Spatial-Temporal Analysis of Grizzly Bear Habitat Use

By
Mary Catherine Alexandra Smulders
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Supervisory Committee:

Dr. Trisalyn A. Nelson, Supervisor
(Department of Geography, University of Victoria)

Dr. Dennis E. Jelinski, Departmental Member
(Department of Geography, University of Victoria)

Dr. K. Olaf Niemann, Departmental Member
(Department of Geography, University of Victoria)

ABSTRACT

Dr. Trisalyn A. Nelson, Supervisor
(Department of Geography, University of Victoria)

Dr. Dennis E. Jelinski, Departmental Member
(Department of Geography, University of Victoria)

Dr. K. Olaf Niemann, Departmental Member
(Department of Geography, University of Victoria)

This research develops spatial-explicit methods to characterize the relationship between wildlife and habitat use and selection. Both home range analysis and resource selection function (RSF) models, two common methods of representing wildlife-habitat associations, are often summarized aspatially. I apply a novel method to home range analysis which quantifies the spatial-temporal patterns of site fidelity and range drift. As a result, the spatial structure of home ranges is described, thus building on current methods which summarize ranges as aspatial metrics, often mean area. Furthermore, I develop a new method to spatially assess the ability of RSF models to predict wildlife occurrence using conditional randomization. As opposed to summarizing RSF model accuracy as a single value, I produce spatially-explicit and mappable outputs. I also demonstrate how this spatial method may be used to improve RSF model results. I apply these two spatial-temporal methods to a case study on adult female grizzly bears (*Ursus arctos*) in the Northeastern slopes of the Canadian Rockies. Through describing the spatial-temporal pattern of grizzly bear home range change, I determine that offspring status and season impact the size and spatial configuration of a bear's home range. By spatially evaluating the predictive success of a RSF model, I locate and quantify the spatial pattern of areas where the model is under-predicting bear occurrence using Local Moran's *I*. Further, I evaluate landscape characteristics at these locations and suggest additions to the model which may increase accuracy. Both home range analysis methods and RSF evaluation techniques could assist in conservation by aiding in the delineation of critical grizzly bear habitat areas in both space and time.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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CO-AUTHORSHIP STATEMENT

This thesis is the combination of two scientific manuscripts for which I am the lead author. The initial project structure was provided by Dr. Trisalyn Nelson, for which spatial-temporal analysis of grizzly bear habitat use was identified as a key research opportunity. For these two scientific journal articles, I performed all research, data analysis, interpretation of results, and final manuscripts preparation. Dr. Dennis Jelinski provided assistance with defining research questions and presenting results. Dr. Scott Nielsen provided assistance with bear biology details and reporting the relevance of the results. Dr. Gordon Stenhouse provided the data. Dr. Nelson, Dr. Jelinski and Dr. Nielsen provided editorial comments and suggestions where required.

1.0 INTRODUCTION

1.1. Research context

In an era of climate change, habitat fragmentation, and human encroachment, wildlife is facing extirpation and extinction on an increasingly short timescale. It is estimated that by the mid 21st century, nearly 30% of all wildlife will be extinct (Wilson 1992; Lawton & May 1995; Primm et al. 1995). A primary requirement for the survival of wildlife is adequate habitat (Morrison et al. 1992). Understanding the relationship between wildlife movements, habitat use, and habitat selection is a cornerstone of managing wildlife populations. Research has shown that both the amount and spatial configuration of habitat has a profound influence on population viability (Ewers & Didham 2006). Wildlife managers need to determine the spatial-temporal relationship between species and their habitat to develop appropriate management strategies for long-term conservation.

Current methods of spatially representing animal habitat use and selection are often based on home ranges or resource selection function (RSF) models. A home range is a concept used in biology to represent the area an animal confines its normal movements to (Burt 1943). Changes in the spatial and temporal characteristics of home ranges can provide important information about the ecological requirements of a species (Mace & Waller 1997). A RSF model spatially represents species habitat selection by predicting the relative probability of species occurrence across a landscape (Manly et al. 1993; Carroll et al. 2001). Due to their predictive ability, RSF models are frequently used in ecological studies to assess habitat use for wildlife (Manly et al. 1993). While both home range analyses and RSF models link wildlife and habitat use, they are often constrained to reporting results aspatially, or at best spatially, and usually lack the capacity to represent explicit spatial-temporal patterns.

Historically, researchers' abilities to conduct spatial-temporal analysis of species have been impeded by logistical limitations, especially for wide-ranging and secretive carnivores (Wieglus & Bunnell 1995). The development of radiotelemetry has provided scientists with the opportunity to collect spatially explicit data on many wildlife species (e.g., whales (Watkin et al. 2002), snakes (Pearson et al. 2003), large cats (Pierce et al. 2000) and bears (Nielsen & Boyce 2005)). Coinciding with the growth of animal location data has been the increased availability of high spatial and temporal resolution remote sensing data (Aplin 2005; Boyd & Danson 2005). Remote sensing data can be used in ecology to identify different vegetation categories and derive animal habitats (e.g., Manson et al. 2003). Existing spatial-temporal analysis methods have not yet adapted to the influx of available animal and habitat data (Young & Shivik 2006). For example, in home range analyses, researchers generally use aspatial metrics such as mean area to describe changes to home range features (e.g., Laver & Kelly 2008). Similarly, researchers often summarize the accuracy of RSF models at predicting species occurrence with a single aspatial measure of overall accuracy (e.g., Nielsen et al. 2002).

With the increase in spatial data available, new methods must be developed to link detailed radiotelemetry and remote sensing data sources to better understand the habitat requirements of species and design successful management and conservation strategies. Researchers need to move beyond aspatial metrics and begin to examine spatial-temporal patterns. In home range analysis, spatial-temporal patterns can provide important details of animal site fidelity and range drift. Site fidelity, whereby animals reuse a particular area, is a strategy employed by animals to enhance their fitness through the predictability of habitat quality and distribution over space and time (Switzer 1993; Wolf et al. 2009). By contrast, home range drift involves an animal leaving an area and may result from competition, protection of offspring, or resource exploration (Wauters et al. 1995; Beisiegel & Mantovani 2006). Methods for assessing home range fidelity and drift can provide wildlife managers with spatially explicit details of important habitat areas.

Similarly, RSF model validation techniques have the opportunity to include details on the spatial-temporal pattern of model accuracy. Researchers have recognized the importance of the spatial pattern of model errors while validating RSF models (e.g., McGwire & Fisher 2001; Pontius & Schneider 2001; Barry & Elith 2006; Lobo et al. 2008) but few attempts have been made to implement spatial evaluation methods. The spatial pattern of inaccuracy may elude ecological processes unaccounted for in the RSF model. Spatially identifying the variation in model accuracy would allow researchers to adjust model input variables or to determine additional environmental variables that would improve the models predictive success.

1.2. Research focus

Given low population densities and low reproductive rates (Craighead et al. 1995), grizzly bears are especially vulnerable to extirpation (Clark et al. 1996; Weaver et al. 1996; Munro et al. 2006). As a result of this population susceptibility and because of the large area needed to sustain populations, grizzly bears are often a flagship species in conservation projects (Noss et al. 1996; Carroll et al. 2001). Since they are omnivores and generalists, grizzly bears consume a diverse variety of ephemerally abundant nutrient-rich food sources, resulting in dynamic spatial and temporal habitat use (Munro et al. 2006). In Alberta, Canada, grizzly bear populations are threatened by development and human activities associated with resource extraction of forests (Nielsen et al. 2004) and energy resources (Popplewell et al. 2003; Linke et al. 2005; Munro et al. 2006). Successful long-term management of grizzly bear populations within resource-extractive landscapes depends on knowledge of critical habitat needs (Nielsen et al. 2004).

1.3 Thesis objectives

This research is concerned with utilizing and developing methods to analyze the spatial-temporal pattern of grizzly bear (*Ursus arctos*) habitat use in the Northeastern slopes of the Canadian Rocky Mountains. The aims of the research are to quantify changes in grizzly bear habitat use through time and to develop new methods to validate grizzly bear habitat models. This aim will be addressed by accomplishing the following objectives:

1) Present a spatially explicit method of quantifying changes in home range fidelity and drift and show the methods importance for wildlife conservation and management.

2) Develop new methods to spatially evaluate the predictive success of RSF models using conditional randomization and demonstrate how this information can enhance the models predictive success.

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2.0 SPATIAL-TEMPORAL PATTERNS IN HOME RANGE FIDELITY AND DRIFT

2.1 Abstract

Animal habitat use, often represented by home ranges, is a pivotal theme in ecological research. Home ranges are commonly characterized by their mean area which negates important spatial characteristics such as home range fidelity and drift. I introduce a new analytical method for characterizing spatial-temporal change in fidelity and home range drift. Spatial-Temporal Analysis of Moving Polygons (STAMP) method was tested on adult female grizzly bears (*Ursus arctos*) during 1999-2003 in the Rocky Mountain foothills region of Alberta, Canada. Home range changes were evaluated on the basis of variable offspring dependency and season. Solitary bears had the greatest amount of site fidelity and had an increase in home range size in mating season, perhaps to increase mating opportunities. Female grizzly bears with offspring experienced substantial home range drift. Bears with cubs-of-the-year offspring had a reduced maternal home range size, especially during mating season, while bears with yearling offspring had an increased home range size. The spatial patterns of home range change were consistent with those expected if mobility and infanticide were the driving ecological mechanism. I conclude that offspring dependency does not impact the proportion of site fidelity but does impact the type of home range drift experienced. I suggest that the aspatial measure of representing home range change between time periods, as mean size, may be too limited and propose the spatial pattern of home range change as a more meaningful

measure for describing space use. A spatially-explicit method of quantifying site fidelity can provide important insight when determining key habitat areas for conservation.

2.2 Introduction

Understanding the relationship between wildlife movements and habitat use is a cornerstone for managing many wildlife populations. Accordingly, radiotelemetry has been widely adopted as a tool for the study of wildlife-habitat relationships as it provides accurate depiction of the activities and area used by animals (e.g., Cochran & Lord 1963; Amstrup & Beecham 1976). Using data on patterns of movement, one can then construct an animal's home range, which Burt (1943:351) defined as " . . . that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range". Home ranges are often used to characterize the relationship between animal behaviour and environmental space use (Morales et al. 2005; Borger et al. 2006b). There are many methods for estimating home ranges (i.e., Minimum convex polygons (Mohr 1947), kernels density estimation (Worton 1987; 1989)), and the typical output is a polygon constructed around a set of animal location points.

A common metric for characterizing these polygonal-depicted home ranges is mean area of used habitat (Carfagno & Weatherhead 2008; Laver & Kelly 2008). While mean home range area may provide useful information, it lacks details on spatial location and structure of the home range. In other words, while the size of a given home range may not change over time, its geometric configuration and spatial location may in fact shift to the extent that a given animal may be using substantially different habitat. This issue becomes particularly problematic for low-density wide-ranging populations in highly heterogeneous landscapes (Wieglus & Bunnell 1995; Apps et al. 2004) or when there is high inter-population variability in behavior (e.g., Wiens 1985).

The notion of shifting home ranges relates to the concept of site fidelity, or its inverse, home range drift. Site fidelity occurs when a particular animal leaves a given site (e.g, foraging ground, nesting area, or home range), say upon migration or hibernation, but returns to the previously occupied and familiar site (Switzer 1993). Edwards et al. (2009) noted that fidelity to a home range can be seen as a cost-benefit challenge. The benefit accrued with familiarity of a habitat (including resources and competition) is contrasted with the costs of venturing into new habitat. Venturing into new habitat becomes cost effective when there is low spatial-temporal predictability of resources within a given home range, while resource acquisition is maximized by venturing into neighboring areas (Wiens 1976; Maehr & Lott 1995). Site fidelity occurs in numerous species belonging to a variety of taxa, including fish (Warner 1988), reptiles (Webb & Shine 1997), amphibians (Gamble et al. 2007), birds (Newton 1993) and mammals (Wolf & Trillmich 2007; Edwards et al. 2009). Unfortunately, there is a dearth of information on home range fidelity in both space and time (Switzer et al. 1997; Borger et al. 2006b). Part of the reason for this may be related to the few existing analytical methods for capturing and characterizing dynamic processes of habitat use.

Accordingly, I introduce a novel analytical method for characterizing home range fidelity based on spatial changes in home range polygons over time. The method, termed Spatial-Temporal Analysis of Moving Polygons (STAMP) (Robertson et al. 2007), uses overlays and unions, as developed by Sadahiro and Umemura (2001), for describing changes in polygons based on their spatial properties. Robertson et al. (2007) added a temporal component to the method to yield *change events* associated with polygon shift. Recently, STAMP has shown to be effective in characterizing the space-time dynamic in mountain pine beetle (*Dendroctonus ponderosae*) infestation of forests in British Columbia, Canada (Robertson et al. in press).

STAMP is demonstrated in this research using radiotelemetry data of female adult grizzly bears in the Rocky Mountain eastern slopes region of Alberta, Canada. Similarly to most mammalian social systems, female grizzly bears provide exclusive parental care (Clutton-Brock 1991). The hypotheses for shifting home ranges in space and time are guided by known general patterns of sex-age habitat segregation related to the movement constraints imposed by offspring of varying dependence (Wielgus & Bunnell 1995; Dahle & Swenson 2003a). More specifically, offspring may constrain maternal home ranges (Blanchard & Knight, 1991; Dahle & Swenson 2003a, 2003b) compared to solitary adult female grizzlies, which often experience large amounts of site fidelity (Blanchard & Knight 1991). Furthermore, females with cub-of-the-year (COY) tend to have smaller home ranges than females with older offspring (Blanchard & Knight 1991; Dalhe & Swenson 2003a; Benson & Chamberlain 2007) and therefore experience notable range drift. Similar offspring-related movement patterns are known for black bears (*Ursus americanus*) (Powell et al. 1997; Benson & Chamberlain 2007).

I test the hypothesis that the presence of offspring variably impacts space-time patterns of home range fidelity and drift along a gradient of offspring dependency: solitary adult females, cub-of-the-year COY(s), and yearling(s). The temporal pattern of seasonal home ranges for five consecutive years is compared. For solitary bears, I predict consistent home range size and site fidelity (Dahle & Swenson 2003a) whereas for bears with offspring, I predict high amounts of drift and variability (Blanchard & Knight 1991; Dahle & Swenson 2003a). Further, I predict home range size and drift will vary across intra-annual foraging seasons with the largest home range changes occurring in spring. These changes will be especially pronounced when offspring are young and the least mobile (Blanchard & Knight 1991; Dahle & Swenson 2003b) compared to home ranges of solitary females or females with yearling offspring.

2.3 Study area

The 38 705 km² study area is situated along the eastern slopes of the Canadian Rocky Mountains in west-central Alberta (53°25'N, 117°34'W, Figure 2.1). The climate is typified by an average temperature range of 11.5°C in the summer to -6.0°C in the winter and an annual precipitation of 538 mm (Beckingham et al. 1996). The local climate is strongly influenced by the elevation which varies from 770 m to > 3500 m. Due to the short growing season, lack of salmon or other high protein foods (Jacoby et al. 1999), grizzly bear populations occur at relatively low population densities (e.g., ≤14 animals/1000 km²) (Nielsen et al. 2006).

The study area is characterized by a gradient of human intensity and development, with protected areas dominating the mountains in the west, and resource extraction in the rolling foothills in the east. The mountainous land cover consists of montane forests, conifer forests, sub-alpine forests, alpine meadows, and high elevation rock, snow and ice (Achuff 1994; Franklin et al. 2001). Approximately one-third of the area is protected, predominately in high elevation mountain area, including Jasper National Park of Canada (10 179 km²), Willmore Wilderness Park (1 791 km²), and Rock Lake – Solomon Creek Wildland Provincial Park (330 km²). These mountainous areas are characterized by extensive recreational use. In contrast, the eastern foothills region is characterized by forestry, mining, oil and gas exploration and development, trapping, hunting and other recreation (Nielsen et al. 2004, 2006; Linke et al. 2005; Stenhouse et al. 2005). The area is intersected with an extensive road and seismic line network as a result of resource extraction activities. Timber harvesting, which began in mid 1950s, occurs at a large-scale resulting in increased fire suppression (Andison 1998; Nielsen et al. 2004). The land cover in the foothills region consists of forests (conifer, mixed, deciduous and regeneration), open treed-bogs, and small herbaceous meadows (Stenhouse et al. 2005).

2.4 Methods

2.4.1 Capture and telemetry

As part of the Foothill Research Institute Grizzly Bear Program, telemetry data were collected from 1999 to 2003 on a sample of 61 grizzly bears (Cattet el al. 2003). Grizzly bears were captured and collared using aerial darting and leg-hold snaring (Stenhouse & Munro 2000). All capture efforts followed protocols accepted by the Canadian Council of

Animal Care for the safe handling of bears (Animal Use Protocol number 20010016). Each captured grizzly bear was fitted with either a Televilt (Lindesberg, Sweden) Simplex GPS radio collar or an Advanced Telemetry System (ATS, Isanti, Minnesota, USA) GPS radio collar. Both types of collars logged a spatial location every four hours, with a positional accuracy of approximately 10–20 m (Stenhouse & Munro 2000; Linke et al. 2005).

Following previous grizzly bear research (e.g., Mace et al. 1996; Mace et al. 1999; Nielsen et al. 2004; Stenhouse et al. 2005; Munro et al. 2006), the telemetry data were partitioned based on the seasonal shifts in food habitats and resource selection patterns into spring, summer and autumn (Nielsen et al. 2003; Nielsen et al. 2004). Spring extends from den emergence, standardized to 1 May, to 15 June (Nielsen 2005). Throughout spring, bears are typically at lower elevation and commonly feed on roots (*Hedysarum* spp.), clover (*Trifolum* spp.) and horsetails (*Equistum arvense*), and carrion or ungulate calves. During summer (16 June – 15 August), bears frequently feed on herbaceous plants such as cow-parsnip (*Heracleum lanatum*), graminoids, sedges and horsetails, and occasionally, ants and ungulate calves. In autumn (16 August – 15 October), bears consume berries such as Canada buffaloberry (*Shepherdia canadensis*), blueberries and huckleberries (*Vaccinium* spp.).

The seasonal home ranges of grizzly bears in two consecutive years, time period 1 (T_1) and time period 2 (T_2), from 1999 to 2003 were examined. The home ranges were partitioned by the age of dependent offspring as follows: (1) solitary adult females in both

T_1 and T_2; (2) solitary in T_1 and COY present in T_2; and (3) COY in T_1 and yearling present in T_2. Included in the second category, solitary in T_1 and COY in $T_{2,}$ was the two instances where a mother lost her yearling in T_1 but had a COY in T_2.

2.4.2 Home range delineation

The precision and accuracy of home ranges increases with the number of telemetry points (Seaman et al. 1999; Leban et al. 2001), and as such, only bears with ≥ 50 telemetry locations for a minimum of two consecutive years, within a given season, were selected for the study. Since the construction of home range polygons can be significantly impacted by the number of telemetry points used in their creation (Borger at al. 2006b), consecutive year seasonal home ranges had to have a similar number of telemetry points in both years. Following these recommendations and the demographic criteria, 11 different adult female bears were analyzed. When the bears were further partitioned by season, 37 pairs of consecutive-year bear location data were used in this study.

Home ranges were delineated using kernel density estimation (see Worton 1989 for details) which is the most common method for characterizing and modelling home ranges (Mace et al. 1996; Seaman & Powel 1996; Borger et al. 2006b) including grizzly bear home ranges (e.g., Mace et al. 1996; Mace & Waller 1997). Following convention, the 95% isopleth of the kernel density was used to define home ranges (e.g., Mace et al. 1996; Garshelis et al. 2005). The methods outlined in this paper could also be used with other methods for delineating home ranges, such as the minimum convex polygon (Mohr 1947; Borger et al. 2006a).

2.4.3 Quantifying change in size and pattern of home ranges

The change in seasonal home range size between T_1 and T_2 was quantified to determine the absolute and relative increase or decrease of area. A positive value of change in home range area indicated a growth in the home range size over time whereas a negative value of change in area indicated a decrease in home range size. The absolute and relative change in range area was calculated for each offspring dependency in the three grizzly bear foraging seasons. To determine if the mean home range area in T_1 and T_2 were significantly different, a Paired Student's *t*-test, which can be applied for small sample sizes of data in consecutive years, was calculated. The test was calculated for offspring dependencies with more than 5 bears.

Each seasonal home range in two consecutive years (T_1 and T_2) was used in the STAMP analysis to quantify temporal changes in home range spatial patterns. Specifically, home range change (HRC) was defined as the union of two seasonal home range polygons for an individual bear in T_1 and T_2. The HRC is composed of STAMP events (i.e., new polygons generated through the union of two home ranges) that describe the spatial relationship that occurred between T_1 and T_2 (Figure 2.2). This study is concerned with three specific STAMP events: stable (fidelity), contraction (drift), and expansion (drift). A stable event, hereafter known as fidelity, occurs when habitat is used consistently in both T_1 and T_2 and indicates that habitat areas were used repetitively. An expansion drift event occurs when new habitat is used in T_2 that was not used in T_1 and indicate areas of home range growth. A contraction drift event occurs when habitat is used in T_1 but is no longer used in T_2 and indicates areas home range loss. To facilitate comparisons of STAMP patterns to changes in home range size, I calculated the absolute area and the relative proportion of each STAMP event (fidelity, contraction drift, and expansion drift) by dividing the area of the event by the total HRC area. To assess whether the area of fidelity, contraction drift, and expansion drift were significantly different a Paired Student's *t*-test was calculated. The test was calculated for offspring dependencies with more than 5 bears.

2.5 Results

2.5.1 Home range delineation

Yearly seasonal home ranges were estimated from 10 580 location data collected on adult female grizzly bears between 1999 and 2003. A total of fifty home ranges were delineated from an average of 212 (SD = 73) locations. The average home range size varied depending on offspring dependency and season (Table 2.1) with solitary bears having an average home size of 352 km^2 (SD = 160 km^2) while bears with COY had an average home range size of 200 km^2 (SD = 110 km^2) and bears with yearling had an average home range size of 332 km^2 (SD = 182 km^2). The large standard deviation values observed alludes to the extensive variations of mean home range size within each offspring dependency.

2.5.2 Home range size

The change in absolute and relative home range size was calculated for 37 pairs of consecutive year home ranges (Table 2.2). There was a decrease in home range size of

21% for solitary bears. The maternal home range of bears that were solitary in T_1 and had COY in T_2 decreased significantly in home range area by 40% ($t = 3.57$, $p = 0.0015$) while bears with a yearling in T_2 increased in home range size by 85% ($t = -1.91$, $p = 0.068$).

Home range size change results were partitioned by grizzly bear foraging season as shown in Table 2.3. Seasonal results for bears remaining solitary showed that the greatest change in relative home range area for these bears occurred in autumn (59%). For bears with offspring, the most substantial changes in relative home range area occurred in spring. During spring, bears with dependent COY had their home range size markedly decrease (70%) whereas bears with dependent yearling had their home range size substantially increase (135%) from the previous year. Changes in relative maternal home range size decreased as the foraging season progressed. Bears solitary in T_1 and with dependent COY in T_2 had their range decrease by 70% in spring, 54% in summer and 7% in autumn. Bears with COY in T_1 and yearling in T_2 had similar range size changes, but with their home range increasing by 135% in spring, 95% in summer and 44% in autumn.

2.5.3 Home range pattern

Within a bears HRC, the average area of home range fidelity was 41% (SD = 18%, range 15-82%) while the area of contraction drift was 32% (SD = 28%, range 0-82%) and expansion drift was 27% (SD = 21%, range 0-79%). Based on offspring dependency, the proportional areas of fidelity, contraction drift and expansion drift within the home ranges was similar to what was expected based on sex-age habitat segregation (Table

2.4). The home range of adult female bears remaining solitary experienced the largest proportion of site fidelity (54% of the area), with contraction drift and expansion drift representing 32% and 14% of the area, respectively. The home range of bears solitary in T_1 and with COY in T_2 had substantial amounts of contraction drift (52% of the area) and smaller amounts of fidelity (35% of the area). The area of contraction drift, expansion drift, and site fidelity were significantly different for the solitary to COY offspring dependency ($p < 0.05$). Contrary to expectations, COY to yearling changes in maternal home range had nearly equal amounts of expansion drift (42% of the area) and fidelity (44% of the area) ($t = 0.451$, $p = 0.66$). The area of contraction drift, however, was significantly different from expansion drift ($t = 2.11$, $p = 0.046$) and fidelity ($t = -3.35$, $p = 0.0026$). There was significant differences in the area of expansion drift ($t = -2.76$, $p = 0.011$) and contraction drift ($t – 3.58$, $p = 0.0015$) between bears that were solitary in T_1 but had a COY in T_2 and those that were had a COY in T_1 but had a yearling in T_2.

The home range fidelity and drift results were partitioned by foraging season (Table 2.5). I compared the amount of fidelity between seasons, regardless of offspring dependency and found no significant differences. When a bear had a COY in T_2, it experienced substantial amounts of contraction drift, especially in spring when contraction drift comprised 73% of the change in area between consecutive years. The proportion of contraction drift decreased in summer (57%) and was the smallest in autumn (33%). When a bear had a yearling in T_2, expansion drift occupied 56% of the change in area in spring, 38% in summer, and 35% in autumn.

2.6 Discussion

The observed spatial-temporal pattern of change in grizzly bear home ranges in Alberta's Rocky Mountain Foothills is similar to those expected if mobility and infanticide were the driving ecological mechanism. As predicted, I found that the relationship between home range size, fidelity, and drift changed along a gradient of offspring dependency. The results also support the notion that season impacts size and fidelity changes whereby the greatest change occurs in spring for bears with COY and yearlings (Blanchard & Knight 1991; Dahle & Swenson 2003b). Similar patterns of young offspring impacting the maternal range have been noted in other species including sea lions (*Zalophus wollebaeki*) (Wolf & Trillmich 2007), leopards (*Panthera pardus*) (Seidensticker 1976; Odden & Wegge 2005), tigers (*Panthera tigris*) (Sunquist 1981), Iberian lynx (*Lynx pardinus*) (Fernandez & Palomares 2000), and mountain lions (*Felis concolor*) (Hemker et al. 1984).

A possible mechanism for maternal home range change, unrelated to offspring status, is resource availability (McLoughlin & Ferguson 2000; Moyer et al. 2007). Home range size should decrease when food abundance increases because individuals are able to obtain sufficient resources in a smaller area (Boutin 1990; Said 2005). This trend has been observed in black bears (Powell et al. 1997) and grizzly bears (Craighead 1995). Changes in resource availability should be especially pronounced in the home ranges of solitary females since they are primarily concerned with foraging and not rearing young. Within the five year study, I found all home range size changes operated similarly regardless of the year. Two years (2001 and 2002) had about a third less precipitation than the 30-year normal, but I did not find evidence that this impacted the bear's movement trends. Perhaps a finer scale study of changes in resource availability would have yielded different results; however, I found no evidence that the home range fluctuations observed were primarily caused by changes in resources availability.

There are several possibly explanations for the offspring related changes in home range size observed. The metabolic, or energetic hypothesis, states that the home range size of mammals should increase with increasing body mass (McNab 1963). Dahle and Swenson (2003a) predicted that the metabolic needs of females with young should exceed those of lone females as offspring are provided with milk, and the total body mass of a family group could be twice that of a lone female. As a result, females with yearlings should have the largest home range, as they have the largest total body mass. Females with COY should have the second largest home ranges and solitary bears should have the smallest ranges. Consistent with this hypothesis, solitary bears had smaller home ranges than females with yearling offspring. However, contrary to the metabolic hypothesis, and in agreement with Dahle and Swenson (2003a) findings, ranges of females with COY were smaller than the results for solitary females and females with yearlings. McLoughlin and Ferguson (2000) also found that body mass related factors were not the most important determinants of grizzly bear home range size.

Another possible explanation for the changes in home range size observed is the limited mobility of young dependent offspring. As suggested by Dahle and Swenson (2003b), in spring and early summer, COY are small and may limit the movements of their mother (and see Lindzey & Meslow, 1977; Blanchard & Knight 1991; Hirsch et al. 1999). In contrast, by autumn when the offspring reach yearling size, their mobility should not limit their mother's movement. Indeed the findings show the decreased home range size of mothers with COY in spring coupled with an increased home range size in autumn. This limited-mobility explanation, however, does not account for the seasonal changes in home range size for solitary bears and bears with yearlings.

Infanticide, a potentially significant cause of grizzly cub mortality (Blanchard & Knight 1991; Wielgus & Bunnell 1995; Powel et al. 1997; Dahle & Swenson 2003b; Rode et al. 2006) may also explain the size changes in the maternal home range. As a counter strategy to infanticide, solitary female bears may increase their home range during the mating season, especially in low density populations, to increase their chances of mating with multiple partners (Bellemain et al. 2006). This promiscuity enhances paternal uncertainty and reduces the possibility of infantcidal behaviour (Hrdy 1979; Ebensperger 1998; Bellemain et al. 2006). Coinciding with these predictions, and similarly to the results found by Dahle and Swenson (2003b), solitary females in the study had the largest home ranges in mating season (spring).

As another counter strategy to infanticide, a female bear with dependent offspring might reduce its home range size to avoid contact with potentially aggressive male bears which are documented to travel widely in search of breeding opportunities (Sandell 1989; Swenson et al. 2001; Dahle & Swenson 2003a). Corresponding to the infanticide hypothesis, my results show that females with COY had home ranges smaller than solitary females and females with yearlings (Blanchard & Knight 1991; Dahle & Swenson 2003b). This reduction in home range size for bears with COY was most pronounced in spring (mating season) when offspring are most vulnerable to infanticide (Dahle & Swenson 2003b; Bellemain et al. 2006). Similar to the home size changes predicted by the infanticide hypothesis, the home range size for bears with COY in autumn (post mating season) increased as the threat of infanticide is alleviated (Swenson et al. 2001). While the support of female's avoidance of males as a counter strategy to infanticide is limited (Ebensperger 1998), it has been proposed to operate in grizzly bear populations by Wieglus and Bunnel (1995) and Dahle and Swenson (2003b). Despite the lack of direct evidence for the immobility of offspring or infanticide, the size changes observed in the female home ranges coincide with what is expected if either process or both were operating.

The changes in spatial pattern of fidelity and drift support the changes in home range size observed. The results suggest female bears in the study area exhibited greater fidelity (41%) than bears observed by Edwards et al (2009) in the Canadian Arctic (24%, range 6-37%). Their study, however, also included male bears which are known to exhibit less fidelity to seasonal and annual home ranges than females (Blanchard & Knight 1991). Similarly to the results of Blanchard and Knight (1991), there were no significant differences in the amount of fidelity between offspring classes although ranges for solitary females remained the most spatially consistent between years.

The amount of fidelity changed seasonally although I was unable to test the statistical significance, due to small sample sizes ($n \leq 5$). It appears however, that bears are most faithful to their seasonal home ranges in summer. This seasonal result is inconsistent with Edwards (2009) who determined that there were no significant differences in grizzly bears seasonal fidelity and Blanchard and Knight (1991) who found female grizzlies showed the greatest fidelity to spring ranges, then autumn, then summer. The increased proportion of fidelity during breeding season compared to non-breeding seasons is common for many species (Greenwood 1980; Wolf & Trillmich 2007). Unlike the rather consistent area of fidelity, the difference between contraction drift and expansion drift varied by offspring dependency; bears with COY experienced significantly more contraction and less expansion than bears with yearlings. These home range drift trends varied seasonal with the greatest magnitude of contraction and expansion drift occurring in spring.

The spatial pattern of contraction drift, expansion drift and fidelity support the home range size change results and provide further evidence of the ecological processes represented in the maternal home range. The spatial pattern in the maternal home range mirrored what was expected if offspring's limited mobility or infanticide were operating. The relatively large amounts of fidelity observed in solitary bears may result from them having no offspring to hinder their movement physically or through intraspecies avoidance. The solitary bears are therefore able to incur the benefits associated with familiarity, such as predictable food resources, by having stable home ranges (Switzer 1993). The substantial amounts of contraction drift experienced by bears with COY shows the confined nature of the maternal home range and may represent the offspring's limited mobility, the mothers counter strategy to infanticide, or a combination of both. These mothers are concentrating their range in areas familiar to them. Some studies suggest that predation risk increases in unfamiliar areas since animals need more time to hide or find escape routes compared to familiar locations (Janmaat et al. 2009). Therefore, the mother may be avoiding infanticide by concentrating its home range in familiar areas. The considerable area of expansion drift experienced by bears with dependent yearling shows a growth in home range size and may allude to the increased mobility of the offspring, the alleviated infanticide threat, or both processes. Coinciding with the results of home range size changes, the results of spatial pattern changes varied seasonally with the greatest amounts of contraction drift or expansion drift experienced in spring.

The spatial pattern of fidelity, expansion drift and contraction drift show the dynamic space use of grizzly bears over time and in relation to offspring. Previous research has shown the impact of age (Schaefer et al. 2000; Janmaat et al. 2009), reproductive success (Switzer 1997), parental territories (Murray et al. 2008), study scale (Janmaat et al. 2009) and resource distribution (Edwards et al. 2009) on animal site fidelity. I have demonstrated the impact of offspring and season on site fidelity and range drift. Simply quantifying temporal patterns in home ranges by reporting mean area or relative area overlooks the importance of fidelity and drift. STAMP enables researchers to spatially and temporally quantify an animal's dynamic space use over multiple consecutive years. Further, STAMP-type results provide managers with a better depiction of the dynamics of species home ranges, which can facilitate better management including more effective delineation of protected areas.

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Table 2.1: Home range size categorized by offspring dependency and season.

Female offspring dependency	Foraging season	$\bar{x}$ (km^2)	SD (km^2)	*n*
Solitary	spring	435	198	5
	summer	366	87	7
	autumn	278	174	7
	average	352	160	
COY[a]	spring	147	83	4
	summer	205	139	8
	autumn	226	86	7
	average	200	110	
Yearling	spring	404	314	5
	summer	354	194	5
	autumn	267	27	3
	average	332	182	

[a] Cub-of-the-year

Table 2.2: Change in home range size categorized by offspring dependency.

Female bear offspring dependency		Change in area			n
T_1	T_2	$\bar{x}$ (%)	$\bar{x}$ (km^2)	SD (km^2)	
Solitary	Solitary	-21	-129	176	3
Solitary	COY[a]	-40	-181	170	13
COY[a]	Yearling	85	117	145	13

[a] Cub-of-the-year

Table 2.3: Change in home range size categorized by offspring dependency and season.

Female bear offspring dependency		Foraging season	Change in area			n
T_1	T_2		$\bar{x}$ (%)	$\bar{x}$ (km^2)	SD (km^2)	
Solitary	Solitary	spring	-10	-29	0	1
		summer	7	19	0	1
		autumn	-59	-376	0	1
Solitary	COY[a]	spring	-70	-390	111	3
		summer	-54	-219	106	5
		autumn	-7	-18	49	5
COY[a]	Yearling	spring	135	246	183	3
		summer	95	121	118	5
		autumn	44	186	37	5

[a] Cub-of-the-year

Table 2.4: Area of site fidelity and drift categorized by offspring dependency.

Female bear offspring dependency		Area of site fidelity and drift									n
		Contraction drift			Expansion drift			Fidelity			
T_1	T_2	$\bar{x}$ (%)	$\bar{x}$ (km^2)	SD (km^2)	$\bar{x}$ (%)	$\bar{x}$ (km^2)	SD (km^2)	$\bar{x}$ (%)	$\bar{x}$ (km^2)	SD (km^2)	
Solitary	Solitary	-32	191	199	14	63	23	54	208	46	3
Solitary	COY[a]	-52	239	164	13	67	41	35	127	42	13
COY[a]	Yearling	-14	70	58	42	177	151	44	155	79	13
Solitary	Yearling	-40	123	68	28	175	123	32	221	151	8

[a] Cub-of-the-year

Table 2.5: Area of range drift and site fidelity categorized by offspring dependency and season.

Female bear offspring dependency		Foraging season	Area of site fidelity and range drift									n
			Drift (contraction)			Drift (expansion)			Fidelity			
T$_1$	T$_2$		$\bar{x}$ (%)	$\bar{x}$ (km^2)	SD (km^2)	$\bar{x}$ (%)	$\bar{x}$ (km^2)	SD (km^2)	$\bar{x}$ (%)	$\bar{x}$ (km^2)	SD (km^2)	
Solitary	Solitary	spring	-26	84	0	17	56	0	57	184	0	1
		summer	-6	19	0	12	39	0	82	271	0	1
		autumn	-64	470	0	13	94	0	23	167	0	1
Solitary	COY[a]	spring	-73	456	129	5	37	48	22	130	35	3
		summer	-57	246	96	7	27	30	36	146	45	5
		autumn	-33	103	59	25	85	49	42	106	35	5
COY[a]	Yearling	spring	-13	46	42	56	292	214	31	113	42	3
		summer	-9	52	84	38	173	127	53	182	88	5
		autumn	-20	76	45	35	113	61	45	154	73	5

[a] Cub-of-the-year

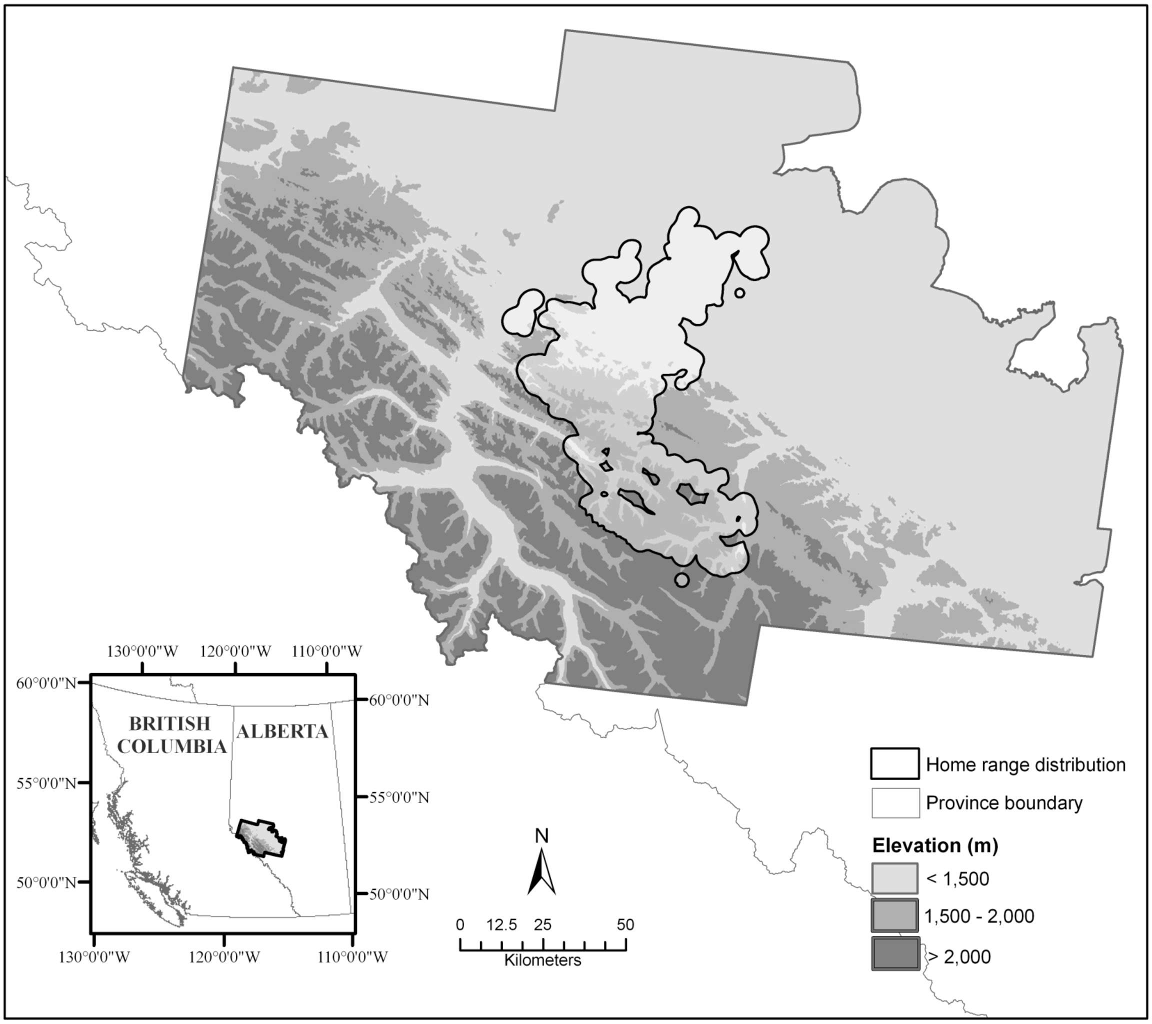

Figure 2.1: Surrounding towns and elevation within the study area. Study area location within Alberta is depicted in the lower left portion of the figure.

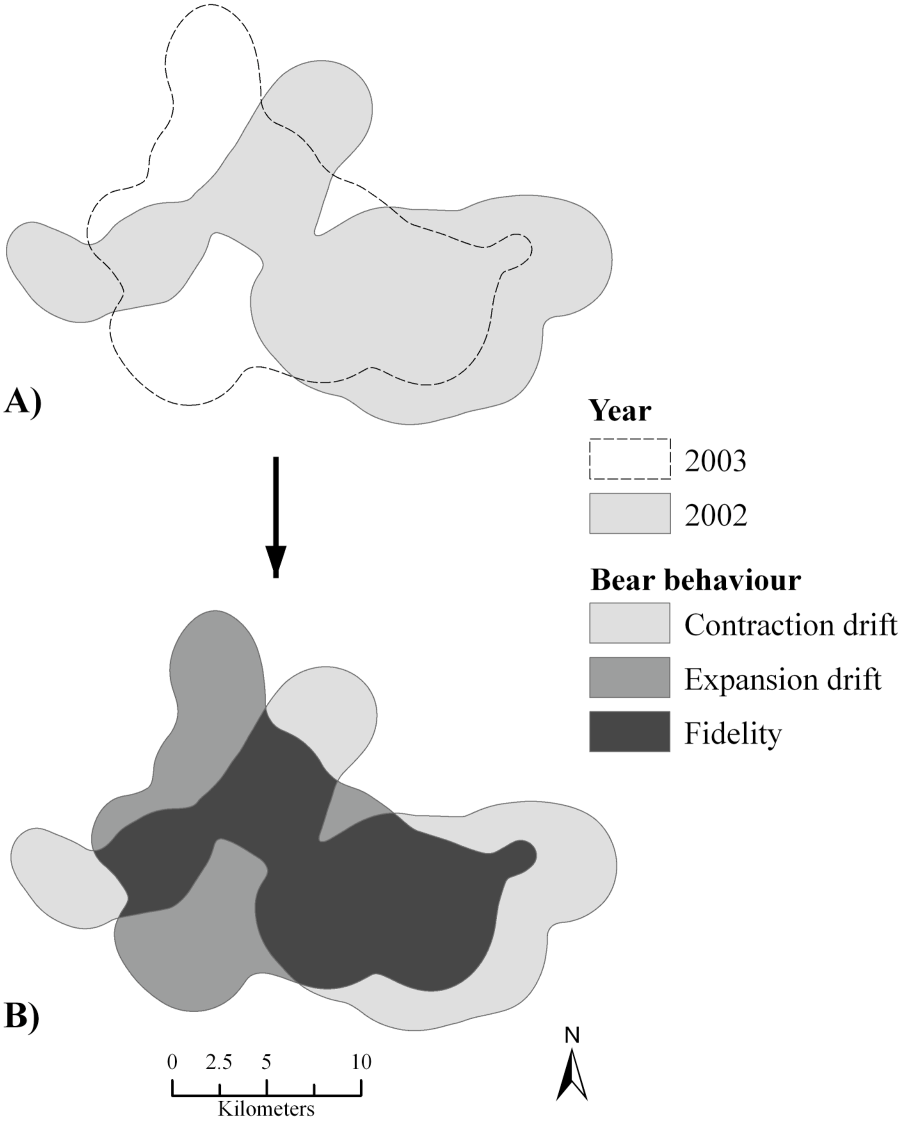

Figure 2.2: Example STAMP input and results for a bear in autumn from 2002-3. The input polygons (A) are the autumn home ranges for a bear in 2002 and 2003. The STAMP results (B) is the home range change (HRC) for the bear; the bear behaviour identified is contraction drift, expansion drift and fidelity.

3.0 SPATIALLY VALIDATING RESOURCE SELECTION FUNCTIONS

3.1 Abstract

Models predicting the spatial distribution of organisms are increasingly used in wildlife management and conservation. The accuracy of these models is typically reported using a single value which represents the overall ability of the model to correctly determine the probability of species occurrence. This accuracy measure does not indicate the spatial location or variation in accuracy. There may be a spatial dependence in error locations which could relate to ecological processes unaccounted for in the original predictive model. The purpose of this research is to explore spatial methods of evaluating resource selection function (RSF) models using conditional randomization. A case study on adult female grizzly bears (*Ursus arctos*) is used to demonstrate this approach. Local test statistics computed from bear telemetry locations are used to identify areas where bears are located more than predicted by the RSF. The spatial pattern of model inaccuracies is evaluated using a measure of spatial autocorrelation, local Moran's *I*. The results show that the RSF model accuracy varied throughout the study area with clusters of inaccuracies located in core, central areas. Model inaccuracies varied both seasonally, with the summer RSF performing the best, and throughout RSF bins, with the least error in high RSF bin values. The landscape characteristics associated with model inaccuracies were examined and factors that may contribute to these unexpected values were identified. I recommend conducting RSF model accuracy assessments spatially and including the spatial accuracy information in model metadata.

3.2 Introduction

A resource selection function (RSF) is a model that predicts the relative probability of finding a species at a given location on the landscape (Manly et al. 2002). RSF models are often used to quantify distribution and abundance of organisms based on species data and environmental variables (Boyce & McDonald 1999; Pearce & Boyce 2006). RSF models statistically correlate species field observations to a set of habitat variables with the intention of reflecting essential elements of the organism's ecological requirements, such as climate, land-cover, and topography. Given that species data are typically collected from a population sample, RSF models can be used to interpolate predicted species use for the entire population across a landscape.

There are a variety of motivations for conducting resource selection studies. RSF models have been used to estimate projected population size for timber wolves (*Canis lupus*) in the American Great Lakes States (Mladenoff et al. 1995). RSF models have also assisted in conservation initiatives by quantifying the long term habitat requirements of a species. For instance, Johnson et al. (2004) created RSF models at different spatial scales to examine the relationship between mountain caribou (*Rangifer tarandus caribou*) and habitat, primarily old growth trees in British Columbia, Canada. Resource selection studies also have analyzed resource partitioning between animals. For example, Voeten and Prins' (1999) studied the impact of exotic domestic cattle (zebu (*Bos indicus*)) on resource partitioning of wild herbivores (zebras (*Equus burchelli*) and wildebeests (*Connochaetes taurinus*)) in Tanzania. Their results suggest that exotic cattle may alter the delicate balance of resource partitioning that occurs between native species as a consequence of evolutionary resource segregation. Studies of resource selection extend beyond animal research. For example, RSF models have been used to relate the pattern of fire susceptibility and landscape composition in northwestern Portugal (Moreira et al. 2001). Resource selection models have also been used to examine ecological theories, such as niche theory in Austin's (2002) study of plant community ecology. Lastly, RSF models can be employed for purely descriptive purposes such as predicting fish distribution (e.g., Olden et al. 2002).

The two common types of RSF models statistically relate species presence and either species absence (presence/absence models) or available habitat locations (presence/available models), to environmental data (biotic and abiotic) (Fielding and Bell 1997; Manly et al. 2002; Pearce & Boyce 2006). Presence sites are locations where the species is known to occur whereas absence sites are locations where the species is known, with some certainty, not to occur. The reliability of absences depends on the species characteristics (Hirzel et al. 2001), abundance (Kéry 2002), and survey methods (Mackenzie & Royle 2005). While researchers may determine plant absence with reasonable confidence, identifying absence sites for wildlife, especially highly mobile and cryptic animals, is difficult (Boyce et al. 2002; Johnson et al. 2006). For example, radiotelemetry methods indicate locations used by wildlife, but many unrecorded locations of use can not be differentiated from unused areas (Boyce et al. 2002). Available sites are locations in the proximity of the species which are not currently being used. While absence sites are entirely exclusive from presence sites, available sites could either become used or unused in the future. Available sites are typically drawn randomly from the study area but also may be selected from a smaller area such as an animal's home range (Buskirk & Millspaugh 2006) or within a defined distance from a presence location (Johnson et al. 2004; Johnson & Seip 2008).

The statistical information about relative species occurrence generated by RSF modeling can be categorized into RSF bins. RSF bins represent ordinal classes of probability often ranging from 1 (relatively low probability of species occurrence) to 10 (relatively high probability of species occurrence). RSF bins are generally created using a decile classification which divides the raw RSF probability values into 10 RSF bins, each roughly equal in area. Since RSF models represent the relative probability of use of an area by a particular species, the majority of presence data is expected to fall within higher RSF bins whereas the majority of absence data, if obtainable, is expected to fall within the lower RSF bins.

The predictive capacity of a RSF is commonly reported as a singular accuracy value (Fielding & Bell 1997) which measures the overall ability of the model to predict species occurrence. Accuracy, in this sense, is defined as the closeness of the model to representing true habitat usage of a specific species (Unwin 1995). Prediction of habitat non-use can only be determined when absence data are available. Although presence/absence and presence/available methods both produce RSF models, development methods and evaluation techniques often differ. Common metrics used to evaluate RSF accuracy are confusion matrix-based (sensitivity, specificity, and the Kappa statistic *K*), receiver operating characteristics (ROC), Spearman rank correlation, Somer's

D and chi-square (χ^2) (Jelinski 1990; Fielding & Bell 1997; Raes & ter Steege 2007). The confusion matrix measures involve selecting a threshold value to separate unsuitable areas where species should be absent from suitable areas where species should be present (Fielding & Bell 1997). With these thresholds, the amount of presence and absence data in suitable and unsuitable areas is tabulated. Sensitivity is the ratio of correctly predicted presence cases to the total number of presences cases. Specificity is the ratio of correctly predicted absences cases to the total number of absences. The Kappa statistic *K* (Cohen 1960) is also derived from the confusion matrix and measures the actual agreement within the confusion matrix minus the agreement expected by chance (Boyce et al. 2002).

Another common method used in RSF model accuracy assessment is the ROC (Metz 1978). The ROC plots sensitivity against (1-specificity) over a number of classification thresholds. The area under the ROC curve (AUC) is a single, threshold independent, metric which evaluates the capacity of the model to correctly predict a higher probability of species occurrence where organisms are present than where they are absent. The confusion matrix based measures and the AUC require both positive and negative data (presence and absence) and are therefore inappropriate for evaluating presence/available RSF models.

The Spearman rank correlation (Spearman 1904), Somer's *D* (Somer 1962) and χ^2 statistic (Neu et al. 1974) are methods used to evaluate a model's predictive success that compare animal locations to RSF bin ranks. These measures do not require negative location data (absences) and are therefore preferable methods for evaluating the predictive success of presence/available RSF models (Boyce et al. 2002). Accuracy assessments with the Spearman's rank correlation quantify the relationship between predicted probability of occurrence for presence data and the frequency of the presence data within the RSF bins. A model has high predictive abilities if there are a greater number of presence locations in bins with high RSF scores (Johnson & Seip 2008). Somer's *D* also measures the relationship between increasing RSF bins and increasing frequency of presences locations. While Spearman's rank correlation assigns weights based on the magnitude of difference in RSF bin ranks, Somer's *D* measures the overall agreement and disagreement of bin ranks (Harrell 2001). The χ^2 goodness of fit test operates by comparing the number of instances (e.g., animal locations) that were expected to fall into specific categories (e.g., RSF bins) with the number of instances that were expected to fall into each category on the basis of some hypothesis (Jelinski 1990). Johnson et al. (2006) for example, determined the expected number of animal locations per RSF bin based on calculating bin utilization values, the area of the bins, and the number of validation observations.

The presence/absence and presence/available validation techniques mentioned above produce an average accuracy value and ignore the spatial variability in accuracy. Different sections of the study area will have an accuracy that is higher or lower than the reported average. Information on the spatial variation and pattern of RSF model accuracy is important to ecologists when assessing data quality and determining how variables and parameters can be modified to improve model outputs (Zhu 2001). Model error, the opposite of model accuracy, is the deviation of the model value from the true proportional habitat usage. While there might be a random component of ecological error that is impossible to know and measure, a bias may also exist where there is a pattern to the deviations from the benchmark (Gottsegen et al. 1999). It may be difficult to produce a map of RSF accuracy because it would require that researchers know the exact location of all individuals within a population, however it is possible to map errors or inaccuracies through comparison with the species sample data.

Previous researchers have recognized and recommended examining the spatial pattern of model errors (e.g., McGwire & Fisher 2001; Pontius & Schneider 2001; Barry & Elith 2006; Lobo et al. 2008). The spatial pattern of model inaccuracies may indicate ecological processes that have not been accounted for or are poorly represented in the RSF model (Fielding & Bell 1997). By characterizing the spatial distribution of model error, locations where the model under performs can be identified. At locations where the RSF model is less accurate, changes to attribute relationships or the inclusion of additional landscape variables may improve predictive success.

A few spatially explicit validation techniques have provided some promising results. Buckland and Elston (1993) explored geographic patterns in model prediction error to understand the spatial pattern of habitat suitability. Prediction errors were modeled by comparing multiple habitat models created through bootstrapping to determine spatially, upper and lower confidence interval areas which represent the models predictive success. Fielding and Bell (1997) describe techniques related to Augustin et al.'s (1996) method of using spatial autocorrelation measures in presence/absence models. Spatial autocorrelation measures examine how similar a feature is to its neighbours and can qualify the spatial pattern of a variable as clustered, dispersed or random. In Augustin et al.'s method, incorrectly predicted species presence are less serious if they are located near real occurrences than if they are further from actual species occurrences. Other researchers recommend that simply calculating different model accuracy metrics (e.g., receiving operating characteristics (ROC)) for subsections within the study area (Osborne & Suarez-Seoane 2002; Barry & Elith 2006) or mapping regression residuals separately for different geographical regions within the study area (Barry & Elith 2006) will aid model evaluation.

The standard method for hypothesis testing in spatial analysis is to compare observed data to a null hypothesis where expected patterns are generated from random processes (formally defined as complete spatial randomness (CSR)) (Fortin & Dale 2005). Randomization is a method for creating a reference distribution from observed data when probability distributions associated with the data are unknown. In some cases, random null hypotheses are unrealistic since researchers can rarely expect ecological phenomenon to have random arrangements (Fortin & Jacquez 2000). Unrealistic null hypotheses lead to Type I errors and trivial results (Legendre & Fortin 1989; Cherry 1998; Legendre et al. 2002). To accommodate more complex null hypotheses, reference distribution can be generated from conditional randomizations. As an example, Nelson and Boots (2005) assessed the spatial pattern of bark beetles using a null hypothesis of randomness that was conditioned on known beetle ecology. Raes and ter Steege (2007) evaluated the accuracy of a species distribution model using a null hypothesis of randomness conditioned on sampling sites thereby correcting for collector-bias in specimen data. Similarly, a conditional randomization approach can spatially assess RSF models. For instance, the null hypothesis of random grizzly bear habitat use can be conditioned on habitat selection represented by the RSF model.

Our goal is to demonstrate how conditional randomization methods can be used to quantify the spatial variability in a presence/available RSF model's predictive success. I outline and demonstrate methods with a case study for grizzly bears in the Northeastern slopes of the Canadian Rockies. The presence/available RSF models were developed as a 30 m by 30 m grid for each grizzly bear foraging season based on food availability and plant phenology (Nielsen et al. 2003; Munro et al. 2006). A conditional randomization is used to identify locations where the RSF model under predicts grizzly occurrence with statistical significance. The spatial pattern of unexpected areas is quantified using local Moran's *I*, a measure of spatial autocorrelation, which will be used to identify clusters and outliers of locations poorly predicted by the RSF model. Environmental conditions at unexpected locations are evaluated to demonstrate assessing RSF model input variables and attribute relationships.

3.3. Study area

The study area is a 10 000 km^2 landscape along the eastern slopes of the Rocky Mountains in west-central Alberta (Figure 3.1). The region contains a strong elevation gradient, ranging from 850 m to > 3200 m. The western mountainous region is dominated by both National and Provincial protected areas, mainly, Jasper National Park. While the parks have controlled use, recreational activities are extensive. Land cover in mountainous regions varies from forest (montane, conifer, sub-alpine) to alpine meadows to rock, snow and glaciers (Achuff 1994). In contrast, the eastern foothills region contains an assortment of resource extraction activities: mining, oil and gas, and forestry (Linke et al. 2005; Stenhouse et al. 2005). Land cover types in the foothills region include forest (conifer, mixed and deciduous), wetlands (open and treed-bogs), early succession forests following harvest, and small herbaceous meadows (Achuff 1994; Franklin et al. 2001).

3.4 Data

3.4.1 Resource selection function

The presence/available RSF models were created by Nielsen (2005) to evaluate third-order (Johnson 1980) habitat selection for grizzly bears using logistic regression which estimates relative likelihoods with an exponential model. The spatial resolution of the RSFs was 30 m by 30 m. To account for seasonal variations in adult female bear habitat use, three RSF models were used representing habitat selection at different stages in bear phenology (Nielsen et al. 2003; Nielsen et al. 2004a). The three seasons are: spring (hypophagia, 1 May to 15 June), summer (early hyperphagia, 16 June to 15 August), and autumn (late hyperphagia, 16 August to 15 October). The seasonal RSF models were classified into ten ordinal RSF bins ranging from 1 (relatively low probability of female bear occurrence) to 10 (relatively high probability of female bear occurrence). Telemetry data (Sect. 3.2) from 1999 – 2002 were used to develop the RSF models. Only data from adult females were used in the RSF models as females have the greatest influence on the development and long-term success of populations (Mace et al. 1996; McLoughlin et al.

2003; Nielsen et al. 2004b). Adult female grizzlies also use habitat more consistently than males and subadults (Blanchard & Knight 1991, Nielsen 2005).

Environmental variables, recorded at presence and available locations, were used to quantify the probability of bear occurrence for the rest of the study area. The variables selected were: land cover type, distance to edge, forest age, compound topographic index, terrain ruggedness index and global solar radiation. The first variable, land cover, was composed of 10 classes; 6 forest classes (closed conifer, open conifer, mixed, deciduous, treed-bog, and regeneration forest), 3 open classes (alpine/herbaceous, non-vegetative, and open-bog/shrub), and 1 anthropogenic class. The second variable, distance to forest/non-forest edge, was calculated at 100 m distance intervals and accounts for grizzly bears preference for edge habitats (Nielsen et al. 2004a). The third variable, forest age, was extracted from Alberta Vegetation Index (AVI) data and GIS maps of fire history from Foothills Model Forest (FMF; Hinton, Alberta). The fourth variable, compound topographic index, was calculated to represent soil moisture, which has been shown to impact the bears use of clearcuts and locations of key food resources (Nielsen et al. 2004a, 2004c). The fifth variable, terrain ruggedness index, was generated by modifying Nellemann and Cameron's (1996) equation which takes into account changes in aspect and elevation. Terrain ruggedness has been used previously to model grizzly bear habitat selection and mortality risk (Nielsen 2004c). The sixth variable, the global solar radiation, was calculated on three days throughout the summer; slope-aspect relationships with solar radiation have been shown to impact predictors of grizzly bear habitat selection (Nielsen et al 2002, 2003, 2004a).

3.4.2 Bear location data

From 1999 to 2003, grizzly bear telemetry location data was collected as part of the Foothills Research Institute Grizzly Bear Research Program. Bears were systematically captured using leg snaring and immobilization techniques in both the forested and non-forest environments (Stenhouse & Munro 2000; Cattet et al. 2003). Bears were collared with either a Televilt (Lindesberg, Sweden) Simplex GPS radio collar or an Advanced Telemetry System (ATS, Isanti, Minnesota, USA) GPS radio collar. The collars collect six locations per day, at four hour intervals, with a spatial accuracy of approximately 10–20 m (Stenhouse and Munro, 2000; Nielsen et al. 2004b; Linke et al. 2005). The telemetry data from 1999-2002 were used to develop the RSF models, while data from 2003 were used for model validation. Adult female bears with ≥ 50 telemetry locations per season were included in this study, as recommended by Leban et al. (2001) since using increasing telemetry points increases confidence in conclusions. In total, I used 3,570 bear location points from nine adult female grizzlies to validate the RSF model (Table 3.1). The telemetry points were fairly evenly dispersed throughout the seasons with 1,102 occurring in spring, 1,249 occurring in summer and 1,219 occurring in autumn.

3.4.3 Supplementary landscape data

Additional landscape data was used to explore characteristics at locations deemed statistically unexpected. The landscape variables selected for comparison were distance to water and elevation. These variables were chosen because of their use in other grizzly bear RSF modeling projects (e.g., Neilsen 2002; Ciarniello et al. 2007). Distance to water was calculated using the straight-line Euclidean distance to the nearest feature. Elevation was examined using a 100 m digital elevation model that exists for the province of Alberta.

3.5 Methods

For individual grizzly bears, locations where bear habitat use is statistically higher than predicted by the RSF, which I refer to as *unexpected locations*, are identified by comparing the observed spatial pattern of bear telemetry points to a reference distribution of spatial pattern. The reference distribution is generated from a randomization conditioned on the RSF (see Figure 3.2). Five steps were used to identify unexpected locations and are listed here to provide context for the methods described below. First, the study area extent was limited to locations available to grizzly bears (Section 3.5.1). Second, the number of telemetry points to randomize to each RSF bin was calculated (Section 3.5.2). Third, telemetry points were randomized conditional on the RSF and accounted for the spatial autocorrelation in the empirical data (Section 3.5.3). The randomization procedure was repeated 99 times. Fourth, I applied a test statistic, quadrat counts, to the observed data and to all randomization outputs (Section 3.5.4). The quadrat count was calculated for high, medium, and low RSF bin groups. Fifth, unexpected locations are identified by comparing the observed quadrat counts to the reference distribution of quadrat counts generated from the 99 randomizations (Section 3.5.5).

3.5.1 Areal restrictions

The spatial extent of each randomization was limited to the grizzly bear's home range, as defined using a minimum convex polygon (MCP). MCP home ranges have previously been used to define available locations for species (e.g., Frair et al. 2004) and ensure that telemetry points are only assigned to areas deemed *available* to the bear (Nielsen et al. 2002; Buskirk & Millspaugh 2006; Thomas & Taylor 2006). The study area was further restricted by excluding water bodies and elevations above 2500 m. Previous researcher has found that adult female bears do not use higher elevations (McLellan & Hovey 2001) and within the observed telemetry data, less than 0.2% of the bear locations were above 2500 m.

3.5.2 Calculating telemetry points per RSF bin

To compare observed bear occurrence with expected bear occurrence, I need to define what "expected" bear occurrence is. A basic premise of a RSF model is that animal occurrence should increase with increasing RSF bin value. If however, RSF bin areas are inconsistent, a bin may be used less frequency than expected because it is rare on the landscape despite having a higher use per unit area (Nielsen 2005). The expected number of animal occurrences in each RSF bin should therefore be a result of the RSF bin value and its area. Johnson et al. (2006) evaluated a presence/available RSF model by comparing expected bin utilization values, the expected proportion of animal occurrences in each RSF bin, to observed bin animal frequencies. The utilization value takes into account the raw RSF bin midpoints and the relative area of the RSF bin within the individual bear home range. The utilization value is used to determine expected bear behaviour; the number of bear occurrence (telemetry points) to randomize in each bin, for each individual bear. The utilization $U(x_i)$ value for each bin i can be calculated through the formula

$$U(x_i) = w(x_i)A(x_i) / \sum_j w(x_j)A(x_j) \quad [1]$$

where $w(x_i)$ is the raw midpoint value of the RSF bin i, $A(x_i)$ is the area of bin i and j is the total number of RSF bins, $j = 1,2,\ldots, 10$ (Boyce & McDonald 1999). The number of expected bear locations in each RSF bin (N_i), was calculated using

$$N_i = N \times U(x_i) \quad [2]$$

where N is the number of observed telemetry points for the particular bear and $U(x_i)$ is utilization function calculated in [1]. Mirroring the expected frequency distribution of bear occurrences, this equation places the largest amount of bear telemetry locations in high RSF bins and the smallest amount in low RSF bins.

3.5.3 Conditional randomization

With the number of telemetry points to be randomized in each bin calculated, I randomized the points conditioned on the RSF and accounted for the spatial autocorrelation present in the empirical data. Given that grizzly bears do not use habitat randomly, animal location data are inherently clustered (Swihart & Slade 1985; Otis & White 1999; Cushman et al. 2005). The spatial autocorrelation in the empirical data was mimicked to ensure that each randomization exhibited a similar level of spatial dependence and thus, reduced the likelihood of Type 1 errors (for a detailed discussion see Fortin & Jacquez 2000). In the empirical data, approximately half of the quadrats contained telemetry points (see Section 3.5.4). To account for this spatial dependence, half of the quadrats were randomly selected and allocated the telemetry data, conditioned on the RSF, to these locations following an inhomogeneous planar Poison process. Without accounting for autocorrelation, randomizations produced point patterns more dispersed than the observed data. The process of randomly selecting quadrats and conditionally allocating points was repeated 99 times.

3.5.4 Test statistic

Quadrat counts are commonly used in biological and ecological studies for summarizing point patterns and as an approach to sampling (e.g., Boyd 2004; Gravel et al. 2008; Kéry et al. 2009). I used quadrat counts as a test statistic and compared the number of telemetry points in each quadrat in the empirical data to the number of conditionally randomized points in the same quadrats. Quadrat counts were chosen because of their familiarity and computing ease allowing for counts to be generated for each quadrat in multiple RSF bin groups. For each quadrat, counts were calculated for RSF bins categorized into three groups; low RSF (bins 1-4), medium RSF (bins 5-7) and high RSF (bins 8-10). Each RSF bin group contained approximately one third of the area within the combined bear home ranges. While a test statistic could be calculated for each RSF bin for greater detail, the complexity of the results would increase. A quadrat size of 2 km by 2 km was selected to ensure that there were an equal number of quadrats containing empirical telemetry points and quadrats remaining empty, as recommended by Getis and Boots (1987). The quadrat count was calculated for observed telemetry data and for each of the 99 randomizations in the three bin groups.

3.5.5 Identifying unexpected locations

For each bear, statistically unexpected locations were detected in the three bin groups by comparing the observed quadrat counts to a reference distribution of count values at each quadrat generated from the 99 randomizations. An unexpected location occurs when the empirical test statistic has a higher value than that of the other 99 permutations. A one-sided 99% (α = 0.01) confidence interval was used to identify such locations. Three unexpected locations categories were generated: 1) a bear using a location more than expected in the low RSF values; 2) a bear using a location more than expected in the medium RSF values; and 3) a bear using a location more than expected in the high RSF values.

Results of individual bear RSF model error were integrated by dividing the number of times the quadrat was unexpected by the total number of bears with a home range that intersected the quadrat. For example, if a quadrat is identified as statistically unexpected for 1 of 4 bears, the quadrat will have an unexpected rate of 0.25. Integrating individual bear results produced maps where quadrats have RSF values that are always, rarely, or never unexpected.

3.5.6 Exploring unexpected locations

Locations identified as unexpected were analyzed by assessing their spatial pattern and underlying environmental characteristics. The spatial pattern of model error was quantified using local Moran's *I* which can be used for ecological data to identify clusters and outliers of extreme values relative to the mean (Anselin 1995; Nelson & Boots 2008).

Areas of high error surrounded by high error are identified as clusters whereas high error surrounded by low error is identified as local high outliers. Clusters therefore represent areas where the RSF is poorly under predicting bear occurrence while outliers represent areas where the RSF is poorly predicting bear occurrence but is surrounded by areas of better prediction.

Landscape characteristics underlying the statistically unexpected quadrats were compared to those of the entire bear home range to explore variables that may be contributing to the under prediction of the RSF model. The two landscape variables selected for analysis were distance to water and elevation. For the low RSF bin group, the relative frequency distribution for the landscape characteristic within the statistically unexpected quadrats was compared to the distribution of values for all quadrats within the home range. For example, if three quadrats within a bear's home range were identified as unexpected in low RSF values, elevation would be extracted at the low RSF values from the three unexpected quadrats and compared to the values extract at the low RSF values from all quadrats in the home range.

Landscape characteristics were assessed for two grizzly bears for the low RSF group in the season spring. Spring was selected since the spring RSF was the least accurate at predicting bear occurrence compared to the other seasonal RSF models. The two grizzly bears chosen had overlapping home ranges and the greatest number of statistically unexpected quadrats; thus their habitat use was particularly problematic for the RSF model's predictive success.

3.6 Results

3.6.1 Conditional randomization

Of the 2655 quadrats generated seasonally for individual bears, 1456 (55%) were part of more than one grizzly bear seasonal home range (Figure 3.3). The RSF was under-predicting bear occurrence at: low RSF values in 152 quadrats (6%), medium RSF values in 153 quadrats (6%) and high RSF values in 100 quadrats (4%) (Table 3.2). The spatial location of unexpected quadrats in each RSF bin group and in all groups is shown in Figure 3.4. The spring RSF model predicts bear occurrence least effectively with 17% of quadrats containing more bear presence then expected, compared to 8% of quadrats in summer and 10% in autumn (Table 3.3).

3.6.2 Characterization of unexpected locations

The spatial pattern of unexpected quadrats for the combined RSF models is shown in Figure 3.5. The unexpected quadrats are spatially clustered, especially in the northeast portion of the study area, while the outliers tend to be located on home range peripheries. The frequency distribution of the landscape characteristics underlying expected and unexpected quadrats for two grizzly bears in low RSF values for spring can be seen in Figure 3.6. The first bear had 9% of their quadrats identified as unexpected through the randomization process while the second had 10% identified as unexpected. The cluster of the unexpected quadrats for these bears can be seen as identified as extreme error in the east-central portion of Figure 3.5. The frequency distribution of values for elevation is similar for both the unexpected and the expected values for both bears. In contrast, for distances to water, the unexpected quadrats in low RSF values occur more frequently at distances between 10 and 14 km than the expected quadrats in low RSF values.

3.7 Discussion

Despite the wide use of RSF models and the recognition of the importance of spatial accuracy assessments, current evaluation methods are largely aspatial. The usefulness of a RSF model depends on its predictive ability which, I argue, can vary in space and time. A new spatially explicit approach to RSF model validation was introduced and demonstrated on a case study of female grizzly bears in Alberta's Rocky Mountains. Overall, the seasonal RSF models predict bear occurrence well, with an average of 5% of the study area identified as under predicting bear occurrence. High RSF bin groups were most accurately characterized while low and medium RSF bin groups were less accurately predicted, but performed roughly the same. The existence of model error in all RSF bin groups indicates that the model is under predicting bear occurrence at all levels of habitat selection. This is an indication that new variables may need to be included in the RSF creation or the input parameters may be adjusted to increase the model's ability to predict bear occurrence.

Although the RSF models performed the best in high RSF bins, the unexpected locations identified in these bins may indicate the need for further relative scaling of the RSF model. The high RSF values may, in fact, not be ranked high enough or may be too inclusive. Since RSF values are categorical, the actual difference in the raw RSF scores varies between each categorical bin. For example, the difference in raw bear selection values between bin 1 and bin 2 is smaller than the difference between bins 9 and 10. The RSF input attribute relationships could also be adjusted to distinguish differences between the high and medium RSF bins more finely.

Identifying locations in high RSF bin groups where bear occurrence is greater than predicted is particularly important to identify spatially for management. These unexpected areas are used more by female grizzly bears than the model has the capacity to predict. They are therefore highly selected by bears and represent important habitat areas for conservation.

The accuracy of the grizzly bear RSF models varied seasonally with the summer RSF model performing the best and the spring RSF model performing the poorest (i.e., rank of performance: summer > autumn > spring). This result contrasts with the results of Nielsen (2005) who, using Somer's *D* and Spearman's rank correlation, found that the autumn RSF model performed best and the summer RSF model performed poorest (i.e., performance rank: autumn > spring > summer). The disparity between the spatial (local measure) and Nielsen's (2005) aspatial (single, global measure) accuracy assessment techniques is interesting considering similar out-of-sample adult female grizzly bear telemetry data was used for both validation processes. The expected proportion of grizzly bear occurrence in each RSF bin was also determined in the same manner, using bin utilization values. The relatively common accuracy techniques used by Nielsen (2005) would produce a perfect accuracy score if there was an increasing amount of bear locations with increasing RSF bins. For example, perfect correlation would be assigned if bin 1 had 2 bear telemetry points, bin 2 had 8 points, bin 3 had 9 points and so on. This method validates the model based on a general pattern of increasing occurrence and is insensitive to the amount of variation between RSF bins. By incorporating process expectations, through the conditional randomization, I use probabilistic comparisons which determine whether bear habitat use is greater than expected based on chance.

Through the use of local spatial statistics, clusters and outliers of extreme error in the unexpected locations were identified. The unexpected clusters were located in core areas which coincided with increased use by the bears modeled in this study. The exception to this is the large, linear cluster of unexpected quadrats in the northeast portion of the study area which resulted from a single bear. Relative to the other bears, this particular bear's seasonal home range had an exceptionally large spatial extent that was more than twice as large as other bear's ranges (1302 km^2 compared to 505 km^2). The bear's telemetry data was spatially characterized by a combination of clusters and highly dispersed locations. Clustered locations occurred when the bear was relatively stationary while dispersed locations indicated fast movement. When the local statistics were used to summarize the observed bear locations, quadrats where telemetry points were clustered experienced increased Type I errors. In other words, the conditional randomization process would seldom allocate the same quantity of telemetry locations to the particular quadrats with empirical clusters, since the home range was so large, and thus all clusters of telemetry points were incorrectly considered significant. This anomalous cluster of unexpected locations resulting from the single bear highlights the importance of examining bears individually. Using individual bear analysis, I was able to identify this cluster as resulting from a bear's individual behaviour and not as an area of high inaccuracy in the RSF model. Similarly, I was able to identify clusters of unexpected quadrats resulting from multiple bears which I focused additional analysis and modeling efforts as they are likely most problematic for model predictive success.

In contrast to the clusters of error, the outliers of error occurred on the peripheries of home ranges, usually in locations of few bears. Outliers are locations where low accuracy is surrounded by high accuracy. In cases where model spatial resolution is quite fine, outliers may have minimal impact. As model spatial resolution becomes coarser, outliers represent a greater area of error and may warrant further investigation since at these locations, model relationships may be unique.

When the observed spatial pattern of habitat use is highly variable, such as in the example above where home range sizes are inconsistent, it may be important to consider randomization algorithms that take into account the observed variation in the spatial pattern of telemetry locations. For example, a frequency distribution of the observed number of telemetry points within each quadrat may be derived. During the randomization process, the number of telemetry points to be allocated to each quadrat may be randomly extracted from the frequency distribution and thus will more appropriately mirror the observed bear behaviour. In some instances, it may also be necessary to vary quadrat size when the spatial extent of the home range is highly inconsistent but the number of telemetry points is similar.

Through distinguishing locations of model inaccuracies, researchers can identify and map errors within the study area and, furthermore, examine characteristics at these locations causing their deviation from the models prediction. Additionally, supplementary environmental data can be suggested for inclusion which may assist in future bear selection models. I tested two variables, elevation and distance to water, that were not included in the creation of the RSF model but were shown relevant in other grizzly bear RSF models (e.g., Neilsen 2002; Ciarniello et al. 2007). While elevation was similar in both expected and unexpected areas, distances to water between 10 km and 14 km were being under predicted by the spring RSF. In other words, there were more bear occurrences than expected in low RSF values within this distance to water. The inclusion of this variable in future RSF modeling may aid researchers in more correctly characterizing grizzly bear habitat use in low RSF values. It is advantageous to examine and adjust how model parameters interact through space and time to increase the success of predictive models (Haggett 1994).

Once the locations of model inaccuracy are identified, there is the opportunity to spatially adjust model parameters to incorporate this and further spatial information. For example, bear occurrence may be higher than predicted in some low RSF bins because of the proximity of these locations to high resource selection. Some low RSF areas may also be used by bears as corridors linking high quality resource patches. Spatially explicit parameters could be incorporated into the creation of the RSF by adding a spatial neighbourhood attribute that considers the relationship between the RSF value of a cell and its neighbours. It may be beneficial for a cell with a low RSF value surrounded by high RSF values to receive a higher value in the final model.

The spatial scale of analysis will impact the RSF validation procedure outlined. Both the spatial analysis extent, defined by the area available, and the spatial analysis grain, defined by the quadrat size, impacts the results. Ecological research has shown the importance of scale (Wiens 1989) and the impact it can have if it is adjusted or improperly defined. The effect of analysis units is explained by the Modifiable Areal Unit Problem (MAUP) (Openshaw & Taylor 1979, 1981; Openshaw 1984) whereby the results generated will change if the size or shape of the quadrat or the available area were altered (Jelinski & Wu 1996). MAUP is ubiquitous in many spatial investigations but can help researchers to understand the structure, function and dynamics of the ecological phenomena they are studying. The 2 km by 2 km quadrat, used in this study, was selected following Getis and Boots (1987) suggestion that there was equal number of quadrats containing empirical telemetry points and quadrats remaining empty. Quadrat size varies depending on the nature of each individual study and must be selected carefully to minimize the MAUP.

Some authors caution that it is dangerous to assume that the accuracy statistic provided for the model will be mirrored throughout the entire study area (McGwire & Fisher 2001) since underlying processes may change across the large and possibly diverse area (Dale & Fortin 2002). Indeed the findings show the spatial variation of accuracy throughout the study area. With the growth of large datasets, spatially assessing model accuracy will become increasingly important, as variations in accuracy are more pronounced over larger areas (McGwire & Fisher 2001). I recommend spatially evaluating habitat models and including an error summary as metadata. Information on geographical variations in model accuracy provided in the metadata might be important to ecologists and decision makers. The conditional randomization method presented not only has the benefits of evaluating accuracy locally, but is also threshold independent unlike most confusion matrix based techniques. While presence/available RSF models are becoming more common than their presence/absence counterparts (Thomas & Taylor 2006), model validation techniques are less developed (Hirzel et al. 2006). The method presented is able to evaluate accuracy on any type RSF model (presence/available and presence/absences) or other kinds of categorical habitat model with associated abiotic or biotic presence data.

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Table 3.1: Number of adult female bear radiotelemetry locations per season

	Bear radiotelemetry locations			
Bear	Spring	Summer	Autumn	Total
g03	96	180	232	508
g10	99	134	142	375
g12	199	170	-	369
g23	106	145	119	370
g28	234	242	273	749
g40	163	181	216	560
g48	-	62	56	118
g60	103	-	-	103
g100	102	135	181	418
Total	1,102	1,249	1,219	3,570

Table 3.2: Quadrats where the number of observed bears is statistically higher than expected based on random process conditioned to the RSF.

RSF value	Number of quadrats
Low	152 (6%)
Medium	153 (6%)
High	100 (4%)

Table 3.3: Amount of quadrats for each season where the number of observed bears is statistically higher than expected based on random process conditioned to the RSF.

RSF value	Number of quadrats[a]		
	Spring	Summer	Autumn
Low	72 (8%)	44 (4%)	36 (5%)
Medium	74 (9%)	39 (3%)	40 (6%)
High	41 (5%)	29 (3%)	30 (4%)

[a] Total number of quadrats: spring = 896, summer = 1056, autumn = 730

Figure 3.1: Study area and surrounding towns. The inset map shows the position of the study area within Canada.

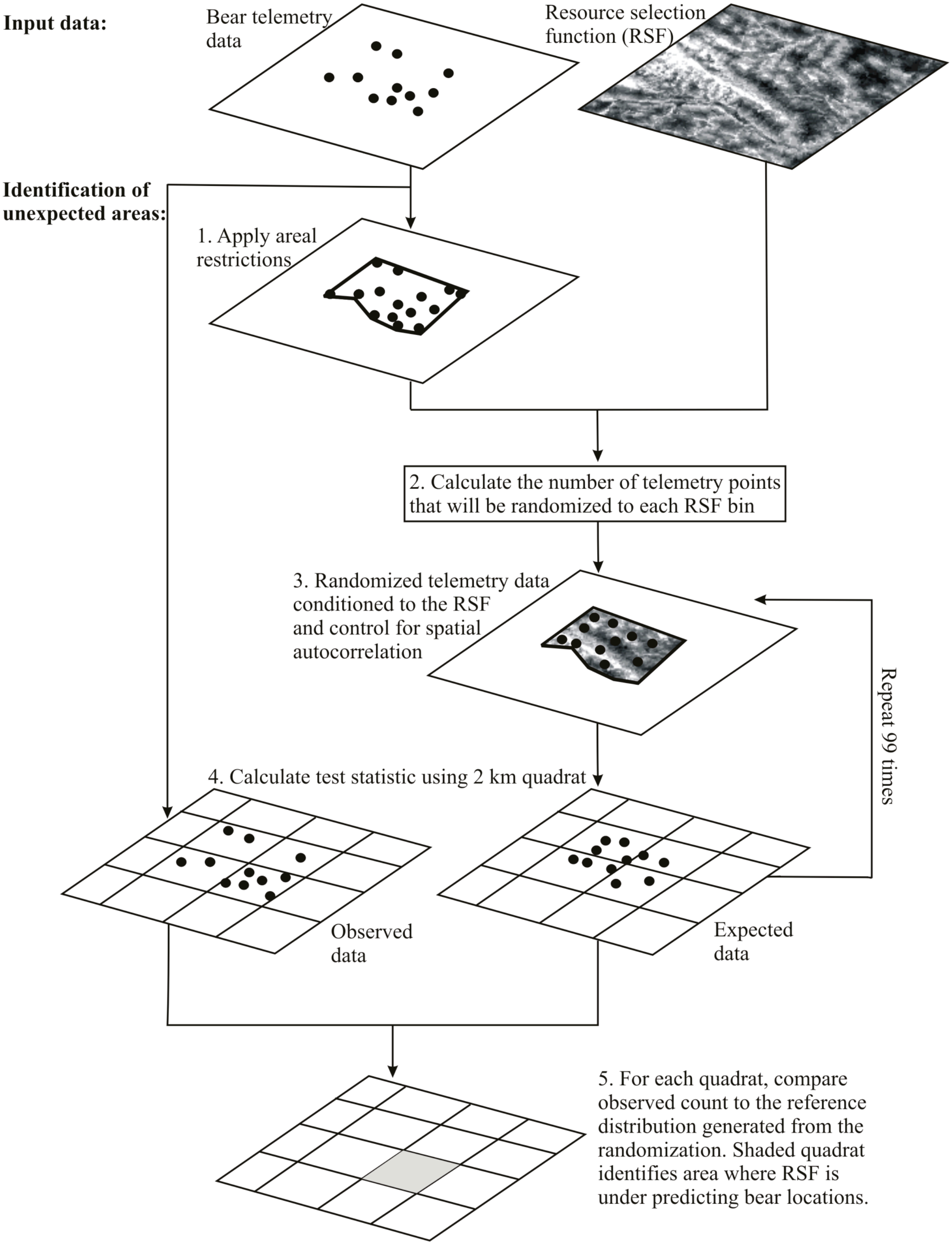

Figure 3.2: An overview of the methods used to indentify unexpected locations.

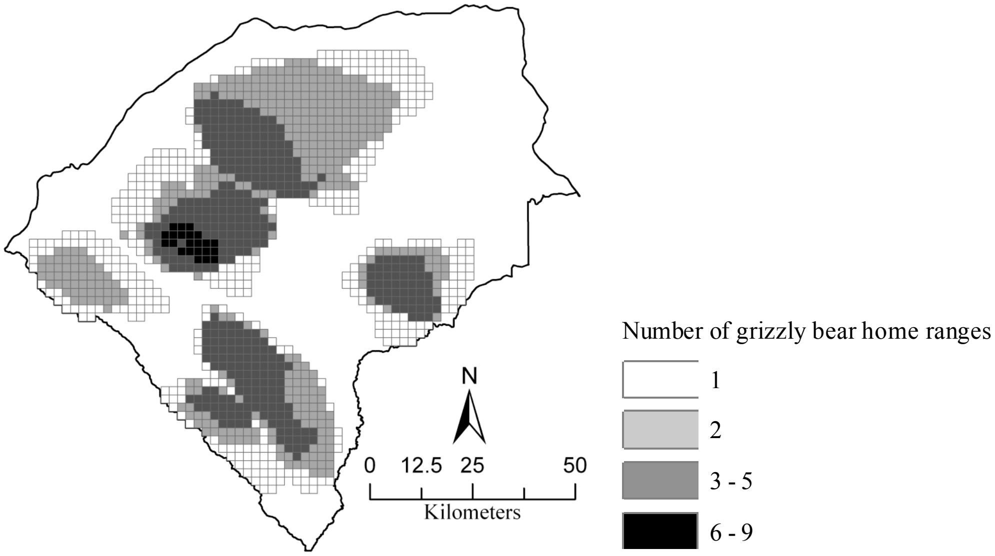

Figure 3.3: Quadrats used for validating the RSF model. Colour indicates the number of individual grizzly bear home ranges observed at each quadrat.

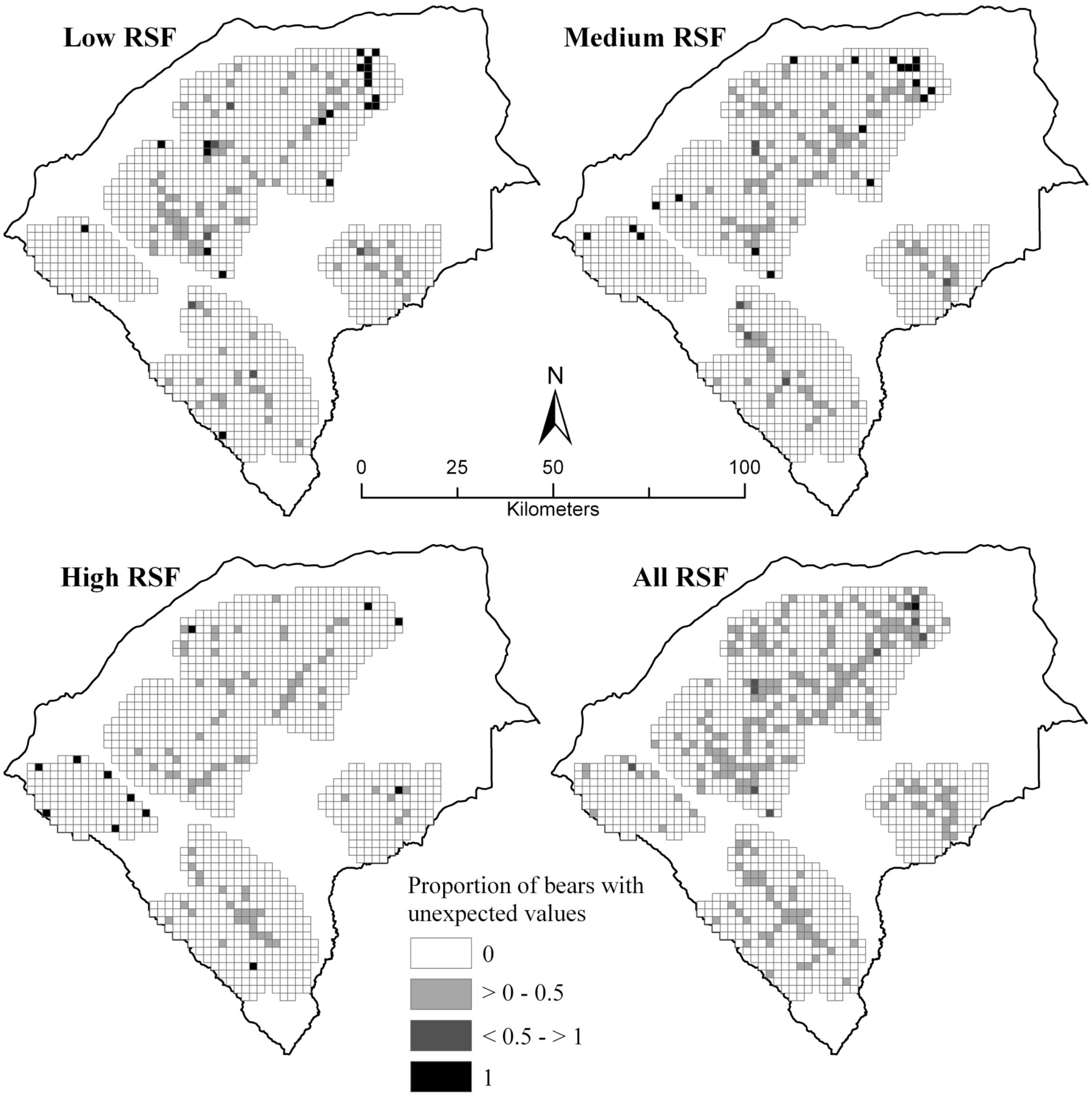

Figure 3.4: Quadrats with unexpected RSF values integrated for all individual bears and seasons. Colour represents the proportion of results indicating unexpected RSF value; calculated as the number of times an individual bear analysis determines values are unexpected divided by the total number of individual bears analyses preformed.

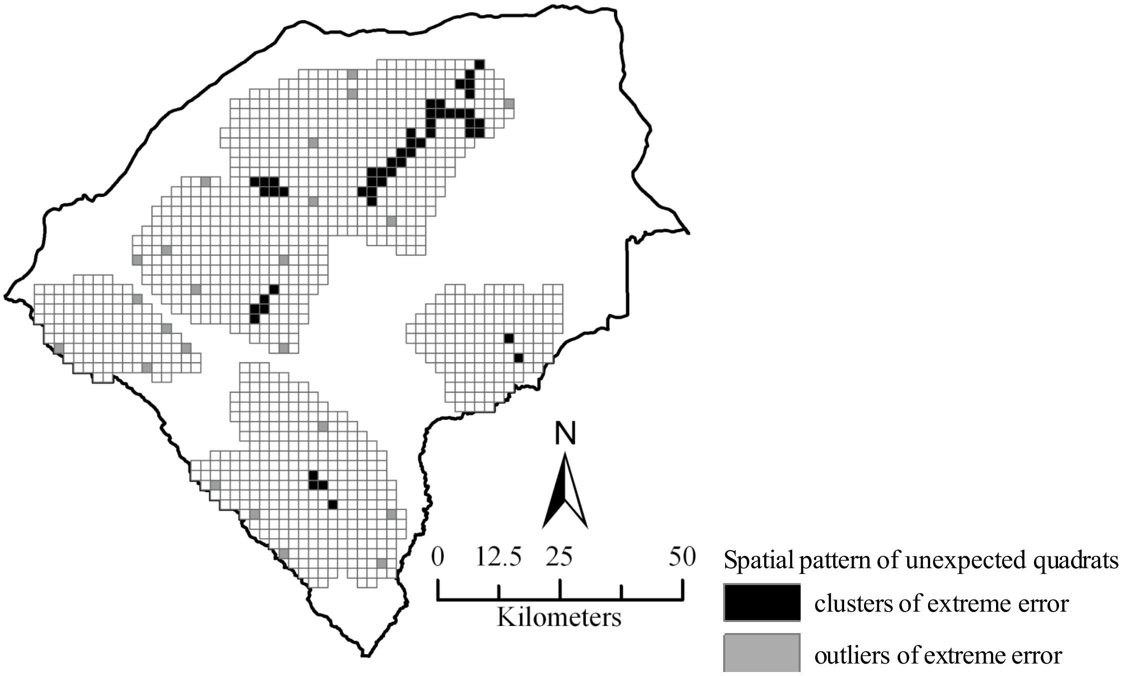

Figure 3.5: Spatial pattern of statistically unexpected quadrats identified by local Moran's *I*.

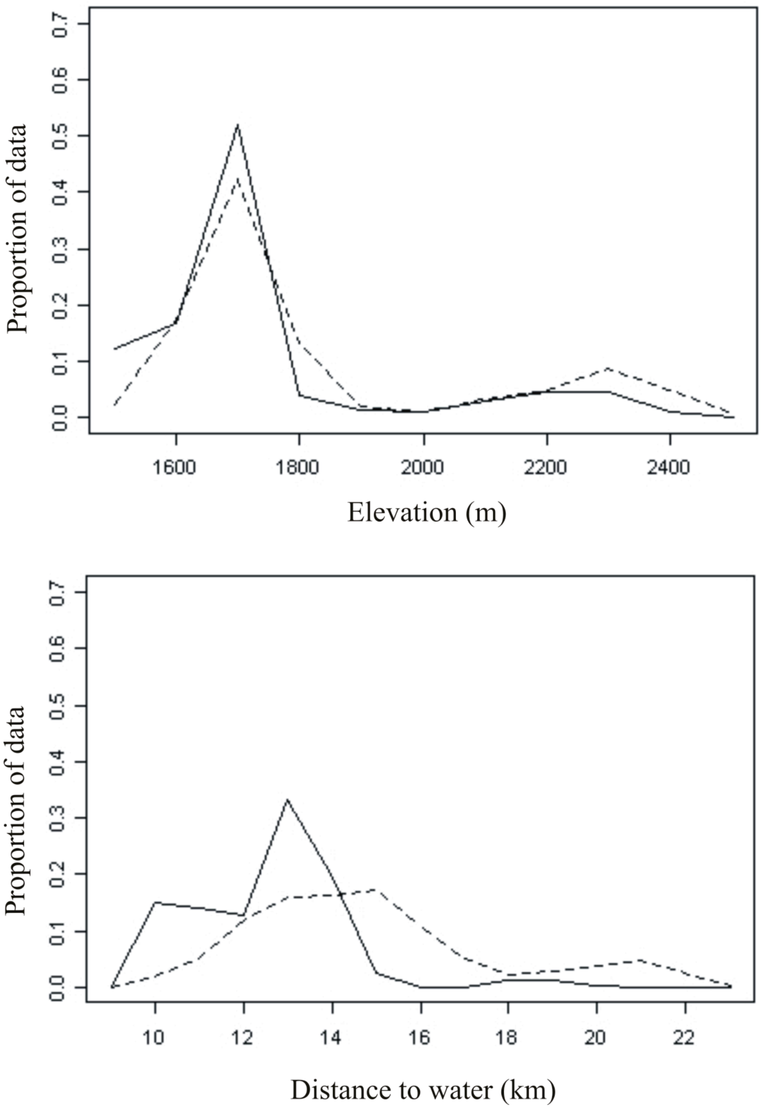

Figure 3.6: Distribution of elevation and distance to water for two bears in low RSF values during spring: unexpected areas are indicated by the solid lines; all locations within the bear’s home ranges are indicated by the dotted lines.

4.0 CONCLUSION

4.1 Discussion and Conclusions

Grizzly bears are considered an umbrella species for conservation since protecting grizzly bears will indirectly protect other species within its ecological community. A fundamental requirement for the survival of wildlife populations is adequate habitat (Morrison et al. 1992). Paquet and Hackman (1995) demonstrated that an additional 403 species were protected by maintaining the habitat needs of grizzly bears, wolves and lynx. Adequate grizzly bear habitat in Canada, however, has declined substantially over the past two centuries such that populations are limited to rugged mountains and surrounding areas where natural conditions have largely restricted human settlement (Banci 1991; McLellan 1999). Since grizzly bears are often used as a measure of ecosystem health (Stenhouse & Munro 2000), the decline in grizzly bear habitat has caused considerable attention to be paid to modeling remaining bear habitat for conservation (e.g., Mace & Waller 1997; Mace et al. 1999; Nielsen et al. 2002). While these modeling efforts have provided promising results, there is a lack of methods to address changes in grizzly bear habitat use in both time and space, especially at an individual-level (Borger et al. 2006).

Critical grizzly bear habitat must be spatially and temporally characterized to ensure that populations are successfully managed and conserved. Both the amount and the spatial configuration of habitat have a considerable impact on population viability (Ewers & Didham 2006). The goal of this research was to employ and develop methods to analyze the spatial-temporal pattern of female grizzly bear habitat use. Female grizzly bears were studied exclusively since they have the greatest influence on the development and long-term success of populations (Mace et al. 1996; McLoughlin et al. 2003; Nielsen et al. 2004b). To meet the research goal, two objectives were addressed: 1) a spatially explicit method was used to quantify changes in home range fidelity and drift over time; and 2) a technique was developed to spatially evaluate the predictive success of resource selection function (RSF) models.

In Chapter 2, I analyzed the variable impact of offspring on size and spatial-temporal pattern change in maternal grizzly bear home ranges. Solitary female bears had a relatively consistent home range size. In comparison, bears with dependent offspring had extensive home range size changes; decreases in size for bears with young offspring (COY) and increases in size for bears with older offspring (yearlings). The amount of change is also seasonally dependent with the greatest change occurring in spring. These results are consistent with what other researcher have hypothesized as resulting from the offspring's limited mobility or female's avoidance of potentially infanticidal male bears (Blanchard & Knight 1991; Dahle & Swenson 2003). The quantified change in the spatial-temporal pattern of home ranges also supports the limited mobility and infanticide hypotheses. For instance, bears with young offspring were observed to contract their home range into familiar areas. Previous research has suggested that predation risk decreases with familiarity since the animal has knowledge of potential escape routes and places to hide (Janmaat et al. 2009).

Analyzing the pattern of home range change over time allows for the spatial and temporal quantification of the species dynamic space use over multiple consecutive years. The area a grizzly bear requires is not static in size or location, but changes and drifts in relation to their offspring dependency and season. As a result of this research, I would recommend wildlife managers consider that protected areas should be large enough to encompass the dynamic nature of female grizzly bear habitat use. Considering the extensive range drift grizzly bears experience, I would also recommend that the delineation of key habitat areas not necessarily exclude habitat because of lack of recent use since these areas may become important in the future. Lastly, I would recommend that managers consider delineating protected areas with locations of site fidelity at their core. The spatial-temporal methods used in this study are important since they can quantify the cohesive home range area needed to accommodate grizzly bear site fidelity, contraction drift, and expansion drift.

In Chapter 3, I presented a new method for spatially evaluating the accuracy of RSF models. Despite the model's widespread use and application, RSF evaluation techniques have been predominantly limited to metrics that report a single value of accuracy for the entire study area (Fielding & Bell 1997). The method I developed is able to identify local pockets of inaccuracy in high, medium, and low RSF values and to investigate the potential causes of these errors. Through the use of local spatial statistics, clusters of error were identified and mapped. Environmental characteristics at locations accurately and inaccurately predicted by the model were compared to suggest modifications that could improve the model's predictive performance.

With the growth in large datasets, reporting accuracy as a single measure becomes increasing problematic since variations in accuracy are more pronounced across large study areas (McGwire & Fisher 2001). Even within my relatively small study area (10 000 km²), the spatial RSF evaluation method showed accuracy varying both spatially and seasonally. Since the spatial accuracy assessment locally identifies particularly problematic areas, additional investigation and sampling efforts can be focused on these locations. The model's predictive success can thereby be most efficiently improved by targeting areas of high inaccuracy. Due to the inevitable variability in RSF accuracy across large study areas, combined with the increased information provided with spatial accuracy assessments, I recommend that wildlife managers consider using this technique to evaluate RSF models. Managers should also consider including metadata with spatial accuracy information to ensure that future users are aware of the variations in model performance.

4.2 Research Contributions

The first major contribution of this research was the novel application of a spatially-explicit method for quantifying and analyzing change in animal home range fidelity and drift. This is a significant contribution to the fields of spatial analysis, biology, and ecology. Previous work has demonstrated the need for methods that have the ability to quantify fidelity and drift in both space and time (Switzer et al. 1997, Borger et al. 2006). By applying STAMP, Spatial-Temporal Analysis of Moving Polygons, (Robertson et al.

2007) to home ranges, I have exposed the research community to tools which can assess fine-scale spatial pattern changes in individual-animal home ranges over time.

Since there are many ecological processes which are difficult, or impossible, to measure explicitly, spatial analysis uses pattern as a surrogate for investigating immeasurable processes. As demonstrated through this research, the application of STAMP allows for inferences to be made about the biological mechanisms and processes causing the observed home range change patterns. This research, thereby, also contributes to biology by analyzing the reasons for changes in grizzly bear habitat use for varying offspring dependency and season. The observed spatial-temporal pattern of home range change coincides with what would be expected if an offspring's limited mobility or infanticide were the dominant ecological processes causing bear home range change. My observations support the notions of Wieglus & Bunnel (1995) and Dahle & Swenson (2003) who have also proposed infanticide as an explanation of grizzly bear behaviour.

The other main contribution of this research was the development of a spatially-explicit method of assessing RSF model accuracy. Despite the recognition that model accuracy undoubtedly varies across a study area (McGwire & Fisher 2001; Dale & Fortin 2002), most habitat-associated studies use a restricted set of error measures, of which percentage of overall accuracy is the most common (e.g., Nielsen 2005). Previous research has recognized and recommended examining the spatial pattern of model error (e.g., McGwire & Fisher 2001; Pontius & Schneider 2001; Barry & Elith 2006; Lobo et al. 2008), but few methods exist. The method I developed allows the user to locally identify areas of weakness within presence/available and presence/absence RSF models. With this knowledge, researchers may target additional efforts to such areas in order to boost the model's predictive capacity. I demonstrated one method of improving the model's accuracy by comparing landscape characteristics between locations where bear occurrence was accurately and inaccurately predicted. Since RSF models are widely used in geography, ecology, and biology, this contribution has the potential to be important to a diverse range of future studies.

4.3 Research Opportunities

The findings in this thesis bring to light many exciting research opportunities. Through spatial-temporal home range analysis, there are opportunities to further decouple the ecological processes resulting in the observed patterns of home range change. Although my results show home range change in relation to offspring status, it would be interesting to assess home range changes in relation to fluctuations in resource availability and human disturbance. Changes in resource availability have been shown to influence site fidelity and drift in Arctic grizzly bear populations (Edwards et al. 2009). While the impact of human disturbance on bear populations have been mixed (e.g., Wieglus et al. 2002, Neilsen et al. 2004a, Linke et al. 2005), it would be interesting to examine the relationship between different types of disturbance and bear fidelity. For example, bears may show increased fidelity and expansion drift towards young clearcut areas as they provide natural openings in a landscape that lacks canopy openings due to multiple generations of fire suppression (Nielsen et al. 2004a).

It would also be interesting to conduct the spatial RSF model accuracy assessment with varying spatial analysis grains and extents to determine if locations of error are consistent at multiple spatial scales. The importance and impact of scale have been demonstrated in a multitude of ecological research (Wiens 1989). The effect of sampling unit scale and configuration, known as the modifiable areal unit problem (MAUP) (Openshaw & Taylor 1979, 1981; Openshaw 1984), occurs when results could change if the size or shape of the quadrat was altered (Jelinski & Wu 1996). Through increasing and decreasing quadrat size, researchers could identify the locations of error that are spatially consistent throughout multiple spatial scales.

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