Evaluating the role of movement behaviour and habitat familiarity on translocated grizzly bear success using an agent-based modelling approach

By

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Abstract

In North America, the grizzly bear (*Ursus arcos*) is one of many species increasingly threatened by the consequences of human-wildlife conflict, with human-bear encounters on the rise due to increased human activity near or in bear habitat. As a result, a growing number of bears are subjected to management measures such as translocations in which animals are moved to areas with lower risk of human conflict, although these measures are not always successful. Previous research has attempted to understand factors associated with translocation success, but new methods are needed to address the continuous and complex nature of issues related to how animals move and learn about their surroundings as well as how they adapt to novel environments. The objective of my MSc thesis is to develop and employ a novel agent-based computer simulation model to analyze how grizzly bears learn and respond following a translocation event. This modelling effort attempts to capture how bears make decisions based on multiple factors, and represent how grizzly bears interact with their environment and make movement decisions based on learned behaviours.

First, an agent-based movement model was developed for female grizzly bears using GPS-location data for bears within a region in west-central Alberta, Canada. The model, which incorporates multi-scale decision-making and machine learning, generated movement patterns similar to those observed in radio-collared females in the study area. Home range sizes and movement metrics produced by the model were consistent with those observed in female grizzly bears in the area. The model was then used to simulate translocation events in which bears with varying “exploration” propensities were translocated to habitats with familiar or novel landscape characteristics. In general, bears translocated to habitats with similar landscape features to their original habitat were more likely to use high-quality habitat than bears moved to areas with very different landscape features. However, while increased exploration led to greater use of high-quality habitat in the long run, exploratory behaviour was found to be mostly detrimental during the first years following a translocation, the period considered critical for translocation success. Model results were found to be scale-dependent with results varying both in time and space, highlighting the need for a multi-scale approach to animal movement studies. The findings presented here also emphasize the need to account for behavioural traits of wildlife and habitat characteristics of the capture and release sites when selecting suitable translocation locations. This work highlights the potential for agent-based modelling as a tool to study animal movement as a continuous and complex process and evaluate conservation policies.

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1. Introduction

1.1 Research context

In the past two centuries, many of the world's large carnivores have been extirpated from their original ranges into isolated populations that struggle to maintain genetic diversity and sustainable population growth (Dirzo et al., 2014). Recent research has highlighted the role of carnivores within their ecosystems in an attempt to encourage conservation efforts, but many populations continue to be threatened by human expansion and activity (Beschta & Ripple, 2009; Estes et al., 2011). In addition to prosecution and overhunting, large carnivores usually have high metabolic demands that result in the use of extensive territories or home ranges and the need for large prey, making them prone to conflict with humans and livestock (Darimont et al., 2015; Ripple et al., 2014). Animals that pose a danger to humans due to repeated interaction are often either killed or translocated to areas where human conflict is less likely. According to the International Union for Conservation of Nature, animal translocations, or the deliberate movement of individuals from one area to another, must yield benefits to the translocated animal as well as the population, species, or ecosystem containing the release site if species conversation is to be a priority (IUCN, 2013). For many of the world's threatened carnivore species, the addition of one individual to a population can aid species recovery by increasing genetic variability and contributing to the reproductive capacity of the population (Miller et al., 1999).

Although translocation is a non-lethal alternative for managing problem wildlife that can support, rather than impede, species conservation efforts (Linnell et al., 1997), the success of this method has varied. In addition to the high financial cost often associated with translocations, most translocated individuals direct their movements towards their original habitat and even return to their release site or die due to hunting, malnourishment, or other unknown causes (Fontúrbel & Simonetti, 2011; Linnell et al., 1997). Furthermore, inconsistencies in criteria used for assessing translocation success as well as the limited efforts in monitoring translocated individuals restrict the availability of data that can be used to study translocation events and increase their efficacy (Fischer & Lindenmayer, 2000).

While it has been recognized that habitat characteristics of the release site are critical for translocation success (Linnell et al., 1997), many studies focus mainly on demographic characteristics such as age and sex of the translocated individual or distance between the capture and release sites (e.g. Alldredge et al., 2015; Bradley et al., 2005; Pinter-Wollman, 2009). However, recent research also supports the notion that behavioural traits of each animal as well as their previous experiences may play an important role in the success of a translocation. For example, simulation models have been used to show that animals that overestimate the quality of an unknown location are more likely to find high-quality habitat due to high exploration rates (Berger-Tal & Avgar, 2012). In a study where two elk groups from different habitats were translocated to a new area, elk familiar with wolf or hunters prior to their release in an area with both of these risk sources were up to 2.2 times more likely to survive their first year than elk that were not familiar with these dangers (Frair et al., 2007). In another study, woodland caribou translocated to a mountainous habitat were more likely to exhibit movement patterns and habitat use similar to the resident population if they originated from other mountainous habitat (Warren et al., 1996). Additionally, mountain individuals were more than twice as likely to survive the first three years after translocation. Aside from studies of translocation events, other research has also suggested that behavioural differences account for individual variation in movement patterns and habitat selection patterns (Ciuti et al., 2012; Found & St. Clair, 2016; Murray & St.

Clair, 2015). The knowledge gained from these studies is invaluable, yet new approaches need to be adopted in order to fully understand the intricacies related to animal movement and the way animals might respond to novel environments. To date, studies of animal movement have mainly focused on studying the relationship between location data and the landscape characteristics in the immediately surrounding area. While results from such studies allow us to understand the way animals respond to individual features within their environment, new approaches are needed to account for the continuous way in which individuals learn about their surroundings and make movement decisions involving factors related to various landscape characteristics at multiple spatiotemporal scales (see Coogan et al., 2018, DeAngelis and Yurek, 2017).

Although relatively new within the field of ecology, simulation modelling can offer tools for evaluating continuous processes such as animal movement and learning (Tang & Bennett, 2010). Agent-based modelling (ABM), in particular, is a computer simulation method that models complex systems and highlights emergent patterns based on behaviour of individuals (i.e. agents) in the system (Railsback & Grimm, 2011). ABM allows for the study of continuous processes and the incorporation of multiple distinct factors into one model (DeAngelis & Diaz, 2019). Agents within the model follow a set of movement rules that dictate when and where they travel to next. These rules allow the agents to consider their internal states (i.e. hunger) as well as environmental variables (i.e. food availability), among other factors, when making these decisions. Additionally, ABM can be used to study complex processes such as animal cognition and can aid in the understanding of animal movement in ways that other methods cannot (Tang & Bennett, 2010).

ABM has been used successfully in the past to assess complex processes including the role of memory on animal migratory behaviour (Bracis & Mueller, 2017), learning and adaptation in mobile agents (Bennett & Tang, 2006), and animal cognition in relation to space-use behaviour (Avgar et al., 2015). Conservation issues such as landscape connectivity of bighorn sheep in British Columbia (Allen et al., 2016) and use of movement corridors by jaguars in Belize (Watkins et al., 2015) have also been addressed using ABM. The knowledge gained from these and other ABM studies shows promise in evaluating the effectiveness of management scenarios and supporting successful conservation of threatened species by increasing our understanding of how animals gather, store, and use information about their environment. Of interest to my thesis research, ABMs have the potential to be useful in aiding animal translocation efforts given their use as tools with which the effects of various factors on translocation success can be evaluated. For this, however, we first need to determine how animals use landscape cues in their resident habitat, and understand how they learn about their environment and use these learned cues to make future movement decisions in a novel environment. The work presented in this thesis aims to address some of these issues with the overall goal of advancing the scientific literature on animal movement and wildlife translocation.

1.2 Research focus

In North America, the increase of industrial activities such as forestry, oil and gas exploration, mining, and agriculture in addition to the urbanization of wildlands has led to a decline in many species that rely on healthy habitat to meet basic requirements (Laliberte & Ripple, 2004). Among other large carnivores, the grizzly bear (*Ursus arctos*), has experienced substantial reduction in its historic range due to human settlement and development (Mattson & Merrill, 2002). Grizzly bears are generalists by nature and hence occupy a wide variety of habitats throughout the year in order to meet their nutritional requirements.

Previous research has demonstrated that grizzly bear movement behavior changes in response to land use patterns, especially those causing alterations to the spatial availability of food sources across seasons (Nielsen et al., 2003). Linear features and forest edges have been shown to provide critical food sources making them a preferred habitat for grizzlies (Stewart et al., 2013). However, major transportation routes have been associated with habitat fragmentation which can limit genetic variability and long-term population success (Proctor et al., 2012). Furthermore, the proximity of bears to humans in areas of high road density has contributed to an increase in bear conflicts with humans and human-caused mortality (Boulanger & Stenhouse, 2014; Cristescu et al., 2016). The complex response of grizzly bears to anthropogenic landscape changes has been the focus of many studies, but further research is necessary to ensure long-term success for grizzly bears in this evolving landscape (see Coogan et al., 2018). While these studies offer invaluable insight into the role of various factors on the way bears interact with their environment, traditional methods, particularly those embedded in spatial statistics, are constrained in their ability to combine this knowledge and represent movement as a continuous process. As bears are challenged by increasingly complex landscape characteristics, it is necessary for ecologists to understand how they navigate through their environment and make movement decisions that depend on multiple factors.

In Alberta, Canada, human-dominated landscapes pose a barrier for population success due to reduced availability of secure habitat and the constant threat of human-bear conflict. Human-caused mortality has long been the number one cause of death for grizzly bears in this area (Boulanger & Stenhouse, 2014; McLellan et al., 1999). Expanding road networks and human activity near grizzly bear habitat have increased the amount of human-bear conflicts (Graham et al., 2010), which often result in the destruction or translocation of individuals. These translocation efforts show mixed success rates, with bears often returning to occupied areas or failing to establish themselves as reproductive individuals within the population in to which they are moved (Milligan et al., 2018). For threatened populations such as the grizzly bears of Alberta, the removal or addition of one reproductive individual may significantly affect the survival of the population. Hence, identifying factors that lead to the success or failure of translocation efforts and understanding how future landscape changes may affect the success of this and other threatened populations is key for conservation management. Understanding how translocated bears perceive and utilize new areas could potentially lead to higher success in translocation events and contribute to more effective management of human-wildlife conflict.

1.3 Thesis objectives and structure

The objectives of this research are to 1) develop an agent-based model to simulate grizzly bear movement behaviour using multi-scale learning and decision-making, and 2) evaluate the role of environmental familiarity and behaviour in the success of grizzly bear translocations. This thesis is structured into four chapters in which relevant context and details on the research are presented. After the first chapter (Introduction), the two research objectives are addressed in chapters two and three, respectively, which are structured as journal publications that will be individually submitted to peer-reviewed journals for publication. The second chapter presents the methodology, including validation and calibration, of a novel agent-based model for grizzly bear movement. Using real landscape data from the Yellowhead Ecosystem in west-central Alberta and positional data for GPS-collared grizzly bears in the area, I developed a simulation model that accounts for various landscape features and highlights the complexities related to grizzly bear movement. I compare results from the simulations to movement and space-use patterns observed in female grizzly bears and demonstrate the validity of the model. In Chapter 3, I implemented the ABM developed in Chapter 2 in order to address the second objective of this thesis. I simulated multiple scenarios in which bears are translocated from a developed area into either a similar environment with landscape features they are acquainted with or a different environment with limited familiar characteristics in order to assess the role of habitat familiarity on potential translocation success. I also tested whether differences in the propensity to explore after a translocation event affect a bear's ability to use high-quality areas at two scales. The final thesis chapter consists of a conclusion that summarizes the accomplishments of this study and discusses important research and management implications stemming from this work.

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2. Simulating multi-scale movement decision-making and learning in a large carnivore using agent-based modelling

2.1 Introduction

Anthropogenic landscape change in many parts of the world is increasingly jeopardizing the survival of wild animals, particularly apex species at the top of their respective food chains (Estes et al., 2011; Ripple et al., 2014). Large predators are especially affected by landscape changes because of their high metabolic requirements and wide-ranging behaviour, making them prone to encounter and conflict with humans and livestock (Ripple et al., 2014). These impacts require such species to constantly adapt to dynamic and complex landscape characteristics in order to find adequate food resources, mates, as well as avoiding areas of human-caused mortality risk (Boulanger & Stenhouse, 2014; Nielsen et al., 2004). Grizzly bears (*Ursus arctos*) are an example of a large carnivore that travels relatively long distances in search of seasonally available food resources, and are hence greatly affected by landscape change (Cristescu et al., 2016). Grizzly bear abundance and distribution has been significantly reduced in North America due to habitat loss and human hunting pressure (Mattson & Merrill, 2002), habitat fragmentation (Proctor et al., 2012), conflict with humans (McLellan et al., 1999), and increased mortality related to anthropogenic features (Northrup et al., 2012; Proctor et al., 2019). Conservation of species like the grizzly bear require that we understand how movement decisions are made based on various landscape features in order to assess how future landscape change might affect the way animals move through their environment.

Grizzly bear home ranges are often used as a measure of habitat and resource selection and have previously helped inform conservation and management efforts (Gibeau et al., 2001;

Roever et al., 2008). An animal's annual home range encompasses the area it moves through in a year for securing food, mating, and caring for young (Burt, 1943). Home ranges emerge from movement decisions which, for grizzly bears, depend mainly on responses to environmental conditions, abundance of food, social dynamics, and human activity that are often learned from the mother as cubs (Pasitschniak-Arts, 1993). Habitat heterogeneity, for example, may affect how much fidelity an individual shows towards a particular area (Edwards et al., 2009; Switzer, 1993). Social hierarchies also impact home range establishment, with dominant animals such as large males often occupying higher-quality habitat, leaving less desired areas for younger males or females with cubs (Bourbonnais et al., 2013; Elfström et al., 2014; Steyaert et al., 2013). Despite the widespread use of home ranges in grizzly bear movement research, our understanding of how movement decisions and the emergence of home ranges is informed by landscape and social dynamics is limited.

Grizzly bear research has shown that individuals sense and react to features in the landscape resulting in modified movement decisions that affect home range size (Dahle et al., 2006) and fidelity (Edwards et al., 2009; Sorensen et al., 2015). Previous studies have highlighted differences in behavioural responses based on age-sex classes and seasonality to linear features such as roads (Graham et al., 2010; Herrero et al., 2012), seismic lines (Finnegan et al., 2018; Linke et al., 2005), and railways (Murray et al., 2017). Studies have also provided evidence that movement is affected by mining (Cristescu et al., 2016) and forest disturbances (Stewart et al., 2012), landscape edges (Larsen et al., 2019; Stewart et al., 2013), and oil and gas infrastructure (Laberee et al., 2014). More recent work using a multi-scale approach tested the influence of landscape disturbance and conditions on the selection of home range and movement (Bourbonnais, 2018). Most markedly in this study, bears were seen to select areas of high productivity and resource availability with topographic complexity while avoiding human development at the home range scale, whereas local movement decisions exhibited a preference for the presence of roads and other anthropogenic disturbances. Thus, observed selection patterns indicated avoidance of high-risk habitat near human activity at large scales and preference for resource availability at finer scales, suggesting that grizzly bears account for and incorporate knowledge at multiple scales when making movement decisions.

While these findings provide invaluable insight into grizzly bear movement behavior, the use of time as a discontinuous variable in these approaches limits our study of the way grizzly bears acquire and use knowledge about their surroundings over time. Cognitive function and its effects on movement behaviour of grizzlies are not well studied despite an understanding that learning and memory play a role in animal migration (Bracis & Mueller, 2017; Turner et al., 1993), site fidelity (Edwards et al., 2009; Switzer, 1993; Van Moorter et al., 2009), and habitat or resource selection (Janmaat et al., 2006; Merkle et al., 2014; Nielsen et al., 2013; Wolf et al., 2009).

As a response to the existing gaps in grizzly bear movement research, simulation modelling offers a spectrum of approaches to model animal movement and decision-making processes for understanding, among other things, the development and use of animal home ranges and territories (Bekoff & Mech, 1984; Carter et al., 2015; Switzer, 1993). Agent-based modelling (ABM), in particular, can be used to represent individual animals as autonomous agents and to simulate how these agents respond to other agents and their environment over time (Railsback & Grimm, 2011). Agents move from one location to another in a modeled environment based on rules informed by internal states, social dynamics, and the environment. ABM approaches have been used to advance large-mammal research focused on habitat connectivity (Allen et al., 2016; Kanagaraj et al., 2013; Rabinowitz & Zeller, 2010; Watkins et al., 2015), space-use based on population dynamics (Carter et al., 2015; Langrock et al., 2014), population dispersal (Bernal-Escobar et al., 2015), and spatial cognition (Avgar et al., 2015; Bennett & Tang, 2005; Semeniuk et al., 2012). Despite their success as tools for animal movement research (DeAngelis & Grimm, 2014; Tang & Bennett, 2010), to date agent-based models have only been used to study bears in the context of mitigating conflict in urban areas (Marley et al., 2017, 2019).

This paper presents a novel ABM with learning mechanisms to help us understand home ranges as an emergent property of grizzly bear movement and space-use. We study the interface between memory and movement decisions and incorporate multi-scale decision-making processes that are representative of complex grizzly bear movement behaviours. We present a computer simulation model informed by animal telemetry and environmental data that accounts for landscape dynamics at two scales and uses a learning algorithm to simulate how grizzly bears acquire information from their surroundings and make informed movement decisions based on that knowledge. With this in mind, the goals of this study are to 1) develop a simulation model of grizzly bear movement and learning using multi-scale decision-making and machine learning algorithms and 2) evaluate the role of learning and memory in home range establishment and an individual's ability to improve habitat and movement selection. In the next section we present the model, followed by a description of how the model was implemented and evaluated using radio collar data from grizzly bears in west-central Alberta, Canada.

2.2 Methods

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing agent-based models (Grimm et al., 2010). The model was implemented in NetLogo 6.1.1 (Wilensky, 1999).

2.2.1 *Purpose*

The purpose of this model is to simulate grizzly bear movement behaviour in a temporally dynamic landscape. The model simulates both global and local movement decisions in a multi-scale decision-making process informed by real landscape data. A reinforcement learning algorithm is used to simulate how individuals gain information about their environment and use this knowledge in future movement decisions. Our model centers on the way bears acquire knowledge about their landscape during the sub-adult and early adult phase (<7 years old) in order to establish habitat selection and space-use patterns. We focus on learning via exploration and memory in order to understand the way informed multi-scale movement decisions lead to the emergence of home ranges.

2.2.2 *Entities, state variables, and scales*

A single mobile agent, representing an individual female bear, is modelled in each run. Females were selected as the focal demographic given their influence on population trends (Proctor et al., 2019). Each agent is characterized by its age and a location, recorded in *xy* coordinates, that changes with each time step as the bear moves throughout the landscape. The agent is considered to be a year-old cub at the start of the simulation with age increasing annually in line with the time elapsed during the simulation.

The environment consists of two landscapes, each covering the entire study area (see Section 2.3) but represented with different spatial resolutions. The first landscape consists of 100 m x 100 m (1 ha) cells characterized by seasonal local utility values u_s, where s represents one of the following three seasonal shifts in grizzly bear food availability: hypophagia (den emergence in spring to early summer), early hyperphagia (early to late summer), and late hyperphagia (late summer to den entrance in late fall) (Nielsen et al., 2010). Local utility values u_s represent the subjective utility value of each cell to bears (see Van Moorter et al., 2009) and are derived at the end of each season from a reinforcement learning algorithm and a local quality index q_s that estimates the probability of a cell being selected by grizzly bears based on landscape characteristics including terrain ruggedness, distance to roads, and food availability (see Section 2.2.5). Utility values u_s decrease with each time step spent in a cell as a consequence of resource depletion or increase in risk due to exposure and increase once the bear moves to a different cell and resources are replenished or risk decreases. While resource consumption and depletion rates may be resource-specific, we do not account for variation between resource types at this stage. This local-scale landscape is used to make immediate movement decisions that depend on fine-scale knowledge of resources and risks in an individual's immediate surroundings.

The second landscape consists of 1 km x 1 km cells that overlap the local-scale landscape cells. Each 1 km^2 cell is characterized by a seasonal global utility value U_s which represents the subjective utility value of the cell to the bear in each of the three seasons. The global utility value U_s is derived seasonally from the reinforcement learning algorithm and a global quality index Q that estimates the probability that a cell is selected by grizzly bears based on land cover type, terrain ruggedness, and density of roads, fires, and harvested areas (see Section 2.2.5). The utility value U_s decreases with continued use by a bear and increases once the bear moves to a different cell in line with changes in risk exposure and an individual's motivation to move (Van Moorter et al., 2009). This global landscape is used by bears to inform coarse-scale movement towards or away from general areas that rely on a basic understanding of the landscape characteristics and terrain type.

2.2.3 *Process overview and scheduling*

Local and global utility values, u_s and U_s, are loaded onto the model during setup and a single female bear is initiated in a predetermined starting point within the study area. The start point was chosen as a centralized cell within the study area with moderate variance in utility values, representing moderately heterogeneous habitat. The bear initially moves following exploratory behaviour consisting of a correlated random walk. The probability of moving by exploiting neighbouring resources (see Appendix Section A1.1) increases at the end of every season according to a search variable function (see Appendix Section A1.2). Throughout the simulation, the bear develops a cognitive map of its surroundings by storing utility value information of all visited cells, which is used to inform subsequent movement decisions through a reinforcement learning algorithm (see Appendix Section A1.3). Yearly measures of success, which help track a bear's ability to secure high-quality cells at the local and global scales, are updated at each time step (see Appendix Section A1.4). Repeated visits to the same area reinforce and increase the use of that area. At the end of a simulation year, the bear is moved to its starting point and all initial settings are restored. Since our model does not simulate denning behaviour, we initialize bears in the same location each year.

2.2.4 *Design concepts*

Objectives. During exploitation, the short-term objective of grizzly bears is to move to surrounding 1 ha cells with high local quality while increasing use of high-quality 1 km^2 cells at the global scale. The long-term objective is to establish a home range consisting of high-quality cells at both scales by relying on knowledge gained about the landscape.

Sensing. Both local and global utility values u_s and U_s, respectively, are used to make movement decisions. Bears perceive all seasonal local utility values, u_s, of all 1 ha cells within a 250 m search radius and seasonal global utility values, U_s, of the 8 neighbouring 1 km^2 cells. Accessing all seasonal values despite the season in which a cell is visited is representative of the way that bears collect information about future resource availability when moving through an area.

Emergence. The first emergent property of the model is the home range, which consists of a general area that is used repeatedly throughout the simulation due to preferential selection and re-use of previously visited cells found to have high quality. The second emergent property is the learning behaviour, which comprises a bear's ability to retain and use information gained from previous movement decisions in order to improve selection of high quality areas.

Learning. A reinforcement learning algorithm is applied at the end of each season that measures the relative success of a bear's movement decisions by comparing the quality of used cells in that season to cells selected during random movement. The algorithm modifies cell utility values at both scales such that it increases the likelihood that cells be revisited in subsequent years. In the wild, adult females transfer knowledge to cubs before weaning (Nielsen et al., 2013) and, while our model does not directly model this process, the landscape quality values used in the model provide simulated bears with an understanding of the relationship between landscape characteristics and quality, similar to the information shared between mothers and cubs.

Interaction. All agents interact with their surrounding environment. Because we simulate a single individual at each time, interactions between agents are not modeled at this stage of our research.

Stochasticity. There are three instances where stochasticity is introduced in the model. First, the correlated random walk performed during exploration is stochastic as it randomly selects a direction of travel between time steps. Second, in years when both exploration and exploitation occur, the probability of a movement being exploitative is defined by the search parameter ε. Third, the model selects a random cell to move to in the case that two cells within the search radius hold the same utility value.

Observation. Data regarding bear location is collected at each time step. Measures of success (i.e. the sum of the quality of all cells visited by bears at the local and global scales) are recorded in a table and used to assess the bear's ability to inform movement decisions and visit high-quality cells at the end of each season. Location coordinates and yearly measures of success are exported after each simulation.

2.2.5 *Initialization*

During initialization, utility values are calculated and loaded into the modelling environment from estimated quality indices at each of the local and global scales. Seasonal local quality values, q_s, were calculated for each 1 ha cell within the study area and represent the probability that a bear will occupy a cell based on distance to the nearest road, terrain ruggedness, and seasonal food availability. Likewise, a global quality value, Q, was obtained for each 1 km^2 cell by estimating the probability that a bear will occupy a cell based on density of roads, fires, and harvested areas as well as the land cover type and the terrain ruggedness. Quality values at the local and global scales were calculated from the GPS data and represent the preference that resident bears exhibit towards landscape features based on the proportion of time spent in each 1ha or 1 km^2 cell, respectively. At the start of the simulation, local utility values u_s for each 1 ha cell are equal to local quality values q_s for the corresponding season. Similarly, all three seasonal global utility values U_s for each 1 km^2 cell are initially equal to the global quality value Q. Utility values are recalculated seasonally using a reinforcement learning algorithm (see Appendix Section 1.1.3). A single female bear is initiated in the starting point; at this time the bear is new to the landscape and has no knowledge of the environment aside from what it can perceive from its starting position. Only information pertaining to the current season is available for bears to use at any given time during the simulation. The search parameter and all outcome values are set to zero at the start of every simulation.

2.2.6 *Input data*

The model input data consists of the local and global quality values, q_s and Q, used to calculate seasonal local and global utility values, u_s and U_s. At the local scale, quality values q_s are available for each of the hypophagia, early hyperphagia and late hyperphagia seasons due to the seasonal nature of the data used to calculate local quality. At the global scale, a single quality data Q is available per 1 km^2 cell. However, because utility values are updated seasonally through a reinforcement learning algorithm, each 1 km^2 cell is characterized by three utility values, U_s, that reflect the utility of a cell in each of the seasons. No other inputs are used in this model.

2.3 Model implementation

The model is applied to an area spanning approximately 11,500 km^2 within the Yellowhead Grizzly Bear management area (BMA) in west-central Alberta, Canada (Figure 2-1). Grizzly bear density in the area has increased in previous years following historic habitat loss, hunting, human conflict and increased industrial activity and is currently among the highest in Alberta (Stenhouse et al., 2015). Following population estimates in 2004 where results suggested approximately 43 individuals within this management area, a hunting moratorium was put into effect in 2006 and the status of grizzly bears was changed from a species of *Special Concern* to *Threatened* in 2010 (Festa-Bianchet, 2010). Continued expansion of forestry, mining, oil and gas exploration, and outdoor recreation and access networks continue to threaten grizzly bear security in the area and have spurred conservation efforts in the past decade. A detailed description of the study area can be found in Nielsen et al. (2001).

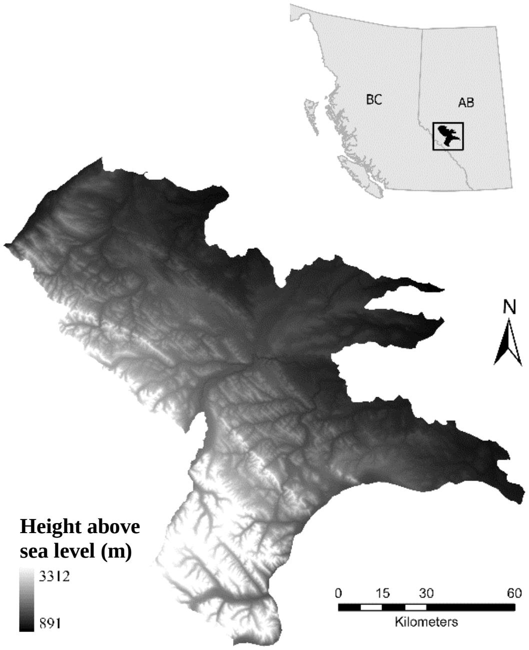

Figure 2-1. Map showing height above sea level in the study area, located within the Yellowhead Bear Management Area in west-central Alberta, Canada.

Movement data was collected by the fRI Research Grizzly Bear Program (fRIGBP) and consisted of radio telemetry data for bears collared between 2013 and 2018. Grizzly bears were captured using culvert traps or helicopter aerial darting (see methods in Cattet et al., 2008) and bears estimated to be over 2 years old were fit with a GPS radio-collar. Positional data was collected at 30 or 60-minute intervals during the non-denning period (approximately April 1 to October 31). Grizzly bear captures were authorized under research permits obtained from Alberta Environment and Parks, Alberta Tourism and Parks, and Parks Canada. All capture and handling protocols were accepted by the University of Saskatchewan Committee on Animal Care. Only bear data from the 2013-2017 period that was fully within the boundaries of the

Yellowhead BMA was used to generate model layers, which resulted in a sample of 10 female bears and 13 male bears for a total of 120 bear trajectories.

Spatial data of landscape features were provided by the fRIGBP, which consisted of the road network throughout the study area, areas of forests that were recently harvested or impacted by wildfires, a digital elevation model (DEM), classification of land cover, and food resource abundance (Appendix Table A1). While previous research has found variation in grizzly bear responses to fire or harvest features at different regeneration stages (Nielsen et al., 2004; Stewart et al., 2012) as well as between types of roads (Graham et al., 2010; Herrero et al., 2012), we did not account for these differences to prevent added complexity that would distract from the study objectives.

2.3.1 *Simulation experiments*

Three scenarios were run in order to assess our objectives: *random*, *learning*, and *learning with memory*. Here, we define *learning* scenarios as instances where bears are learning to increasingly exploit high-quality areas and move away from random movement as a response to a seasonal increase in the search parameter ε. While the *learning* scenario simulates an increase in exploitation, it does not implement the reinforcement learning algorithm representative of bear memory. Memory is assessed with the *learning with memory* scenario, in which bears not only learn to exploit their environment but have reinforcement of movement decisions based on the success obtained throughout the simulation. Model simulations were run for 30 years, where a year is considered a 5-month period during which bears are active in the Yellowhead BMA and for which food resource data was available (May – Sept). Within the model, each time step represents one hour. Each simulation scenario was run 100 times.

2.3.2 *Model validation*

Model validation was performed by comparing model outputs for the total area of bear home ranges, daily and yearly total distance travelled, and daily displacement to observations seen in the radio-collared bears. Home range is calculated using a minimal convex polygon (MCP); a method used previously in grizzly bear home range analysis (e.g. Nielsen et al. 2013). Daily and yearly distances travelled were calculated as the linear distance between each of the location points obtained during a day or year, respectively. Daily displacement is the linear distance between the first and last locations in a day, which can be indicative of circular movement or reuse of the same areas in a day.

Validation of the model was completed using a subset of the 2013-2017 data as well as data collected during 2018 chosen based on the availability of location points throughout the year (n = 12). Only female bear trajectories were used during validation. In line with other studies (Nielsen et al., 2013; Sorensen et al., 2015), only trajectories from radio-collared bears that contained over 50 locations each season were used. When bears met the criteria on multiple years, the year with the most days with locations was selected. Only days with over 20 or 40 locations for trajectories collected every hour and every half hour, respectively, were used for validation of distances travelled and daily displacement. Simulation data used for validation consisted of yearly bear trajectories from the *learning with memory* scenario produced after year 7 of the simulation. While three scenarios were run to assess the effects of learning and memory on grizzly bear movement, only the *learning with memory* scenario is meant to be representative of real grizzly bear movement behaviour and hence only results from this scenario are used for validation.

2.4 Results

2.4.1 *Model validation*

Simulated bear trajectories produced results consistent with measurements obtained from radio-collared females. Average home range size for simulated bears ranged from 83.97 km^2 to 1475.64 km^2 (μ = 338.68 km^2, σ = 180.35) while radio-collared home range sizes were between 73.57 km^2 and 820.73 km^2 (μ = 335.58 km^2, σ = 199.99). A Welch two-sample t-test (two-sample t (11.10) = 0.05, p = 0.96) suggests that there is not a significant difference between the home range sizes of the radio-collared females and the home range sizes of the simulated bears. This supports the ability of our model to accurately simulate movement decisions that lead to the emergence of home ranges similar in size to those emerging from the movement decisions of real female grizzly bears (Figure 2-2).

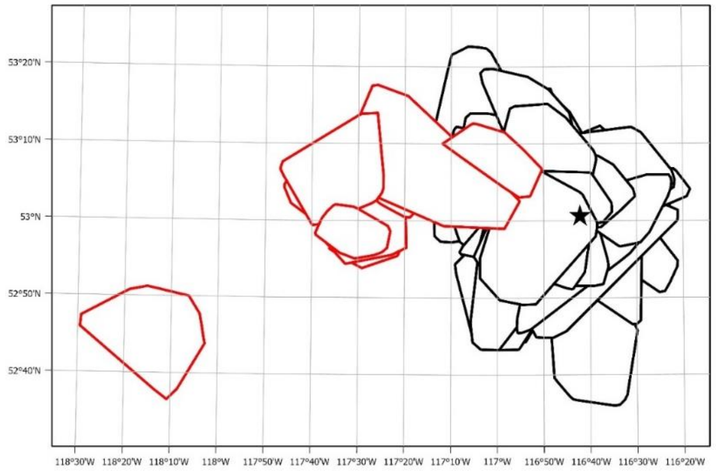

Figure 2-2. Home ranges of simulated grizzly bears from year 15 of the *learning with memory* scenario (n = 100, black) and from radio-collared bears (n = 9, red). Only home ranges from radio-collared bears within a 100 km radius of the starting point of simulated bears (black star) are shown.

Radio-collared female bears travelled between 0.36-31.76 km (μ = 7.56 km, σ = 4.64) each day and between 607-1472 km yearly (μ = 1006 km, σ = 305). This concurs with previous reports of female grizzly bear movement rates of 292 m/h (Graham & Stenhouse, 2014), equivalent to 7 km a day and just over 1000 km in the May – October period. Simulated bears travelled less than radio-collared bears on average, with a mean daily distance travelled of 3.74 km (σ = 0.49) and a yearly mean distance travelled of 572.3 km (σ = 59.95). Daily displacement of simulated bears (0-3.78 km, μ = 1.52 km, σ = 0.49) was similar to that estimated for radio-collared bears (0-18.28 km, μ = 2.90 km, σ = 2.69).

2.4.2 *Simulation results*

In order to evaluate the role of learning and memory in grizzly bear movement behaviour and home range establishment, we compared results from the three scenarios (*random*, *learning*, and *learning with memory*) in terms of average and annual home range sizes as well as the annual measures of success. Comparison of average home range sizes for each of the three simulations was done using all simulation years of the *random* scenario but only trajectories generated in years >7 in the *learning* and the *learning with memory* scenarios. Average annual home range sizes were considerably larger for bears in the *random* scenario (range 173.4-1921.2 km^2, μ = 709.2 km^2, σ = 246.70) and the *learning* scenario (range 175.4-1647.6 km^2, μ = 678.8 km^2, σ = 214.76) than for bears in the *learning with memory* scenario (range 73.57-820.73 km^2, μ = 379.81 km^2, σ = 238.41) (Figure 2-3).

Annual home range sizes for bears in the *random* scenario did not change throughout the simulation. Meanwhile, bears in the *learning* scenario experienced an increase in home range size during the first 10 years of the simulation and bears in the *learning with memory* scenario saw a reduction in home range size during the same period. Only home ranges emerging in the *learning with memory* scenario coincided with average adult female home range sizes observed in radio-collared bears (Figure 2-4).

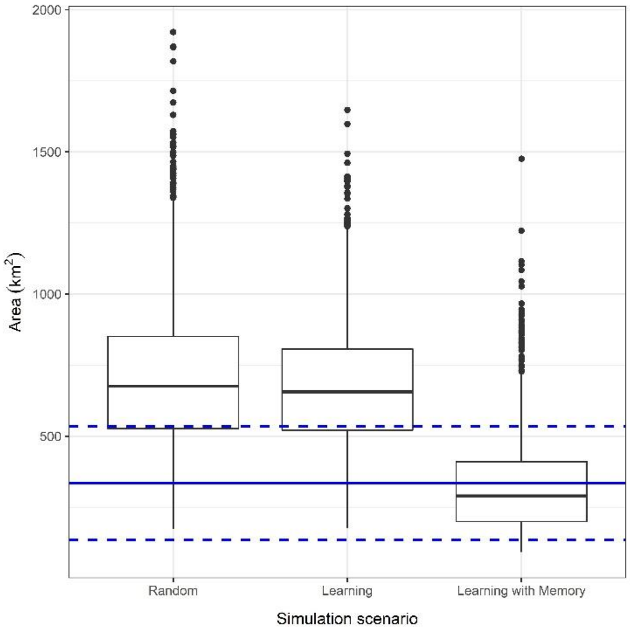

Figure 2-3. Boxplot showing home range sizes for all bears in the *random* scenario and bears >7 years old in the *learning* and *learning with* memory scenarios. Blue lines show mean home range size (solid) and standard deviation (dashed) for radio-collared bears.

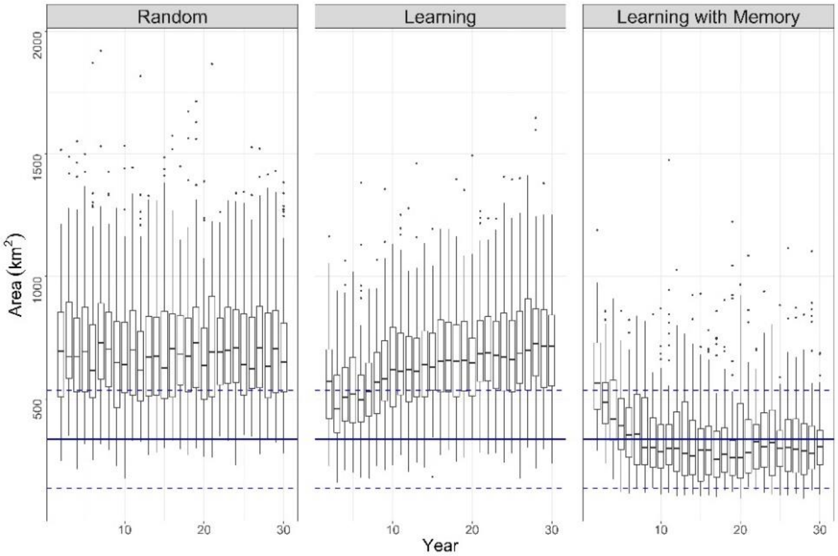

Figure 2-4. Average annual home range sizes for *random*, *learning*, and *learning with memory* scenarios. Blue lines show mean home range size (solid) and standard deviation (dashed) for radio-collared female bears.

We additionally compared yearly measures of success, MoS, at the local and global scales in each of the three scenarios in order to determine the role of learning and memory in the ability of bears to exploit high-quality areas. The average MoS at the global scale remained low throughout the simulation for bears in the *random* scenario in comparison to the global MoS obtained by bears in the *learning* and *learning with memory* scenarios (Figure 2-5). As expected, an increase in exploitation coinciding with an increase in the search parameter in the *learning* and *learning with memory* scenarios resulted in an increase of global MoS during the first years of each of these scenarios. Improvement in the global MoS for both scenarios occurs rapidly during the first eight years of the simulation in line with the rapid increase in the search parameter during this time. However, the *learning with memory* scenario continues to show increase in MoS beyond the years during which the search parameter is increasing, with leveling off occurring in year 10 instead of year 7, as seen in the *learning* scenario. Both the *learning* and *learning with memory* scenarios result in a similar overall landscape MoS after year 10 of the

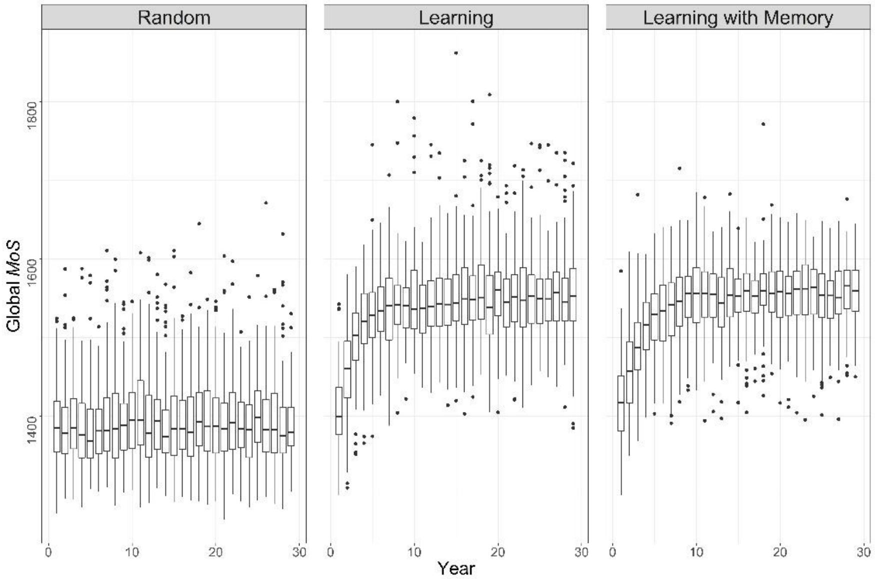

Figure 2-5. Yearly global $\boldsymbol{MoS_s}$ obtained by each bear (n = 100) during the *random*, *learning*, and *learning with memory* scenarios.

simulation. Local MoS for the three scenarios show similar results, with MoS in the *random* scenario remaining low throughout the simulation compared to the *learning* and *learning with memory* scenarios, which show an increase in local MoS during the first 10 years of the simulation before levelling off (Figure 2-6). In contrast to global MoS, local MoS level off slightly higher in the *learning* scenario than the *learning with memory* scenario.

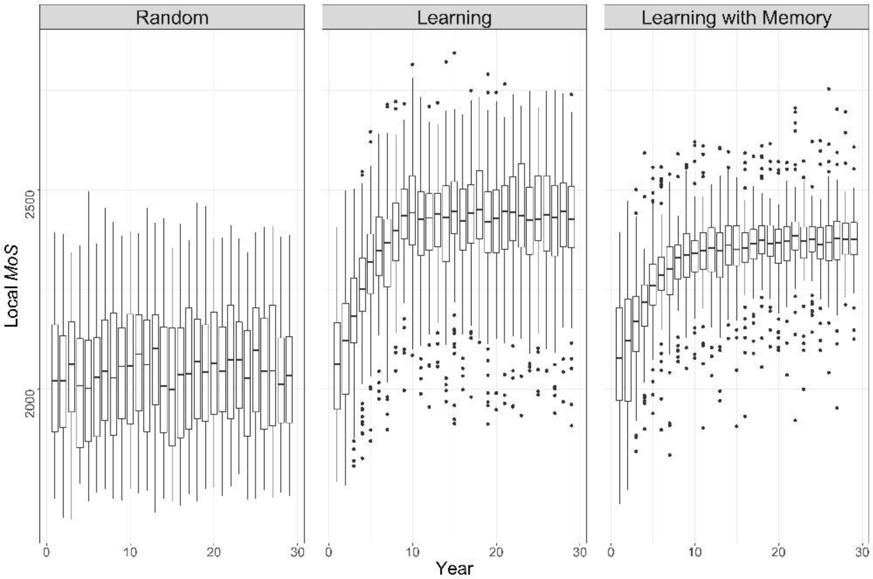

Figure 2-6. Yearly local $\boldsymbol{MoS_s}$ obtained by each bear (n = 100) during the *random*, *learning*, and *learning with memory* scenarios.

2.5 Discussion

The model presented here provides insights into the role of cognition and movement in the emergence of home ranges in grizzly bears using agent-based modelling. Validation of our model showed agreement between home range sizes of simulated bears and grizzly bears radio-collared in the Yellowhead BMA. Although reported home range sizes for adult female bears in west-central Alberta are larger than those reported here (Boulanger et al., 2018; Graham & Stenhouse, 2014; Smulders et al., 2012), this could be due to differences in the way home range sizes were calculated and the limited length of our modelled period. Depending on their reproductive status, female adults in the area enter their winter dens between the first and third week of November and emerge in mid or late-April (Graham & Stenhouse, 2014), and the smaller home range sizes reported here could likely be a result of the reduced time period used to determine home range sizes in this project. Furthermore, travel distances and displacements resulting from our model are realistic in terms of grizzly bear movement, but do not accurately represent the variance seen in measures of radio-collared grizzly bears. Although our model could be parameterized to produce higher and more varied movement rates, it is important to note that the purpose of the model is not to represent movement paths, but instead to capture the emergent properties of movement such as home range size.

After validation, evaluating three scenarios with our model allowed us to differentiate between effects of directed movement, learning, and memory on home range emergence and success in occupying high-quality areas. In the *random* scenario, bears did not use information about their surroundings to make movement decisions and strictly moved following a correlated random walk. As a result, no movement patterns suggesting home range emergence were seen and no behavioural differences developed throughout the simulation. In our model, the implementation of a memory component in the *learning with memory* scenario integrates the concept of cognition by allowing bears to store information gained from previous visits to an area. Out of the three scenarios tested, only the *learning with memory* scenario led to the emergence of home ranges showing the success of our model in simulating repeated space-use by grizzly bears and that, similar to real grizzly bears, simulated bears will return or visit spaces close to previously used areas (Nielsen et al., 2013). Establishing a home range has many benefits as animals incur energetic costs related to locomotion, gaining familiarity, and establishment every time they settle in a new area (Switzer, 1993). Grizzly bears rely on information concerning availability and distribution of food and other resources as well as social dynamics that may lead to mating, competition, or conflict with conspecifics while selecting suitable habitat and establishing an annual home range. By using memory and returning to previously visited areas, grizzly bears are able to exploit resources within an area and avoid unnecessary travel to new and unknown habitats. The *learning* scenario, which simulated use of landscape information in order to exploit high-quality areas, did not result in home range emergence since bears had no incentive to return to previously used areas. Bears in this scenario occupied areas similar in size to those produced by bears in the *random* simulation, suggesting that the use of landscape information in the context of our model does not lead to a restriction in the area used. While this may be different if bears had been initiated in an area consisting of high-quality cells surrounded by low-quality cells, bears simulated in a heterogeneous landscape are likely to exploit surrounding cells and eventually reach high-quality areas, even if they are far from the starting point. While this movement behavior may be true for some species, grizzly bears benefit from establishing a home range given the seasonal nature of the food resources they rely on and the potential energy costs of relocating to new areas.

Compared to the *random* scenario, both the *learning* and the *learning with memory* scenarios resulted in higher overall measures of success at both the local and global scales. While this is partly a direct result of the increase in exploitation behavior given an increase in the search parameter, these results suggest that the use of memory does not necessarily translate into improved exploitation of high-quality areas. This is consistent with the notion that animals may settle in areas of lower quality based on factors such as variability of quality within the area, reproductive outcome predictability, population pressures, or limited knowledge of alternate areas (Switzer, 1993). It is also important to note that our results are constricted by the fact that bears are initiated in the same cell each year and are not allowed to permanently settle in areas away from the starting point, as can be true for grizzly bears. In the wild, bears identify high quality or low risk areas while moving through their environment and may choose to establish a new home range that ensures higher probability of survival than areas previously used, especially during dispersal in the first years of independence (Blanchard & Knight, 1991; Graham & Stenhouse, 2014) or in heterogeneous landscapes with low resource predictability (Edwards et al., 2009). While female bears often remain close to the maternal home range (Pasitschniak-Arts, 1993), grizzly bears may show annual shifts in habitat use related to changes in resource availability and social dynamics (Edwards et al., 2009). Incorporating denning behaviour and allowing bears to start in different points each year based on annual landscape characteristics may have provided a more accurate representation of annual home range shift in grizzly bears. Despite being restricted to one starting point, however, simulated bears in the *learning with memory* scenario were able to reach similar success measures than bears in the *learning* scenario. While the latter generally travel further within the study area and reach high-quality areas far from the starting point, grizzly bears in the *learning with memory* scenario were able to secure similar quality spaces by developing a detailed cognitive map of previously visited areas and using it to inform future movement decisions. These results may suggest that, if allowed to relocate away from the starting point, bears in the *learning with memory* scenario would be more effective in securing high-quality areas.

In summary, our model was successful in simulating multi-scale movement decisions in a dynamic landscape and promoting the emergence of home ranges through the use of reinforcement learning and memory. Further dynamic models should implement increasingly complex movement behaviours that include social dynamics as well as landscape change throughout the simulation in order to address some of the shortcomings of the current model. Our findings, however, highlight the applicability of agent-based modelling in animal movement and support previous research in that memory is a key component in the emergence of home ranges in non-territorial species (Van Moorter et al., 2009). The current model is useful for assessing the role of memory-informed movement in optimal use of resources and may support future research in this area. Additional studies could focus on utilizing this model as a tool for assessing movement and learning behaviours in wide-ranging species like the grizzly bear. There is high potential for using ABM as a tool to understand how landscape changes might affect wildlife space-use and the ability of individuals to access adequate resources in new environments. We encourage further research to expand on our work and develop similar models that can help inform future management and conservation of threatened species like the grizzly bear by, for example, including additional landscape features and assessing how movement behaviour changes as anthropogenic features develop in a landscape.

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3. Evaluating the role of environmental familiarity and behaviour in the success of wildlife translocation: A grizzly bear case study using agent-based modelling

3.1 Introduction

Increased human activity in wildlife habitat has led to a surge in human-wildlife conflicts (Ripple et al., 2014). As a consequence, animal translocation, defined by the IUCN as the deliberate movement of organisms from one site for release in another (IUCN, 2013), has been used as a mechanism to remove problematic carnivores from areas of conflict to locations assumed to have less risk of human-wildlife interactions. Support for animal translocations has increased in recent decades since this method offers an alternative to euthanization of an individual that can contribute to, rather than impede, species conservation efforts (Linnell et al., 1997). Despite this, translocations can be costly and results show varying levels of success, with translocated animals frequently directing their movements towards the area of capture and often returning to their original habitat (i.e. homing), becoming involved in repeated conflict, or dying due to hunting, malnourishment, or other unknown causes (Fischer & Lindenmayer, 2000). As the only non-lethal alternative that allows problem animals to remain in the wild, translocations harness immeasurable value to the overall success of threatened populations. However, translocation success must be increased if this is to become a standard management measure when dealing with problem wildlife.

Translocation methods have been used to relocate a variety of species including birds (Kemink & Kesler, 2013), ungulates (Frair et al., 2007; Warren et al., 1996), and carnivores (Bradley et al., 2005; Hayward et al., 2007; Terhune et al., 2010). Within large carnivore species, however, the grizzly bear (*Ursus arctos*) is perhaps the most often subject of translocations related to human-wildlife conflict due to their high propensity to seek food near human establishments and the potential danger they pose towards humans (Linke et al., 2013; Marley et al., 2017; Northrup et al., 2012). While translocation efforts may reduce wildlife mortality rates due to human conflict and have the potential to contribute individuals to declining or endangered populations, the success of grizzly bear translocations has shown mixed results (Kasworm et al., 2007; Milligan et al., 2018; Riley et al., 1994).

While translocation methods and techniques have remained constant throughout the years, in the last three decades more studies have monitored translocated bears in an attempt to improve success rates, with most assessments focusing on differences in age, sex, and reason for failure including homing behaviour (Beeman & Pelton, 1976; Fies et al., 1987; Landriault et al., 2009; Miller & Ballard, 1982). Previous research has also highlighted the importance of social dynamics on the fate of a translocated bear (Riley et al., 1994), and it has been suggested that placing bears in high-quality habitat, particularly in areas with low human activity and reduced hunting pressure, may increase translocation success and justify the related costs (Alldredge et al., 2015; Letty et al., 2007). To date, an assessment of the role of landscape characteristics and time of year has only been explicitly accounted for in one study (Milligan et al., 2018). By comparing translocation outcomes from bears moved between 1974 and 2014 in Alberta, Canada, this study found that translocated bears were most likely to succeed if moved earlier in the year. Additionally, decreased mortality risk related to road density, water, and edge features also led to higher success rates. Understanding what factors related to landscape characteristics affect the outcome of a translocation will allow managers to select more suitable areas for release. While these findings provide critical knowledge to assist with conservation, it is important to understand the role of landscape characteristics in more detail and acknowledge the role of variables aside from an individual's demographic characteristics and the social hierarchies that may impede individuals from establishing an active role within the new population. For example, there is a need to recognize that behavioural differences between individuals may play a role in translocation outcome (Found & St. Clair, 2016; Réale & Festa-Bianchet, 2003) and should also be considered when assessing translocation outcomes.

Recent grizzly bear research has highlighted the propensity of individual variation to dictate movement behaviour in this species (Hertel et al., 2017, 2019). Although some of this variation is in part due to easily identifiable characteristics such as age or sex, it has also been suggested that behaviour may be dependent on intrinsic personality traits such as boldness (Hertel et al., 2019). In this last study, authors found that there exists positive correlation between travel distance, displacement, and diurnality, which may indicate differences in exploratory behaviour and potentially boldness in the bear population studied. It is believed that bears that travel more through exploration usually spend less time foraging and expend more energy by moving larger distances, but they also have a higher probability of finding high-quality habitat that is safe and offers plentiful resources. While considerations of animal personality are relatively new in the conservation field, particularly when it comes to large animals that are difficult to observe such as the grizzly bear, there is large potential for use of animal behavioural syndromes supporting management actions such as translocations.

This study aims to highlight the importance of considering both landscape characteristics and behavioural profiles for providing new information on the potential success of grizzly bear translocation. We use an agent-based simulation modelling approach to assess how differences between resident and translocated habitat as well as how the role of exploration influences the ability of individuals to adapt to novel environments. Simulation modelling has shown promise for ecological purposes as it offers the ability to assess scenarios that can be invaluable in cases when experimental management scenarios are implausible (DeAngelis & Yurek, 2017). Our study is based on an existing ABM of multi-scale decision-making, learning, and memory in grizzly bears (Chapter 2). We test four behavioural profiles with varying approaches to exploration, representing different levels of boldness in different translocation scenarios, where boldness is used as an indicator of higher exploration, and hence increased activity and movement as per Hertel et al. (2019). By comparing the habitat quality accessed and two measures of movement, we aim to determine how boldness and landscape characteristics affect a bear's ability to access high-quality habitat. Specifically, we evaluate the assumptions that (1) bolder behaviours, consisting of more exploration post-translocation, will eventually lead to increased use of high-quality habitat, (2) bolder behaviours will lead to increased movement measures, with bold bears using larger areas, and (3) boldness will have a lesser effect in individuals translocated to environments similar to their original habitat. Through this analysis, we aim to highlight the need for more specific monitoring of translocated individuals and their habitat preferences as well as showcase the use of ABM for conservation purposes.

3.2 Methods

3.2.1 *Study Area*

Our study takes place in the Yellowhead Bear management area (BMA 3) of west-central Alberta, Canada (Figure 3-1). The study area, spanning approximately 11,500 km^2, comprises various land-use and resource management areas. It is characterized by protected areas on the west side of the region where development and anthropogenic activities are limited, and by boreal forest foothills on the east that host a variety of natural resource extraction industries and support a high level of human activity. Local changes in climate and resource availability reflect the area's topographic complexity (elevation ranges from 900-2700 meters above sea level).

Mean precipitation ranges between 450-800 mm a year, and temperature ranges from 12°C in the summer to −7.5°C in the winter (Bourbonnais et al., 2014). Common bear foods in the region include alpine sweetvetch *(Hedysarum alpinum),* cow-parsnip *(Heraculeum lanatum),* horsetail *(Equisetum),* clover *(Trifolium),* buffaloberry *(Shepherdia canadensis),* huckleberry *(Vaccinium sp),* and bearberry *(Arctostaphylos uva-ursi),* as well as ungulates and insects (Munro et al., 2006; Nielsen et al., 2010).

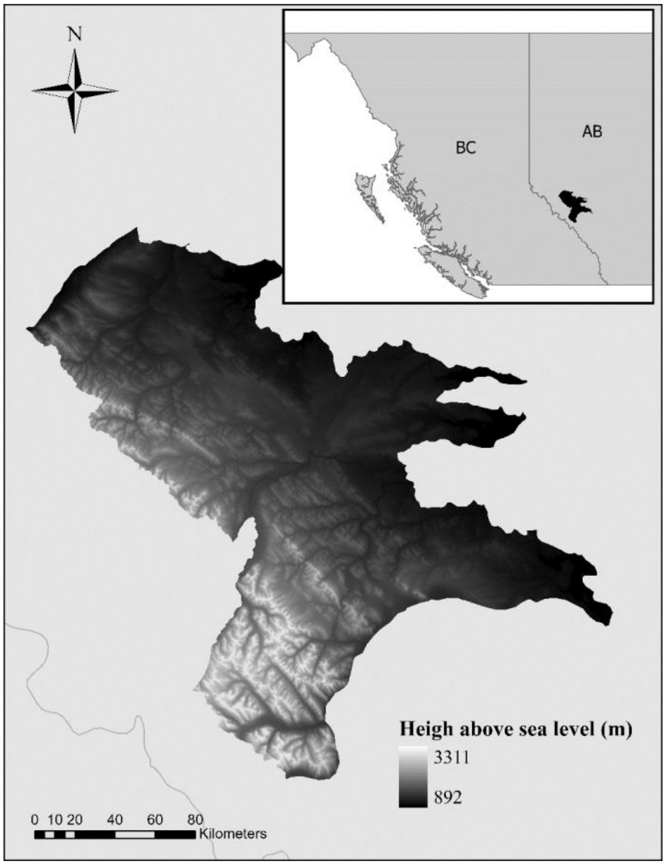

Figure 3-1. Map of study area showing height above sea level (m).

The Yellowhead area is home to a recovering population of grizzly bears, which has recently increased following historic high levels of disturbance primarily due to human development in the surrounding areas (Stenhouse et al., 2015). Despite this population increase, reasons for grizzly population growth in the region remain uncertain due in part to the translocation of conflict bears into areas with declining numbers (Proctor et al., 2012; Stenhouse et al., 2018). A hunting moratorium was established in 2006 following estimates that suggested a population size of 43 individuals, and the status of the species was changed from *Special Concern* to *Threatened* in 2010 (Festa-Bianchet, 2010). Although these efforts have increased the level of protection and support for grizzly bear conservation in the area, human conflict and increasing human activity in bear habitat continues to jeopardize the specie's success.

3.2.2 *Data*

Resident bear location data was collected by the fRI Research Grizzly Bear Program (fRIGBP) between 2013 and 2017. Grizzly bears, captured using culvert traps or helicopter aerial darting (see methods in Cattet et al., 2008), were fit with a GPS radio-collar if over 2 years old. During the non-denning period (approximately April 1 to October 31), positional data was collected every 30 or 60 minutes. Grizzly bear captures were authorized under research permits obtained from Alberta Environment and Parks, Alberta Tourism and Parks, and Parks Canada and all capture and handling protocols were accepted by the University of Saskatchewan Committee on Animal Care. A subset of twenty-three bears (10 female bears and 13 male bears) whose locations were within the boundaries of BMA 3 was used to generate model layers for a total of 120 bear trajectories (n = 120).

Spatial data of landscape features were provided by the fRIGBP, which consisted of the road network throughout the study area, areas of forests that were recently harvested or impacted by wildfires, a digital elevation model (DEM), classification of land cover, and food resource abundance. Road and harvested area layers are products of the 2016 Human Footprint Inventory of Alberta (Alberta Biodiversity Monitoring Institute, 2018), and hence are representative of landscape conditions circa 2016. The road layer consists of paved and unpaved roads, trails, and major highways; no distinction was made between types of road during this study despite evidence that individual bears respond differently to these features (Graham et al., 2010; Herrero et al., 2012) to prevent added complexity that would distract from the study objectives. Harvested areas represent areas in which forestry harvesting operations have occurred in the past 100 years. Fire data from the Government of Alberta includes all recorded fires in the area since 1936. While we acknowledge that features at varying ages serve different purposes for grizzly bear use (Stewart et al., 2012), we also did not account for variation in grizzly bear responses to features at different regeneration stages. The DEM layer was used to calculate a Terrain Ruggedness Index (TRI) which measures the elevation difference between adjacent cells and provides a measure of terrain heterogeneity (Riley et al., 1999). The land cover layer represents eight land cover classes including upland and wetland trees, upland and wetland herbs, shrubs, water, barren, snow/ice, agricultural land, and anthropogenic disturbances composed of mines, pipelines, railways, reservoirs, roads, active and abandoned wellsites, harvested areas, and transmission lines. Resource abundance data consists of ten bi-weekly (May 1 – September 30) food models of absolute probability of twenty key food items for grizzly bears representing root digging, frugivory, herbivory, or carnivory. Food models use 2015 landscape data and are therefore most representative of resource abundance in 2015. Resource abundance was estimated using presence-absence, species distribution, and an importance weight calculated using digestible dry matter reported for each of the bi-weekly periods (see Nielsen et al., 2010 for details).

3.2.3 *Simulation model*

We use an existing ABM for simulating grizzly bear multi-scale decision making and learning that highlights the process by which grizzly bears explore, learn, and exploit their surroundings while moving through landscapes. The purpose of the model implementation in this study is to assess (1) the degree to which translocation to a similar environment is more likely to lead to a successful outcome and (2) how differences in behaviour related to exploration (i.e. boldness) affect translocation outcome. We present a general overview of the model environment and processes; see (Chapter 2) for a full description of the model's details.

Model Landscape

In the model, grizzly bears move through two conceptualized gridded landscapes with different spatial resolutions, both of which cover the entire study area. Rather than values of cells in the grid representing observed landcover or topographic attributes, the values are estimates of information that bears utilize at each time step of the model to determine if they should continue to reside in their current cell or move to a neighbouring cell. The first landscape, used by bears to make "global-scale" decisions, consists of 1 km^2 cells, c, characterized by three variables: cell quality, Q, which denotes the value of a cell to resident bears; the memory, M_s, which constitutes the learned value of a cell for translocated bears based on previous experience; and the utility value, U_s, which represents the subjective value of a cell to the bear. While each cell only has one quality value, Q, memory and utility values are available seasonally and hence presented with a subscript s, indicating the season. The three seasons are defined by shifts in grizzly bear food availability: hypophagia (den emergence in spring to early summer), early hyperphagia (early to late summer), and late hyperphagia (late summer to den entrance in late fall) (Nielsen et al., 2010). The value for each of these variables is estimated as follows:

- Using data from radio-collared data collected by FRIGBP between 2013 and 2017, we estimate Q as the preference that resident bears exhibit towards landscape features based on the proportion of time spent in each 1 km^2 cell. We accounted for changes in the density of roads, wildfires and harvested areas as well as the land cover type and terrain ruggedness index (TRI). For example, a cell with high Q represents a cell where many GPS-location points were found, suggesting a strong preference of radio-collared bears towards the landscape features associated with that cell.

- Values of M_s represent the preference simulated bears show towards the selected landscape features and was calculated in the same way as global quality values. Memory values were obtained by simulating bears in a designated point within the study area and calculating the proportion of time spent in each 1 km^2 cell. Simulated bears have different landscape preferences than radio-collared bears since they are familiar with only the environment they experienced, as opposed to the joint preference of radio-collared bears familiar with various areas within the study area. In addition, resident bear space-use is also dependent on other environmental factors as well as social dynamics within the population, which the simulated bears are not influenced by.
- Values of U_s are estimated seasonally based on the cell memory value, M_s, the cell quality Q, and a reinforcement algorithm. At the start of the simulation all global utility values, U_s, are equal to the memory value M_s. Utility values are updated seasonally based on the global quality value of each cell and an algorithm that reinforces use of the cell based on the increase in use of high-quality cells. Reinforcement learning operates by rewarding decisions that lead to successful outcomes (Sutton & Barto, 1998); in our case, the algorithm increases the U_s of visited cells that led to a high seasonal *Measure of Success* (MoS_s, the cumulative quality of all cells visited in a season), so as to increase their attractiveness and

promote revisiting. Utility values are increased proportionally to the percentage increase in the MoS_s. This process represents a bear gaining familiarity with the quality of a cell and reinforcing the use of that cell with increasing visits.

The second landscape consists of 100 m x 100 m (1 ha) cells that overlap the global landscape and is used by bears to make local level decisions. At the local scale, we considered distance to roads as well as TRI and resource availability. Given the seasonal nature of resource availability, local seasonal values were calculated for each of the hypophagia, early-hyperphagia, and late-hyperphagia periods. Values for the local quality, q_s, were once again calculated based on the preference shown towards certain features by resident radio-collared bears within each 1 ha cell. Local memory values, m_s, were similarly calculated using locations of simulated bears. Local utility values, u_s, are initially equal to m_s and are updated seasonally based on local quality values, q_s, and the reinforcement algorithm. While quality and memory values are static throughout the simulation, utility values at both the global and local scales are updated seasonally to reflect changes in a bear's attraction towards and individual cell based on increased familiarity gained through repeated use.

Bear movement

The ABM simulates bear movement using a wildlife simulation modelling approach in which an animal compares trade-offs between staying at their current location (i.e. cell) or moving to a cell in the surrounding neighbourhood (those cells surrounding their current location). There are numerous approaches to govern how bears make these decisions; in this study, a bear either uses either an "explore" or "exploit" tactic to decide where to move. Whether a bear explores or exploits is dependent on their assigned behavioural profile (i.e. bold, conservative, shy, or greedy) and the corresponding search parameter formula. The search parameter, ε, which determines the percentage of moves in which bears will exploit, increases seasonally based on the profile-specific formula (Figure 3-2).

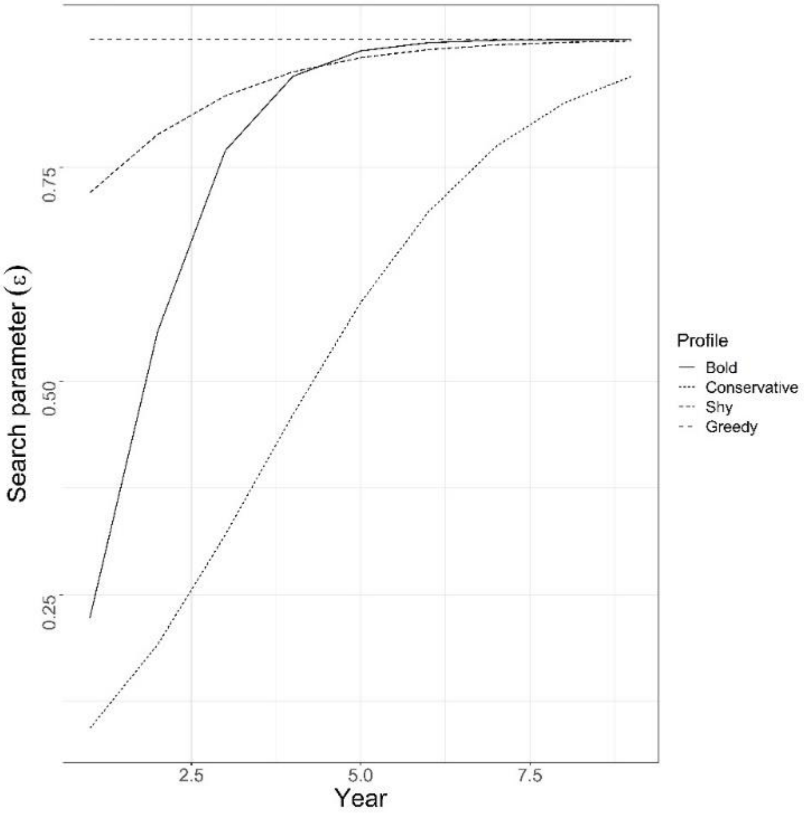

Figure 3-2. Search parameter functions for the four behavioural profiles tested, where larger search parameters translate to a higher probability that a movement will be exploitative.

When employing the explore tactic, bears perform a correlated random walk (Codling et al., 2008) in which they turn based on an angle extracted randomly from a normal distribution ($\mu = 0, \sigma = 20$) and move 100 m forward each time step. If a bear is using the exploit tactic, it will make movement decisions based on utility values of cells at the two scales described above. Model calibration was used to determine how U_s dictates where bears move: if U_s of the currently occupied 1 km^2 cell is above 0.15, the bear will select the cell within a 250 m radius with the highest local utility value, u_s, and move towards it. Otherwise, the bear assesses the eight surrounding 1 km^2 cells and selects the one with the highest U_s. Then, the bear faces a random 1 ha cell within the selected 1 km^2 cell and move towards it by selecting the 1 ha cell within a visual cone of 90 degrees and 250 m with the highest u_s. This process is repeated with a different 1 ha cell within the target 1 km^2 cell chosen each time until the bear reaches the selected 1 km^2 cell. Global and local utility values are reduced by 20% and 65% each time step, and replenished at a rate of 20% and 1%, respectively. The selection of the various movement parameter values were tested and validated in Chapter 2.

Memory and learning

Representations of memory and learning are implemented into the ABM using an approach called reinforcement learning (Sutton & Barto, 1998). This type of machine learning operates by reinforcing decisions an agent makes while interacting with its environment which lead to a successful outcome. In our model, reinforcement learning is employed by first recording the bear's location at each time step as well as a seasonal measure of success (MoS_s) at cell c for each of the two scales. The global $MoS_{G,s}$ is calculated after each step by adding the global quality value, Q, of the occupied 1 km^2 cell. Similarly, the local $MoS_{l,s}$ is calculated using the local quality value, q_s, of the occupied 1 ha cell. All MoS_s are set to zero at the start of a simulation and at the start of every season. At the end of each season, global and local utility values, U_s and u_s, of all cells visited within that season are updated using the reinforcement algorithm. Reinforcement is always positive but the effect is proportional to the ratio between the MoS_s obtained in the current simulation year and that of year 1 in the same season. Hence, cells visited in a year in which the MoS_s are much higher than in year 1 will be reinforced more than cells visited in years in which MoS_s improvement is not as great. Cells frequented in multiple occasions are subject to multiple reinforcement events and hence hold a larger utility value to bears.

3.2.4 *Simulation experiments*

As stated above, this study aims to test three assumptions: (1) bolder behaviours, consisting of more exploration post-translocation, will eventually lead to increased use of high-quality habitat, (2) bolder behaviours will lead to increased movement measures, with bold bears using more cells and larger areas, and (3) boldness will have a lesser effect in individuals translocated to environments similar to their original habitat. To accomplish this, our simulation design includes a comparison of bear behaviour in a landscape that is *Similar* to that which the bear experienced before translocation, and a second landscape representing a very different "*Different*" landscape. These landscapes were selected by analyzing the landscape and topographic attributes in the study area to determine starting points (i.e. the area in which the bear is placed at the beginning of a simulation) that are similar and different to where a bear existed prior to translocation. As a result, our simulated site of capture and the *Similar* release site are both located within the foothills region of BMA 3, while the *Different* release site is located in the mountains.

Four different exploration scenarios were tested in both the *Similar* and *Different* landscapes. The first scenario, "*bold"*, consisted of high exploratory movements in the year after translocation followed by a rapid increase in exploitation. A second scenario, *"conservative"*, tested the same learning curve used in the original model (see Chapter 2), with initial movements dominated by exploration and a slow increase in exploitation during subsequent years. A *"shy"* scenario consisted of bears exploring only 30% of the time immediately after translocation, with a slow increase in exploitation in subsequent years. The fourth and final scenario, *"greedy"*, tested movements dominated by exploitation from the start. In all eight scenarios "*Different-bold*", "*Different-conservative*", "*Different-shy*", "*Different-greedy*", "*Similar-bold*", "*Similar-conservative*", "*Similar-shy*", and "*Similar-greedy*", bears only ever reach a maximum search parameter, ε, of 0.9. Each scenario was run 100 times for a duration of 9 years, with the first year of the simulation representing the first year after a translocation event. Preliminary results include global and local MoS_s obtained in each of the eight scenarios as well as the number of 1 km^2 cells used each year and the annual home range size. Home range is calculated using a minimal convex polygon (MCP); a method shown to provide robust results (Börger et al., 2006; Van Moorter et al., 2009) and used previously in grizzly bear home range analysis (e.g. Nielsen et al. 2013). Global and local MoS_s and home range sizes for resident bears are also presented in order to provide a comparison for translocation results.

3.3 Results

Global and local MoS_s obtained by resident bears initiated in the $Similar$ and $Different$ habitats (following modelling methodology from Chapter 2) are shown in Figures 3-3 and 3-4. Figure 3-3 shows resident bears in the $Similar$ environment having an overall lower global MoS than resident bears in the $Different$ environment. In other words, bears in the $Similar$ habitat have less access to high-quality habitats at the global scale. In both cases, bears increased their global MoS during the first years of the simulation, with higher variation in global MoS_s obtained by resident bears in the $Different$ environment indicating increased variability in cell quality at this scale. At the local scale, resident bears in the $Similar$ environment increased their local MoS_s during the first years of the simulation (Figure 3-4). In the $Different$ environment, resident bears initially secured high local MoS_s which subsequently dropped to similar levels as that obtained by bears in the $Similar$ environment, suggesting that habitat quality at the local scale is higher in areas away from the *Different* starting point that are only accessed during years of high exploration in which animals travel far by chance. Bears translocated to a *Similar* environment had larger home ranges than bears translocated to *Different* environments, likely as a consequence of the differences in quality of each area. These differences are consistent with previous studies that have found grizzly bear home ranges to be smaller in the mountain regions of Alberta, where our *Different* starting point is located, than in the foothills region, where our *Similar* starting point is located (Milligan et al., 2018).

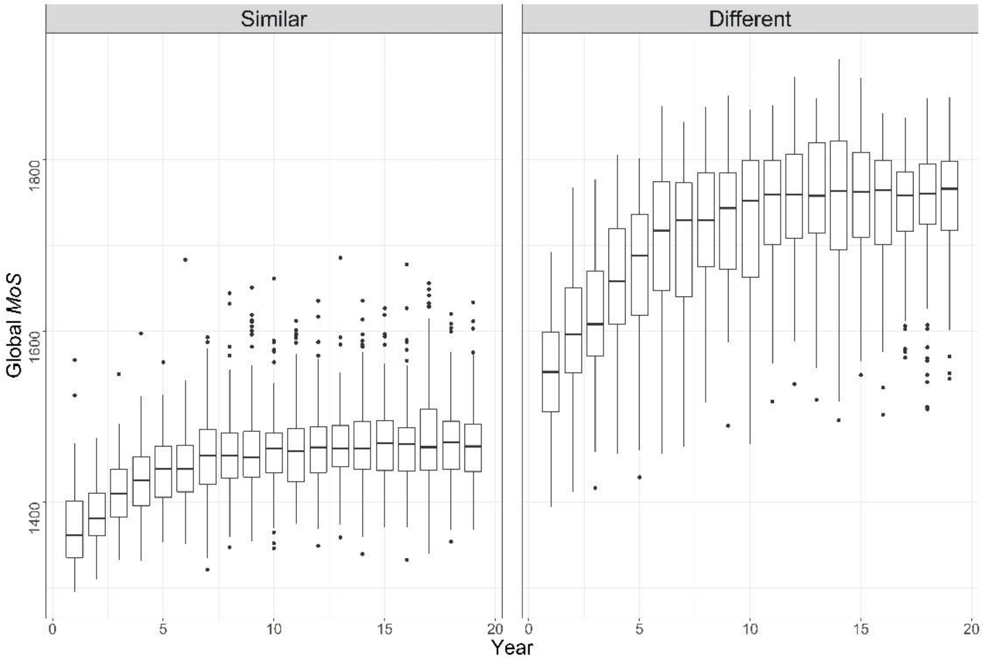

Figure 3-3. Yearly global $\boldsymbol{MoS_s}$ obtained by resident bears (n = 100) initiated in the *Similar* and *Different* environments.

The results from the model simulations are presented in a sequence of time series plots below (Figures 3-5 through 3-8), where each plot shows the global or local MoS_s corresponding to translocated bears in the *Similar* or *Different* scenarios. These results are also summarized in

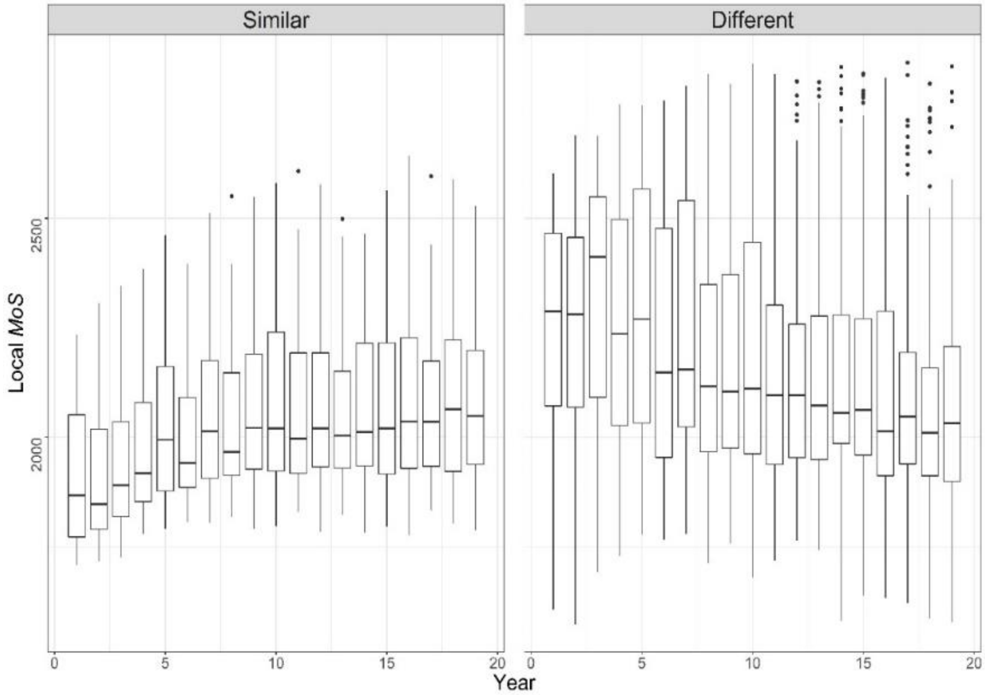

Figure 3-4. Yearly local $\boldsymbol{MoS_s}$ obtained by resident bears (n = 100) initiated in the *Similar* and *Different* environments.

Table 3-1, which indicates the success of translocated bears in terms of the average short- and long-term MoS_s compared to that obtained by resident bears. Short-term observations refer to results from the first two years after translocation, while long-term observations concern the last two years of the simulation (years >8). The table also presents a ranking of success, with 1 meaning the highest MoS_s out of all behavioural profiles and 4 (or 3 in the case of equal results between two profiles) representing the lowest MoS_s.

In general, bears translocated to a *Similar* environment were able to obtain similar MoS_s than resident bears at the global scale, although their performance was reduced at the local scale. Bears translocated to a *Different* environment, on the other hand, were able to reach similar MoS_s as resident bears at the local scale but not at the global scale. While long-term outcomes in both habitats did not differ between behavioural profiles, boldness had an effect in short-term results at the global scale for bears translocated to the *Similar* habitat and at the local scale for bears translocated to the *Different* environment.

Table 3-1. Summary of results comparing global and local median $\boldsymbol{MoS_s}$ of all eight scenarios to the median $\boldsymbol{MoS_s}$ obtained by resident bears in the short (<2 years) and long (>8 years) term after translocation. Simulated median $\boldsymbol{MoS_s}$ were either equal (=), greater than (+), or less than (-) the median $\boldsymbol{MoS_s}$ obtained by resident bears in the same habitat. A ranking of highest (1) to lowest (3 or 4) is assigned to each behavioural profile based on the median $\boldsymbol{MoS_s}$ obtained compared to other profiles within the same scenario.

Starting point		*Similar*				*Different*			
Behavioural profile		*Bold*	*Conservative*	*Shy*	*Greedy*	*Bold*	*Conservative*	*Shy*	*Greedy*
Global MoS_s	*Short-term*	=	=	+	+	-	-	-	-
		3	4	2	1	4	3	2	1
	Long-term	=	=	=	=	-	-	-	-
		1	2	4	3	2	1	3	2
Local MoS_s	*Short-term*	-	-	-	-	+	+	=	=
		2	2	3	1	1	1	2	3
	Long-term	-	-	-	-	+	+	+	+
		1	2	4	3	1	4	2	3

Bears translocated to the *Similar* environment improved their global MoS_s following translocation, but exploratory behaviour affected the way bears performed, particularly during the first two years after translocation (Figure 3-5). Bears of all scenarios reached similar global MoS_s by the end of the simulation, which was comparable to the global MoS_s reached by resident bears in the same environment, with minor improvement seen after year six of the simulation. However, individuals in the *bold* and *conservative* scenarios obtained lower global MoS_s, similar to the global MoS_s obtained by resident bears in the first year of simulation, than their *greedy* or *shy* counterparts in the first two years. *Bold* bears performed slightly better than *conservative* bears in the first year and showed the most rapid increase in global MoS_s out of all scenarios. There are no notable differences in variation between the four scenarios and variation was in general similar to that seen in resident bears.

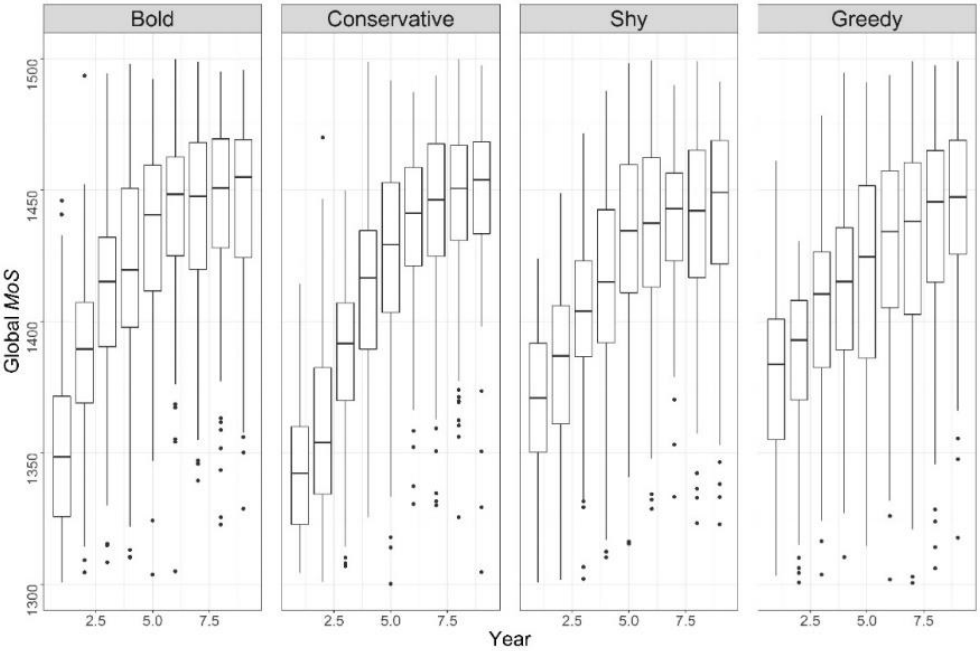

Figure 3-5. Yearly global $\boldsymbol{MoS_s}$ obtained by translocated bears (n = 100) in each of the *bold, conservative, shy,* and *greedy* scenarios starting in the *Similar* environment.

The different behavioural profiles also had an effect on local MoS_s for bears translocated to a *Similar* environment (Figure 3-6). Bears in all four scenarios were able to reach similar local MoS_s by the end of the simulation, with constant increase throughout the nine years. While global MoS_s performance rivalled that of resident bears, local MoS_s remained lower for translocated bears in all scenarios. Unlike the global MoS_s, however, local MoS_s continues to improve during the entire duration of the simulation. While all behavioural profiles performed similarly in the later years of the simulation, *bold* and *conservative* individuals obtained higher local MoS_s in the first year following translocation. Variation in results from translocated bears is considerably less than that of resident bears with the exception of the first year in *bold* and *conservative* bears.

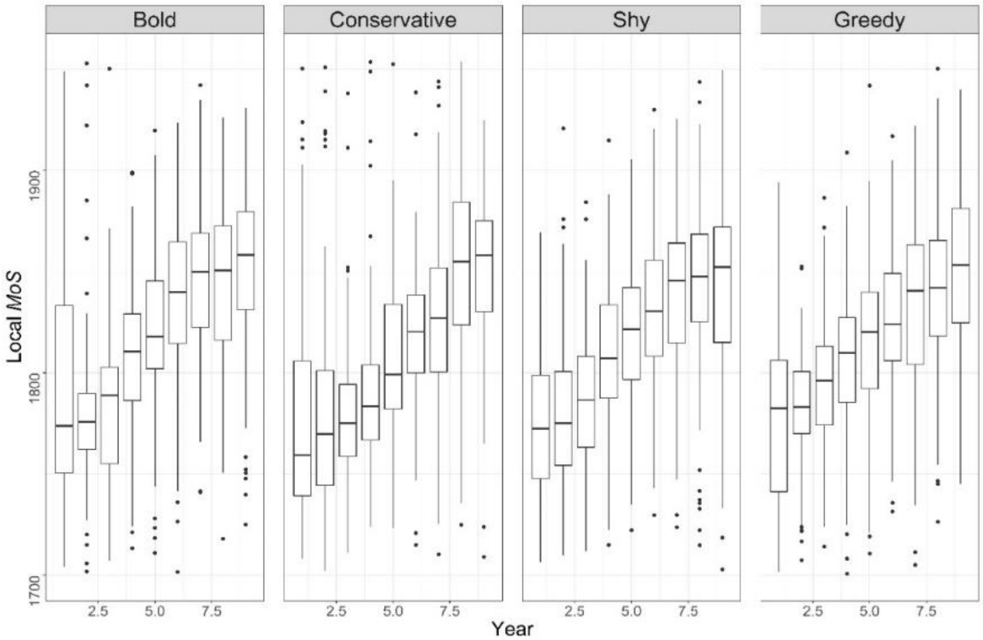

Figure 3-6. Yearly local $\boldsymbol{MoS_s}$ obtained by translocated bears (n = 100) in each of the *bold, conservative, shy,* and *greedy* scenarios starting in the *Similar* environment.

Bears initiated in a *Different* environment also showed some differences in global MoS_s (Figure 3-7) and local MoS_s (Figure 3-8) depending on behaviour. At the global scale, all four scenarios led to a similar global MoS_s by the end of the simulation that was slightly lower than the global MoS_s obtained by resident bears. However, *conservative* bears improved their global MoS_s most rapidly and reached the highest potential results, with some individuals reaching similar global MoS_s than resident bears. Higher exploration behaviours led to lower global MoS_s during the first year, with *greedy* bears obtaining the highest global MoS_s. In year two, *bold* bears obtained a similar global MoS_s to *greedy* individuals, while *conservative* bears continued to have the lowest global MoS_s. Variation was similar between resident and translocated bears, although large variation is seen in the *conservative* scenario, particularly during the last years of the simulation.

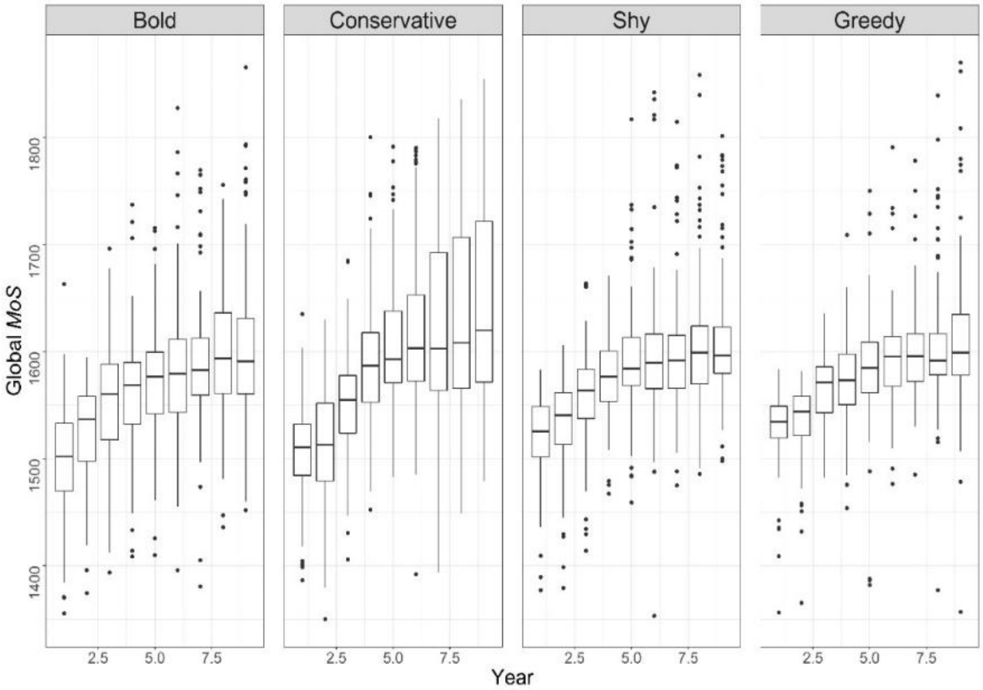

Figure 3-7. Yearly global $\boldsymbol{MoS_s}$ obtained by translocated bears (n = 100) in each of the *bold*, *conservative, shy,* and *greedy* scenarios starting in the *Different* environment.

At the local scale, translocated bears were able to obtain higher local MoS_s than adult residents in the *Different* environment, particularly *bold* individuals which obtained the highest local MoS_s of all scenarios. *Bold* and *conservative* individuals achieved high local MoS_s in year one and maintained that throughout the simulation, while *shy* and *greedy* bears improved their performance during the simulation but had slightly worse performances in the first three years of the simulation. Variation in this case was much lower compared to resident bears, with translocated results showing more variation as exploration increased. Variation was high during the first year for both *bold* and *conservative* bears, and *conservative* bears showed much higher variation in the last years of the simulation. Overall, *bold* bears were most successful at this scale given their ability to reach higher local MoS_s during the first year and consistently throughout the simulation.

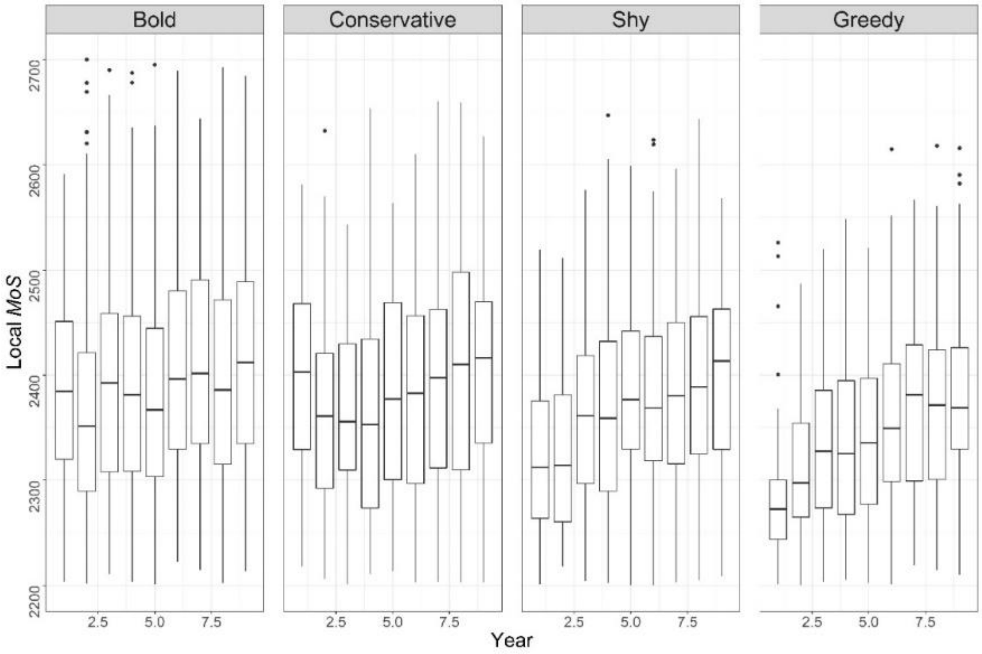

Figure 3-8. Yearly local $\boldsymbol{MoS_s}$ obtained by translocated bears (n = 100) in each of the *bold, conservative, shy,* and *greedy* scenarios starting in the *Different* environment.

The number of 1 km^2 cells used by translocated individuals was similar in scenarios initiated in the *Similar* environment but differed for bears in the *Different* environment (Figure 3-9). In the *Similar* environment, translocated bears in the *bold*, *greedy*, and *shy* scenarios reduced the amount of cell used each year during the first six years of the simulation, after which cell use remained constant. Bears in the *conservative* scenario continued to reduce their use of new cells throughout the entire simulation. Variation increased as the simulation progressed, with the smallest variation seen in year 1 in all four scenarios. In the *Different* environment, all four scenarios converged on a similar number of cells used by the end of the simulation. However, *bold* and *conservative* bears had significantly less number of cells used during the first two years after translocation. In subsequent years, *greedy* and *shy* individuals reduced the number of cells quickly and, by the third year, had equalled the number of cells used by *bold* bears and declined past the number of cells used by *conservative* bears.

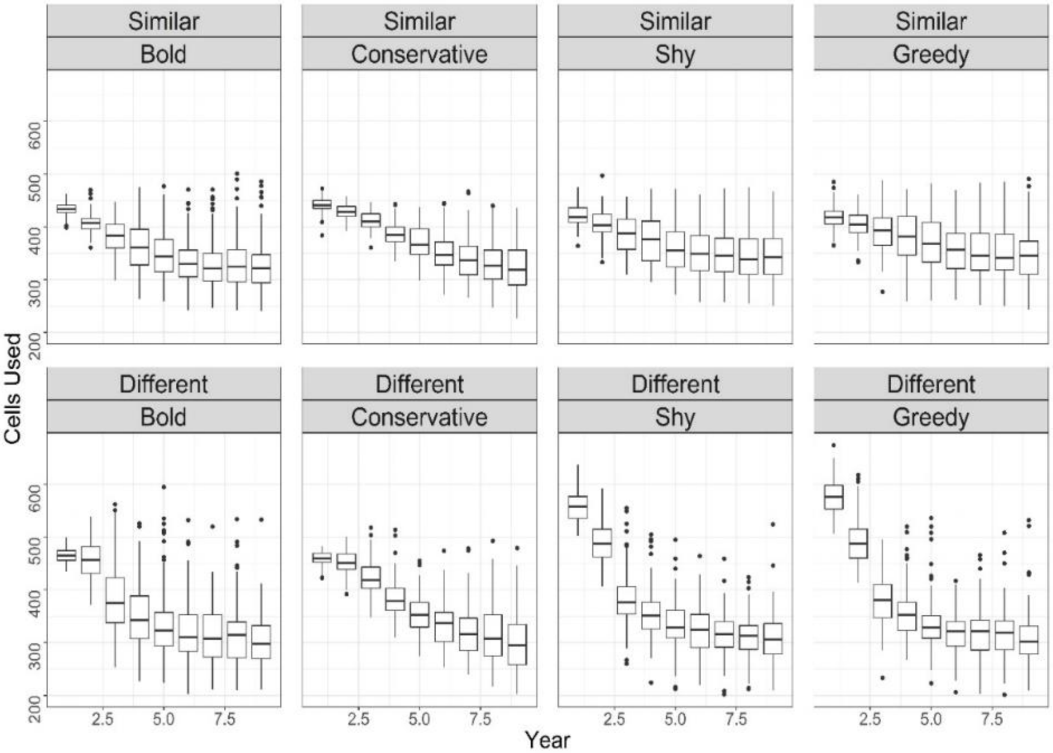

Figure 3-9. Number of cells used annually by bears in each of the eight scenarios.

Home ranges for translocated bears were different for each of the starting points but remained consistent with observed home ranges from radio-collared resident females in the study area (Figure 3-10). Bears translocated to a *Similar* environment had larger home ranges than bears translocated to *Different* environments, although in both cases home ranges were much smaller than those reported for translocated bears in the area (Milligan et al., 2018; Stenhouse et al., 2018). In both cases, *conservative* bears had the largest home ranges immediately after translocation, with *bold* and *greedy* bears following closely. *Bold* and *conservative* bears in the *Similar* environment reduced their home range size gradually during the first years of the simulation, whereas *greedy* bears underwent a slower change and *shy* bears remained somewhat constant for the first four years of the simulation before reducing the home range size. A similar pattern is seen in the *Different* environment, with *bold* bears experiencing the most considerable decrease in home range size between the first and second year and all bears, with the exception of the *shy* individuals, decreasing their annual home range size in the first years of the simulation. Variation was constant between simulations started in the same area but home range sizes from bears initiated in the *Similar* environment were more disparate than those from bears in the *Different* environment.

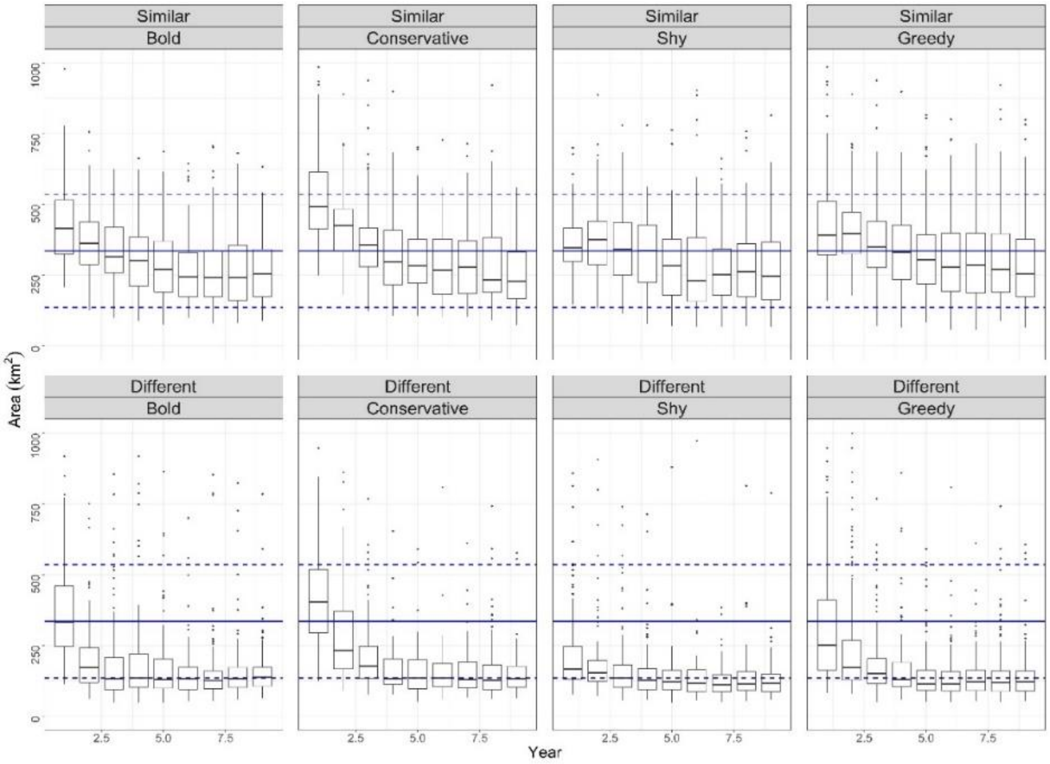

Figure 3-10. Average annual home range sizes for all eight scenarios. Blue lines show mean home range size (solid) and standard deviation (dashed) for radio-collared female bears.

3.4 Discussion

The objective of this study was to implement an ABM in order to evaluate the role of habitat familiarity and behaviour on the ability of translocated bears to use high-quality habitat. Overall, the results demonstrate that bears were more successful in environments with familiar landscape characteristics. Increased exploration behaviour was beneficial in the long run but in most cases, bears with higher exploratory behaviour did poorly in the first two years after translocation. Increased exploration did not lead to increased number of 1 km^2 cells used. Bears translocated to a *Different* environment used more cells if they had lower exploratory behaviour, while bears translocated to a *Similar* environment used equal number of cells regardless of behaviour. Home range sizes were comparable for all scenarios within each translocated environment after year 3, but higher exploration led to larger home ranges in the first two years after translocation.

In the case of resident bears, the results obtained when starting in a *Similar* point were congruent with results obtained in Chapter 2 at both scales. The decrease in local MoS_S seen in the *Different* environment could indicate that higher quality habitat at the local scale is available far from the starting point and bears have more access to it when exploration is high. Once a home range is established and bears remain close to the starting point, however, they are limited in their use of high-quality habitats to those close to the starting point, limiting the potential local MoS_S. The high variation seen in local MoS_S for bears in the *Different* environment suggests that there is high variation in the landscape and that while some bears are able to learn and consistently use higher quality cells, others remain unfamiliar with these areas and are limited to using lower quality habitats. In general, these results indicate that landscape quality at the global scale is higher in the *Different* environment, and that, at the local scale, both starting points have comparable quality available to bears.

In terms of the results for translocation events, our findings indicate that when translocated to a *Similar* environment bears overall perform similarly to resident bears at the global scale. While bears from all behavioural profiles were able to reach similar global MoS_S by the end of the simulations, exploratory behaviour was detrimental in the first years post-translocation. Bears in the *bold* and *conservative* categories, who explored most out of the four behavioural profiles, attained the lowest global MoS_s. In addition, it has been suggested that exploratory behaviour could lead to higher energy expenditures and reduced foraging, with more time spent searching and moving actively than utilizing resources within an area (Hertel et al., 2019). Our results support the notion that, when translocated to similar environments, bears that perform less exploratory behaviour have an advantage in that they can successfully seek high-quality habitats that they are already familiar with. This is consistent with previous research that found wild translocated ungulates adapted better to habitats they were familiar with, particularly in terms of predation risk (Frair et al., 2007). While exploratory behaviour may allow bears to become familiar with new environments that lead to increased use of high-quality habitats in future years, this results in bears occupying less suitable habitat during the first year post-translocation, when the ability to secure high-quality habitat is critical in order to ensure translocation success. At the local scale, however, boldness was related to higher local MoS_s in the first years after translocation to a *Similar* environment. These results likely differ from those found with global MoS_s since, at the global level, bears are more likely to follow larger scale cues that can be generalized to similar environments. At the local scale, bears are familiar with more specific cues that may not be as transferrable to new landscapes with similar, but not equal, cues. Individual differences observed in selection of food resources near railways (Murray et al., 2017), for example, supports the idea that bears differ in their preference for food resources and may develop individual foraging behaviours based on local cues that may hence limit generalization to other environments regardless of similarity.

The differences seen in bears translocated to a *Different* environment indicates that bears moved to habitats they are unfamiliar with are generally unable to exploit resources at the global scale as well as resident bears. However, while boldness is generally detrimental during the first years at this scale, increased exploration allows bears to become familiar with more high-quality habitats that can be exploited in later years, although the large variation seen in *conservative* bears in the last years of the simulation suggests that not all individuals were able to identify and exploit high-quality habitats at the global scale. At the local scale, however, translocated bears generally performed better than resident bears in the *Different* environment, particularly when exhibiting high exploratory behaviours. Given the importance of short-term success for translocated bears, bolder personalities prone to higher levels of exploration might be more successful at the local scale when the release site is unfamiliar and the chances of encountering high-quality habitat are high through exploration.

Previous research has indeed suggested that high exploration is beneficial for adaptation as it increases the chances of encountering unfamiliar but high-quality habitat (Berger-Tal & Avgar, 2012). Increased exploration, however, also has the potential to expose individuals to situations where repeated conflict is likely or areas of high mortality such as roads (Nielsen et al., 2004). Research on elk movement, for example, has shown that increased movement related to bolder personalities is correlated to higher use of open fields and areas near roads where hunters are more common, resulting in higher mortality of individuals with bolder behavioural profiles (Ciuti et al., 2012). Mortality risk is an important factor determining translocation success, with bears translocated to novel environments needing to learn the location of risky habitat or the novel sources of risk related to their new environment.

Results from previous research using multi-scale movement analysis in grizzly bears has suggested that bears avoid high-risk habitat related to human development at the larger scale (i.e. global scale) but select for roads and other anthropogenic features at the local scale (Bourbonnais, 2018). Critical grizzly bear foods are often found in edge habitats artificially created by disturbances such as roads (Roever et al., 2008) and forestry cutblocks (Larsen et al., 2019; Nielsen et al., 2004), but these habitats often pose high mortality risk due to the increased exposure to human activity (Gibeau et al., 2001). Given our results, bolder bears would be likely to access more high-quality habitat at the local scale but not the global scale, meaning they are able to secure adequate food resources at the expense of higher risk exposure. These results are congruent with previous research which has suggested that bold personalities, related to increased movement rates and exploration, tend to access higher quality habitat at the expense of higher risk exposure (Hertel et al., 2019). In our case, individuals exploring more during the first year indeed were able to occupy higher quality cells at the local scale, which is highly resource-dependent, but jeopardized security at the global scale and were exposed to the lowest quality cells of all behavioural profiles. Individuals in the *greedy* profile, which relied mostly on exploitation, were most successful at the short-term in *Similar* environments. Previous research conducted on caribou (Warren et al., 1996) supports our findings that animals translocated to environments they are familiar with are most successful given their ability to recognize and exploit resources, although this is not the case when translocated to *Different* environments. In general, increased exploration is beneficial for long-term success given that individuals are able to become familiar with areas with higher habitat quality. However, boldness is only beneficial immediately after translocation when the release site is not similar to the capture site and only at the local scale.

In this study, movement measures (consisting of the number of 1 km^2 cells used each year as well as the annual home range size) differed between behavioural profiles and similarity in release site. While the number of cells used was comparable in all behaviours for bears translocated to the *Similar* environment, bears translocated to the *Different* habitat exhibiting increased exploitation behaviour used more cells in the first two years post-translocation than bolder bears. Previous research has found that, when exposed to a novel environment, animals that overestimate the value of an unfamiliar area tend to perform better given higher rates of exploration (Berger-Tal & Avgar, 2012). Given our use of utility values to dictate movement decisions, *shy* and *greedy* bears in our simulation are likely following cues leading them to lower quality areas that hence encourage faster transitions between cells, indirectly promoting higher movement. While bears exploring move randomly, bears exploiting exhibit directed movement that, combined with misleading cues, results in increased movement that may expose them to higher-quality habitat. Unlike number of cells used, home range analysis for our simulated bears did show larger area use for bears exhibiting higher exploratory behaviour. This is likely a result of lower revisiting rates; although cells are reinforced seasonally, bears do not revisit reinforced cells unless they are exhibiting exploiting behaviours and using landscape information to make movement decisions. Hence, *bold* and *conservative* bears, which explore more during the initial years, exhibit larger home ranges because they are not revisiting previously used cells and benefiting from the gained familiarity. While our analysis does not implicitly look at revisitation, we acknowledge the potential role of this behaviour in explaining some of the observed patterns and suggest further revisitation analysis (e.g. Bracis et al., 2018).

Although home range sizes for translocated bears were consistent with observed grizzly bear home ranges in the wild, previous analyses of translocated bear home ranges have found that home range sizes of translocated bears are much larger than that of resident bears in the same environment (Milligan et al., 2018; Stenhouse et al., 2018), a pattern we did not observe in our results. While our model incorporates some variables used by bears to make movement decisions, there are many other factors affecting movement rates and home range sizes that we do not account for. Our model does not simulate social dynamics which can lead to social segregation (Steyaert et al., 2013), forcing less dominant bears into less desirable habitat, or directed movement related to mate finding during the mating season (Stenhouse et al., 2005). Previous research has found strong homing behaviour in translocated bears which suggests individuals are able to identify the direction of their original habitat and direct movement towards it (Miller & Ballard, 1982), something our model also does not simulate. The disparity in our results and observed patterns from translocated bears in the area are indicative of the importance of homing behaviour and suggest that bears may not only be making movement decisions based on landscape cues, but that motivation to return to their original habitat or seek familiar environments is leading to increased travel distances and home range sizes.

In summary, our study demonstrated that individual behaviour and general habitat characteristics have the potential to affect the outcome of grizzly bear translocations. While bold behaviours did not always lead to increased use of high-quality habitat in the long term, bears with a bold behavioural profile did eventually obtain higher MoS_s at the local and global scales than all of the other bears in the *Similar* environment, and boldness was generally correlated with higher MoS_s at both scales in the *Different* environment. However, it is important to note that monitoring of translocated bears is limited and most assessments of translocation success will only focus on the initial years after release. Opposite to our original hypothesis that bolder behaviours would result in higher movement measures, we found that behaviour did not influence the number of cells used for animals translocated to a *Similar* environment and that *bold* and *conservative* individuals in the *Different* habitat used less cells than *shy* and *greedy* bears. However, boldness did result in larger home range sizes in both the *Similar* and *Different* habitats during the first year after translocation. While the effect of boldness on indicators of movement is stronger in the *Different* environment, we did not find that boldness had a stronger influence on the ability of translocated bears to use high-quality habitat in one type of habitat than the other. Our results, however, suggest that scale is an important determinant of success, with bears often able to exploit high-quality areas at one scale but not another. We therefore suggest animal movement researchers continue to incorporate a multi-scale component in their analysis.

Our study highlights the use of agent-based simulation models for conservation and management purposes by presenting hypothetical scenarios applicable to a current wildlife management issue. We encourage future studies to elaborate on the current model and consider other factors that may affect translocation success such as population dynamics and added landscape complexity. While our model offers initial insights into the role of personality and environment on translocation success, a more complex model could potentially be used to determine adequate release sites for translocated bears based on landscape characteristics, social dynamics of the resident population, and individual characteristics of the translocated animal. For our translocated scenarios, we selected two starting points that consisted of similar or different landscape characteristics to the capture site. Previous research has found that increased distance between the capture and release sites can increase translocation success, often due to reduced homing behaviour (Landriault et al., 2009; Milligan et al., 2018; Rogers, 1986). While landscape characteristics are not commonly accounted for in assessments of translocation success (but see Milligan et al., 2018), it is often the case that a release site closer to the capture site will have more similar habitat than a release site that is further away. In our study, the *Similar* release site is indeed closer to the capture site than the *Different* release site. However, our model does not account for homing behaviour; we suggest future studies assess the role of both distance and habitat differences in determining an appropriate release site that will offer a familiar environment but where homing behaviour is discouraged. While personality studies are not common in wild species, we support previous findings that introduce personality into conservation issues (Ciuti et al., 2012; Found & St. Clair, 2016; Hertel et al., 2019; Leclerc et al., 2016) and demonstrate here the need to account for individual differences in animal movement studies. Understanding how ideal release sites might differ between individuals depending on their age, sex, personality, and area of capture will aid conservation efforts and contribute to the success of future translocation events, ultimately offering a more viable option for managing problem wildlife.

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4. Conclusion

The goals of this research were to develop an ABM for simulating grizzly bear movement behaviour and to implement that model in order to evaluate the role of behavioural and landscape traits on translocation success. I designed, calibrated, and validated a novel ABM using landscape and GPS data in an attempt to provide new insights into the way behaviour and habitat familiarity may affect translocation success.

For the development of the model, we used traditional machine learning algorithms rooted in the way agents acquire knowledge while moving through their environment as well as the way that knowledge is used in making subsequent movement decisions. We based our design of movement rules on results from previous research indicating that grizzly bears asses their surroundings at multiple scales and have varying preferences depending on scale and the type of feature (Bourbonnais, 2018). We also implemented a reinforcement learning algorithm and tested the role of learning and memory on movement behaviour. Data provided by the FRIGBP was used to 1) generate indices of habitat quality at two scales for grizzly bears within the Yellowhead region, and 2) validate the model using measures of movement including daily and yearly distance travelled, daily displacement, and annual home range size. Our results show that a model simulating multi-scale decision making, learning, and memory can be used to generate movement with spatial and temporal patterns consistent with those observed in radio-collared bears. At the same time, I acknowledge that our model does not incorporate many of the complexities related to social dynamics, demographics, and additional landscape characteristics that have been shown to affect grizzly bear movement behaviour (e.g. Friesen, 2016; Larsen et al., 2019; Stenhouse et al., 2005; Stewart et al., 2012; Steyaert et al., 2013).

Implementation of the model in Chapter 3 allowed us to assess the role of behaviour and familiarity with the release site on the likelihood of success of a translocation event. We tested four different behavioural profiles, each with varying levels of exploratory behaviour in the initial years after a translocation event, in two different release sites representing habitats that were either similar (familiar) or different (novel) to the capture site. Although previous research has found that increased exploration is beneficial when animals are exposed to novel environments (Berger-Tal & Avgar, 2012), our results suggest that this effect is dependent on the characteristics of the release site and the scale at which movement is being assessed. We found that higher exploration usually leads to increased use of high-quality habitat long-term, but this pattern was only seen in the two years following a translocation event in bears released in unfamiliar habitats. Overall, our study highlights the importance of incorporating behaviour into movement research and showcases one of the many potential uses of an ABM in conservation.

4.1 Management implications

One of the biggest limitations of current large carnivore research is the reliance on long-term datasets and the inability to manipulate ecosystems and conditions in order to perform experimental studies. While the availability of positional data for wide-ranging species has increased dramatically in previous decades (Cagnacci et al., 2010), manipulation of wildlife and large ecosystems is and will always remain limited due to ethical and practical reasons. The research presented here, along with other instances in which ABM has successfully been used to address wildlife management and conservation issues (e.g. Allen et al., 2016; Avgar et al., 2015; Grosman et al., 2009; Rabinowitz & Zeller, 2010), provides support for the use of simulation modelling in this field. By simulating animal behaviours such as movement, population dynamics, and interactions with the environment, agent-based modelling allows researchers to understand continuous processes such as animal movement and cognition. Validated models can then be used as tools to assess future scenarios, providing a sustainable and accessible way to perform hypothetical experiments on wild populations and ecosystems. Given current rates of anthropogenic development and landscape changes, it is necessary for new approaches such as ABM to become a more common tool for ecologists.

Although ABM is still a relatively new approach in ecology, these models have demonstrated a utility in testing management strategies, such as the reduction of moose vehicle collisions using salt pool removal and displacement (Grosman et al., 2009), the creation of various wildlife corridors on jaguar movement (Watkins et al., 2011), and the role of human education programs on black bear conflict reduction (Marley et al., 2017). While this last example is the only instance of ABM use regarding bears found throughout our research, the promising results of that study in addition to the results of the research presented in my thesis highlight the uses of ABM for studying bear behaviour. In particular, we believe that management issues such as animal translocations would benefit tremendously from this type of modelling. Despite extensive monitoring efforts and the existence of large-scale datasets on this species, the small sample size of translocated bears and the lack of monitoring pre-translocation limits what researchers can conclude using traditional methods (Stenhouse et al., 2018). While compiling data from various sources has been used previously to provide insight into the factors affecting translocation success (Milligan et al., 2018), issues may arise when using data collected with multiple protocols and from animals of varying environments, which are likely to behave differently. Such studies, however, still offer valuable guidance for the development of agent-based models, which can then be used to generate large sample sizes and test multiple translocation scenarios in order to evaluate success, such as the work presented here. The development of more complex simulation models will allow for more specific assessments and could potentially serve as tools for selecting increasingly adequate release sites.

The work presented here provides support for the use of simulation modelling to study management scenarios and offers insight into issues related to translocation of wildlife to novel environments. In particular, our findings support the need for a multi-scale approach not only to animal movement studies but also to the assessment of release site for translocation events. The results of this thesis suggest that the ability of a bear to access high-quality habitat after a translocation event may vary depending on scale and the level of familiarity with the new landscape. Management measures must hence consider not only landscape features of a particular release site, but also the overall characteristics of the surrounding environment. Given that exploratory behaviour is common following translocation, it is important to account for the potential area an individual may encounter during this exploratory phase and ensure that it is suitable. While the model presented here does not implicitly incorporate mortality risk into the landscape, we acknowledge that this is an important element of the landscape that bears must incorporate into movement decisions. With this in mind, we suggest that translocation efforts account for mortality risk present in the broader environment a bear might encounter after translocation.

4.2 Future research

There are many intricacies related to grizzly bear movement behaviour that were not incorporated into our model. We encourage future studies to develop sub-models that can be added to the current model in order to account for some of these factors. In particular, we suggest that social dynamics be assessed as they are known to have measurable effects on grizzly bear movement patterns, especially during the mating season (Stenhouse et al., 2005) and in regards to spatiotemporal segregation (Libal et al., 2011; Steyaert et al., 2013). With the increasing availability of landscape data in mind, we also advocate for the inclusion of additional landscape features as well as a more continuous approach to the generation of the simulation environment in order to capture a more accurate picture of bear behaviour. While most previous research has also used a seasonal approach when studying bears, we support the use of smaller time frames such as those used to generate the original food models used to develop our model (Nielsen et al., 2010) in order to capture temporal variations in behaviour and within the landscape. Incorporating more complex representations of movement behaviour will allow future research to more closely assess factors affecting translocation efforts. Additionally, ABM models stemming from this work can be used to evaluate how future changes in the landscape may affect grizzly bear movement. Understanding how bears, and other animals, respond to various landscape features and guide their movement based on these responses will allow future studies to assess how increased development within wildlife habitat may alter current space-use patterns.

Overall, this thesis presented a novel ABM for simulating complex decision-making in grizzly bears that accounts for learning and memory and provided an example of how such models can be applied. Our work provides insight into how ABM can be used to test scenarios and supports the need for a more in-depth approach to evaluating translocation efforts. We additionally incorporated behaviour and habitat characteristics to our evaluation of translocation efforts, and our results suggest that these factors have the potential to determine translocation success to an extent. While there is substantial potential for developing the current model to address various conservation efforts, our work serves to support the use of simulation modelling in this field. We demonstrated that simulation modelling can be a powerful tool to understanding how wildlife make movement decisions and can subsequently be used to evaluate management issues in grizzly bears and other species.

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Appendix

A.1 Submodels

A.1.1 Movement

Bears move by either exploring or exploiting their surroundings; the type of movement performed at each time step is randomly selected following a probability defined by the search parameter ε. Exploration is characterized by a correlated random walk where the bear turns based on an angle extracted randomly from a normal distribution ($\mu = 0, \sigma = 20$) each time step and moves 100 m forward. In the case that a bear reaches the edge of the study area, it will move to a random cell within a 500 m radius that is within the study area. While this movement does not represent real processes relating to grizzly bear movement, contact with the edge occurs infrequently and only during the first years of the simulation when bears are roaming larger areas, making the potential effects of this decision-making in the model results negligible.

During exploitation, bears remain in a 1 km^2 cell and move to the 100 m x 100 m cell with the highest local utility value, u_s, within the 250 m perception range as long as the utility value, U_s, of the occupied 1 km^2 remains above 0.15. At the local scale, utility values are reduced by 65% per time step during occupancy and replenished by 25% each time step after the bear has moved to a different cell. Utility values of 1 km^2 cells are reduced and replenished at a rate of 20% and 1%, respectively. These values were selected since they ensured short residency times and appropriate return rates representative of real movement patterns in radio-collared bears. Because utility depletion occurs exponentially and diminishes over time, a depletion value of 0.15 ensures that bears do not remain in a single cell indefinitely. Once a 1 km^2 cell has been depleted, bears select the neighbouring 1 km^2 cell with maximum utility, U_s, face a random 1 ha cell within this new target 1 km^2 cell, and move towards it by selecting 1 ha cells with maximum utility, u_s, within a visual cone of 90° and 250 m radius (Figure A1). This process is repeated by randomly selecting a different 1 ha cell within the target 1 km^2 cell and following the highest local utility values within the visual cone until the target is reached.

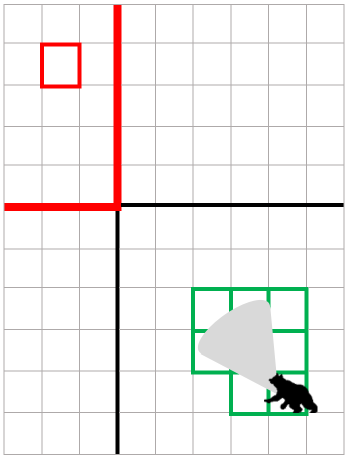

Figure A1. Diagram depicting bear movement during exploitation. Once the current 1 km^2 cell (black border on bottom right) is depleted, the bear assesses the eight neighbouring 1 km^2 cells and selects the one with the highest utility value, $\boldsymbol{U_s}$, (red border on top left) and faces a random 1 ha cell within the target 1 km^2 cell (red border). The bear then moves towards this target by selecting the 1 ha cell with the highest utility value, $\boldsymbol{u_s}$, within a visual cone of 90° and 250 m radius (grey cone, available cells for selection shown in green).

A.1.2 Search parameter

The search parameter ε determines the probability that a movement will be based on exploitation at each time step and increases yearly based on the following formula:

$$\varepsilon_y = \varepsilon_{max} - \frac{1}{1 + e^{\beta(y-\alpha)}} \qquad (6)$$

where ε_{max} is the maximum value desired for the search parameter, β is a real number less than 1.0 that defines the slope of the curve, y is the current simulation year, and α is a positive integer that dictates the overall shape of the curve. We used a ε_{max} value of 0.9, limiting exploitation to 90% of movement decisions, in order to account for the fact that exploration is often advantageous in heterogeneous landscapes (Boyer & Walsh, 2010). Because learning occurs predominantly during the first years of a bear's life, we used $\beta = 0.6$ and $\alpha = 3$ to define a function where a rapid increase in the probability of exploitation is seen during the first 7 years of a simulation. The search parameter was modified seasonally in order to accurately simulate periodical increases in learning. Seasonal increases in exploitation occur proportionally to the length of each season during a simulation year with a maximum annual increase in the search parameter defined by the search parameter formula.

A.1.3 Reinforcement learning

At the end of each season, a reinforcement learning algorithm is applied that modifies the utility values U_s and u_s of all cells visited during that season. The new values depend on the utility values of the cell during the same season of the previous year, the cell qualities Q and q_s, and a reinforcement factor that reflects the improvement in success. The new local utility value u_s of a cell is calculated with the formula:

$$u_{s_{y+1}} = \frac{u_{s_y} + (q_s * r_l)}{2} \tag{2}$$

where s is the season, y is the year, and r_l is a local reinforcement factor that determines the strength of reinforcement. The local reinforcement factor is the ratio between the obtained MoS_s and the MoS_s achieved during that same season the first year of the simulation ($y = 0$) such that:

$$r_l = \left(\frac{MoS_{l,s_y}}{MoS_{l,s_0}}\right)^{10} \tag{3}$$

Similarly, utility values U_s for all 1km^2 cells visited are updated by calculating a global reinforcement factor based on the global MoS_s:

$$r_G = \left(\frac{MoS_{G,s_y}}{MoS_{G,s_0}}\right)^{10} \tag{4}$$

And calculating the new utility values:

$$U_{s_{y+1}} = \frac{U_{s_y} + (Q * r_G)}{2} \tag{5}$$

This reinforcement learning algorithm results in a larger positive reinforcement of cells visited in seasons with higher success, rewarding the bear for making movement decisions that led to increased time spent in high-quality areas. Grizzly bears are known to occupy heterogeneous areas with varying levels of resources (Denny et al., 2018) which may result in the use of low-quality areas that facilitate the access or use of nearby higher-quality areas. The use of seasonal MoS_s, which reinforces all cells contributing to improved quality in a season, is relevant as it does not penalize the use of low-quality cells as long as the seasonal MoS_s is positive relative to previous years.

A.1.4 Measures of success (MoS_s)

Seasonal local and global MoS_s consist of the cumulative local and global qualities of each 1 ha or 1 km^2 cell occupied by the bear in a season, respectively, and are used to guide bear learning through the reinforcement algorithm. At each time step, the local measure of success $MoS_{l,s}$ increases by the local seasonal quality value, q_s, of the occupied cell in each time step such that:

$$MoS_{l,s} = \sum_{i=1}^{N} q_{s_{x_i y_i}} \tag{1}$$

Where $x_i y_i$ represent the x and y coordinates of cell i and N is the total number of time steps in a season. A single cell can contribute to the $MoS_{l,s}$ on multiple occasions if a bear spends more than one time step in a cell either by remaining in the cell or by revisiting it. The global measure of success $MoS_{G,s}$ increases by the global quality value Q following the same formula as for $MoS_{l,s}$. Yearly local and global measures of success, $MoS_{l,y}$ and $MoS_{G,y}$, respectively, are calculated at the end of each year by compiling seasonal MoS_s and used to assess the overall ability of the bear to move through high-quality areas. An improvement in yearly MoS_s would indicate that the bear spent more time in high-quality areas in the current year than in previous years.

Table A1. Summary of landscape features used to generate model landscapes

Feature	Details	Products	References
Roads	Product of the 2016 Human Footprint Inventory of Alberta (HFI2016) consisting of paved and unpaved roads, trails, and major highways.	Road density (1 km^2) and distance to nearest road (1 ha)	Alberta Biodiversity Monitoring Institute, 2016
Harvested Areas	Product of the 2016 Human Footprint Inventory of Alberta (HFI2016) consisting of areas in which forestry operations have occurred in the past 100 years	Harvested area density (1 km^2)	Alberta Biodiversity Monitoring Institute, 2016
Wildfires	All fires in the area recorded by the Government of Alberta since 1936	Wildfire density (1 km^2)	
DEM	Digital elevation model (25 m)	Terrain Ruggedness Index (TRI) (1 km^2 and 1 ha)	Riley et al., 1999
Land Cover	Classes include: upland and wetland trees, upland and wetland herbs, shrubs, water, barren, snow/ice, agricultural land, and anthropogenic disturbances composed of mines, pipelines, railways, reservoirs, roads, active and abandoned wellsites, harvested areas, and transmission lines.	Land cover class (1 km^2)	
Resource abundance	Bi-weekly (May 1 – September 30) food models of absolute probability of twenty key food items for grizzly bears representing root digging, frugivory, herbivory, or carnivory in 2015.	Seasonal (May 1 – June 15, June 15 – August 15, August 16 – September 30) resource abundance (1 ha)	Nielsen et al., 2010

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