
1.2	Adult Male	19.32% (0.59%)
1.4	Adult Male	32.65% (0.64%)
1.6	Adult Male	43.47% (0.74%)

6.2 The minimum hourly energy consumed by agents, *minimum-hourly-energy-coeff*

The parameter *minimum-hourly-energy-coeff* controls the minimum amount of digestible energy a grizzly bear agent can consume per hour based on sex-and-age-class. I could not derive this parameter value from literature sources and exploratory analyses suggested its value could influence model results. Hence, I inversely determined the parameter value of *minimum-hourly-energy-coeff* by choosing a range of parameter values and conducted multiple (replicate) simulation for each parameter value. In total, I had 330 model runs (each parameter value was replicated 5 times with an *active-coeff* value of 1.2; see section 6.1). I chose final values based on the change in body mass between den exit and den entry for adult females, adult males, sub-adult females, and sub-adult males that best match literature sources.

Table S3: The inverse determination of the minimum hourly energy coefficient, *minimum-hourly-energy-coeff*. I report the mean and standard error of the mean in the relative change in body mass between den exit and den entry (i.e., fall body mass relative to spring body mass) for adult female, adult male, sub-adult female, and sub-adult male agents. An *active-coeff* value of 1.2 was used across model runs (see section 6.2 and Table S2 for details). The final values are as follows: adult females = 2700; adult males = 3000; sub-adult females = 2200; and sub-adult males = 2400. These values were used in the final model because they most closely matched empirical mass gain values, when considering an *active-coeff* value of 1.2. Final values and associated change in body mass are bolded.

Minimum hourly energy value (kcal)	Sex	Relative Change in Body Mass of Females (SE)	Relative Change in Body Mass of Males (SE)
2000	Adult	9.05% (2.17%)	18.12% (1.73%)
2100	Adult	13.25% (2.56%)	18.59% (1.76%)
2200	Adult	16.31% (2.54%)	15.12% (1.90%)
2300	Adult	19.23% (2.37%)	18.78% (1.70%)
2400	Adult	25.92% (2.72%)	19.33% (1.93%)
2500	Adult	34.34% (2.55%)	18.72% (1.87%)
2600	Adult	35.40% (3.10%)	18.72% (1.86%)
2700	Adult	**45.49% (3.20%)**	18.50% (2.02%)
2800	Adult	38.86% (3.09%)	17.13% (1.97%)
2900	Adult	48.93% (3.50%)	23.08% (2.13%)
3000	Adult	56.49% (3.35%)	**27.04% (2.44%)**

2000	Sub-adult	29.01% (3.70%)	26.69% (4.53%)
2100	Sub-adult	36.18% (4.55%)	29.37% (3.66%)
2200	Sub-adult	**36.00% (5.62%)**	23.11% (4.42%)
2300	Sub-adult	39.54% (7.47%)	44.24% (6.77%)
2400	Sub-adult	55.60% (7.54%)	**32.40% (5.45%)**
2500	Sub-adult	59.38% (7.77%)	55.92% (7.58%)
2600	Sub-adult	61.03% (7.27%)	59.70% (7.50%)
2700	Sub-adult	70.27% (7.73%)	59.35% (8.01%)
2800	Sub-adult	86.57% (8.43%)	55.55% (7.15%)
2900	Sub-adult	91.18% (6.96%)	58.54% (6.98%)
3000	Sub-adult	90.43% (9.34%)	57.03% (7.42%)

7 Model analysis

Summary:

I performed a global sensitivity analysis to understand how varying parameter values influenced model results by using regression-based methods. I selected 7 key variables (model parameters) and ran 250 simulations with randomized parameter sets. I did this to assess the influence of each parameter on model outputs by partitioning the variance among parameters using linear modeling techniques. In general, female BCI and male BCI, and female and male survival rates were insensitive to changes in parameter values.

7.1 Sensitivity of model results to changes in parameter values

Here, I explored how the uncertainty in parameter values influenced model results by using regression-based methods that assessed the relative influence of each parameter on model outputs (ten Broeke et al., 2016). I first selected 7 key variables (model parameters) that were associated with some uncertainty and that I considered to have an important influence on model outputs (Table S4). I then chose a range of values (interval) that spanned a reasonable level of uncertainty for each parameter and subsequently uniformly (random) sampled each parameter interval, from which I created 250 parameter sets. For each parameter set, I ran a single model (250 in total). I only used uncertainty intervals to conduct a global sensitivity analysis, whereas single parameter values (Table S4) were used in the final simulation. Finally, to conduct 250 model runs, I used the R package *RNetLogo* to pass parameter sets to NetLogo via a software link connected to R (Thiele et al., 2014).

I used four variables (model outputs) that met the objectives of the model outlined in Section 1 to assess the influence of parameter values on model results. The model outputs were: 1) female (adult and sub-adult) body condition at the end of the simulation (active period); 2) male (adult and sub-adult) body condition at end of the simulation; 3) female (adult and sub-adult) survival rates related to road crossing frequency at the end of the simulation; and 4) male (adult and sub-adult) survival rates related to road crossing frequency at the end of the simulation.

I use linear modeling to assess the influence of each parameter on model outputs by partition the variance among parameters. I implemented the analysis in R by running a single linear model for each output variable, each of which were considered a response variable, and for each of the 7 key parameters, which made up the predictor variables. To that end, each linear model had 250 observations from which I calculated η^2, which describes the proportion of variance in model outputs that is explained by each of the 7 key parameters. High η^2 values indicate that model outputs are sensitive to uncertainty in parameter values.

Table S4: Sensitivity of model outputs to uncertainty in model parameters. I report the proportion of variance, η^2, in model outputs (female and male body condition index, female and male survival rate) explained by each of the 7 key model parameters. BCI refers to body condition index.

Parameter	**Uncertainty Level**	**Output Variables**			
		Female BCI	**Male BCI**	**Female Survival Rate**	**Male Survival Rate**
Sensing radius (60 m interval)	1 - 4	0.013	0.009	0.001	< 0.001
Female BCI threshold	-2 - +2	0.008	< 0.001	0.006	< 0.001
Male BCI threshold	-2 - +2	< 0.001	0.010	0.002	0.015
Forage probability when BCI < BCI threshold	0.5 - 1	0.020	0.015	0.055	0.090
Forage probability when BCI >= BCI threshold	0.5 - 1	0.058	0.059	0.064	0.106
Forage or move probability	0.5 - 1	0.011	0.013	< 0.001	< 0.001
Bear density	5 – 15/ 1000 km^2	<0.001	< 0.001	< 0.001	< 0.001
Residuals		0.897	0.900	0.862	0.794

In general, female BCI and male BCI, and female and male survival rates were insensitive to changes in parameter values (Table S4). However, varying some parameters had moderate effects on some output variables (model outputs). For instance, forage probability when BCI < BCI threshold explained 5.5% and 9% of the variance in female survival rate and male survival rate, respectively. Likewise, forage probability when BCI >= BCI threshold explained between 5.8% and 10.6% of the variance when considering all output variables (model outputs).

8 Model output corroboration

Summary:

In this section I validate (corroborate) the model using pattern-oriented modeling. The goal here is to have the model reproduce patterns not included in model design. The model reproduced empirical results of grizzly bear mass gain patterns, bioenergetics, body condition index, movement patterns, and distribution patterns related to food resources and body condition index. Specifically, I reproduce patterns on how grizzly bears gain mass from den exit to den entry, the daily rate of mass gain, the body condition index as recorded in spring, and the distance traveled from den exit to den entry. I also show how the distribution of grizzly bears on a real landscape is linked to the distribution of food resources (digestible energy) and early seral forests, and how this relates to body condition index (a measure of health).

To validate (corroborate) the model, I used pattern-oriented modeling (POM; Grimm et al., 2005). The idea here is to have the model reproduce patterns observed in real systems that were not included, or preferably not known, during model design to understand the model's internal organization while the model was developed, parameterized, and verified. Thus, the model's emergent (reproduced) patterns act as indicators of the model's underlying structure and processes, effectively reassuring users that the model contains the correct mechanisms to address the problem, that the model is structurally realistic, and to make useful predictions that can be trusted to some degree (Grimm et al., 2005; Grimm and Railsback, 2012; Grimm et al., 2014; Railsback and

Grimm, 2019). Furthermore, a model that reproduces patterns of a real system at multiple levels (both agent and system level) and at different scales reduces the risk that the model is completely unrealistic (Grimm et al., 2014), thus reassuring users of the model's utility. Here, I compare some model outcomes (patterns) that were not part of model design to empirical results previously published on grizzly bear bioenergetics, body condition (health), movement, and distribution.

8.1 Mass gain and loss patterns

Depending on the availability and quality of spring food resources, grizzly bears can continue to lose body mass over the course of spring until food resources recover during summer and fall (Blanchard, 1987; Schwartz et al., 2003). Mass gain and loss patterns between den exit and den entry are an important aspect of grizzly bear physiology and condition. Blanchard (1987) reported results on mass gain and loss patterns in grizzly bear populations residing in interior North America (Yellowstone) and found that both male and female adults loss mass from den emergence through approximately July, whereas male and female sub-adults loss mass from den emergence through approximately August (although with limited data). The model produced similar patterns where both male and female adults and sub-adults loss mass from den emergence through approximately June and regained much of their emergence weight sometime in July (~ day 200), although this varied based on the sex-and-age-class (Figure S5). Grizzly bear agents continued to gain mass from July onwards and this probably reflects the increased availability of digestible energy arising from berries. Given the model was mostly parameterized with data originating form Alberta and the above-mentioned empirical study was conducted on grizzly bear populations residing in Yellowstone, slight differences in patterns were to be expected.

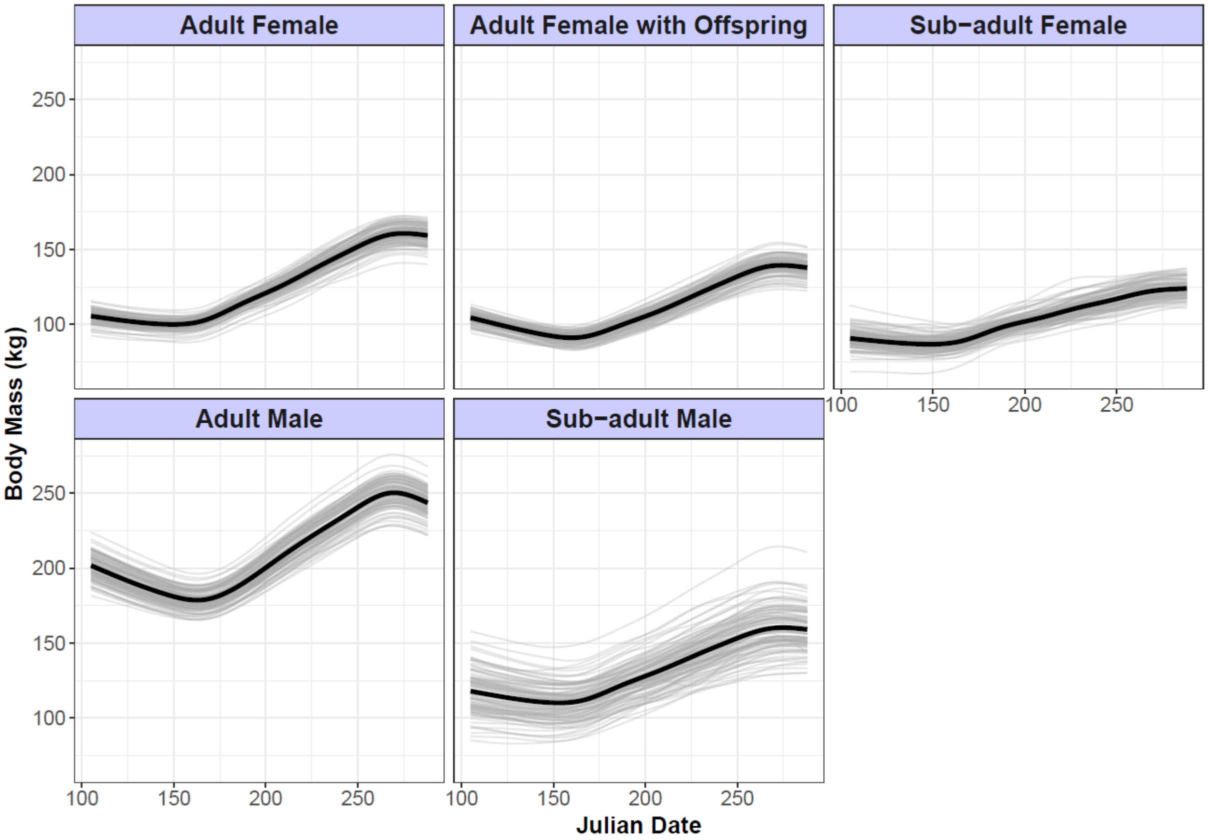

Figure S5: Patterns of mass gain between den exit and den entry. Each gray line represents a single model run (average of agents within each run) whereas the thick black line represents the average across 100 model runs.

Several studies have quantified the differences in mass between den exit and den entry in grizzly bear populations residing in interior North America. Differences in mass gain between den exit (spring) and den entry (fall) are thought to range between 30-70% for adult females, 15-45% for adult males, and approximately 40% for sub-adults for grizzly bear populations residing in interior North America (Kingsley et al., 1988; Schwartz et al., 2003; McLellan, 2011). Females are thought to have greater weight fluctuations than males because of the energy expended for gestation and lactation (Kingsley et al., 1988; Schwartz et al., 2003), and so I expect lone adult females to have greater weight fluctuations than adult females with offspring (reduction in energy because of attendant offspring), which are results corroborated (Figure S6). The spring-to-fall weight gain differences were as follows: adult female (50%), adult female with offspring (32%), sub-adult female (35%), adult male (21%), sub-adult male (34%). The values fall within the range detailed in previously published studies and are similar to results published from grizzly bear populations residing in southeastern British Columbia. For instance, McLellan (2011) found spring-to-fall weight gain differences of grizzly bears in southeastern British Columbia as follows: adult female (33%), sub-adult female (41%), adult male (16%), and sub-adult male (38%). If I pool lone adult female and adult female with offspring classes together, spring-to-fall weight gain in this model was 41%. Given this model is parameterized with data mostly originating from Alberta, exact similarities between model results and empirical results derived from field data in neighboring and more southern populations were not necessarily expected.

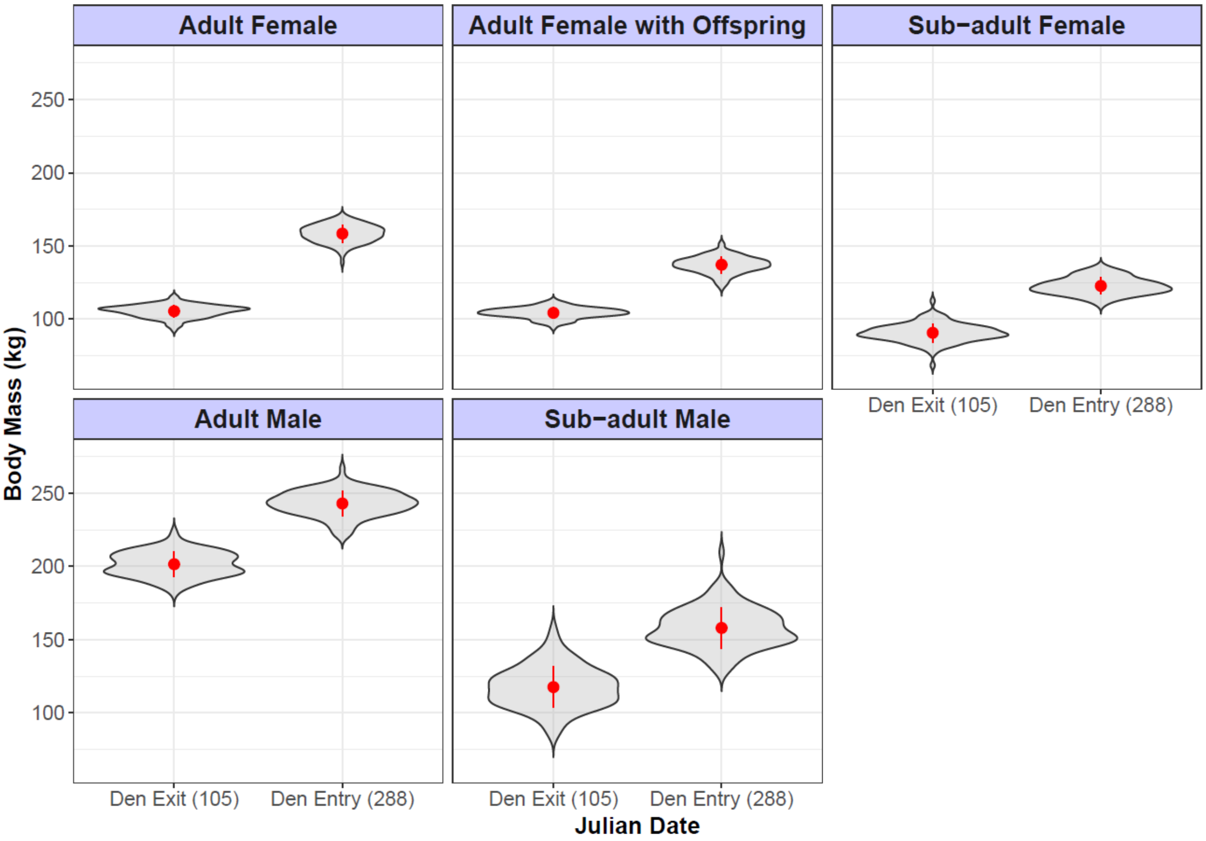

Figure S6: Differences in grizzly bear agent mass between den exit and den entry for 100 model runs represented with violin plots, which depict the distribution of the data at different values smoothed with a kernel density estimator. For each sex-and-age-class, the red circle represents the average mass whereas the red line represents the standard deviation.

8.2 Bioenergetics and body condition

Empirical studies have quantified mass gain per day of wild (free-ranging) populations and captive grizzly bears. The capacity for rapid mass gain allows bears to meet maintenance demands as well as demands required for dormancy, gestation, and lactation (Bunnell and Hamilton, 1983; Hilderbrand et al., 1999). Mass gain can range from 0.2-1 kg/day for both wild and captive populations (Pearson, 1975; Nagy and Russell, 1978; Bunnell and Hamilton, 1983; Kingsley et al., 1983; Blanchard, 1987; Hilderbrand et al., 1999; Rode et al., 2001). Using two captive bears, Bunnell and Hamilton (1983) found that the male gained 0.63 kg/day whereas the female gained 0.51 kg/day per day. Similarly, a male bear from the Yukon gained on average 0.41 kg/day (Pearson, 1975; Bunnell and Hamilton, 1983). Blanchard (1983) found females gained 0.4 kg/day on average in Yellowstone, whereas Rode et al. (2001) reported that a 120 kg captive bears can gain weight at 0.53 kg/day. Daily mass gains for wild sub-adult male and female bears were 0.39 kg/day and 0.28 kg/day, respectively (Nagy and Russell, 1978). I did not find any literature values on mass gain per day for adult females with offspring. The model produced similar values of mass gain per day to those documented in previous studies (Table S5), especially those from wild populations, suggesting the model can be partly thought as structurally realistic.

Table S5: The mean mass gain per day of grizzly bear agents between the onset of continuous mass gain (approximately early June; see Figure S5 for further details) and den entry averaged from 100 model runs. Data is summarized within each model run and subsequently summarized across 100 model runs.

Sex-and-Age-Class	Mean kg/day	95% CI kg/day
Adult Female	0.43	0.42–0.43
Adult Female with Offspring	0.38	0.37–0.39
Sub-adult Female	0.26	0.26–0.27

Adult Male	0.53	0.52–0.53
Sub-adult Male	0.35	0.35–0.36

Following Cattet et al. (2002) I used BCI to assess the body condition of grizzly bear agents (see sections 2.7, 3, and 7 for further details). Similar to wild populations reported by McLellan (2011), grizzly bear agents had lower BCI in spring than in fall and BCI of adult males was less variable between seasons compared to other sex-age-classes (Figure S7). McLellan (2011) reported BCI values to be at their lowest in May and increased thereafter until August. I find similar patterns, where grizzly bear agents had their lowest BCI values in early June and BCI values peaked in early-to-mid September. Differences between empirical results and model results should be expected for two reasons: 1) on account of the higher latitudes encountered in this model study area, plant phenology likely lags behind those found in south-eastern British Columbia, which would create a temporal mismatch in BCI values when comparing both areas, and 2) parameterization of den emergence (spring) mass (which influences BCI) was accomplished using von Bertalanffy growth curves using data from the population unit in west-central Alberta.

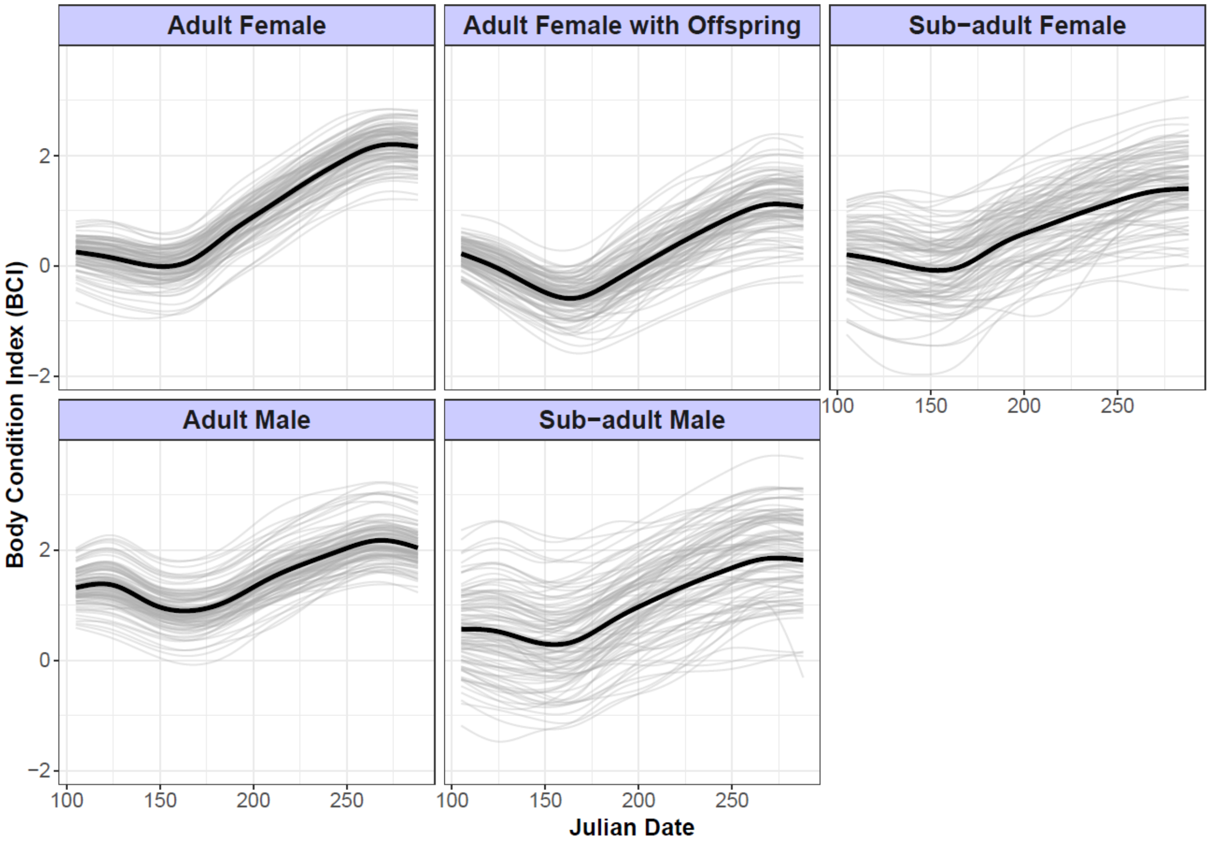

Figure S7: Changes in body condition index (BCI) between one day after den exit (day 106) and den entry. Since BCI was updated at the end of each day, I could not record BCI data until day 106 (one day after den exit – day 105). Each gray line represents a single model run (average of agents within each run) whereas the thick black line represents the average across 100 model runs.

Again, similar to McLellan (2011) adult females had lower BCI in spring than adult males, however, BCI values were more similar in fall just prior to den entry (Figure S8). Overall, sub-adult males had higher BCI than sub-adult females, again, similar to results reported in McLellan (2011). Note that the BCI values are reported on a single day whereas those from McLellan (2011) are pooled across seasons.

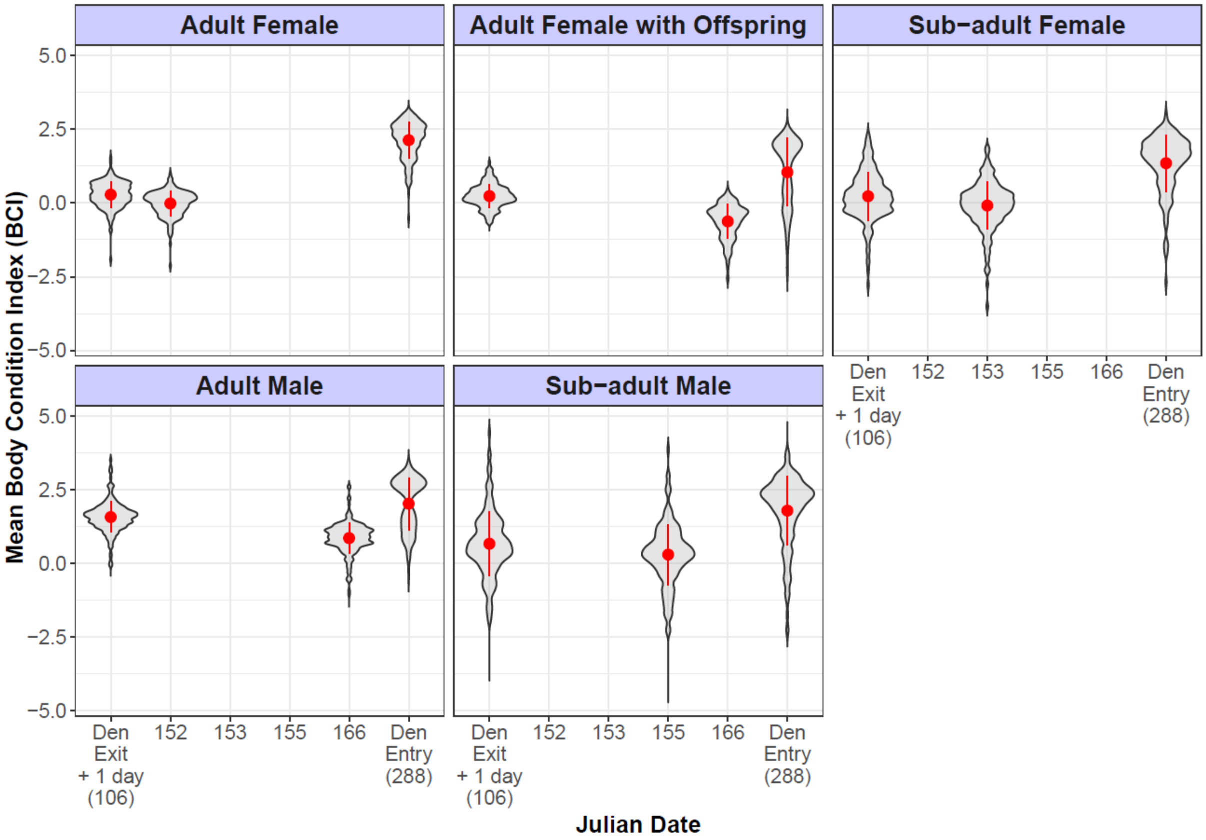

Figure S8: Differences in mean BCI one day after den exit, day with lowest BCI unique to each sex-and-age-class, and den entry, summarized from 100 model runs represented with violin plots, which depict the distribution of the data at different values smoothed with a kernel density estimator. For each sex-and-age-class, the red circle represents mean BCI whereas the red line represents the standard deviation across 100 model runs. Data is summarized within each model run and subsequently summarized across 100 model runs.

The spring BCI values (Table S6) are comparable to those found in McLellan (2011) and Bourbonnais et al. (2014), which I report here to allow comparison to the model results. I report results from McLellan (2011) first followed by those from Bourbonnais et al. (2014) as follows: adult female (-0.47; -0.28), adult male (0.09; 0.76), adult female with offspring (NA; -0.43); sub-adult female (-0.26; -0.48), and sub-adult males (-0.33; -0.11). The model results are more similar to those reported by Bourbonnais et al. (2014) and should be expected given both study areas occurred in the same region. Overall, the spring BCI patterns between sex-and-age-classes are comparable to both McLellan (2011) and Bourbonnais et al. (2014), where adult males have higher BCI than other reproductive classes and females of all reproductive classes generally have poorer

BCI than either adult males or sub-adult males. If pooling all classes together, then the average BCI is -0.25 for McLellan (2011), -0.11 for Bourbonnais et al. (2014), and 0.09 for the model here.

Table S6: The average body condition index (BCI) of grizzly bear agents on day with lowest recorded BCI (approximately early June; see Figure S7 for further details) across 100 model runs. Data is summarized within each model run and subsequently summarized across 100 model runs.

Sex-and-Age-Class	**BCI**	**95% CI BCI**
Adult Female	-0.02	-0.03–(-0.004)
Adult Female with Offspring	-0.62	-0.64–(-0.61)
Sub-adult Female	-0.09	-0.11–(-0.06)
Adult Male	0.86	0.84–0.87
Sub-adult Male	0.30	0.26–0.33

8.3 Movement patterns

To explore how grizzly bear agents were influenced by food resources and road density it was important to understand the movement patterns of bear agents themselves. Grizzly bears can move considerable distances during the active period (outside of den) while searching for food, mates, and secure habitat while navigating natural and human-caused disturbances (Schwartz et al., 2003). A consistent finding in grizzly bear literature is that adult male bears have larger ranges of movement than other sex-and-age-classes, likely owing to searching for food to support a larger body mass and/or searching for reproductive females (Blanchard and Knight, 1991; McLoughlin et al., 1999; Schwartz et al., 2003). In contrast, females with attendant offspring have reduced mobility because offspring lack mobility and the need for security to reduce the risk of infanticide by male bears (Blanchard and Knight, 1991; Steyaert et al., 2013). The model reproduced movement patterns (distance covered during the active period) similar to results reported in previous studies located in west-central Alberta (Table S7). For instance, Graham and Stenhouse

(2014) found that adult females with offspring traveled approximately on average 1071 km, whereas Boulanger et al. (2013) reported that for the same sex-and-age class bears traveled approximately on average 892 km. Model results from other sex-and-age classes cover similar movement distances as those reported in Graham and Stenhouse (2014) and Boulanger et al. (2013). I do note, however, that the model results have smaller movement (distance) variance than what was reported in Graham and Stenhouse (2014). This is expected as I built the model to sample from a movement (distance) distribution with a small variance. I expect that sampling from a movement distribution with a larger variance would create larger confidence intervals in distance traveled, although I expect that mean distance to be the approximately the same as reported here.

Table S7: The average distance traveled by grizzly bear agents between den exit and den entry (recorded on last tick) across 100 model runs. The model runs with the lowest and highest recorded mean distance are summarized as minimum and maximum distance, respectively. Data is summarized within each model run and subsequently summarized across 100 model runs.

Sex-and-Age-Class	Mean Distance (km)	95% CI Mean Distance (km)	Minimum Distance (km)	Maximum Distance (km)
Adult Female	1283	1278–1289	1214	1337
Adult Female with Offspring	1056	1048–1064	944	1202
Sub-adult Female	1415	1406–1425	1319	1558
Adult Male	1637	1633–1642	1582	1701
Sub-adult Male	1456	1445–1466	1318	1582

8.4 Distribution pattern and BCI related to forestry and food resources

To explore the distribution patterns of grizzly bear agents across a landscape, I spatially mapped the relative location density of grizzly bear agents against BCI (Figure S12). I provided additional spatial maps of total digestible energy (Figure S9), standard deviation in digestible energy (S10), and area disturbed by early seral forests (Figure S11) to contrast areas where bear agents have the highest probability of gaining body condition across gradients of food resources and forested areas. Here I compare model patterns using male agents (Figure S12), although similar patterns were found with female agents as well. The model reproduced similar geographic patterns in BCI change relative to gradients of forested areas as those reported in Boulanger et al. (2013) for captured bears. Grizzly bear agents tended to have higher BCI values in areas with high amounts of digestible energy, large variation in digestible energy, and areas with higher proportions of early seral forests (<= 30 years), suggesting anthropogenic activity, especially regarding forestry disturbances, may benefit grizzly bear health and thus could conceivably help with population recovery efforts. These patterns are similar to Boulanger et al. (2013), where gains in body condition were associated with regenerating forest habitats, whereas reductions in body condition were associated with older forests.

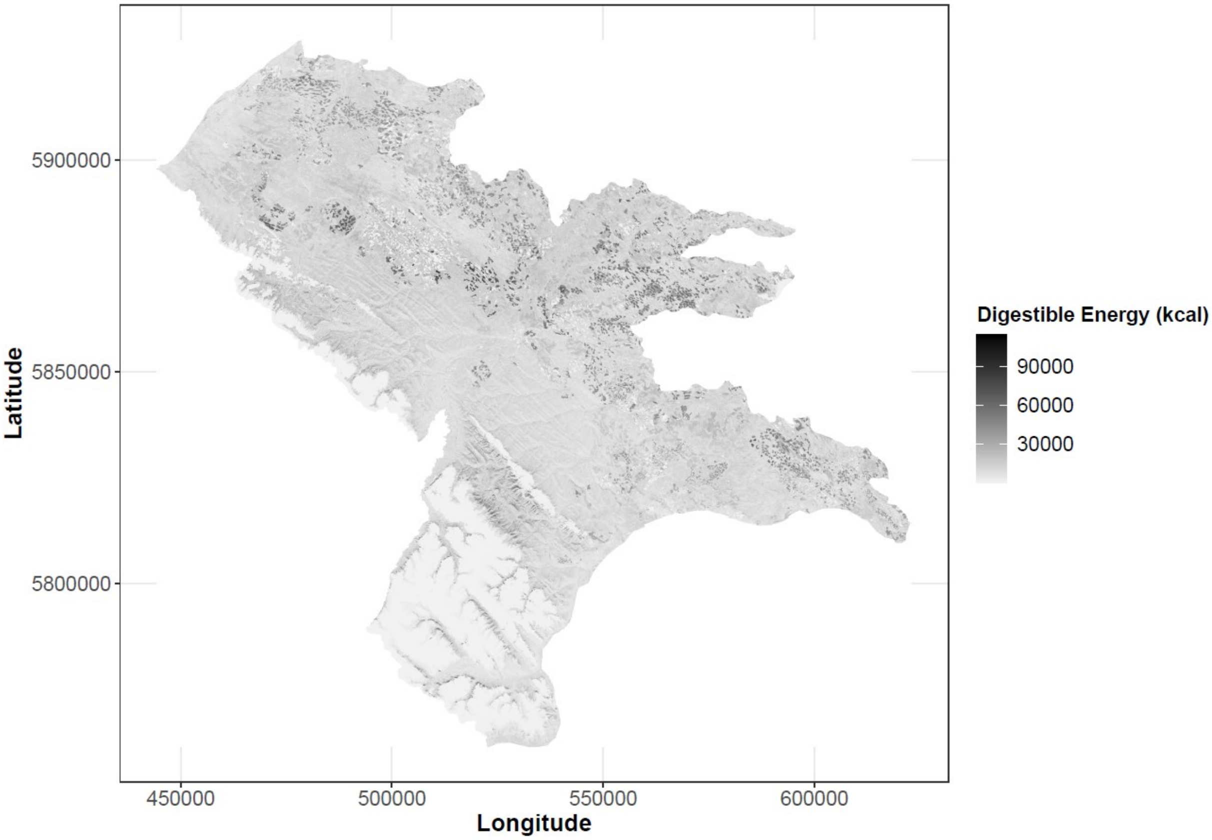

Figure S9: The total amount of digestible energy (kcal) available on the landscape summarized from individual food groupings (fruit, forb, horsetail, sweetvetch roots, ant, and ungulate).

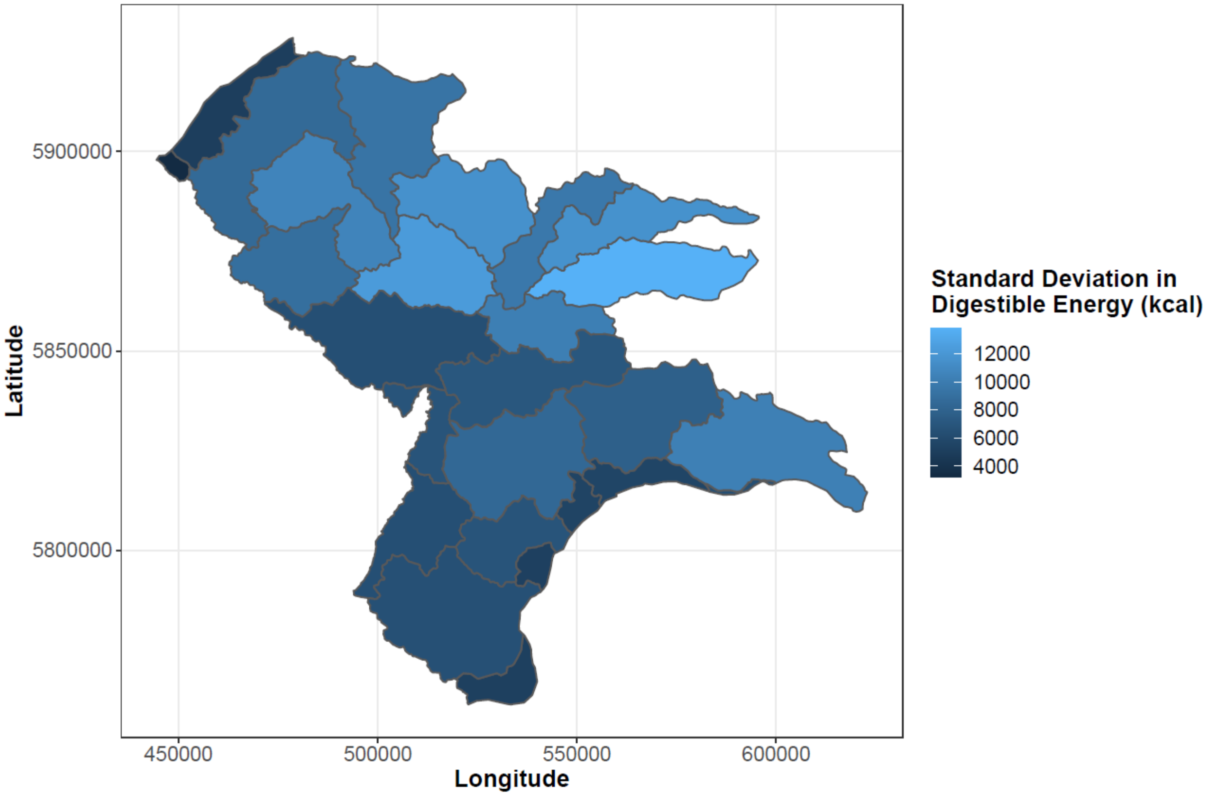

Figure S10: The standard deviation in the total amount of digestible energy (kcal) available on the landscape summarized from individual food groupings (fruit, forb, horsetail, sweetvetch roots, ant, and ungulate) in each Alberta watershed.

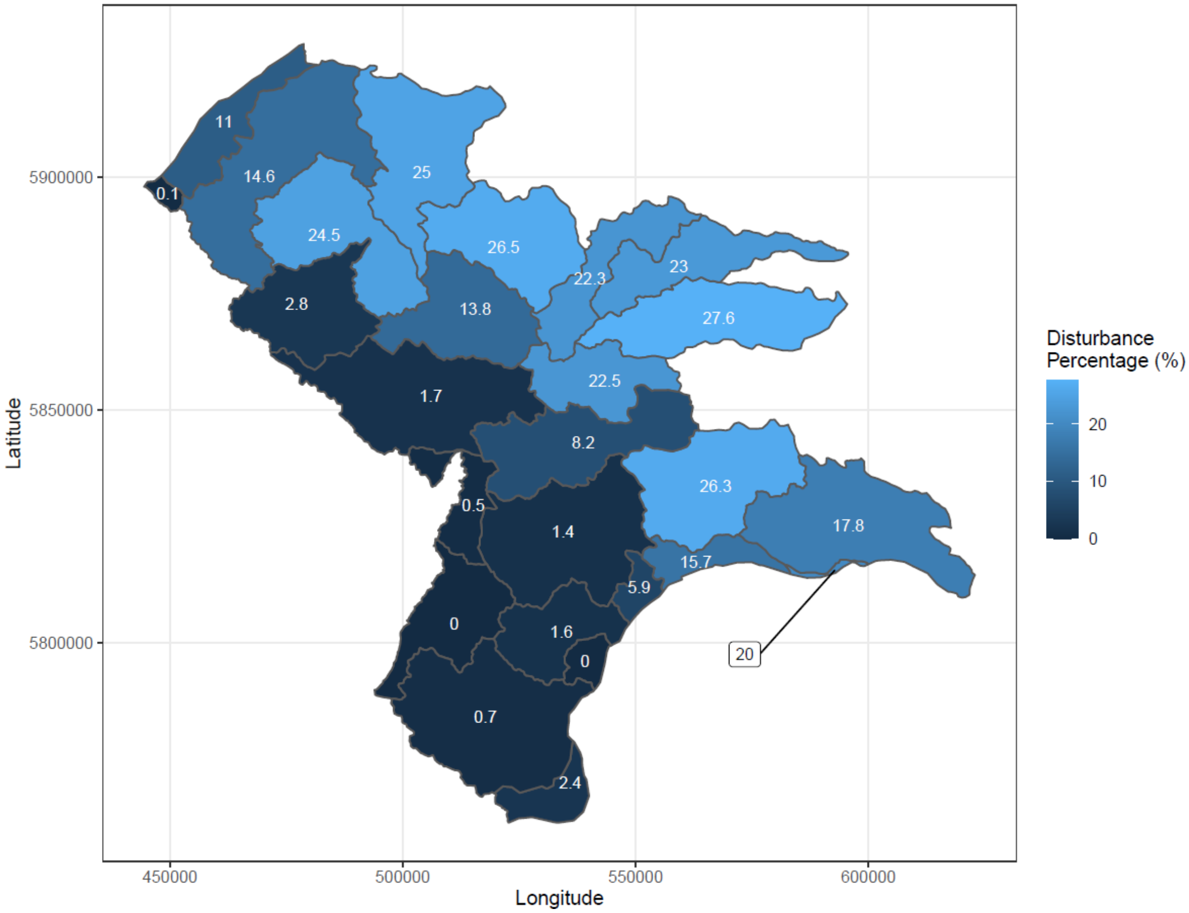

Figure S11: The percentage of surface area disturbed by early seral forests (<= 30 years) in each Alberta watershed.

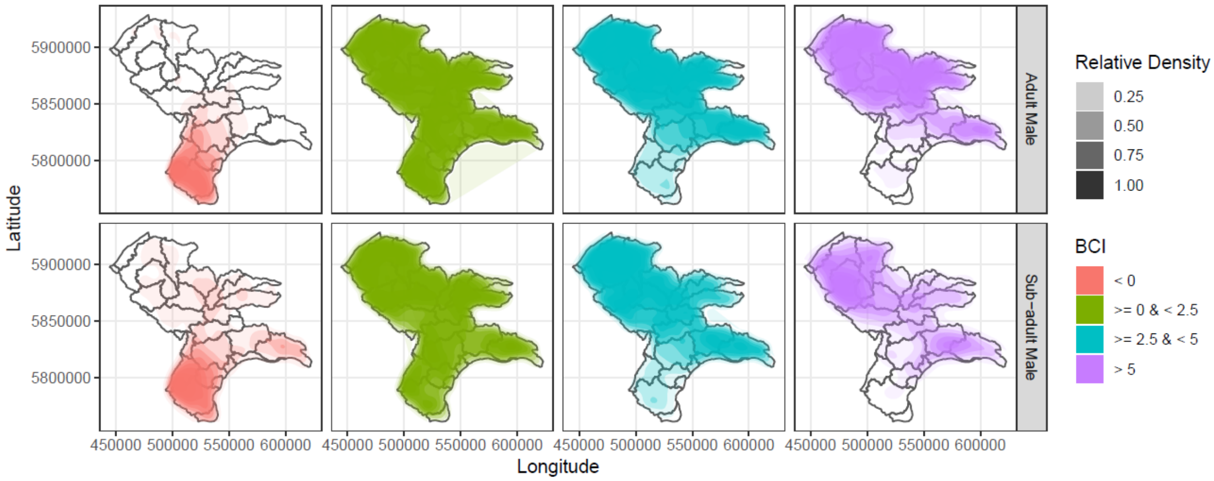

Figure S12: Relative location density contrasted against BCI values of male bear agents. Locations are recorded once per day (at the beginning of each day) throughout the simulation and contrasted, for visualization purposes, against end-of-active period BCI values. Data is not summarized within each model run, rather it is pooled here across 100 model runs.

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Appendix 4.2. NetLogo code of the main simulation model.

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;;;;;;;        ENTITIES AND STATE VARIABLES        ;;;;;;;
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extensions [ gis rnd csv profiler ]


globals
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  ;; landscape-related or patch-related
  fruit-dataset
  forb-dataset
  horsetail-dataset
  sweetvetch-dataset
  ant-dataset
  ungulate-road-dataset
  lat-dataset
  long-dataset
  hour-of-day
  day-of-year
  day-of-month
  month
  year
  mod-mask ;; shapefile to set envelope
  roads
```

```
  landscape-energy
  annual
  core-secondary
  dig-energy-patches
  ;sensing-radius; global switch
  ;active-coeff; global switch
  ;minimium-energy-hourly-coeff; global switch when calibrating coefficient
  ;draw-watersheds? ; global switch


; turtle-label-on? global variable used as slider


 ;; bear-related
  age-sex-list ; (e.g. [[5 "male"] [12 "female"]])
  survival-rates ; list of annual bear survival rates
  length-mass-rates ; length and mass parameters derived from von Bertalanffy regressions
  active-prob ; the mean probability that bears are active for each month from April 1st to
November 15
  cub-cost ; cost of lactation in cubs-of-the-year


;; patch-related
  energy-weights
  potential-foraging-patches
  this-patch
  watershed-dataset
```

```
; end of simulation outputs
 bear-who
 bear-age
 bear-sex
 bear-age-class
 bear-spring-body-mass
 bear-body-mass
 bear-survival-rates
 bear-survive
 bear-road-freq
 bear-road-dens
 bear-total-dist
 bear-current-bci
 bear-dig-energy
 bear-cub
 bear-yearling
 ;bear-yearling-age

 ; hourly (tick) location outputs
 location-who
 location-xcor
 location-ycor
 location-spring-body-mass
 location-body-mass
```

```
  location-current-bci
]

breed [males male]
breed [females female]

turtles-own
[
  age
  sex
  age-class; (i.e., cub, yearling, sub-adult, or adult, with associated age)
  dig-energy-spring
  max-energy-hourly
  min-energy-hourly
  hourly-energy
  body-mass
  spring-body-mass
  body-length
  spring-body-length
  mean-dist-timestep ; mean distance per timestep/time interval
  sd-dist-timestep ; standard deviation of mean distance per timestep/timeinterval
  state
  substate
  should-I-rest?
  should-I-active?
```

```
  should-I-forage?
  I-am-localized?
  I-am-moving?
  hours-awake
  hours-resting
  current-step-dist
  previous-step-dist
  road-freq
  total-dist
  current-bci
  previous-bci
  diff-bci
  bear-watershed-id
  bear-watershed-dens
  bear-survival-rate
  bear-survive?
]

males-own[]

females-own
[
  attendant-cub?
  attendant-yearling?
```

```
  yearling-age
]

patches-own
[
  fruit-energy
  forb-energy
  horsetail-energy
  sweetvetch-energy
  ant-energy
  ungulate-energy
  dig-energy; digestible energy of every single patch as layed out by GIS pixel values
  latitude-value
  longitude-value
  I-am-out-of-bounds? ; boolean vavlue - only patches off-map area (black)
  I-am-road? ; boolean value stating road
  weights-applied? ; has the patch been updated this time period with weights
  current-tick ; the tick number/value that last updated the patches + 1
  ;hourly-patch-energy ; patch energy adjusted for per hour with old framework
  weighted-patch-energy ; available energy weighted to phenology. This is calculated only when
bear occupies patch which is needed for computational efficiency
  available-patch-energy; available energy after substracting energy consumption from previous
bear
  energy-consumed ; energy consumed by bears
  patch-consumed? ; has the patch energy been previously consumed by a bear
  freq-consumed ; frequency of patch consumption by bears
```

```
  will-forage?
  area-id
  watershed-dens
  watershed-id
]



;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;  SETUP FUNCTIONS/MAIN INTERFACE PROCEDURES   ;;;;;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;


to setup-landscape
  ca ; clear-all
  set core-secondary gis:load-dataset
("../../IBMData/NLogo/gb_uf_veg_Dissolve_core_sec.shp")
  set watershed-dataset gis:load-dataset     ("../../IBMData/NLogo/wts_corsec4MP.shp")
  set fruit-dataset gis:load-dataset         ("../../IBMData/NLogo/fruit_int_60.asc")
  set forb-dataset gis:load-dataset          ("../../IBMData/NLogo/forb_int_60.asc")
  set horsetail-dataset gis:load-dataset     ("../../IBMData/NLogo/equ_int_60b.asc")
  set sweetvetch-dataset gis:load-dataset    ("../../IBMData/NLogo/hed_int_60b.asc")
  set ant-dataset gis:load-dataset           ("../../IBMData/NLogo/ant_int_60b.asc")
  set ungulate-road-dataset gis:load-dataset ("../../IBMData/NLogo/ung_ro_int_60b.asc")
  set lat-dataset gis:load-dataset           ("../../IBMData/NLogo/latitude.asc")
  set long-dataset gis:load-dataset          ("../../IBMData/NLogo/longitude.asc")
```

```
  ;set core-secondary gis:load-dataset
("../../IBMData/NLogo/gb_uf_veg_Dissolve_core_sec.shp")


  gis:set-world-envelope (gis:envelope-union-of (gis:envelope-of fruit-dataset) ; set world-
envelope to raster datasets
                                                (gis:envelope-of forb-dataset)
                                                (gis:envelope-of horsetail-dataset)
                                                (gis:envelope-of sweetvetch-dataset)
                                                (gis:envelope-of ant-dataset)
                                                (gis:envelope-of ungulate-road-dataset)
                                                (gis:envelope-of lat-dataset)
                                                (gis:envelope-of long-dataset))

  gis:apply-raster fruit-dataset fruit-energy
  gis:apply-raster forb-dataset forb-energy
  gis:apply-raster horsetail-dataset horsetail-energy
  gis:apply-raster sweetvetch-dataset sweetvetch-energy
  gis:apply-raster ant-dataset ant-energy
  gis:apply-raster ungulate-road-dataset ungulate-energy
  gis:apply-raster lat-dataset latitude-value
  gis:apply-raster long-dataset longitude-value


      foreach gis:feature-list-of core-secondary [
    a -> ask patches gis:intersecting a [ ; two or more arguments require brackets, i.e., [x y] -> ask
patches...
      set area-id gis:property-value a "HABITAT"
```

```
    ]
  ]


      foreach gis:feature-list-of watershed-dataset [vector-feature ->
    ask patches gis:intersecting vector-feature [ ; two or more arguments require brackets, i.e., [x y] -> ask patches...
      set watershed-dens gis:property-value vector-feature "km_km2"
      ;set watershed-dens precision watershed-dens 4
      set watershed-id gis:property-value vector-feature "id"
    ]
  ]




  ;resize-world 0 gis:width-of ungulate-dataset - 1 0 gis:height-of ungulate-dataset - 1; [gis:width-of landscape-energy - 1] removes the last column because the first column in NetLogo starts at 0 and not 1, which ArcMap does


  ask patches [


    ; set patches to proper boundary and color identifier
    ifelse (isNAN(fruit-energy))
    [
      set I-am-out-of-bounds? TRUE
      set dig-energy 0 set fruit-energy 0 set forb-energy 0 set horsetail-energy 0 set sweetvetch-energy 0 set ant-energy 0 set ungulate-energy 0 set latitude-value -9999 set longitude-value -9999
```

```
    set pcolor black
   ]
   [
    set I-am-out-of-bounds? FALSE
    set dig-energy (fruit-energy + forb-energy + horsetail-energy + sweetvetch-energy + ant-energy + ungulate-energy)
    set pcolor green
   ]
   if (dig-energy = 0 and I-am-out-of-bounds? = FALSE) [set pcolor black set I-am-out-of-bounds? TRUE] ; rectifies the last column on the right
  ]

  let min-dig-energy min [dig-energy] of patches with [pcolor = green]
  let max-dig-energy max [dig-energy] of patches with [pcolor = green]

  ask patches [

   ; color road patches gray
   if (ungulate-energy = 1) or (ungulate-energy = 2) [ ; 1 refers to core area and 2 refers to secondary area
    ifelse (ungulate-energy = 1)
    [ set pcolor 4 ] ; medium gray
    [ set pcolor 7 ] ; light gray
   ]
```

```
  ; green patches (energy) get rescaled according to their dig-energy value

  if (pcolor = green) [set pcolor scale-color green dig-energy (min-dig-energy - 10000) (max-dig-energy + 10000)]


  if (dig-energy = 1) and (area-id = "S") [ set area-id "C" ] ; set area-id that overlap the boundary line between the core and secondary areas to the proper area-id - dig-energy used as references

  if (dig-energy = 2) and (area-id = "C") [ set area-id "S" ] ; ditto


  ; substract ungulate energy from dig-energy for patches that are considered roads

  if (ungulate-energy = 1) or (ungulate-energy = 2) [ ; 1 refers to core area and 2 refers to secondary area

    ifelse (ungulate-energy = 1)

    [ set dig-energy dig-energy - 1] ; medium gray

    [ set dig-energy dig-energy - 2] ; light gray

  ]


  ; make sure to out-of-bounds areas have the correct identification

  ifelse (pcolor = black)

  [set dig-energy 0 set I-am-out-of-bounds? TRUE]

  [set I-am-out-of-bounds? FALSE] ;after adjusting patch color and area-id, set non-green patches (roads and black area [formely dig-energy NaN]) dig-energy to 0


  ; if road, set road TRUE and all energy layers to 0

  ifelse (pcolor = 4 or pcolor = 7)

  [set I-am-road? TRUE set dig-energy 0 set fruit-energy 0 set forb-energy 0 set horsetail-energy 0 set sweetvetch-energy 0 set ant-energy 0 set ungulate-energy 0]

  [set I-am-road? FALSE]
```

```
   ;set patch-with-energy patches with [dig-energy > 0]
    ;set hourly-patch-energy (dig-energy / ((319 + 1) - 97) / 24) ; hourly patch energy
    set weighted-patch-energy 0
    set patch-consumed? FALSE ;0



  ]


   set energy-weights
  [
    [0.11 0.03 0.06 0.08 0.11 0.00 0.48 0.67 0.70 1.00 0.44 0.16] ; fruit
    [0.53 0.00 0.13 0.17 0.73 1.00 1.00 0.60 0.43 0.10 0.20 0.00] ; forb
    [0.14 1.00 0.86 0.71 0.43 0.43 0.00 0.00 0.00 0.00 0.00 0.00] ; horsetail
    [0.68 0.99 0.67 0.14 0.03 0.01 0.00 0.14 0.30 0.06 0.58 1.00] ; sweetvetch
    [0.00 0.00 0.17 0.00 0.50 0.83 1.00 0.50 0.67 0.00 0.00 0.00] ; ant
    [0.31 0.20 0.43 1.00 0.55 0.41 0.29 0.24 0.16 0.16 0.22 0.16] ; ungulate
  ]


  ask patches
  [ ; these are adjusted for peak weight. i.e. values in patch represent the month with max energy
(1.00 of energy weights rows). This is done so that when use apply weights, energy is distributed
according phenology and patch total energy.
    set fruit-energy fruit-energy / sum item 0 energy-weights
    set forb-energy forb-energy / sum item 1 energy-weights
    set horsetail-energy horsetail-energy / sum item 2 energy-weights
```

```
    set sweetvetch-energy sweetvetch-energy / sum item 3 energy-weights
    set ant-energy ant-energy / sum item 4 energy-weights
    set ungulate-energy ungulate-energy / sum item 5 energy-weights
    set weights-applied? FALSE
  ]

  reset-ticks
end

to setup-agents
  clear-ticks
  reset-ticks
  clear-turtles
  clear-all-plots
  clear-output
  clear-drawing
  set turtle-label-on? TRUE
  set hour-of-day 0
  set day-of-year 105 ; April 15
  set day-of-month 15 ; April 15
  set month 4 ; april
  set year 1
  set age-sex-list[]
  set survival-rates [0.56 0.88 0.74 0.67 0.95 0.84 0.75] ; cubs-of-the-years (< 1), yearlings(>= 1
and < 2), sub-adult female (>= 2 and < 5), sub-adult male (>= 2 and < 5), adult female (>= 5 and
< 20), adult male (>= 5 < 20), senescent adult (> = 20)
```

```
  sex-age-dist
  if (males-on? = TRUE) [ setup-males ] ; global switch
  if (females-on? = TRUE) [ setup-females ] ; global switch

  assign-age-class

  ifelse(file-exists? (word "../output/sex-age-distribution_simulation_" behaviorspace-run-number ".csv"))
  [
    carefully
    [
      file-delete (word "../output/sex-age-distribution_simulation_" behaviorspace-run-number ".csv")
    ]
    [print error-message]
  ]
  [
    file-open (word "../output/sex-age-distribution_simulation_" behaviorspace-run-number ".csv")
    file-close
  ]

  if(behaviorspace-run-number = 1)
  [
    ifelse(file-exists? (word "../output/nonBehaSpace_results.csv"))
  [
```

```
  carefully
  [
   file-delete (word "../output/nonBehaSpace_results.csv")
   file-open (word "../output/nonBehaSpace_results.csv")
   file-print csv:to-row (list "run number" "ticks" "bear-who" "bear-age" "bear-sex" "bear-age-class" "bear-spring-body-mass" "bear-body-mass" "bear-survival-rates" "bear-survive" "bear-road-freq" "bear-road-dens" "bear-total-dist" "bear-current-bci" "bear-cub" "bear-yearling")
   file-close
  ]
  [print error-message]
 ]
 [
  file-open (word "../output/nonBehaSpace_results.csv")
  file-print csv:to-row (list "run number" "ticks" "bear-who" "bear-age" "bear-sex" "bear-age-class" "bear-spring-body-mass" "bear-body-mass" "bear-survival-rates" "bear-survive" "bear-road-freq" "bear-road-dens" "bear-total-dist" "bear-current-bci" "bear-cub" "bear-yearling")
  file-close
 ]
 ]

 ifelse(file-exists? (word "../output/location_results_" behaviorspace-run-number ".csv"))
 [
  carefully
  [
   file-delete (word "../output/location_results_" behaviorspace-run-number ".csv")
   file-open (word "../output/location_results_" behaviorspace-run-number ".csv")
```

```
      file-print csv:to-row (list "run number" "ticks" "location-who" "location-xcor" "location-ycor" "location-spring-body-mass" "location-body-mass" "location-current-bci")
      file-close
    ]
    [print error-message]
  ]
  [
    file-open (word "../output/location_results_" behaviorspace-run-number ".csv")
    file-print csv:to-row (list "run number" "ticks" "location-who" "location-xcor" "location-ycor" "location-spring-body-mass" "location-body-mass" "location-current-bci")
    file-close
  ]

  set length-mass-rates [180 0.402 -1.420 158 0.647 -1.190 231 0.297 -1.518 106 0.582 -1.578 ] ; male length; male length growth rate, male age at size 0 for length; female length; female length growth rate; female age at 0 size for length
                                                                                          ; male mass, male mass growth rate, male age at 0 size for mass; female mass, femlae mass growth rate, female age at 0 size for length
  set active-prob [[4 0.1875] [5 0.3225] [6 0.4975] [7 0.592] [8 0.59] [9 0.555] [10 0.454] [11 0.215]]; April, May, June, July, August, September, November (first two weeks)
  ;set active-prob [[4 0.1875] [5 0.3225] [6 0.4975] [7 0.9] [8 0.9] [9 0.555] [10 0.454] [11 0.215]];
  set cub-cost [[4 2200] [5 3200] [6 3500] [7 3500] [8 3200] [9 2200] [10 400]]
  set bear-who [] set bear-age [] set bear-sex [] set bear-age-class [] set bear-spring-body-mass [] set bear-body-mass [] set bear-survival-rates []
  set bear-survive [] set bear-road-freq [] set bear-road-dens [] set bear-total-dist [] set bear-current-bci [] set bear-cub[]
```

```
  output-print (word "Core area has " item 0 area-check " patches and secondary area has " item 1 area-check " patches\ncategorized as secondary area and core area respectively,\nafter taking into account road patches that overlap boundaries.")
  output-plot
  update-outputs
end


to setup-males
  create-males sex-ratio * initial-num-bears
  [
    set shape "default"
    set color blue
    set size 50
    let p random length age-sex-list
    set age item 0 item p age-sex-list
    set sex "male"
    move-to one-of patches with [ pcolor != blue and pcolor != yellow and pcolor != black ] ; "green" string doesn't cover all patches with green shade per se, so exclude other colors to get generate bear on "green" shaded patches
  ]
end


to setup-females
  create-females abs(sex-ratio - 1) * initial-num-bears
  [
    set shape "default"
    set color cyan
```

```
    set size 50
    let p random length age-sex-list
    set age item 0 item p age-sex-list
    set sex "female"
    move-to one-of patches with [ pcolor != blue and pcolor != yellow and pcolor != black  ] ;
same for females
    set attendant-cub? FALSE set attendant-yearling? FALSE
  ]
end


to initialize-bear-param
ask turtles [
    determine-spring-length-mass
    determine-dist-timestep
    determine-min-energy-hourly
    set hours-awake 0
    set hours-resting random 24
    set hourly-energy 0
    set max-energy-hourly (240 * spring-body-mass) / 13 ; Average maximum daily intake in kcal
DE of bears * BM (kg) divided by the mean hours spent foraging per day
    if (max-energy-hourly < min-energy-hourly)[set max-energy-hourly min-energy-hourly];
Minimum energy consumed by any bear over an hour
    ;set max-energy-hourly 3000
    set I-am-localized? TRUE
    set total-dist 0
    set current-step-dist 0
```

```
    set previous-step-dist 0

    set current-bci 0

    set previous-bci 0

    set diff-bci 0

]

end


to draw-watersheds

  ifelse (draw-watersheds? = TRUE) ; global switch

  [

    gis:set-drawing-color white

    gis:draw watershed-dataset 1

  ]

  [clear-drawing]

end


;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

;;;;;;;                RUN FUNCTIONS                ;;;;;;;

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;


to go

  record-time

  ask turtles [

    update-patch-energy

    update-state
```

```
    determine-status
    if (turtle-label-on? = FALSE) [set label ""]
    if (hour-of-day = 0)
    [
      daily-energy-to-mass
      update-body-condition
    ]
  ]


  if year > 1 [stop]
    ask turtles [
      set bear-survival-rate survival-rate (road-freq)
      ifelse (random-float 1 < bear-survival-rate)
      [set bear-survive? TRUE]
      [set bear-survive? FALSE]
    ]
  record-location ; don't need to ask all turtles, else this will repeat printing location to file and
slow simulation down
  update-plot
  tick
end


;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;             BEAR PROCEDURES              ;;;;;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
```

```
; set age classes according to assigned age and whether females have attendant-cub? or attendant-yearling?
to assign-age-class
  ask turtles [
    ifelse (age < 5)
    [set age-class "sub-adult"]
    [
      ifelse(age >= 5 and age < 20)
      [set age-class "adult"]
      [set age-class "older-adult"]
    ]
    if (sex = "female" and age-class = "adult" and age >= 5); might want to change this to >= 6, currently old-adult age-class cannot have attendant cubs or yearlings
    [
      ifelse (random-float 1 < 0.333) ; 0.333 prob of female being assigned cub, 0.33 prob of female being assigned yearling, 0.33 prob of female being assigned no young
      [set attendant-cub? TRUE]
      [if (random-float 1 < 0.5) [
        set attendant-yearling? TRUE
        ifelse (random-float 1 < 0.5) [set yearling-age 1] [set yearling-age 2]
        ]
      ]
    ]
  ]
end
```

```
to sex-age-dist
 repeat 10000 [
  let z list random 25 random-sex
  set age-sex-list lput z age-sex-list
 ]
 repeat 1000 [
  set age-sex-list map [i -> ifelse-value(last i = "female")
  [ ;female true
   ifelse-value(first i >= 5 and first i < 20)
   [ ;adult true
    ifelse-value (random-float 1 > item 4 survival-rates)
    [list (random (4 - 3 + 1) + 3) (random-sex)] ; forces random number to be ages 3 or 4
    [list (first i + 1) (last i)] ; aging, same for others
   ] ;adult true
   [ ;adult false
    ifelse-value(first i >= 2 and first i <= 4)
    [ ;sub-adult true
     ifelse-value (random-float 1 > item 2 survival-rates)
     [list (random (4 - 3 + 1) + 3) (random-sex)]
     [list (first i + 1) (last i)]
    ];sub-adult true
    [ ;sub-adult false
     ifelse-value (first i >= 20 and first i < 35)
     [ ;older adult  true
```

```
        ifelse-value (random-float 1 > item 6 survival-rates)
        [list (random (4 - 3 + 1) + 3) (random-sex)]
        [list (first i + 1) (last i)]
      ] ;older adult true
      [ ;over 35
        ifelse-value (first i >= 35)
        [list (random (4 - 3 + 1) + 3) (random-sex)]
        [list (first i + 1) last(i)]
      ] ;over 35
    ] ;sub-adult false
  ] ;adult false
] ;female true

[ ;female false ;male true
  ifelse-value(first i >= 5 and first i < 20)
  [ ;prime adult true
    ifelse-value (random-float 1 > item 5 survival-rates)
    [list (random (4 - 3 + 1) + 3) (random-sex)]
    [list (first i + 1) (last i)]
  ] ;prime adult true
  [ ;prime adult false
    ifelse-value(first i >= 2 and first i <= 4)
    [ ;sub-adult true
      ifelse-value (random-float 1 > item 3 survival-rates)
      [list (random (4 - 3 + 1) + 3) (random-sex)]
```

```
          [list (first i + 1) (last i)]

        ];sub-adult true

        [ ;sub-adult false

          ifelse-value (first i >= 20 and first i < 35)

          [ ;older adult true

            ifelse-value (random-float 1 > item 6 survival-rates)

            [list (random (4 - 3 + 1) + 3) (random-sex)]

            [list (first i + 1) (last i)]

          ] ;older adult true

          [ ;over 35

            ifelse-value (first i >= 35)

            [list (random (4 - 3 + 1) + 3) (random-sex)]

            [list (first i + 1) last(i)]

          ] ;over 35

        ] ;sub-adult false

      ] ;adult false

    ] ;female false ;male true

] age-sex-list]

end


to determine-spring-length-mass

  ifelse (sex = "male")

  [

    set body-length (item 0 length-mass-rates * (1 - exp(1) ^ (- item 1 length-mass-rates * (age -
item 2 length-mass-rates))))     ; von Bertalanffy model growth for male length
```

```
    set body-length random-normal body-length 11
; random variation introduce to male length value

    set body-mass (item 6 length-mass-rates * (1 - exp(1) ^ (- item 7 length-mass-rates * (age -
item 8 length-mass-rates))) ^ 3)   ; von Bertalanffy model growth for male mass

    set body-mass random-normal body-mass 43.2
; random variation introduce to male mass value

  ]

  [

    set body-length (item 3 length-mass-rates * (1 - exp(1) ^ (- item 4 length-mass-rates * (age -
item 5 length-mass-rates))))     ; von Bertalanffy model growth for female length

    set body-length random-normal body-length 8.1
; random variation introduce to female length value

    set body-mass (item 9 length-mass-rates * (1 - exp(1) ^ (- item 10 length-mass-rates * (age -
item 11 length-mass-rates))) ^ 3) ; von Bertalanffy model growth for female mass

    set body-mass random-normal body-mass 17.6
; random variation introduce to female mass value

  ]


  if(sex = "male" and (body-length < 135 or body-length > 206)) [determine-spring-length-mass]
; min/max posssible value for male length due to the stochastic nature of introducing random
variation producing unrealistic values

  if(sex = "female" and (body-length < 126 or body-length > 176)) [determine-spring-length-
mass] ; min/max posssible value for female length due to the stochastic nature of introducing
random variation producing unrealistic values

  if(sex = "male" and (body-mass < 49 or body-mass > 311)) [determine-spring-length-mass]
; min/max posssible value for male mass due to the stochastic nature of introducing random
variation producing unrealistic values

  if(sex = "female" and (body-mass < 35 or body-mass > 163)) [determine-spring-length-mass]
; min/max posssible value for female mass due to the stochastic nature of introducing random
variation producing unrealistic values
```

```
  set spring-body-length body-length

  set spring-body-mass body-mass


  ;set hours-awake random round(24 * item 1 item 0 active-prob) ; retrieve a random number between 0 and [24 hours * active-prob for April (=5)]

  ;set hours-awake 0

  ;set hours-resting random 24

  ;ifelse(hours-awake <= round(24 * item 1 item 0 active-prob)) [set should-I-forage? TRUE][set should-I-forage? FALSE] ; if hours awake is less than or equal to 5 hours, set should-I-forage to TRUE

end


to determine-min-energy-hourly

    if (sex = "male" and age >= 5) [set min-energy-hourly 3000]

    if (sex = "male" and age < 5) [set min-energy-hourly 2400]

    if (sex = "female" and age >= 5) [set min-energy-hourly 2700]

    if (sex = "female" and age < 5) [set min-energy-hourly 2200]

end


;to determine-dist-timestep ; mean movement rate per hour / ; 60 m

;  ifelse (sex = "male")

;  [

;    if (age >= 5) [set mean-dist-timestep (408 + 2 * 649.7) set sd-dist-timestep (408 + 3 * 649.7)] ;34

;    if (age >= 2 and age < 5) [set mean-dist-timestep (342 + 2 * 522.3) set sd-dist-timestep (342 + 3 * 522.3) ] ;27

;  ]
```

```
; [
;    if (attendant-cub? = TRUE) [set mean-dist-timestep (191 + 2 * 317.8) set sd-dist-timestep (191 + 3 * 317.8)] ;16 also set survival rates for following year
;    if (attendant-yearling? = TRUE) [set mean-dist-timestep (297 + 2 * 449.6) set sd-dist-timestep (297 + 3 * 449.6)] ;24 also set surival rates for following year
;    if (age >= 5 and attendant-cub? = FALSE and attendant-yearling? = FALSE) [set mean-dist-timestep (292 + 2 * 459.6) set sd-dist-timestep (292 + 3 * 459.6)] ;24
;    if (age >= 2 and age < 5 and attendant-cub? = FALSE and attendant-yearling? = FALSE) [set mean-dist-timestep (366 + 2 * 506.4) set sd-dist-timestep (366 + 3 * 506.4)] ;27
; ]
;end


to determine-dist-timestep ; mean movement rate per hour / ; 60 m
  ifelse (sex = "male")
  [
    if (age >= 5) [set mean-dist-timestep 4200 set sd-dist-timestep 100] ;34 ; 4000
    if (age >= 2 and age < 5) [set mean-dist-timestep 3940 set sd-dist-timestep 100] ;27 ; 3353
  ]
  [
    if (attendant-cub? = TRUE) [set mean-dist-timestep 2200 set sd-dist-timestep 100] ;16 also set survival rates for following year
    if (attendant-yearling? = TRUE) [set mean-dist-timestep 3000 set sd-dist-timestep 100] ;24 also set surival rates for following year
    if (age >= 5 and attendant-cub? = FALSE and attendant-yearling? = FALSE) [set mean-dist-timestep 3300 set sd-dist-timestep 100] ;24 ; 2862
    if (age >= 2 and age < 5 and attendant-cub? = FALSE and attendant-yearling? = FALSE) [set mean-dist-timestep 4040 set sd-dist-timestep 100] ;27 ; 3588
  ]
```

```
end

to check-out-of-bounds
  if (I-am-out-of-bounds? = TRUE) [right 180 fd (current-step-dist + 10)]
end

to check-rest
  ifelse(hours-resting < 24 - (round(24 * activity-pattern (active-prob-coeff (active-prob))))) [set
should-I-rest? TRUE][set should-I-rest? FALSE]
end

to check-active
  ifelse(hours-awake < round(24 * activity-pattern (active-prob-coeff (active-prob))))
  [set should-I-active? TRUE]
  [set should-I-active? FALSE set should-I-rest? TRUE]
end

to check-stop-for-forage
  ifelse (diff-bci < 0)
  [
    ifelse (random-float 1 < 0.95)
    [set should-I-forage? TRUE]
    [set should-I-forage? FALSE]
  ]
  [
```

```
    ifelse (random-float 1 < 0.85) [
    ifelse (mean-radius-energy > active-energy-cost)
    [set should-I-forage? TRUE]
    [set should-I-forage? FALSE]
  ]
  [
    set should-I-forage? FALSE
  ]
  ]
end

to update-state
  check-out-of-bounds
  check-rest
  ifelse (should-I-rest? = TRUE)
  [set state "rest"]
  [check-active
    ifelse(should-I-active? = TRUE)
    [check-stop-for-forage
      ifelse(should-I-forage? = TRUE)
      [set state "active-foraging"]
      [set state "active-moving"]
    ]
    [set state "rest"]
  ]
```

```
end

to determine-status
  if (state = "rest")            [rest set label "resting"]
  if (state = "active-foraging") [active forage set label "active-foraging"]
  if (state = "active-moving")   [active move set label "active-moving"]
end

to rest
  ;if (I-am-out-of-bounds? = TRUE) [right 180 fd 100]
  set hours-resting hours-resting + 1 ; make bear rest and count time
  set hourly-energy (hourly-energy - resting-energy-cost)
  if(hours-resting > 24 - (round(24 * activity-pattern (active-prob-coeff (active-prob))))) [set hours-awake 0 set hours-resting 1]; if resting time exceeds threshold, set hours-awake to 0 and hours-resting to 1
  set bear-watershed-id [watershed-id] of patch-here
  set bear-watershed-dens [watershed-dens] of patch-here
end

to active
  set hours-awake hours-awake + 1
  ;ifelse (hours-awake = 1) [set I-am-localized? TRUE][set I-am-localized? FALSE]
end

to forage
  ;if (I-am-out-of-bounds? = TRUE) [right 180 fd 100]
```

```
road-decision
set previous-step-dist current-step-dist
set current-step-dist 1
set total-dist (total-dist + 0.06) ; patch size in KM

ifelse (random-float 1.0 < 0.9)
[
  uphill available-patch-energy ; move deterministically to higher neighoring patch
]
[
  move-to one-of neighbors ; move randomly to neighboring patches with prob 0.1

]

ifelse ([available-patch-energy] of patch-here < max-energy-hourly)
[
  set bear-watershed-id [watershed-id] of patch-here
  set bear-watershed-dens [watershed-dens] of patch-here
  set hourly-energy (hourly-energy + available-patch-energy - active-energy-cost)
  set energy-consumed (energy-consumed + available-patch-energy)
  set pcolor white
  set patch-consumed? TRUE
  set freq-consumed (freq-consumed + 1)
]
[
```

```
    set bear-watershed-id [watershed-id] of patch-here

    set bear-watershed-dens [watershed-dens] of patch-here

    set hourly-energy (max-energy-hourly - active-energy-cost)

    set energy-consumed (energy-consumed + max-energy-hourly)

    set pcolor white

    set patch-consumed? TRUE

    set freq-consumed (freq-consumed + 1)

  ]

end


to move

  set previous-step-dist current-step-dist

;  if (I-am-out-of-bounds? = TRUE)

;  [

;    right 180

;    fd (previous-step-dist + 10) ; fd extra 10 will cover any agent who makes a big step into out-of-bounds to come back into in-bound region

;    set total-dist (total-dist + (previous-step-dist + 10) * 0.06) ; KM

;  ]

  set hourly-energy (hourly-energy - active-energy-cost)

  set current-step-dist step-dist

  set road-freq (road-freq + frequency (true) ([i-am-road?] of patches-ahead (step-dist))) ; check how many patches ahead are roads and count them, to detect how many roads were crossed by taking large movement steps between ticks

  fd current-step-dist

  set total-dist (total-dist + (current-step-dist * 0.06)) ; KM
```

```
    while [([I-am-road?] of patch-here)] ; if on road, cross it
  [
    ifelse (patch-ahead 1 = nobody) ; if on the edge of world and patch-ahead is nobody, then turn around and move forward 1
    [right 180 forward 1]
    [forward 1] ; if not on edge world (i.e. in watershed-home-id), move forward until across road
  ]

  if(any? other turtles-here) [move-to one-of neighbors with [I-am-out-of-bounds? = FALSE or I-am-road? = FALSE]]

  set bear-watershed-id [watershed-id] of patch-here
  set bear-watershed-dens [watershed-dens] of patch-here
end

to road-decision
  if (I-am-road?) [set road-freq road-freq + 1] ; count if hit road
  while [([I-am-road?] of patch-here)] ; if on road, cross it
  [
    ifelse (patch-ahead 1 = nobody) ; if on the edge of world and patch-ahead is nobody, then turn around and move forward 1
    [right 180 forward 1]
    [forward 1] ; if not on edge world (i.e. in watershed-home-id), move forward until across road
  ]
end
```

```
to daily-energy-to-mass
  let daily-intake (hourly-energy / (body-mass ^ 0.75))
  let daily-energy ((0.106 * daily-intake) - 10.8)
  let daily-mass ((daily-energy * (body-mass ^ 0.75)) / 1000)
  set body-mass (body-mass + daily-mass)
  if (body-mass <= 0) [set body-mass 0.01]
  set hourly-energy 0
end

to update-body-condition
  set previous-bci current-bci
  set current-bci body-condition-index (body-mass) (body-length)
  set diff-bci (current-bci - previous-bci)
end


;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;         LANDSCAPE/PATCH PROCEDURES          ;;;;;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to record-time
  ifelse (hour-of-day < 23)
  [set hour-of-day hour-of-day + 1]
  [set hour-of-day 0]
```

```
  if (hour-of-day = 0) [set day-of-year day-of-year + 1 set day-of-month day-of-month + 1]


  if (day-of-year >= 105 and day-of-year <= 120) [set month 4]
  if (day-of-year >= 121 and day-of-year <= 151) [set month 5 if (day-of-year = 121) [set day-of-month 1]]
  if (day-of-year >= 152 and day-of-year <= 181) [set month 6 if (day-of-year = 152) [set day-of-month 1]]
  if (day-of-year >= 182 and day-of-year <= 212) [set month 7 if (day-of-year = 182) [set day-of-month 1]]
  if (day-of-year >= 213 and day-of-year <= 243) [set month 8 if (day-of-year = 213) [set day-of-month 1]]
  if (day-of-year >= 244 and day-of-year <= 273) [set month 9 if (day-of-year = 244) [set day-of-month 1]]
  if (day-of-year >= 274 and day-of-year <= 304) [set month 10 if (day-of-year = 274) [set day-of-month 1]]
  if (day-of-year >= 305)                    [set month 11 if (day-of-year = 305) [set day-of-month 1]]


  ;if (day-of-year >= 105 and day-of-year <= 120) [set day-of-month


  if (day-of-year > 288) ; greater than October 15
  [
    record-results
    set year year + 1
    set month 4
    set hour-of-day 0
    set day-of-year 97
```

```
 ]
end


to apply-weights
 let z [[4 15] [5 1] [5 15] [6 1] [6 15] [7 1] [7 15] [8 1] [8 15] [9 1] [9 15] [10 1]]
 foreach z [x ->
  ifelse (item 1 x = 15)
  [
   if (month = item 0 x and day-of-month >= 15) [
    if (weights-applied? = FALSE) [
     set fruit-energy fruit-energy * item 0 weights energy-weights
     set forb-energy forb-energy * item 1 weights energy-weights
     set horsetail-energy horsetail-energy * item 2 weights energy-weights
     set sweetvetch-energy sweetvetch-energy * item 3 weights energy-weights
     set ant-energy ant-energy * item 4 weights energy-weights
     set ungulate-energy ungulate-energy * item 5 weights energy-weights
     set weights-applied? TRUE
     ;set patch-consumed? FALSE
    ]
   ]
  ]
  [
   if (month = item 0 x and day-of-month >= 1 and day-of-month < 15)
   [
    set weights-applied?  FALSE
```

```
    if (weights-applied? = FALSE) [
     set fruit-energy fruit-energy * item 0 weights energy-weights
     set forb-energy forb-energy * item 1 weights energy-weights
     set horsetail-energy horsetail-energy * item 2 weights energy-weights
     set sweetvetch-energy sweetvetch-energy * item 3 weights energy-weights
     set ant-energy ant-energy * item 4 weights energy-weights
     set ungulate-energy ungulate-energy * item 5 weights energy-weights
     set weights-applied? TRUE
     ;set patch-consumed? FALSE
    ]
   ]
  ]
 ]
end

to update-patch-energy
   ; may need to adjust for roads and out-of-bounds patches, though they will never sample there because there is no available-patch-energy
 let potential-patches [patches in-radius sensing-radius] of patch-here ; patches in radius of 2-patches from the patch in which the turtle is currently on
 let ideal-patch max-one-of potential-patches [weighted-patch-energy] ; of potential-patches, patch with maximum weighted-patch-energy value

 ask potential-patches
 [
  apply-weights
```

```
    set current-tick (ticks + 1)
    set weighted-patch-energy (fruit-energy + forb-energy + horsetail-energy + sweetvetch-energy + ant-energy + ungulate-energy)
    set available-patch-energy weighted-patch-energy
    if (patch-consumed? = TRUE) [set available-patch-energy (available-patch-energy - energy-consumed) ] ; substracts energy that has already been consumed by previous bears which visited the patch
    if (available-patch-energy < 0) [set available-patch-energy 0]
  ]
end


;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;        MODEL OUTPUTS AND REPORTERS          ;;;;;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;


; end of year results
to record-results
  if(results-on? = TRUE)
  [
    ; globals outputs used in BehaviorSpace; data is sorted by turtle id
    set bear-who map[x -> [who] of x] sort turtles
    set bear-age map [x -> [age] of x] sort turtles
    set bear-sex map [x -> [sex] of x] sort turtles
    set bear-age-class map [x -> [age-class] of x] sort turtles
    set bear-spring-body-mass map [x -> [spring-body-mass] of x] sort turtles
    set bear-body-mass map [x -> [body-mass] of x] sort turtles
```

```
    set bear-survival-rates map [x -> [bear-survival-rate] of x] sort turtles
    set bear-survive map [x -> [bear-survive?] of x] sort turtles
    set bear-road-freq map [x -> [road-freq] of x] sort turtles
    set bear-road-dens map [x -> precision ([0.04268 + 0.005212 * road-freq] of x) 7] sort turtles
    set bear-road-dens intercept-zero (0.04268) (0) (bear-road-dens)
    set bear-total-dist map [x -> [total-dist] of x] sort turtles
    set bear-current-bci map [x -> [current-bci] of x] sort turtles
    let m n-values (count turtles with [sex = "male"]) [false]
    let fc map [x -> [attendant-cub?] of x] sort turtles with [sex = "female"]
    set bear-cub sentence m fc
    let fy map [x -> [attendant-yearling?] of x] sort turtles with [sex = "female"]
    set bear-yearling sentence m fy
  ;bear-dig-energy


    ; this is to double check results of BehaviorSpace; which uses sorted results from above
    file-open (word "../output/nonBehaSpace_results.csv")
    file-print csv:to-row (list behaviorspace-run-number ticks bear-who bear-age bear-sex bear-age-class bear-spring-body-mass bear-body-mass bear-survival-rates bear-survive bear-road-freq bear-road-dens bear-total-dist bear-current-bci bear-cub bear-yearling)
    file-close
  ]
end


to record-location
  if(location-results-on? = TRUE)
  [
```

```
    ; this is for behavior space, results are sorted by turtles
  set location-who map[x -> [who] of x] sort turtles
  set location-xcor map[x -> [longitude-value] of x] sort turtles
  set location-ycor map[x -> [latitude-value] of x] sort turtles
  set location-spring-body-mass map[x -> [spring-body-mass] of x] sort turtles
  set location-body-mass map[x -> [body-mass] of x] sort turtles
  set location-current-bci map[x -> [current-bci] of x] sort turtles
  ; this is to double check results of behavior space; which uses sorted results from above
  file-open (word "../output/location_results_" behaviorspace-run-number ".csv")
  file-print csv:to-row (list behaviorspace-run-number ticks location-who location-xcor location-ycor location-spring-body-mass location-body-mass location-current-bci)
  file-close
  ]
end


to update-outputs ; opens on pressing go and writing variables and closes on pressing stop - can do this as many times as needed
  file-open (word "../output/sex-age-distribution_simulation_" behaviorspace-run-number ".csv")
  ;file-print  word(map [[i] -> first i] sex-age-dist, "," map [[i] -> last i] sex-age-dist)
  ;file-print  map [[i] -> last i] sex-age-dist
  ;csv:to-file "sex-age-distribution.csv" sex-age-dist
  csv:to-file (word "../output/sex-age-distribution_simulation_" behaviorspace-run-number ".csv") age-sex-list
  ;csv:to-file "sex-age-distribution_simulation.csv" map [i -> first i] sex-age-dist
  file-close
```

```
end


to output-plot
   ; histogram of bear age
  set-current-plot "Age Distribution of Bears"
  set-histogram-num-bars 35
  histogram [age] of turtles
end


to update-plot
  ; plot of mean body-mass by sex and age-class
  set-current-plot "Mean Body Mass of Bears"
  set-current-plot-pen "adult male"
  plot mean [body-mass] of turtles with [sex = "male" and age >= 5]
  set-current-plot-pen "sub-adult male"
  plot mean [body-mass] of turtles with [sex = "male" and age < 5]
  set-current-plot-pen "adult female"
  plot mean [body-mass] of turtles with [sex = "female" and age >= 5 and attendant-cub? =
FALSE and attendant-yearling? = FALSE]
  set-current-plot-pen "adult female with cub"
  plot mean [body-mass] of turtles with [sex = "female" and age >= 5 and attendant-cub? =
TRUE]
  set-current-plot-pen "adult female with yearling"
  plot mean [body-mass] of turtles with [sex = "female" and age >= 5 and attendant-yearling? =
TRUE]
  set-current-plot-pen "sub-adult female"
```

```
  plot mean [body-mass] of turtles with [sex = "female" and age < 5]


  ; plot mean distance traveled of sex and age-class in KM
  set-current-plot "Distance Traveled by Bears"
  set-current-plot-pen "adult male"
  plot mean [total-dist] of turtles with [sex = "male" and age >= 5]
  set-current-plot-pen "sub-adult male"
  plot mean [total-dist] of turtles with [sex = "male" and age < 5]
  set-current-plot-pen "adult female"
  plot mean [total-dist] of turtles with [sex = "female" and age >= 5 and attendant-cub? = FALSE and attendant-yearling? = FALSE]
  set-current-plot-pen "adult female with cub"
  plot mean [total-dist] of turtles with [sex = "female" and age >= 5 and attendant-cub? = TRUE]
  set-current-plot-pen "adult female with yearling"
  plot mean [total-dist] of turtles with [sex = "female" and age >= 5 and attendant-yearling? = TRUE]
  set-current-plot-pen "sub-adult female"
  plot mean [total-dist] of turtles with [sex = "female" and age < 5]


  ; plot of mean road crossing frequency by sex and age-class
  set-current-plot "Road Crossing Frequency"
  set-current-plot-pen "adult male"
  plot mean [road-freq] of turtles with [sex = "male" and age >= 5]
  set-current-plot-pen "sub-adult male"
  plot mean [road-freq] of turtles with [sex = "male" and age < 5]
  set-current-plot-pen "adult female"
```

```
  plot mean [road-freq] of turtles with [sex = "female" and age >= 5 and attendant-cub? = FALSE and attendant-yearling? = FALSE]
  set-current-plot-pen "adult female with cub"
  plot mean [road-freq] of turtles with [sex = "female" and age >= 5 and attendant-cub? = TRUE]
  set-current-plot-pen "adult female with yearling"
  plot mean [road-freq] of turtles with [sex = "female" and age >= 5 and attendant-yearling? = TRUE]
  set-current-plot-pen "sub-adult female"
  plot mean [road-freq] of turtles with [sex = "female" and age < 5]


  ; plot percentage of bears that survive (true) each day by sex and age-class
  set-current-plot "Percentage of Bears that Survive Each Day"
  if (hour-of-day = 0)
  [
  set-current-plot-pen "adult male"
  plot (count turtles with [sex = "male" and age >= 5 and bear-survive? = TRUE] / count turtles with [sex = "male" and age >= 5]) * 100
  set-current-plot-pen "sub-adult male"
  plot (count turtles with [sex = "male" and age < 5 and bear-survive? = TRUE] / count turtles with [sex = "male" and age < 5]) * 100
  set-current-plot-pen "adult female w/wo yearlings 2+"
  plot (count turtles with [(sex = "female" and age >= 5 and attendant-yearling? = FALSE and attendant-cub? = FALSE and bear-survive? = TRUE) or (sex = "female" and age >= 5 and attendant-yearling? = TRUE and yearling-age = 2 and bear-survive? = TRUE)] /
        count turtles with [(sex = "female" and age >= 5 and attendant-yearling? = FALSE and attendant-cub? = FALSE) or (sex = "female" and age >= 5 and attendant-yearling? = TRUE and yearling-age = 2)]) * 100
  set-current-plot-pen "sub-adult female"
```

```
  plot (count turtles with [sex = "female" and age < 5 and bear-survive? = TRUE] / count turtles with [sex = "female" and age < 5]) * 100
  set-current-plot-pen "adult female w/ coy or yearlings 1"
  plot (count turtles with [(sex = "female" and age >= 5 and attendant-cub? = TRUE and bear-survive? = TRUE) or (sex = "female" and age >= 5 and attendant-yearling? = TRUE and yearling-age = 1 and bear-survive? = TRUE)] /
        count turtles with [(sex = "female" and age >= 5 and attendant-cub? = TRUE) or (sex = "female" and age >= 5 and attendant-yearling? = TRUE and yearling-age = 1)]) * 100
  ]


  ; plot mean survival-rate of bears by sex and age-class
  set-current-plot "Mean Survival Rate of Bears"
  set-current-plot-pen "adult male"
  plot mean [bear-survival-rate] of turtles with [sex = "male" and age >= 5]
  set-current-plot-pen "sub-adult male"
  plot mean [bear-survival-rate] of turtles with [sex = "male" and age < 5]
  set-current-plot-pen "adult female w/wo yearlings 2+"
  plot mean [bear-survival-rate] of turtles with [(sex = "female" and age >= 5 and attendant-yearling? = FALSE and attendant-cub? = FALSE) or (sex = "female" and age >= 5 and attendant-yearling? = TRUE and yearling-age = 2)]
  set-current-plot-pen "sub-adult female"
  plot mean [bear-survival-rate] of turtles with [sex = "female" and age < 5]
  set-current-plot-pen "adult female w/ coy or yearlings 1"
  plot mean [bear-survival-rate] of turtles with [(sex = "female" and age >= 5 and attendant-cub? = TRUE) or (sex = "female" and age >= 5 and attendant-yearling? = TRUE and yearling-age = 1)]
end
```

```
to-report isNaN [z]
  report not ( z > 0 or z < 0 or z = 0 )
end


to-report area-check
  let c count patches with [area-id = "C" and dig-energy = 2] ; patches with area-id = core and dig-energy = 2 (secondary); should equal zero after running setup-landscape
  let s count patches with [area-id = "S" and dig-energy = 1] ; patches with area-id = secondary and dig-energy = 1 (core); should equal zero after running setup-landscape
  report list s c
end


to-report random-sex
  ifelse random-float 1 < 0.5
  [report "female"]
  [report "male"]
end


to-report weights [a]
  let z [[0 4 15] [1 5 1] [2 5 15] [3 6 1] [4 6 15] [5 7 1] [6 7 15] [7 8 1] [8 8 15] [9 9 1] [10 9 15] [11 10 1]]
  foreach z [x ->
    ifelse (item 2 x = 15)
    [
      if (month = item 1 x and day-of-month >= 15) [report map [i -> item (item 0 x) i] a]
    ]
```

```
    [
      if (month = item 1 x and day-of-month >= 1 and day-of-month < 15) [report map [i -> item (item 0 x) i] a]
    ]
  ]
end


to-report active-prob-coeff[a] ; multiplies active-coeff of slider button by active-prob (item 1 i) for calibration purposes
  report map [i -> list (item 0 i)(active-coeff * item 1 i)] a
end


to-report activity-pattern [a]
  foreach a [x -> if(item 0 x = month) [report item 1 x]]
  ;report item 1 item 3 a
end


to-report resting-energy-cost
  let bm body-mass
  if (bm < 0) [set bm 0]
  let basal-metab-rate (61.9 * (bm) ^ 0.77) / 24 ; kcal/hour
  ifelse (sex = "female" and attendant-cub? = TRUE)
  [report basal-metab-rate + (cost-of-cub cub-cost / 24)]
  [report basal-metab-rate]
end
```

```
to-report active-energy-cost
  let active-metab-rate (2.57 * (body-mass) - 0.316) * 0.341 ; kcal/hour ; 0.341 km is the mean
hourly movement rate (sub-adults and adults, table 6, Graham, 2014)
  ifelse (sex = "female") [
    ifelse (attendant-yearling? = TRUE)
    [ ; yearling TRUE
      ifelse (yearling-age = 1)
      [report active-metab-rate + ((2.57 * (60) - 0.316) * 0.341)] ; yearling-age 1
      [report active-metab-rate + ((2.57 * (91) - 0.316) * 0.341)] ; yearling-age 2
    ] ; yearling TRUE
    [ ; yearling FALSE
      ifelse (attendant-cub? = TRUE)
      [report active-metab-rate + (cost-of-cub cub-cost / 24)] ; cub TRUE
      [report active-metab-rate]; no cub, no yearling
    ]
  ]
  [
    report active-metab-rate ; male
  ]
end


to-report cost-of-cub [a]
  foreach a[x -> if (item 0 x = month) [report item 1 x]]
end
```

```
to-report foraging-patches
  let b [patches in-radius 1] of patch-here
  report b
end

to-report mean-radius-energy
  let b [patches in-radius sensing-radius] of patch-here
  let c sum [available-patch-energy] of b / count b ; average weighted-patch-energy over 13 patches if radius is 2 (includes 2 patches from patch-here on vertical and horizontal planes (8), and 1 patch from patch-here on diagonal planes (4), plus patch-here (1))
  report c
end

to-report step-dist
  let z random-normal mean-dist-timestep sd-dist-timestep
  while [z < 0] [set z random-normal mean-dist-timestep sd-dist-timestep]
  report ceiling(z / 60) ; cell size of 60 meters, MUST change according to pixel cell size
end

; reports the patches ahead by a certain step/distance, instead of 1 with just the primitive patch-ahead
to-report patches-ahead [ step ]
  report patch-set map patch-ahead n-values step [i -> i + 1]
end

; filter a list by an item and reports the total length, true is used here with "an-item" in the to-move submodel
```

```
to-report frequency [an-item a-list]
   report length (filter [i -> i = an-item] a-list)
end


to-report body-condition-index [m l]
  let z ((ln(m) - 3.21 * ln(l) + 11.64) / (0.29 - 0.017 * ln(l)))
  report z
end


; replace 0.04268 (intercept of road-freq crossing to road density rate formula) with 0
to-report intercept-zero [interc new the-list]
  report map [x -> ifelse-value (x = interc) [new][x]] the-list
end


to-report survival-rate [rf]
  ; road-freq crossing rate converted to road-density
  let rd 0.04268 + 0.005212 * rf


  ; adult male
  if (sex = "male" and age >= 5) [
    ifelse (rd <= 3.7)
    [report (0.946014 - (0.042284 * rd) - (0.031795 * rd ^ 2) - (0.006340 * rd ^ 3))]
    [report 0]
  ]
```

```
  ; sub-adult male
  if (sex = "male" and age < 5) [
    ifelse (rd <= 3)
    [report (0.942445 + (0.080035 * rd) - (0.353526 * rd ^ 2) + (0.075524 * rd ^ 3))]
    [report 0]
  ]

    ; adult female alone or adult female with yearlings 2+
  if ((sex = "female" and age >= 5 and attendant-yearling? = FALSE and attendant-cub? =
FALSE) or (sex = "female" and age >= 5 and attendant-yearling? = TRUE and yearling-age = 2))
[
    ifelse (rd <= 4.6)
    [report (0.984809 - (0.009914 * rd) - (0.042663 * rd ^ 2))]
    [report 0]
  ]

      ; adult female with cub-of-year or with one year-old yearlings
  if ((sex = "female" and age >= 5 and attendant-cub? = TRUE) or (sex = "female" and age >= 5
and attendant-yearling? = TRUE and yearling-age = 1)) [
    ifelse (rd <= 2.1)
    [report (0.97954 - (0.11163 * rd) + (0.14217 * rd ^ 2) - (0.14685 * rd ^ 3))]
    [report 0]
  ]

      ; sub-adult female
  if (sex = "female" and age < 5 ) [
```

```
    ifelse (rd <= 3)
    [report (0.96643 + (0.11602 * rd) - (0.21249 * rd ^ 2) + (0.02300 * rd ^ 3))]
    [report 0]
  ]
end
```

Appendix 4.3. NetLogo code of the road model.

```
extensions [gis]


globals [
  watershed-dataset
  road-dataset
  ;tick-step
]



patches-own [
  I-am-out-of-bounds?
  I-am-road?
  watershed-dens
  watershed-id
  road-value
]

turtles-own [
  watershed-home-id
  watershed-home-dens
  road-freq
]
```

```
to setup-landscape
  ca ; clear-all
  set watershed-dataset gis:load-dataset ("../../IBMData/NLogo/wts_corsec4MP.shp")
  set road-dataset gis:load-dataset ("../../IBMData/NLogo/ung_ro_int_60b.asc")

  gis:set-world-envelope gis:envelope-of road-dataset
  gis:apply-raster road-dataset road-value



  ask patches [
        ; set patches to proper boundary and color identifier
    ifelse (isNAN(road-value))
    [
      set I-am-out-of-bounds? TRUE
      set pcolor black
      set road-value 0
    ]
    [
      set I-am-out-of-bounds? FALSE
      set pcolor green
    ]
    if (road-value = 0 and I-am-out-of-bounds? = FALSE) [set pcolor black set I-am-out-of-bounds? TRUE] ; rectifies the last column on the right

    ifelse (road-value = 1 or road-value = 2)
```

```
    [
      set pcolor 7
      set I-am-road? TRUE
    ]
    [
      set I-am-road? FALSE
    ]
  ]

  foreach gis:feature-list-of watershed-dataset [vector-feature ->
    ask patches gis:intersecting vector-feature [ ; two or more arguments require brackets, i.e., [x
y] -> ask patches...
      set watershed-dens gis:property-value vector-feature "km_km2"
      ;set watershed-dens precision watershed-dens 4
      set watershed-id gis:property-value vector-feature "id"
    ]
  ]

  ask patches [
    if (I-am-out-of-bounds? = TRUE) [set watershed-dens 999 set watershed-id 999 set road-value
999]
  ]

end

to setup-agents
```

```
  clear-ticks

  reset-ticks

  clear-turtles


  foreach gis:feature-list-of watershed-dataset [ vector-feature ->

      let centroid gis:location-of gis:centroid-of vector-feature

      ; centroid will be an empty list if it lies outside the bounds

      ; of the current NetLogo world, as defined by our current GIS

      ; coordinate transformation

      ;if not empty? centroid

      create-turtles 1

        [ set xcor item 0 centroid ; if you want turtle to be created at center of vector-feature, also
use to center watershed-home-id and watershed-home-dens

          set ycor item 1 centroid ; ditto

          set color blue

          set size 25


    ]

  ]


  ask turtle 13 [set xcor 2478 set ycor 914] ; causing issues, so set manually

  ask turtle 7  [set xcor 1134 set ycor 1160]; ditto, centroid is outside the boundaries, so move
inside

  ask turtles

  [

    let centroid-patch [watershed-id] of patch xcor ycor
```

```
    set watershed-home-id [watershed-id] of patch xcor ycor
    set watershed-home-dens [watershed-dens] of patch xcor ycor
    set watershed-home-dens precision watershed-home-dens 4

    let x [watershed-home-id] of self
    move-to one-of patches with [watershed-id = x]
    ;OR
    ;move-to one-of patches with [watershed-id = [watershed-home-id] of myself]; myself because
patch is asking a turtle, A patch can't access a turtle variable without specifying which turtle.

    ; if random patch in watershed-id of turtles is not the same as watershed-home-id of turtle,
then move to centroid-patch
    ; here to make sure no turtle ends up in wrong polygon because of a random-error glitch
    if ([watershed-id] of patch-here != x) [
    set xcor item 0 centroid-patch
    set ycor item 1 centroid-patch
    ]
  ]
end

to draw-watersheds
  gis:set-drawing-color white
  gis:draw watershed-dataset 1
end

to random-walk
```

```
  ask turtles
  [
    set heading ((random 4) * 90)
    watershed-random watershed-home-id
    ;right-random
    forward 1
    move-to patch-here ; center turtle in patch
    hit-road
  ]
  tick
  if ticks >= tick-step [stop] ; stop experiment according to tick-step slider
end


to right-random
   while [patch-ahead 1 = nobody]
   [
     right ((random 4) * 90)
   ]
end


to watershed-random [a]
  while [(patch-ahead 1 = nobody) or ([watershed-id] of patch-ahead 1 != a) or ([watershed-id] of
patch-ahead 1 = nobody)]
  [
    right ((random 4) * 90)
```

```
  ]
end


to hit-road
  if (I-am-road?) [set road-freq road-freq + 1] ; count if hit road
;  while [patch-ahead 1 = nobody] [
;    right 180
;    forward 10
;  ]
  while [([I-am-road?] of patch-here) and ([watershed-id] of patch-here = watershed-home-id)] ;
only cross road if watershed-id is the same as watershed-home-id
  [
    ifelse (patch-ahead 1 = nobody) ; if on the edge of world and patch-ahead is nobody, then turn
around and move forward 1
    [right 180 forward 1]
    [forward 1] ; if not on edge world (i.e. in watershed-home-id), move forward until across road
  ]
end


to random-coor
  ask turtles [
    let x [watershed-home-id] of self
    move-to one-of patches with [watershed-id = x]
    ;OR
    ;move-to one-of patches with [watershed-id = [watershed-home-id] of myself]; myself because
patch is asking a turtle, A patch can't access a turtle variable without specifying which turtle.
```

```
  ]
end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;;;        MODEL OUTPUTS AND REPORTERS           ;;;;;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;


to-report isNaN [z]
  report not ( z > 0 or z < 0 or z = 0 )
end



    ;foreach gis:feature-list-of watershed-dataset [ vector-feature -> let x gis:location-of
gis:centroid-of vector-feature] show
```

Chapter 5: General Conclusions

5.1. Summary of Findings

The findings presented in this thesis provide insights into the effects of landscape change, large-scale disturbances, and the quality, abundance, and distribution of food resources on grizzly bear food and habitat supply, habitat selection, and the tradeoff between individual health (body condition) and survival (mortality risk as it related to roads). Overall, the findings contribute to a growing body of literature showing that by shifting the quality, abundance, and distribution of food resources (via landscape change and large-scale disturbances), such disturbances may benefit a threatened bear population by increasing access to high-quality foods in human-modified areas. In turn, this can influence overall health, and ultimately reproduction and fitness, if mortality risk is lowered. These results broaden our understanding of the effects of landscape change on grizzly bears and how this can be used to inform grizzly bear management practices. A key (and ongoing) management challenge for grizzly bears inhabiting human-modified areas is how to best minimize the negative effect of anthropogenic disturbances (e.g., increased mortality risk), while simultaneously enhancing their positive effect (e.g., access to high-quality food resources) (Nielsen et al., 2008).

In chapter 2, I explored whether harvested areas can act as surrogates to wildfires for grizzly bear food supply by comparing and quantifying grizzly bear food supply in post-harvest and post-fire disturbance types and at relatively early stages of forest regeneration. Results indicated that there were no significant differences between digestible energy available from fruit and forbs when comparing between post-harvest and post-fire stands within any age-class, whereas significant differences were evident between age-class. Results also provide evidence that harvested areas can potentially act as surrogates to wildfires in relation to grizzly bear food supply and could thus be used as a management tool to maintain or enhance food supply to support population recovery efforts, especially in areas of wildfire suppression. Human access, however, remains a key challenge given harvested areas are often associated with increases in road density and human presence.

In chapter 3, I explored the degree to which grizzly bears may trade off foraging strategies (food resource heterogeneity vs. homogeneity) depending on how food resources are spatially allocated and investigated these patterns on seasonal habitat (food resource) selection. In general, models that included heterogeneity coupled with homogeneity were most supported and best explained grizzly bear habitat (food resource) selection across all seasons. Most importantly however, results suggest that bears may alternate between foraging strategies (heterogeneity vs. homogeneity) given they were more likely to use high contrast areas (patchiness) when digestible energy is more widely distributed, and conversely, use resource dense areas when digestible energy distribution is constrained. Results herein combined with the fact that forest harvesting has largely replaced natural wildfire as the main disturbance agent in the study area, could offer a way to increase the probability of bears encountering and exploiting high-quality patches in a human-modified area, preferably in secure locations with reduced mortality risk. Although wildfires are predicted to become more frequent and severe in the future (Coogan et al., 2019), thus forest harvesting may not be as necessary with increasing wildfire activity. For instance, > 2 million hectares were burned during the 2023 Alberta wildfires (Ministry of Environment and Protected Areas, 2023), exceeding any previous year on record.

In chapter 4, I present a novel spatially explicit individual-based model (IBM) that simulates the interaction between grizzly bear agents, a spatiotemporal dynamic landscape of key grizzly bear foods, and differing road density levels for a threatened grizzly bear population in Alberta, Canada. Results suggest that a tradeoff between health and survival may be occurring given the survival rate of bear agents peaked at body condition index values near zero (i.e., when survival was influenced by both road density and low body condition index values). Bear agents that tended to be located in resource poor areas had higher survival rates yet were in lower body condition, whereas the opposite pattern occurred in resource rich areas. Lastly, the model showed that the relationship between displacement and body condition index was contingent on whether bear agents foraged in resource rich or poor areas. Thus, the findings in combination with the model per se could be used as a spatial planning tool to help support ongoing recovery efforts in a threatened grizzly bear population. Moreover, the model could be expanded upon via testing and exploring alternative scenarios and conditions when proposing long-term management plans.

5.2. Future Research

There are several pathways by which future studies can extend upon the findings presented in this thesis; hence I will discuss this in the context of chapters 2-4.

Regarding chapter 2

One possible extension might involve teasing apart whether differences in high productive vs. low productive wildfires (i.e., magnitude of disturbance in relation to bear food resources and energy) contribute to differences in the structural characteristics of understory (and overstory) forests and comparing this to harvest and non-harvested areas. Given that productivity can substantially vary between wildfires, bears may preferentially frequent the areas disturbed by the most productive wildfires. Thus, accounting for wildfire productivity when comparing to harvested areas should be taken into account in future studies. Also, given this study was located in a transition zone (foothills) between montane and boreal ecoregions, future research focusing on differences in overstory characteristics (e.g., canopy cover, tree height, basal area) and seeing how this relates to the forest understory might also be of scientific value.

A question that might be of direct value to grizzly bear conservation in Alberta: do grizzly bears use, or perhaps more importantly, acquire energy in harvested areas at the same rate as when they frequent or forage in areas disturbed by wildfire irrespective of the occurrence, quantity, or availability of energy? For instance, during field work I often observed bear scat in high productive wildfires but rarely, if at all, in harvested areas (pers. obs.). This is an important question for three reasons: First, whether because of understory and/or overstory forest structure, high variability in wildfire productivity, landscape permeability, behavioral and evolutionary reasons, or combination thereof, if bears acquire energy at a greater rate in areas disturbed by wildfire, then the utility of harvested areas as a habitat surrogate may not be as effective as described in chapter 2. Second, if bears do acquire energy at a higher rate when using areas disturbed by wildfire, then limiting wildfire suppression, especially in high productive areas may allow bears to acquire their energetic needs while constraining their movements. This higher rate of energy acquisition in wildfire areas can benefit bears by increasing their rate of fat deposition while simultaneously decreasing their exposure to roads, thus lowering their mortality risk. Third, if knowledge of habitat selection is acquired via imitation of maternal behavior (Nielsen et al., 2013), then shifting foraging behavior (i.e., use and rate of energy acquisition) from wildfire to harvested areas may take generations. Using field methods and/or landscape simulation, future research should consider the rate at which grizzly bears acquire energy in disturbed areas, preferably distinguished by high productivity (magnitude of difference) in key bear foods. Although this type of research would benefit from considering how body size, bite size, and bite rate influence the rate of energy acquisition, given large-bodied grizzly bears with relatively smaller bite sizes (e.g., males) need to consume more energy to overcome the constraints imposed by herbivory. For instance, male bears from vegetation-based populations are much more carnivorous (dietary meat) than females (Rode et al., 2001), suggesting that meat should be included when investigating productivity differences in disturbed areas with respect to key bear foods.

Another area of research should consider the effects of mechanical scarification and herbicide application on key bear foods in harvested areas. Site preparation can destroy rhizomes and delay plant recovery and growth of berry producing shrubs (Martin, 1983; Zager et al., 1983), whereas herbicide application may delay flowering and seed reproduction in many target and non-target plants (Boutin et al., 2014). This not only has direct effects on food availability, but also promotes the canopy to close more quickly (contrasted with wildfire), triggering a decline in habitat value with respect to bears. Moreover, silvicultural thinning practices that increase light penetration would likely delay canopy closure and extend the window of time bears benefit from harvested areas (i.e., light gap that creates small areas for growth of bear foods) (Sullivan et al., 2002). Active maintenance of fruiting species in harvested areas, coupled with road access restrictions, would likely also benefit bears. This could be done by maintaining fruiting shrubs across many harvest blocks or concentrating shrubs within food plots (Braid et al., 2016).

Regarding Chapter 3

Extending the results from this chapter could involve a study that explicitly focuses on macronutrient (protein, lipid, and carbohydrate) selection rather than food resource selection (digestible energy) in the context of habitat selection studies. This way, researchers could investigate the proportion of macronutrients driving grizzly bear foraging decisions, if any. For instance, diets of wild bear populations are often more variable and typically contain a higher proportion of protein relative to lipid or carbohydrate, although foods high in lipid or carbohydrate become, in general, most available in summer and autumn during the hyperphagic period prior to hibernation (Coogan et al., 2014; Coogan et al., 2018). Exploring the degree to which grizzly bears trade off foraging strategies (heterogeneity vs. homogeneity) in the context of macronutrient selection could help shape not only where to focus conservation efforts, but also on what to focus (types of plants) and by how much (proportion of each plant). For instance, if bears use high contrast areas (patchiness) when energy is more widely distributed, and these areas coincide with a higher proportion of a particular macronutrient component, then focusing conservation efforts on these areas would be justified in the case of habitat use and the ability of bears to maximize a particular macronutrient component. Furthermore, if high contrast areas increase the probability of a bear locating high-quality patches, then identifying which factor (e.g., digestible energy vs. macronutrient proportions) is driving the cue for exploitation becomes important when making conservation decisions.

Another important aspect to consider when looking at macronutrient selection is the digestible energy profile. For instance, if two high-quality patches have equal energy levels but the digestible energy profile of one patch is entirely made of protein while the digestible energy profile of the latter patch is a mix of lipid and carbohydrate components, then bears may not only be selecting for digestible energy in high-quality areas per se; rather they may also be selecting areas to optimize macronutrient components in their diet. This is relevant to conservation efforts since most mass gain is accumulated during the late mesophagic and hyperphagic periods and is critical for over-winter survival. This is particularly the case for females given there is strong correlation between their prehibernation body mass and reproductive success (e.g., lactate longer, earlier parturition, and larger litter size; Hilderbrand et al., 2000; McLellan, 2011; López-Alfaro et al., 2013; Friebe et al., 2014). Considering bears in Alberta are threatened, and females have relatively smaller body size, younger age at primiparity, smaller litter size, and longer interbirth interval compared to other interior bear populations residing in more productive environments (e.g., Flathead River, BC) (Hilderbrand et al. 1999; Ferguson and McLoughlin 2000; COSEWIC, 2002; 2012), conservation efforts that integrate macronutrient selection could help complement, and perhaps bolster, the suite of bear management tools already employed by the Alberta government.

Apart from investigating habitat selection at varying levels of granularity, integrating long-term spatial and temporal covariates of shifting forestry, wildfire, insect outbreak, road, and human-density patterns into habitat selection studies should help in understanding how these factors shape grizzly bear populations in an ever-changing landscape, particularly for Alberta. For instance, given the long-term GPS telemetry data as well as population monitoring data available for grizzly bears residing in Alberta (i.e., genetic sampling and dead bear recovery data), future studies could explore whether shifting patterns in landscape covariates contribute to changes in individual behavior across time and space. Could evidence of learning, whether partly heritable (Shafer et al., 2014) or maternally learnt (Nielsen et al., 2013), be changing over time as a direct response to human-altered resource patterns?

<u>Regarding Chapter 4</u>

There are likely many ways to extend the results of chapter 4; however, I will only discuss a small number of extensions here.

The IBM would probably benefit from incorporating a denning sub-model (López-Alfaro, 2014) to capture an important component of grizzly bear biology, especially if researchers are interested in understanding how navigating a human-modified and dynamic landscape translates into female reproductive success. Seasonal food layers (maps) estimated on an annual or semi-annual basis, via backcasting and forecasting, could be leveraged to simulate changes in key bear foods (e.g., succession with and without the effects of climate change for instance) across different types of bear habitat using both short-term (e.g., 5–20 years) and long-term time horizons (e.g., 60–80 years). This could be coupled with simulating a suite of forest harvest patterns, wildfire predictive layers, and changes in road density thresholds, traffic, and closures, to gain a better understanding of the interaction between bottom-up and top-down factors in the context of grizzly bear management. For example, simulating scenarios that exhibit a high degree of spatiotemporal variation in the landscape over longer horizons could help clarify our understanding of landscape carrying capacity and source-sink dynamics in a landscape perpetually modified by humans for the foreseeable future. Other submodels that could be improved upon include movement, perhaps by incorporating memory (Lewis et al., 2021; Thompson et al., 2022) and/or sampling distances (from the location of the bear agent) dynamically under known statistical distributions. Lastly, in line with extensions discussed above, simulating a landscape punctuated by areas with high resource quality (and preferably low road and human density) and exploring this effect on female reproductive success could be beneficial in understanding how adult females meet their resource/energetic needs in such critical areas. For example, if meeting resource needs in high-quality areas reduces movement, and thereby reduces conflict and exposure to human-caused mortality, then these areas may present safe havens for reproductive females. Thus, they should be identified not only under present conditions but also forecasted under various landscape and climate change scenarios. These areas could prove vital to boosting grizzly bear populations in Alberta under continued landscape change and worsening climate change.

Computationally, the IBM could be improved in a few ways. The use of a more high-level general-purpose programming language that supports multiple programming paradigms (e.g., object-oriented and functional programming, robust parallel computing, and modern model automation tools) could help expand on the findings of the IBM, including exploring more complex and ecological valuable scenarios (e.g., larger spatiotemporal scale or higher dimensionality data) as well as establishing a model automation process. Practitioners or other interested parties, for example provincial wildlife managers, would likely benefit from this type of implementation. The IBM could also benefit from model validation that uses more sophisticated techniques such as approximate Bayesian computation (Beaumont, 2010; Hartig et al., 2011; van der Vaart et al., 2016), especially if future research involves forecasting and backcasting over longer horizons with uncertainty in model predictions. Movement decisions could be implemented in a Bayesian probabilistic framework (e.g., Markov chain Monte Carlo methods) given prior information (e.g., t-*n* steps) representing existing knowledge or preferences can be updated with new experiences gained from moving through a landscape (Lewis et al. 2021).

Alternatively, reinforcement learning (RL) approaches, largely overlooked compared to better-known supervised learning and unsupervised learning paradigms, might also show promise in the ecological and conservation sciences (e.g., Fonnesbeck, 2008; Wang et al., 2020;

Lapeyrolerie et al., 2022). Although RL involves the interaction between an environment and an agent, similar to individual-based modeling, it differs in that agents are not provided with rules, but must instead observe the current state of the environment and then perform an action with the goal of learning to maximize a cumulative reward. By performing an action from the set of available actions, the environment transitions to a new state (s_{t+1}) with the reward (r_{t+1}) associated with the newly transition state transmitted to the agent (Sutton and Barton, 2018). That being said, here are three potential ways to expand or improve the IBM in the context of RL. (1) By way of example, investigating how a bear (agent) may be more likely to forage in resource rich areas (positive reinforcement via rewards, for instance, satiation or maximizing lipid and carbohydrate intake) but less likely to forage in the same area because of increased mortality risk associated with roads (inhibitory learning via avoidance of unpleasant stimuli; that being increased exposure to humans near roads leading to death) could be an interesting application of RL (Lewis et al., 2021). Without being told the rules, the agent would discover which actions yield the highest cumulative reward. The focus here is on finding a balance (tradeoff) between exploitation (of current knowledge) and exploration (of unknown or undiscovered resources). (2) Another potential use of RL lies in searching for solutions to hard decision-making problems in conservation (Lapeyrolerie et al., 2022) and forest management (Malo et al., 2021). For instance, perhaps by using predicted food resource covariates (e.g., GIS layers) adjusted for seasonality and phenology, there is a potential to simulate the successional trajectory of key bear foods under a suite of harvesting (including road placement), wildfire, and climate change scenarios over various time horizons. Using these forecasted layers to simulate an RL environment, a bear agent could thus learn to take actions (and generate plausible future states) to maximize some cumulative reward (e.g., fitness). By tailoring the transition dynamics, states, actions, and reward function, the RL environment could be used to explore an array of bear management and decision-making problems/states. (3) Lastly, analyzing the outputs of individual-based models can be challenging. Ever-increasing amounts of data can encourage users to build models with complex interactions (i.e., increasingly realistic), often resulting in high-dimensional parameter space and nonlinear relationships between inputs (initial conditions and parameters) and outputs, which can lead to significant demands in computational power. Surrogate modeling, via implementing machine learning methods, has been proposed to approximate the relationships between an IBM's inputs and outputs via exploring the model's parameter space (Lamperti et al., 2018). Compared to more computationally costly Monte Carlo methods, this has the advantage of lowering a model's running time and computational cost while assessing the importance of individual parameters and making calibration processes more computationally tractable, especially when dealing with nonlinear relationships (Angione et al. 2022; Sivakumar et al., 2022). Although RL methods have been used to infer and refine optimal rule-sets of agents and decision-making processes – effectively learning an IBM's rules, and thus acting as a complement or alternative to classical IBM approaches (DeAngelis and Diaz, 2019; Sivakumar et al., 2022) – few, if any, RL methods have been used to calibrate IBM models. Given the stochastic and nonlinear nature of ecological data, as well as conservation decision-making being increasingly informed by forecasting (Dietze et al., 2018), new tools such as those presented here could be explored in future research.

5.3. Management Implications

There are many management challenges associated with recovering a threatened grizzly bear population in a human-disturbed landscape. In general, however, because of increases in resource extraction, recreational access, and human density, implementing road management strategies that control or limit human access to bear habitat (and hence decreases mortality risk) becomes a difficult management challenge in Alberta. An alternative approach to bear management involves enhancing access to high-quality food resources. For instance, limiting fire suppression (i.e., allowing wildfires to burn, especially in high-quality habitat located in remote areas with adequate security) or habitat surrogacy via timber harvesting (preferably coinciding with areas distant to roads and humans) are two potential ways to increase access to high-quality food resources. However, there are some drawbacks to approaching bear management from a bottom-up framework. For instance, there is likely a limited ability to shift behavior away from ecological traps given behavior is often maternally learnt (e.g., habitat selection and site fidelity, especially for females) (Nielsen et al., 2013, Schwartz et al., 2003). Increases in human density coinciding with access to high productive areas will likely increase the rate of conflict in bears. Furthermore, as bear movement is often wide-ranging and partly driven by seasonal food sources (Schwartz et al. 2003), open areas near humans may become more appealing in the future owing to rising temperatures advancing the development of plants, thereby creating a phenological mismatch between key bear foods and feeding behavior. This phenological mismatch has the potential to alter reproductive behavior in an already threatened population (Laskin et al., 2019).

If the conservation goal is to at least maintain, although preferably expand, grizzly bear population levels in Alberta to a healthy level (e.g., social carrying capacity, biological carrying capacity, population size exceeding 1000 individuals), then management should follow examples set by Sweden. Brown bear populations in Sweden have expanded from less than 150 individuals in the 1930s to over 3000 individuals today, having been hunting since the 1940s and coexisting in a human-dominated landscape where commercial timber harvesting has occurred for over a century (Swenson et al., 1995; Linder and Östlund, 1998; Kindberg et al., 2011). Yet, even while pursuing commercial timber exploitation, and despite bears being subjected to persistent hunting pressure, Sweden has effectively managed roads and changed attitudes towards bears while recovering their population to sustainable levels. In light of this, short-term conservation efforts in Alberta should continue to employ road access management, thereby limiting mortality risk, as well as access to high-quality habitat, preferably in remote areas with sufficient security cover (Nielsen et al., 2006). In the long-term, however, acrimonious attitudes towards bears should lessen over time with the goal of reducing human-bear conflict (Hughes and Nielsen, 2018), thus contributing to steady-state in human-bear coexistence in Alberta.

Collaboration is a key component of modern research, and likely a necessary enterprise to effectively implement wide-ranging and long-term conservation and wildlife management programs. In collaboration with industry, academia, indigenous-led conservation, and government partners, future studies that leverage adaptive management and/or robust ecological forecasting and decision making under uncertainty could further strengthen management and population recovery efforts for grizzly bears in Alberta. This action is even more necessary if ecological systems that have already been perturbed by humans are more apt to experience sudden and dramatic changes in the future.

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