

**Identifying mechanisms of population change in two  
threatened grizzly bear populations.**

by

Michelle L. McLellan

A thesis submitted to Victoria University of Wellington  
in fulfilment of the requirements for the degree of

Doctor of Philosophy

2020



Identifying mechanisms of population change in two threatened grizzly bear populations.

Ph.D. thesis © Michelle L. McLellan 2020

This thesis was conducted under the supervision of

Dr. Heiko U. Wittmer (primary supervisor)

School of Biological Sciences

Victoria University of Wellington

Wellington, New Zealand

and

Dr. Rahel Sollmann (secondary supervisor)

Department of Wildlife, Fish, and Conservation Biology

University of California – Davis

Davis, California, U.S.A.

## Abstract

Identifying the mechanisms causing population change is essential for conserving small and declining populations. Substantial range contraction of many carnivore species has resulted in fragmented global populations with numerous small isolates in need of conservation. Here I investigate the rate and possible agents of change in two threatened grizzly bear (*Ursus arctos*) populations in southwestern British Columbia, Canada. I use a combination of population vital rates estimates, population trends, habitat quality analyses, and comparisons to what has been described in the literature, to carefully compare among possible mechanisms of change.

First, I estimate population density, realized growth rates ( $\lambda$ ), and the demographic components of population change for each population using DNA based capture-recapture data in both spatially explicit capture-recapture (SECR) and non-spatial Pradel robust design frameworks. The larger population had 21.5 bears/1000km<sup>2</sup> and between 2006 and 2016 was growing ( $\lambda_{\text{Pradel}} = 1.02 \pm 0.02 \text{ SE}$ ,  $\lambda_{\text{secr}} = 1.01 \pm 4.6 \times 10^{-5} \text{ SE}$ ) following the cessation of hunting. The adjacent but smaller population had 6.3 bears/1000km<sup>2</sup> and between 2005 and 2017 was likely declining ( $\lambda_{\text{Pradel}} = 0.95 \pm 0.03 \text{ SE}$ ,  $\lambda_{\text{secr}} = 0.98 \pm 0.02 \text{ SE}$ ). Estimates of apparent survival and recruitment indicated that lower recruitment was the dominant factor limiting population growth in the smaller population.

Then I use data from GPS-collared bears to estimate reproduction, survival and projected population change ( $\lambda$ ) in both populations. Adult female survival was 0.96 (95% CI: 0.80-0.99) in the larger population (McGillvary Mountains or MM) and 0.87 (95% CI: 0.69-0.95) in the small, isolated population (North Stein-Nahatlatch or NSN). Cub survival was also higher in the MM (0.85, 95%CI: 0.62-0.95) than the NSN population (0.33, 95%CI: 0.11-0.67). This analysis

identifies both low adult female survival and low cub survival as the demographic factors associated with population decline in the smaller population. By comparing the vital rates from these two populations with other small populations, I suggest that when grizzly bear populations are isolated, there appears to be a tipping point (de Silva and Leimgruber 2019) around 50 individuals, below which adult female mortality, even with intensive management, becomes prohibitive for population recovery. This analysis provides the first detailed estimates of population vital rates for a grizzly bear population of this size, and this information has been important for subsequent management action.

To determine whether bottom-up factors (i.e. food) are limiting population growth and recovery in the small isolated population I use resource selection analysis from GPS collar data. I develop resource selection functions (RSF) for four dominant foraging seasons: the spring-early summer season when bears feed predominantly on herbaceous plants and dig for bulbs, the early fruit season where they feed on low elevation berries and cherries, the huckleberry season and the post berry season when foraging behaviours are most diverse but whitebark pine nuts are a relatively common food source. The differences in overall availability of high-quality habitats for different food types, especially huckleberries, between populations suggests that season specific bottom-up effects may account for some differences in population densities. Resource selections are a very common tool used for estimating resource distribution and availability, however, their ability to estimate food abundance on the ground are usually not tested. I assessed the accuracy of the resulting RSF models for predicting huckleberry presence and abundance measured in field plots. My results show that berry specific models did predict berry abundance in previously disturbed sites though varied in accuracy depending on how the models were categorized and projected across the landscape.

Finally, I combine spatially explicit capture-recapture methods and models developed from resource selection modelling to estimate the effect of seasonal habitat availability and open road density, as a surrogate for top-down effects, on the bear density in the two populations. I found that population density is most strongly connected to habitats selected during a season when bears fed on huckleberries, the major high-energy food bears eat during hyperphagia in this area, as well as a large baseline difference between populations. The abundance of high-quality huckleberry habitat appears to be an important factor enabling the recovery of the larger population that is also genetically connected to other bears. The adjacent, smaller and genetically isolated population is not growing. The relatively low abundance of high-quality berry habitat in this population may be contributing to the lack of growth of the population. However, it is likely that the legacy of historic mortality and current stochastic effects, inbreeding effects, or other Allee effects, are also contributing to the continued low density observed. While these small population effects may be more challenging to overcome, this analysis suggests that the landscape can accommodate a higher population density than that currently observed.

## Acknowledgements

I would like to thank my supervisor, Heiko Wittmer, for his academic guidance, generosity and friendship. I appreciate that many of our best discussions were on two wheels climbing up Makara peak. I would also like to thank Rahel Sollmann for her thoughtful recommendations, useful feedback, and for taking time for me when I needed it most.

My family has been an integral part of this project. I thank my father and mentor, Bruce, for his unparalleled insights and perspectives, and above all, for the fun times. I thank my mother, Céline, for coming in the field with me and for looking after my kids, often for weeks on end, but mostly I am grateful that she's kind, adventurous and knows when it's time to stop working for the day. I thank my brother, Charlie, for his encouragement and his unique time management insights. I thank Jonathan, for moving back and forth across the world so that I could pursue this, and for his enduring support, even when it involved carrying rotten blood. I thank my daughters, Tia and Elise, for keeping me balanced and engaged over the last few years, and for knowing the difference between huckleberries and blueberries before they could talk. I also thank Sarah and Alli for listening during the more difficult times.

The contributions in time and support for this project have been numerous. I thank Tony Hamilton for hiring me in 2005 to “find out what the bears are doing”. I thank Yvonne Patterson for years of fieldwork and even more years of friendship. Bryce Bateman, Robin Steenweg, and Rhys Walter contributed hundreds of field days and countless good times. Steve Rochetta provided data, lots of blood, and good humour. Clayton Apps has always been insightful, encouraging, and helpful. Clayton Lamb inadvertently convinced me that it was time to go back to school. Thanks to the excellent piloting of Dave Mair, Clay Wilson and Scott Taylor, we are

all still alive and have collected so much data. I thank Gary Pavan for mentoring me in both GIS analysis and deep-snow snowmobiling. I thank Rob Serrouya for hiring me to do all sorts of wildlife work that led me here. I also thank both Francis Iredale and Jolene Patrick for their interest in the project, support, and fieldwork. Justine McCulloch, John Redan, Kathleen Street, Dorian Leech, Awan Ned and Alicia Krupek contributed to data collection. Finally, Mark Ritchie, Jen Reid and Sarah Littlejohn kindly proof-read parts of this thesis.

I would like to acknowledge that this research was carried out in the traditional territory of the St'at'imc people.

I am grateful to Victoria University of Wellington for a doctoral scholarship, Habitat Conservation Trust Foundation, the Province of British Columbia and the Grizzly Bear Foundation for financial support.

## **Statement of authorship**

All experimental design, data collection, analyses, and writing were conducted by the author with advice from Heiko Wittmer and Rahel Sollmann. All data chapters are intended for publication.

The following collaborations contributed to the completion of this thesis:

**Chapter 2:** Data collection was conducted by the author and Clayton Apps, Bryce Bateman, Celine Doyon, Jonathan Foulger, Bruce McLellan, Steve Rochetta and pilot Scott Taylor.

A version of chapter 2 was published as:

McLellan, M. L., B. N. McLellan, R. Sollmann, C. T. Lamb, C. D. Apps, and H. U. Wittmer. 2019. Divergent population trends following the cessation of legal grizzly bear hunting in southwestern British Columbia, Canada. *Biological Conservation* 233:247–254.

**Chapter 3:** Data collection was conducted by the author and Bruce McLellan, Yvonne Patterson, Steve Rochetta, Tony Hamilton and pilot Clay Wilson.

**Chapter 4:** Data collection was conducted by the author and Bruce McLellan, Yvonne Patterson, Bryce Bateman, Robin Steenweg, Rhys Walter, Francis Iredale, Justine McCulloch, John Redan, Kathleen Street, Dorian Leech, Awan Ned and Alicia Krupek.

**Chapter 5:** Analysis was conducted by the author and included the results of chapter 2 and 4.





This thesis is dedicated to Tex.

## Table of Contents

Abstract .....	iii
Acknowledgements .....	vi
Statement of authorship.....	viii
List of Figures .....	xiii
List of Tables.....	xviii
Chapter 1 .....	1
General Introduction .....	1
1.1 How to identify the rate and causes of population change in threatened populations. ....	1
1.2 Thesis Structure.....	9
1.3 Study Area.....	10
Chapter 2.....	15
Divergent population trends after ending the legal grizzly bear hunt.....	15
2.1 Abstract .....	15
2.2 Introduction .....	16
2.3 Methods.....	19
2.3.1 DNA Capture-Recapture .....	19
2.3.2 Changes in population density.....	21
2.3.3 Apparent survival and recruitment .....	23
2.4 Results .....	25
2.5.1 Spatial Mark-Recapture Density Trends .....	27
2.5.2 Demographic components of trends .....	30
2.5 Discussion .....	33
Chapter 3.....	38
Vital rates underpinning trends of small and endangered large carnivore populations. ....	38
3.1 Abstract .....	38
3.2 Introduction .....	39
3.3Methods.....	42
3.3.1 Bear Capture and Monitoring.....	42
3.3.2 Survival Analysis.....	44

3.3.3 Age of primiparity and Litter size .....	46
3.3.4 Reproductive Rate and State Transition .....	46
3.3.5 Population Growth and Stable Age Distribution .....	48
3.4 Results .....	49
3.4.1 Causes of mortality .....	50
3.4.2 Survival of independent females .....	50
3.4.3 Age of primiparity and Litter size .....	51
3.4.4 Survival of dependent offspring .....	53
3.4.5 Stable reproductive state distribution (SRSD).....	53
3.4.6 Population growth.....	54
3.4.7 Stable age distribution .....	57
3.5 Discussion .....	58
Chapter 4.....	64
The influence of habitat on the trend of two threatened grizzly bear populations & ground testing habitat selection models.....	64
4.1 Abstract .....	64
4.2 Introduction .....	65
4.2 Methods .....	70
4.2.1 Capture and Collaring.....	70
4.2.2 Seasonal Delineation .....	71
4.2.3 RSF Model Development .....	72
4.2.4 Environmental Variables .....	75
4.2.5 Comparing seasonal habitats between the populations. ....	78
4.2.6 Bear foraging sites .....	78
4.2.7 Huckleberry productivity plots .....	81
4.2.8 Huckleberry Season Model Testing Analysis .....	82
4.3 Results .....	85
4.3.1 Capture and Collaring.....	85
4.3.2 Seasonal RSF Models .....	85
4.3.3 Habitat distribution among populations .....	95
4.3.4 Berry Foraging Site Attributes .....	97
4.3.5 Test Plots and RSF Predictions .....	99

4.4 Discussion .....	105
Chapter 5 .....	111
Estimating the role of bottom-up processes in the recovery of endangered populations of a large carnivore. ....	111
5.1 Abstract .....	111
5.2 Introduction .....	112
5.3 Methods .....	115
5.3.1 DNA Capture-Recapture .....	115
5.3.2 Habitat and road density covariates .....	116
5.3.3 Analysis methods .....	119
5.3.4 Detection parameters .....	120
5.3.5 Density surfaces .....	121
5.4 Results .....	122
5.5 Discussion .....	127
Chapter 6 .....	131
General Discussion .....	131
6.1 Discussion .....	131
6.2 Applications in Conservation Biology .....	135
6.2 Project Legacy .....	140
Literature Cited .....	141
Supplementary Material .....	162

## List of Figures

**Figure 1.1:** **a)** Extant (blue), vagrant (ochre) and extirpated (red) distribution of grizzly bears in central and western North America (McLellan et al. 2016). **b)** The southern extent of grizzly bear distribution in western North America highlighting the two peninsulas of occupancy (blue). The Yellowstone population is the large isolate at the southeastern tip of the current distribution in the United States. The study area boundary is outlined in the red dashed line and spans the genetic population fracture between the McGillvary Mountains (MM) part of the South Chilcotin population and the northern part of the Stein-Nahatlatch (NSN) populations. These populations are at the southern tip of the grizzly bear distribution in the Coast Mountain ranges in southwest British Columbia, Canada. .... 13

**Figure 1.2:** The southwestern extent of grizzly bear distribution in North America: extant (blue), vagrant (ochre) and extirpated (red) (McLellan et al. 2016). The population boundaries are outlined in black. The northern MM population has some degree of connectivity to the north and west while the NSN population has very little connectivity to other neighbouring populations. The effective sampling area for this research is outlined in a red dash. Grizzly bear capture occurred within both the study area (red dash) and the population boundary (black line)..... 14

**Figure 2.1** Model average density estimates  $\pm$  SE (shaded) of annual density estimate over time from spatial capture-recapture models for the North Stein-Nahatlatch (NSN) and McGillvary Mountain (MM) portions of the South Chilcotin grizzly bear populations, British Columbia, Canada..... 28

**Figure 2.2** Pradel robust design model-averaged parameter estimates ( $\pm$ SE) for apparent survival ( $\phi$ ), apparent recruitment ( $f$ ) and population growth ( $\lambda$ ). Left panels (a,c,e) are model-averaged estimates where both sex and population were included as covariates. Right panel (b,d,f) model-averaged estimates for each population independent of sex. .... 32

**Figure 3.1:** The relationship between population growth rate ( $\lambda$ ) and population size from this research and other populations highlighting that connected, or larger populations are more likely to be growing than smaller, isolated populations. The isolated North Stein Nahatlatch population (■) and other isolated populations (●); the connected McGillvary Mountain population (□) and other connected populations (○); augmented populations (+) (Clevenger et al. 1987, Wakkinen and Kasworm 2004, Garshelis et al. 2005, Palomero et al. 2007, Chapron et al. 2009, Kindberg et al. 2011, Proctor et al. 2012, Pérez et al. 2014, Gervasi et al. 2017). ..... 56

**Figure 3. 2** Density plots of **a)** the stable reproductive state distribution estimated using in multistate transition models on reproductive data from collared adult female grizzly bears ( $\geq 6$  years). **b)** bootstrapped estimates of the stable age distribution estimated from vital rates for grizzly bears in the McGillvary Mountain and North Stein Nahatlatch populations in southwestern British Columbia, Canada. .... 57

**Figure 4.1** Proportion of bear use locations in the top 6 RSF bins where each bin represents 1% of available habitat in the model construction area. All models are projected across the population areas. HERB (May-early July) season diet is dominated by herbaceous forage, roots and bulbs. EARLY fruit (July-mid Aug.) diets are dominated by fruit from tall shrub species (see text). DTOP & DINT (mid-Aug.– late Sept.) without and with interactions respectively, these models predict diet consists almost entirely of huckleberries; this model only considers selection in previously disturbed sites. BTOP & BINT (mid-Aug - late Sept) without and with interactions respectively, these models predict habitat selection for huckleberry foraging but consider use and availability within the home range including undisturbed sites. POST (Sept.-Oct.) follows the huckleberry season and includes many food types. All models scored highly in Spearman’s rank correlation coefficient  $>90\%$  ..... 96

**Figure 4.2** The proportion of habitat that is high-quality ( $\geq$  RSF bin 95) for each foraging season in the McGillvary Mountain (MM) and North Stein Nahatlatch (NSN) grizzly bear populations. HERB (May-early July) season diet is dominated by herbaceous forage, roots and bulbs. EARLY fruit (July-mid Aug.) diets are dominated by fruit from tall shrub species (see text). DIST (mid-

Aug.– late Sept.) diet consists almost entirely of huckleberries; this model only considers selection in previously disturbed sites. BERRY predicts habitat selection for huckleberry foraging but considers use and availability within the home range including undisturbed sites. POST (Sept.-Oct.) follows the huckleberry season and includes many food types. .... 98

**Figure 4.3** Huckleberry season RSF model testing plot locations in the McGillvary Mountain (MM) and the North Stein Nahatlatch (NSN) grizzly populations in the south Coast Ranges of British Columbia, Canada. RSF model development area (pink outline) included both populations and all test plots were in sites previously disturbed by wildfire or forest harvest. . 100

**Figure 4.4** Non-linear relationships estimated using generalized additive models between the predicted top huckleberry RSF model (BINT) and huckleberry (VM) metrics measured at model test plots across the McGillvary Mountain and North Stein Nahatlatch grizzly bear populations. See text for abundance definitions and supplementary material Figures S2, S.3, S.4 for other RSF model comparisons. .... 103

**Figure 4.5** Bin specific estimates of model performance metrics including precision, sensitivity, specificity, accuracy and F1 score for four RSF huckleberry habitat selection models developed from seasonally specific bear locations. BTOP and BINT predict within home range habitat selection across all available habitats while DTOP and DINT are limited to disturbed sites based on the a priori exclusion of all others. BDTOP is the BTOP model binned within disturbed sites like DTOP and DNT, but only as a reference for comparison between the effects of binning and model structure..... 104

**Figure 5.1:** Seasonal food-based habitat and open road density maps for grizzly bears in southwest British Columbia, Canada. Units are scaled habitat quality from binned resource selection functions for HERB, EARLY fruit, BERRY seasons. Whitebark pine cover is percent cover (WBP) and open road density (OP\_RD) in km/ km<sup>2</sup> models is a surrogate for increased mortality risk. The BERRY \*depicts shows the footprint of potential black huckleberry patches in disturbed sites while BERRY reflects the RSF model projected across the landscape. The

boundary between the MM and NSN follows the most centre line of increased road density crossing the study area noticeable on the OP\_RD panel. .... 118

**Figure 5.2:** Probability densities of home range centres for detected individuals using the top detection model for density estimation of grizzly bears in the MM and NSN populations in southwestern British Columbia Canada. The projected densities are limited to the study area boundary to reduce edge bias in density estimates resulting from increased distance from trap location. Red dash marks the boundary between the populations delineated along the highway and settled areas. .... 123

**Figure 5.3** Relationship between density and scaled huckleberry habitat estimated from the top density surface model for the McGillvary MM and NSN grizzly bear populations in southwestern British Columbia, Canada. Lower panel is the probability density function for the scaled huckleberry habitat in each population. Huckleberry habitat quality is the scaled output of foraging specific resource selection functions projected across the populations where 0 is low quality habitat and 1 is high-quality habitat. Most selection for huckleberries occurs between 0.75 and 1.0 (see chapter 4 for details). .... 126

**Figure S.1** Hair trap array for capture-recapture population monitoring in the North Stein Nahatlatch (NSN) and McGillvary Mountain (MM) grizzly populations in southwestern British Columbia, Canada, between a) 2005 and 2012 and b) 2013-2017. Panels are separated for clarity only. Red line shows the study area boundary and the search area for areal capture described in chapter 3. .... 163

**Figure S.2** Non-linear relationships estimated using generalized additive models between the predicted top huckleberry RSF model (BTOP) and huckleberry (VM) metrics measured at model test plots across the McGillvary Mountain and North Stein Nahatlatch grizzly bear populations. See text for abundance definitions in section 4.3.5. .... 167



**Figure S.3** Non-linear relationships estimated using generalized additive models between the predicted top huckleberry RSF model (DTOP) and huckleberry (VM) metrics measured at model test plots across the McGillvary Mountain and North Stein Nahatlatch grizzly bear populations. See text for abundance definitions in section 4.3.5. .... 168

**Figure S.4** Non-linear relationships estimated using generalized additive models between the predicted top huckleberry RSF model (DINT) and huckleberry (VM) metrics measured at model test plots across the McGillvary Mountain and North Stein Nahatlatch grizzly bear populations. See text or abundance definitions in section 4.3.5..... 169

## List of Tables

<b>Table 1.1:</b> Multiple-hypotheses framework for comparing mechanisms of population change (row) and associated demographic, habitat quality and trend predictions (columns). Metrics for various predictions are comparative (low/high) relative to the other study population and other populations described in the literature. COD is the cause of death. ....	5
<b>Table 2.1</b> Summary of capture statistics from DNA population monitoring in the McGillvary Mountains (MM) and North Stein Nahatlatch (NSN) grizzly bear populations in southwest British Columbia, Canada. Statistics calculated by year and population including the number of detections, the number of individual grizzly bears, the mean number of recaptures per bear, the maximum number of recaptures, the number of new individuals, the average distance between recaptures, and the maximum distance between recaptures. ....	26
<b>Table 2.2</b> Spatial capture-recapture model selection for estimating trend in population density for the McGillvary Mountains (MM) and North Stein Nahatlatch (NSN) grizzly bear populations in southwest British Columbia, Canada. The null model ( $D \sim 1$ ), indicating no change in density between years, was compared to models where density was different among years ( $D \sim \text{session}$ ) and where density was changing as a linear function of time ( $D \sim \text{year}$ ) indicating population growth or decline. I included trap-type and sex as covariates for the probability of detection at the activity center of an individual ( $g0$ ) and sex as a covariate for the scale parameter of the detection function ( $\sigma$ ). See supplementary material table S.1 for model selection results for detection parameters. ....	27
<b>Table 2.3</b> Model-averaged parameter estimates $\pm$ SE from spatial capture-recapture models for the McGillvary Mountains (MM) and North Stein Nahatlatch (NSN) grizzly bear populations in southwest British Columbia, Canada. Detection probability for each population and sex at individual home range centre ( $g0$ ), scale parameter of the half-normal detection function ( $\sigma$ ) in km. See figure 2.1 and Supplementary Material Table S.2 for model structure.....	29

<b>Table 2.4</b> Pradel robust design models to estimate apparent survival ( $\phi$ ) and apparent recruitment ( $f$ ), for both the McGillvary Mountains (MM) part of the South Chilcotin and North Stein (NSN) part of the Stein-Nahatlatch grizzly bear populations in southwest British Canada. Models fit using common detection probability ( $p$ ) estimated in a prior analysis $p \sim \text{sex} + \text{type} + \text{effort} + (\text{sex} * \text{type})$ . Effort refers to the number of traps per occasion and type refers to whether the trap was a hair trap or rub tree. ....	31
--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------	----

<b>Table 3.1</b> Possible reproductive state transitions for adult female brown bears. Reproductive states are defined by the presence and age of accompanying offspring. ....	47
--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------	----

<b>Table 3.2</b> Model Selection results for Kaplan-Meier estimates independent bear survival from collared grizzly bears in McGillvary mountains and the North Stein Nahatlatch populations. Age is subadults from 2 to 5 years and adult bears are $\geq 6$ years. ....	51
---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------	----

<b>Table 3.3</b> Vital rates estimated using Kaplan-Meier estimator from monitoring collared grizzly bears in the McGillvary mountains (MM) and North Stein Nahatlatch (NSN) populations. Reproductive rates estimated based on monitoring females with cubs. ....	52
--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------	----

<b>Table 3.4</b> Reproductive state transition rates estimated using multi-state models on reproductive data from collared adult female grizzly bears ( $\geq 6$ years) in the McGillvary Mountain and North Stein Nahatlatch populations in southwestern British Columbia, Canada. ....	54
------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------	----

<b>Table 3.5</b> Latent variables derived from bootstrapped vital rates estimated with age-structured population matrix for collared grizzly bears in the McGillvary Mountains (MM) and North Stein Nahatlatch (NSN) populations in southwestern British Columbia, Canada. ....	55
---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------	----

<b>Table 4.1</b> Spatial covariates used for seasonal RSF model development for grizzly bear habitat in southwestern British Columbia, Canada. ....	79
-----------------------------------------------------------------------------------------------------------------------------------------------------	----

**Table 5.1** Model selection results for covariates influencing grizzly bear encounter rate ( $g0$ ), and movement scale ( $\sigma$ ) and density ( $D$ ) without density surface integration. See text for covariate definitions. Only the top 4 models are shown, all models are included in supplementary material Table S.4. .... 124

**Table 5.2** Model selection results comparing destiny surfaces including habitat and road density covariates as well as population. Detection parameters were consistently defined for all models  $g0$  (trap-type \* sex)  $\sigma$ (sex). .... 124

**Table S.1** Model selection for detection parameters estimated using spatial capture-recapture methods in each the MM part of the South Chilcotin and NSN part of the Stein-Nahatlatch grizzly bear populations in southwest British Columbia, Canada, between 2005 and 2017. **a)** Step one: candidate models compare usage defined as the number of days a trap is open or closed per occasion (days) with usage defined as a binary indicating whether a trap was open or not during an occasion, while density could vary among years ( $D \sim \text{session}$ ). **b)** Step 2: candidate models for detection parameters ( $g0$  and  $\sigma$ ) while density could vary among years ( $D \sim \text{session}$ )..... 164

**Table S.2** Candidate models for detection probability ( $p$ ), estimated using Pradel robust design capture-recapture. Apparent survival ( $\phi$ ) and apparent recruitment ( $f$ ) could vary by sex and population.  $\phi$  ( $\sim \text{sex} + \text{pop}$ ) and  $f$  ( $\sim \text{sex} + \text{pop}$ ). Recapture probability ( $c$ ), was the same as  $p$ . **a)** Step one compared effort defined as the number of traps open per occasion ( $\sim \text{effort}$ ) with the number of traps times length of the occasion in days ( $\sim \text{both}$ ). **b)** Step two used the top model from step one to compare other covariates affecting capture probability  $p$ . .... 165

**Table S.3** Model coefficients for the top five Pradel robust design models to estimate apparent survival ( $\phi$ ) and apparent recruitment ( $f$ ) and derived population growth ( $\lambda$ ), for both the McGillvary Mountains (MM) part of the South Chilcotin and North Stein (NSN) part of the Stein-Nahatlatch grizzly bear populations in southwest British Columbia, Canada. Models fit using common detection probability ( $p$ ) estimated in a prior analysis  $p$  ( $\sim \text{sex} + \text{type} + \text{effort} +$

(sex*type). Effort refers to the number of traps per occasion and type refers to whether the trap was a hair trap or rub tree. ....	166
-------------------------------------------------------------------------------------------------------------------------------------	-----

<b>Table S.4</b> Model selection results for covariates influencing grizzly bear encounter rate ( $g\theta$ ), and movement scale ( $\sigma$ ) and density ( $D$ ) without density surface integration. See section 5.32 for covariate definitions.....	170
---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------	-----

# Chapter 1

## General Introduction

### 1.1 How to identify the rate and causes of population change in threatened populations.

*“ . . . . when the bear was a few paces of the Shore I Shot it in the head. . . . the men hauled her on Shore and proved to be an old Shee which was so old that her tusks had worn Smooth, and Much the largest female bear I ever saw.”*

*-William Clark, 1806*

When Lewis and Clark were making their famous journey across the North American continent, on a quest to explore newly acquired territory and find a route to the Pacific, they were heading an era of human population expansion and increased permanent settlement, quickly leading to the large-scale extirpation of some species. Meanwhile, thousands of kilometres away, on an island where brown bears had long been extirpated, Thomas Malthus had just published the first works on population limitation and regulation (Malthus 1798).

Persecution is a unique form of top-down population limitation that is spatially predictable and historically well documented. It is often density-independent and therefore has frequently resulted in extirpation where humans and that species overlapped (Mattson and Merrill 2002, Laliberte and Ripple 2004). The ensuing patterns of occupancy are large continuous populations where human density is low or where landscape complexity limits effective persecution by humans. Therefore, the distribution of most large carnivore species is

currently or historically restricted by both continental-scale climate patterns and persecution by humans (Woodroffe 2000, Mattson and Merrill 2002).

Global brown bear (a.k.a. grizzly bear *Ursus arctos*)<sup>1</sup> distributions, for example, can be explained by large scale ecosystem changes following the last ice age and deliberate extirpation by humans for millennia in Europe and for centuries in the rest of the northern hemisphere (Curry-Lindahl 1972, Mattson and Merrill 2002). Between 1850 and 1970, grizzly bears became extirpated from 48% of their historical North American range. Humans caused this decline by direct persecution and habitat conversion. Mortality and subsequent extirpations were associated with the dominant food sources of the time; particularly predictable and low elevation food sources that concentrated bears near people, such as salmon, accelerated the rate of decline (Mattson and Merrill 2002). The resulting pattern of extirpation left islands and peninsulas of occupancy forming the contemporary distribution of grizzly bears. A similar pattern of extinction happened in Europe, Asia and North Africa, over many centuries. Brown bears now only persist in several isolated populations limited to mountainous regions of Europe and Asia, however populations become more contiguous to the north (McLellan et al. 2016).

In North America, the continuous distribution of grizzly bears becomes increasingly restricted towards the southern fringe and ends in two long peninsulas and islands of occupancy (Figure 1.1): one along the interior mountain ranges and the other along the coastal mountains (Proctor et al. 2012). Grizzly bear populations in the interior mountains have been relatively well studied (McLellan 1989, Schwartz et al. 2006, Eberhardt et al. 2008, Kendall et al. 2009). In the

---

<sup>1</sup> Grizzly bear and brown bear are common names for the same species, *Ursus arctos*. In general, the term grizzly bear is used in north America and brown bear is used in Europe and Asia, however in some areas of North America such as parts of coastal Alaska, they are also referred to as brown bears. In this thesis I will call North American bears “grizzlies” and Eurasian bears “brown bears” but in discussions where both are considered, I will use them interchangeably unless the continent of origin is important to the discussion.

southern Rocky Mountains of British Columbia, grizzly bears are continuously distributed and had sufficient abundance to support a sustainable harvest when the provincial hunt was stopped in 2017 for other reasons (Mowat and Lamb 2016, McLellan et al. 2017a). This interior population is continuous into the United States where it is considered threatened but is now growing and has more than 800 individuals. Two-hundred kilometers south the Yellowstone grizzly population is a large (>500 individuals), but isolated population that has been growing for around 45 years (Schwartz et al. 2006, Mace et al. 2012). Interior populations west of the Rockies were more fragmented and, as a result, were considered threatened and not hunted in Canada or the United States.

In stark comparison, very little is known of the ecology and abundance of grizzly bears living in the southern coastal mountain ranges, other than that their status is extremely tenuous in some if not most areas (Romain-Bondi et al. 2004). Grizzly bears have been recently extirpated from two areas in the southern coastal mountains; additionally, five mostly isolated populations are considered threatened, and there may not be any bears left in the United States portion of the most southerly population (Schwartz et al. 2003, McLellan et al. 2016).

The imbalance in research emphasis and apparent status of grizzly bears between interior and coastal mountain ranges led to the beginning of a research project in the coastal mountains in 2004. The first estimates of grizzly bear abundance and distribution were measured using a broad scale, DNA capture-recapture program across approximately 40,000 km<sup>2</sup> spanning some of these populations (Apps et al. 2007). This study identified major geographic and genetic population fractures; however, it did not estimate population trends or identify specific mechanisms that influence them. Therefore, in addition to the broad-scale, DNA based inventory, researchers initiated a finer-scale radio telemetry project in 2005 to investigate population trends and



associated mechanisms. The finer scale research program was established in two of the threatened populations that had an adjacent geographical boundary but was thought to lack genetic connectivity (Apps et al. 2007). As part of this research I began to monitor mortality and reproductive rates of collared bears as well as conduct field investigations of habitat use and associated behaviours. Following the first few years of research, the suspected difference in adult survival rates between the two threatened populations sparked the initiation of an ongoing DNA based mark-recapture population monitoring program in 2010. This program shared similar boundaries to the telemetry project and was conducted in parallel.

This dissertation is the synthesis of that research. Here, I describe how I identified the rates and likely causes of population change in two threatened populations. I use data from this ongoing research to identify rates of population change, and in a multiple competing hypothesis framework, I address the possible agents of change (Caughley 1994) to establish whether these populations are declining and, if so, why?

A common challenge for conservation research stems from the inherent difficulties obtaining meaningful inferences from small sample sizes characteristic of small populations. Because the few individuals remaining are often at very low densities, documenting population status and identifying major limiting factors for small populations is much more challenging than for large, healthy populations. However, research on the relatively easily studied large populations may provide hypotheses for the decline that can focus investigation in small populations.

The enormous amount of research on interior bears enabled me to begin with three *a priori*, but not mutually exclusive, hypotheses on why these grizzly populations are small, threatened, and doing relatively poorly (Table 1.1). First, the top-down hypothesis or, for grizzly

bears, that human-caused mortality (HCM) rates are unsustainable. In the United States, reducing HCM has been the dominant approach for recovering grizzly bears and in some areas, including Yellowstone and Northern Montana, this strategy has been highly successful (Schwartz et al. 2006, Mace et al. 2012). A similar effort to reduce HCM in the Cabinet/Yahk ecosystems of Montana and Idaho, as well as the Banff area of Alberta, however, has not resulted in dramatic increases in bear densities (Garshelis et al. 2005, Proctor et al. 2012, Sawaya et al. 2012), suggesting other factors may be more important there.

**Table 1.1:** Multiple-hypotheses framework for comparing mechanisms of population change (row) and associated demographic, habitat quality and trend predictions (columns). Metrics for various predictions are comparative (low/high) relative to the other study population and other populations described in the literature. COD is the cause of death.

<b><u>Hypotheses</u></b>	<b><u>Predictions</u></b>			
	<b>Adult Survival</b>	<b>Reproduction &amp; Recruitment</b>	<b>Habitat Quality/Food</b>	<b>Population Trend</b>
<b>Top-Down Factors (HCM)</b>	Low COD= HCM	High	Abundant	Stable/Declining
<b>Recovering (from past HCM)</b>	High COD = Rare, mostly natural	High Large Litters High survival	Abundant	Increasing
<b>Bottom-up Factors (Food availability)</b>	High COD = Rare, mostly natural	Low Small litters Old primiparity	Low or absent high energy foods	Stable
<b>Small Population Effects</b>	Slightly lower than average  COD = variable	Low Low cub survival Small litters Old primiparity	Relatively abundant	Erratic/Declining

If top-down factors are limiting these populations, I predict that adult mortality (1-survival) is higher than recruitment, and both should be high compared to other populations

because the population would be far below carrying capacity and limited by HCM. If HCM has been unsustainably high in the past, but the populations are now recovering, we would expect both survival and reproduction to be high compared to other populations, and the population to be increasing. In addition to these predicted demographic responses to top-down limitation by HCM, I expect that if HCM is currently unsustainable, the leading cause of mortality for collared adults and sub-adults will be HCM, otherwise, I expect very little adult mortality and lower recruitment rates similar to those for populations near carrying capacity (Keay et al. 2018).

Second, the bottom-up hypothesis is that south-coastal ecosystems have a limited abundance of high energy foods for grizzly bears to feed on. Research in the interior mountains of British Columbia found an abundance of high-energy foods, primarily huckleberry (*Vaccinium membranaceum*), but also buffalo berry (*Shepherdia canadensis*), consumed during late summer, enabled bears to have high reproductive rates and maintain a relatively high population density (McLellan 2011, 2015). Similarly, in the Yellowstone ecosystem, grizzly bear reproductive output was strongly influenced by whitebark pine (*Pinus albicaulis*) seed crops that bears consume in the autumn (Schwartz et al. 2006). Hilderbrand et al. (1999) suggested that the over two orders of magnitude range of grizzly bear density in North America is due to the amount and availability of high-energy foods (in particular spawning salmon) available to bears.

The second hypothesis is more complicated than the first, requiring several steps beginning with the identification of dominant food sources and associated seasonal variations in resource use among individual bears and within these populations (Nielsen et al. 2004b, McLellan and McLellan 2015). The careful identification of dominant food types allows subsequent analyses of resource selection to be season-specific. This is useful for understanding the potential contribution of habitat, and specifically, which seasonal habitats, to the observed

densities and reproductive rates. Resource selection function (RSF) modelling uses GPS telemetry data to compare use sites to available sites to make inferences about habitat selection (Johnson 1980, Manly et al. 2002, Gillies et al. 2006), ultimately providing a spatial estimate of habitat quality that can then be linked to density and other population traits.

Although useful, RSF models are not mechanistic and usually do not indicate why animals use the habitats they do (Boyce and McDonald 1999). For this analysis, I also investigate the efficacy of RSFs for predicting food abundance by measuring berry abundance in areas predicted by a berry season-specific RSFs to be selected by grizzlies. I compare the values predicted by the model to the abundance of berries at sites selected by bears to assess the accuracy and precision that can be applied to estimates of food availability within a specific spatial scale, such as a home range. This information will be useful for estimating the accuracy of RSF models for predicting food abundance, and therefore as a utility for testing hypotheses related to food-based (bottom-up) mechanisms of population regulation.

If food is limiting, I expect that the relative availability of high-energy food, such as huckleberries or whitebark pine, which have shown to drive population growth in other populations, to be low or absent (Robbins et al. 2006, McLellan 2015). I also expect specific demographic outcomes of bottom-up limitation including moderate to high adult bear survival (because few are being killed by people), and low recruitment and low population density that is either stable or declining (because of the low recruitment) (McLellan 2015, Keay et al. 2018). In addition, I hypothesize that habitat abundance where low energy foods including herbs, roots and bulbs are consumed by bears in the spring will have relatively little effect on population parameters, whereas the abundance of late summer habitat, where bears consume high-energy foods, will affect population density and reproductive rates.

The third competing hypothesis is that the bear populations have been reduced by historic agents of decline, such as prolonged persecution, and now remain as small, isolated populations. Population smallness has specific consequences limiting a population's chance for recovery; in small populations the dynamics are often determined by the specific fate of its few individuals. Also, the smaller the population, the more frequent pairings occur between related individuals, possibly resulting in reduced fecundity and increase mortality (Caughley 1994, Courchamp et al. 1999, Chapron et al. 2009). Genetic analysis of the initial population grid identified near-complete isolation of two grizzly populations in this area. Proctor et al. (2005, 2012) have shown that settled valleys with highways restrict inter-population movements of grizzly bears. Although some male movements may mediate gene flow, valleys with > 20% settlement appear to stop female movement and therefore isolate populations demographically. I hypothesize that severe inbreeding will result in reduced survival and fertility of offspring from related individuals (Charlesworth and Willis 2009, Kenney et al. 2014). Furthermore, if this is the case, cub survival and recruitment rates should be lower than predicted by the estimates based on measured availability of high-quality resources. Symptoms of non-genetic Allee effects may include skewed sex ratios caused by stochastic natal sex-ratios or net positive emigration rates exceeding replacement. Finally, small populations could experience increased rates of sexually selected infanticide if the number of females available to mate (i.e. without cubs) is low and there is a high proportion of adult males in the population (McLellan 2005).

One final consideration is that it is likely that more than one agent is responsible for the current population status for these two bear populations at the extreme edges of their current range. It is also likely that the relative importance of the various agents shifts over time. Regardless, careful analysis of the components that contribute to current population change and

successful identification of even some of the independent and/or synergistic causes of population decline and smallness will inform recovery initiatives and the use of this framework for the future conservation of grizzly bears and other species.

## **1.2 Thesis Structure**

In this thesis I investigate the mechanisms driving the population trend of two threatened grizzly bear populations using multiple competing hypotheses (Table 1.1). In the second chapter, I use spatial capture-recapture techniques and long-term population monitoring data to estimate the density and trends of the populations. I also estimate the demographic components of population change, including apparent survival and apparent recruitment. In the third chapter, I use survival and reproduction data from collared bears to quantify age-specific survival, causes of mortality, and the components of reproduction, including litter size, juvenile survival, interbirth intervals and age of primiparity. This results in one of the only detailed accounts of population demographics for a large carnivore population with fewer than 25 individuals.

The fourth chapter aims to estimate habitat selection and infer habitat quality in the two populations. In chapter four I use GPS collar location data and apply commonly used resource selection modelling to test bottom-up hypotheses. In that analysis, I delineate seasons according to diet composition so that interannual and individual variations in seasonal habitat selection are accounted for. I then test the efficacy of the resulting habitat model for the huckleberry foraging season by conducting ground truth investigations across the study area where I measure resource abundance. The ground-truthing exercise tests the huckleberry selection model independently of bear use, thereby validating it in areas where no bears were collared. The resulting habitat

models can then be confidently applied to assess and compare habitat quality in both threatened populations.

In the final chapter, I combine the resource selection functions developed in chapter 3 with spatially explicit capture-recapture methods to examine the effects of habitat quality on density. I continue to test the hypothesis that possible bottom-up factors are contributing to the difference in density between threatened populations by measuring spatial correlations between seasonal habitat quality and density. In addition, by applying a spatial component to the comparison between habitat quality and density, I expose areas for potential recovery.

### **1.3 Study Area**

This research was conducted near the southern tip of North America's coastal mountain grizzly bear range (Figure 1.1). The human history of the area is focused around a series of long inland lakes and the Fraser River, both with large annual salmon runs. These geographic features also form the contemporary boundaries of remnant grizzly populations. Anthropologists have estimated that in the 3,000 years preceding European colonization several large villages, with populations ranging from 500-1,000 people, were common along the lakes and Fraser River (Hayden and Ryder 1991). Although the historical relationship between grizzly bears and native North American people is somewhat mysterious, we can safely assume that large commonalities in their diets brought the two into contact. Toward the end of the nineteenth century, thousands of people flooded the area in pursuit of gold. The two main travel arteries from the coast to the interior of the province also followed these lakes and the Fraser River, which flanks the currently

isolated Stein-Nahatlach grizzly population. The relationship between bears and humans during this time is less mysterious; bears were shot on sight, without exception.

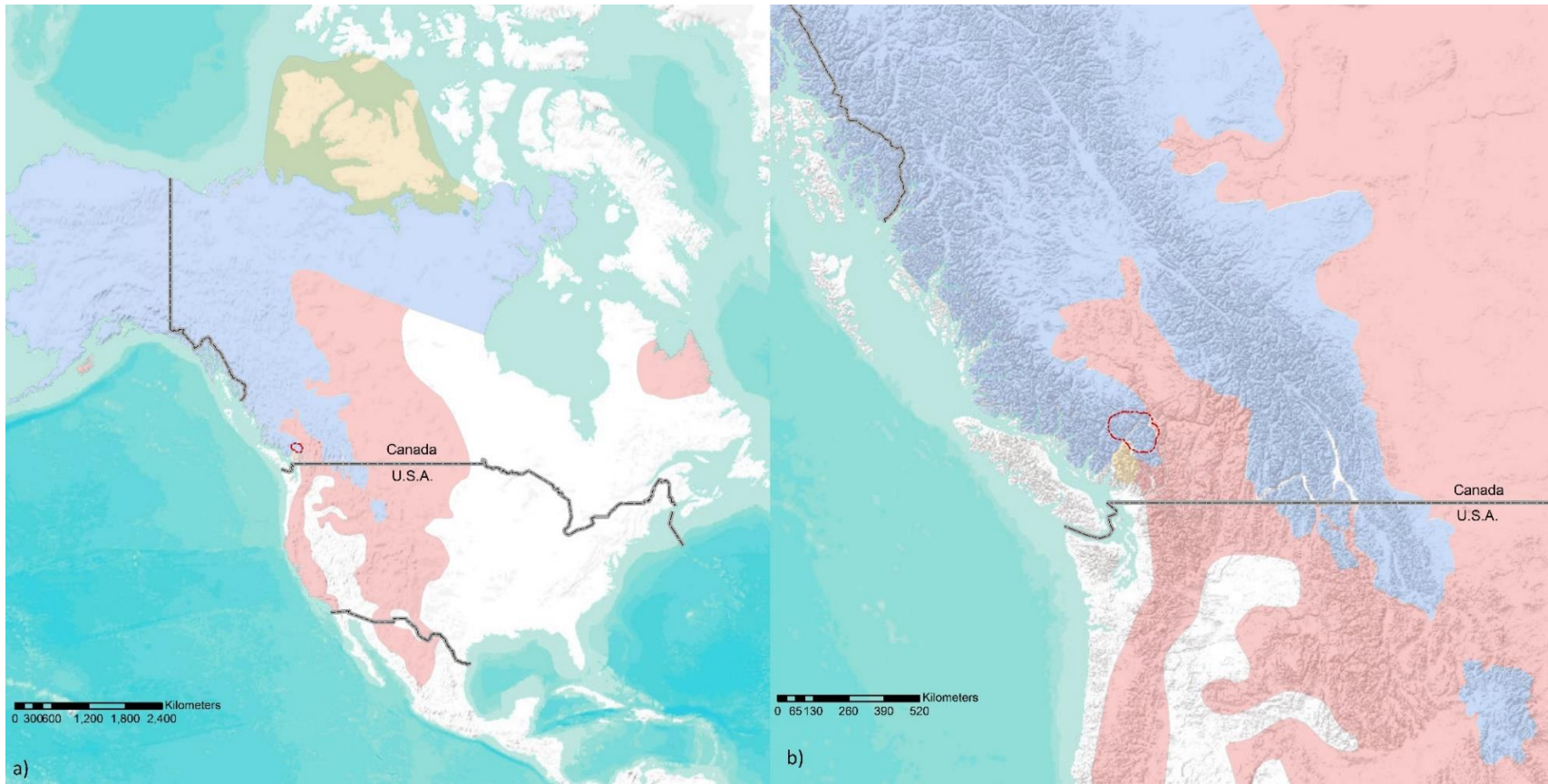
My study area spans 5,625 km<sup>2</sup> in portions of two “threatened” grizzly bear population units (GBPU) in southwestern British Columbia, Canada: the northern portion of the Stein-Nahatlach (NSN) and the southern portion of the South Chilcotin population referred to as the McGillvary Mountains (MM) population (50.6°N, 122.5°W; Figure 1.2). These populations are identified to be genetically separate with little interbreeding (Apps et al. 2007). The populations are divided by two large lakes approximately 45 km long and 1.5 km wide and the rural settlements along a minor paved highway between several small communities. A highway also bisects the NSN population, but there is no human settlement along this highway, and collared male bears cross it regularly. The southern boundary of the study area is the Stein River, located in the centre of a large (1,300 km<sup>2</sup>) and un-roaded protected area. The northern boundary of the MM study area is Carpenter Reservoir.

Both populations are in the eastern portion of the rugged Coast Mountain Range, elevations in the study area range from 240 m to 2,920 m. Air masses moving eastward from the Pacific Ocean dominate the climate and result in temperate rain forests on the west side of the mountain range, but conditions are increasingly drier moving eastward across the study area. Near the lowest elevation at the centre of the study area, the 25-year average daily maximum and minimum temperatures were 28.2 °C and 11.0 °C in July, and 0.6 °C and -2.9 °C in January. The average annual precipitation at this elevation is 500 mm. In the mountains at 1830 m, the average daily maximum and minimum temperatures are 17.0 °C and 5.3 °C in July and -3.5 °C and -9.5 °C in January. On the wetter side of the study area, the average annual precipitation is 1,080 mm,

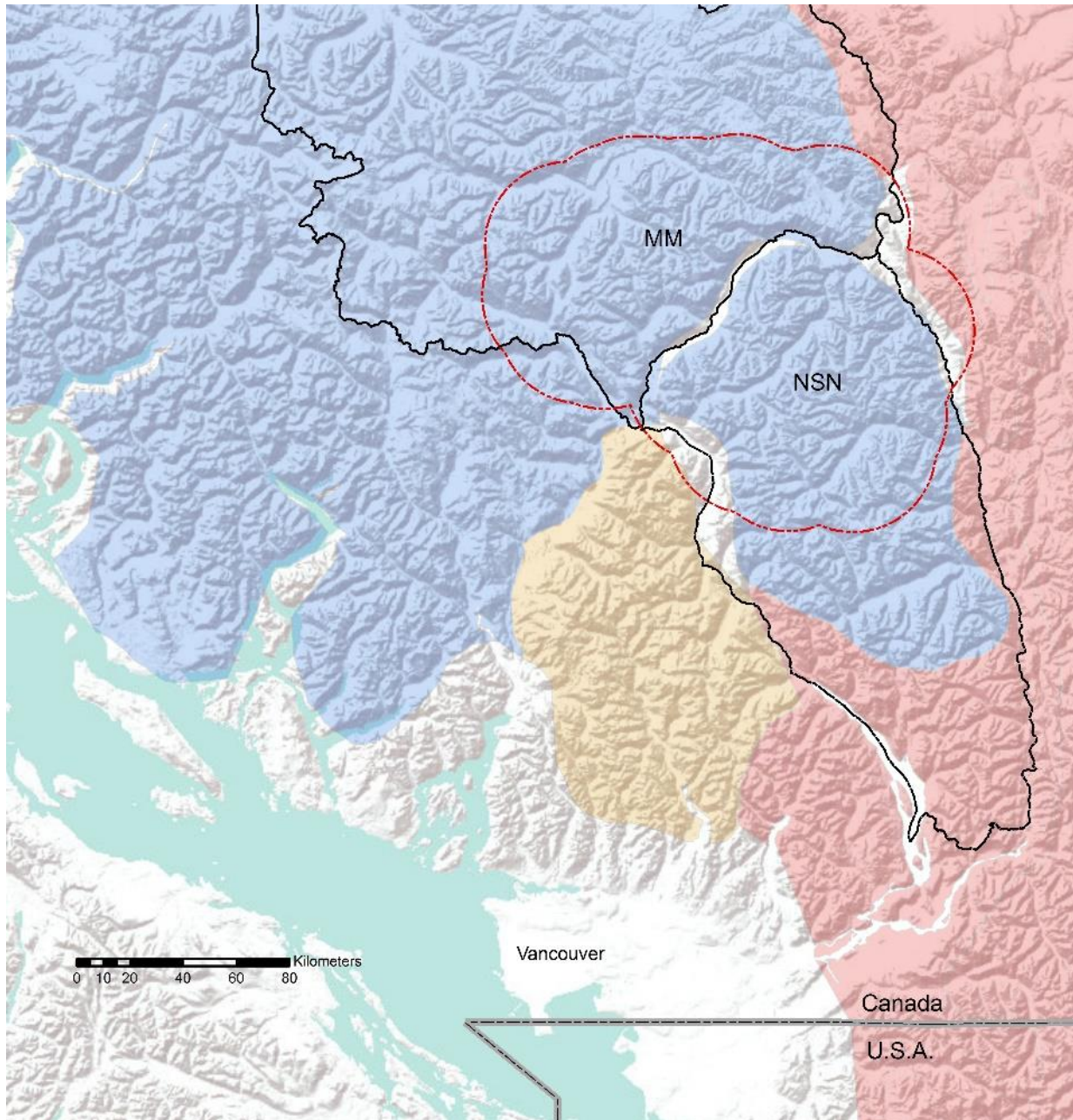


while in the mountains on the dry side of the study area the average annual precipitation is 780 mm.

Vegetation in the study area reflects the influence of high mountains, the transition of precipitation, and natural plus human-caused disturbances. Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) are the most common conifers at lower elevations with cottonwood (*Populus trichocarpa*) and western red cedar (*Thuja plicata*) along streams. On the western side of the study area, mid-elevation forests are dominated by cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) and moving eastward Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) become most common. In the transition between wet and dryer forests there are a few 10 to 20 ha patches of whitebark pine (*Pinus albicaulis*) creating a subalpine parkland. Due to high snowfall and rugged mountains, avalanche chutes are common throughout most of the study area and are rich in glacier lilies (*Erythronium grandiflorum*), Canada thistle (*Cirsium edule*), cow parsnip (*Heracleum lanatum*) and other foods preferred by grizzlies in the spring. At higher elevations, subalpine fir grows in clumps, which are often stunted forming krummholz within extensive alpine meadows. Mountain peaks are rock and rise far above the alpine meadows. There are several small glaciers in the study area.



**Figure 1.1:** **a)** Extant (blue), vagrant (ochre) and extirpated (red) distribution of grizzly bears in central and western North America (McLellan et al. 2016). **b)** The southern extent of grizzly bear distribution in western North America highlighting the two peninsulas of occupancy (blue). The Yellowstone population is the large isolate at the southeastern tip of the current distribution in the United States. The study area boundary is outlined in the red dashed line and spans the genetic population fracture between the McGillvary Mountains (MM) part of the South Chilcotin population and the northern part of the Stein-Nahatlatch (NSN) populations. These populations are at the southern tip of the grizzly bear distribution in the Coast Mountain ranges in southwest British Columbia, Canada.



**Figure 1.2:** The southwestern extent of grizzly bear distribution in North America: extant (blue), vagrant (ochre) and extirpated (red) (McLellan et al. 2016). The population boundaries are outlined in black. The northern MM population has some degree of connectivity to the north and west while the NSN population has very little connectivity to other neighbouring populations. The effective sampling area for this research is outlined in a red dash. Grizzly bear capture occurred within both the study area (red dash) and the population boundary (black line).

## Chapter 2

# Divergent population trends after ending the legal grizzly bear hunt

### 2.1 Abstract

I conducted DNA capture-recapture monitoring of grizzly bears (*Ursus arctos*) from 5 to 17 years after hunting was stopped in two adjacent but genetically distinct populations in southwestern British Columbia, Canada. I used spatial capture-recapture and non-spatial Pradel robust design modelling to estimate population density, realized growth rates ( $\lambda$ ), and the demographic components of population change for each population. The larger population had 21.5 bears/1000km<sup>2</sup> and was growing ( $\lambda_{\text{Pradel}} = 1.02 \pm 0.02 \text{ SE}$ ,  $\lambda_{\text{secr}} = 1.01 \pm 4.6 \times 10^{-5} \text{ SE}$ ) following the cessation of hunting. The adjacent smaller population had 6.3 bears/1000km<sup>2</sup> and was likely declining ( $\lambda_{\text{Pradel}} = 0.95 \pm 0.03 \text{ SE}$ ,  $\lambda_{\text{secr}} = 0.98 \pm 0.02 \text{ SE}$ ). Estimates of apparent survival and apparent recruitment indicated that lower recruitment was the dominant factor limiting population growth in the smaller population. Factors limiting reproductive rates and population density could include poor habitat quality, particularly the abundance of high-energy foods, genetic Allee effects due to a long period of population isolation, or demographic effects affecting infanticide rates. The cessation of hunting was insufficient to promote population recovery for the low density, isolated population. My research highlights the importance of considering mortality thresholds in addition to small population effects and habitat quality when recovering large carnivore populations.

## 2.2 Introduction

Over half of the world's terrestrial large carnivore populations are declining because of habitat fragmentation, habitat loss, and human-caused mortality (HCM) (calculated for species > 50 kg from IUCN, 2015, Myhrvold et al. 2015). Large carnivores are often killed by humans because they pose real or perceived threats to personal safety and property such as livestock. Besides, some large carnivore species are also hunted for sport, animal parts (Weber and Rabinowitz 1996), or because they are in competition with humans for prey (e.g., Riley et al. 2004). The result is a common geographic pattern of extinction that begins with the contraction of species distribution into peninsulas and islands of occupancy which are then sequentially extirpated over time (van Oort et al. 2011, Proctor et al. 2012, Henschel et al. 2014, Kenney et al. 2014). Extirpation is accelerated because, in addition to mechanisms initiating the decline, isolated populations face synergistic effects of population smallness such as vulnerability to stochastic change as well as genetic and demographic Allee effects (Caughley 1994, Berec et al. 2007, Brook et al. 2008).

The distribution and population size of brown and grizzly bears (*Ursus arctos*) have declined globally over the past two centuries as a result of habitat loss, habitat fragmentation, and persecution by humans (Mattson and Merrill 2002, McLellan et al. 2016). For example, grizzly bears in North America have been extirpated from approximately 42% of their historical range (calculated from IUCN spatial information; McLellan et al. 2016). Extirpation has primarily occurred in the lower 48 states of the USA and the prairies, boreal forest and taiga of central and northeastern Canada (Figure 1.1a). The northern portion of their current North American distribution is expansive but towards their southwestern extent, grizzly bears are now



restricted to two narrow peninsulas of occupancy; one along the interior Rocky and Columbia mountain ranges, and the other along the Coastal Mountain ranges (Figure 1.1a). Both peninsulas of occupancy end in isolated populations of varying sizes (Kendall et al. 2009, McLellan 2015) fragmented by natural landscape features and human settlements.

There have been numerous grizzly bear research projects along the interior peninsula of North American occupancy that identified HCM as the primary limiting factor (Garshelis et al. 2005, Kendall et al. 2009, Mace et al. 2012, Proctor et al. 2012). As with many other large carnivores, HCM for grizzly bears includes legal hunting, defence of human life or property, road and rail kills, and poaching. Reducing HCM has been the dominant approach for recovering grizzly bears and in some areas, including the Yellowstone and Northern Continental Divide ecosystems in the USA and northern Sweden, this strategy has been highly successful (Schwartz et al. 2006, Kindberg et al. 2011, Mace et al. 2012). Populations limited by HCM have relatively high adult mortality rates and will often have high recruitment rates because populations are perpetually below carrying capacity (Miller et al. 2003, McLellan 2015). In such conditions reducing HCM is expected to increase adult survival rates allowing populations to grow toward carrying capacity.

In contrast to the interior populations of North America, there has been very little research along the coastal peninsula of grizzly bear occupancy. The limited available information suggests that the status of at least some populations appears extremely tenuous (Romain-Bondi et al. 2004, Apps et al. 2014). Specifically, the provincial government of British Columbia, Canada, considered the five most southerly populations to be Threatened (Grizzly Bears - Environmental Reporting BC 2012) and in 2000, declared a moratorium on grizzly bear hunting there due to suspected low population density and probable decline. Five years after the hunt ended, a DNA-

based population study that included 4 of these Threatened populations, identified major geographic and genetic fractures as well as large differences in grizzly bear density among populations (Apps et al. 2014). Based on genetic evidence, this study also suggested reconnection and possibly population expansion in some areas, but actual trends or demographic mechanisms were not addressed.

My goal was to quantify population trends and the relative contribution of survival and reproduction to population change in portions of two adjacent but mostly disjunct portions of Threatened grizzly bear populations at the southwestern extent of their range, the McGillivray Mountain (MM) and the North Stein-Nahatlatch (NSN) populations (Figure 1.1b). As a result of the hunting moratorium, both populations experienced a decline in known HCM; between 1978 and 1999 the known HCM has declined from 0.72 bears/year in the MM and 0.50 bears/year in the NSN to 0.12 bears/year in both populations (Grizzly Bears - Environmental Reporting BC 2012). I wanted to establish whether populations were recovering following the cessation of the legal hunt and, if not, whether adult mortality or low recruitment were limiting growth.

Based on what is known of grizzly bear ecology and conservation from studies in the interior mountains (Garshelis et al. 2005, McLellan et al. 2007, Mace et al. 2012, McLellan 2015), I derived three alternative hypotheses and corresponding predictions: (1) The grizzly bear populations were limited by HCM in the past, but due to the reduction in HCM following the hunting moratorium, they are now recovering. If this hypothesis is supported, I predict high population growth rates resulting from high recruitment and high adult survival rates. (2) The grizzly bear populations remain limited by high HCM; restricting population recovery. If this alternative hypothesis is supported, I predict relatively low adult survival but high recruitment rates because populations are being held below carrying capacity. (3) The grizzly bear population

growth is not solely being limited by HCM but by other effects such as poor habitat quality. If this hypothesis is supported, I predict moderate to high adult survival because few adult bears are being killed by HCM; but low recruitment rates.

To measure the support for these hypotheses, I used non-invasive DNA sampling of hair traps (Woods et al. 1999) and rub-trees (Kendall et al. 2009) to estimate population densities, trends and the demographic components of population change. I used spatial capture-recapture (SCR) techniques to estimate population-specific density and trends (Efford 2004, Borchers and Efford 2008). I then used a robust design Pradel capture-recapture model for open populations to estimate apparent survival ( $\phi$ ) and apparent recruitment ( $f$ ), and identify their relative contributions to the realized population growth ( $\lambda$ ) for each population (Pradel 1996, Nichols et al. 2000).

## **2.3 Methods**

### **2.3.1 DNA Capture-Recapture**

I used DNA capture-recapture data from two different studies. The first occurred in 2005 and 2006 when Apps et al. (2014) estimated grizzly bear population density across the southern Coast Mountain ranges. The second study occurred annually from 2010 to 2017 and spanned the MM and NSN portion defined as the study area (Figure 1.1b). For both studies, hair traps consisted of one barbed wire strand tightly strung between trees, approximately 50 cm above the ground, forming a small corral around a pile of debris and scent lure (Woods et al. 1999). I visited traps every 2 to 5 weeks starting in late June to remove hair and re-bait. Each visit



constituted a capture occasion, and for each occasion, traps within a population were visited within 3 days of one another. The number of occasions each year varied from 3 to 6. Wildlife Genetics International (Nelson, British Columbia) screened samples, extracted DNA, carried out genotyping to 22 microsatellite loci, and identified individuals following established techniques (Paetkau 2003). The extent of the trap arrays remained nearly identical among years, though specific trap locations were often moved (Supplementary material Figure S.1). The annual minimum convex polygon (MCP) surrounding the trap arrays was 587 km<sup>2</sup> (SD = 41 km<sup>2</sup>) in the NSN and 646 km<sup>2</sup> (SD = 80 km<sup>2</sup>) in the MM. The average seasonal MCP home range for GPS collared females in these populations is 146 km<sup>2</sup> (N = 24; unpublished data) therefore the trap array was large enough to encompass home ranges of multiple females, with multiple traps within each home-range.

For the first study (2005-2006), one trap was placed in each 10 x10 km cell resulting in 13 traps per population amounting to approximately 1 trap in every major drainage within the study area. For the second study (2010-2017), the number of traps used in each population varied from 12 to 43 among years. At least 1, and often 2 or 3 hair-traps were set within each drainage, depending on the size of the drainage (Supplementary material Figure S.1).

For the second study, known rub trees were used in addition to hair traps to collect hair samples. One strand of barbed wire was attached to the rub tree and then revisited at the same occasion schedule as the hair traps. Because new rub trees were discovered, and old ones were sometimes removed by logging, the number of rub trees varied across years between 0 and 19 trees for the MM and 0 and 22 for the NSN. Trap-type and differing capture efforts among years (number of traps) and occasions (length) were included as covariates in the population models (see 2.3 and 2.4).

### 2.3.2 Changes in population density

I estimated changes in population density ( $\hat{D}$ ) for the MM and the NSN populations by fitting SCR models by maximizing the full likelihood (Borchers and Efford 2008) using *secr* package v.3.1.0 (Efford 2018) in program R. I treated each population separately and intra-annual capture-recapture occasions were nested within independent annual sessions. Grizzly bears only have offspring during winter and therefore populations were assumed to be closed across occasions of the same year (no births, deaths, immigration or emigration) and open between consecutive years (sessions). Both hair traps and rub trees allow capture of multiple individuals at a detector on one occasion and an animal may be caught in multiple traps on one occasion. In *secr*, traps with these characteristics are defined as “proximity” detectors and the capture probabilities are estimated accordingly (Efford et al. 2013). I defined the state space of density models (i.e. the area from which bears could potentially be captured) using a buffer around the hair trap/rub tree polygon of 3 times the root pooled spatial variance of each individual’s location dispersion (Efford 2004). I limited the resulting state-space at known population fractures using a spatial mask. SCR models estimate individual and trap-specific detection probabilities as a declining function of the distance between a trap and the individual’s estimated activity center. I used a half-normal detection function governed by two parameters: the baseline detection probability  $g0$ , describing detection probability at the individual’s activity center, and the scale parameter  $\sigma$ , which governs how quickly detection probability declines with distance and is related to how far animals move (e. g. Borchers and Efford 2008, Efford 2004).

I used a three-step model comparison approach with differing detection and density covariates to estimate density trends in each population while minimizing the number of models

compared. The objective of the first two steps was to incorporate potential variability in detection probability parameters  $g0$  and  $\sigma$  due to individual heterogeneity and sampling design. In the first step, I compared a model where traps were either used or unused for each occasion (binary), with a model where closed traps were classified as unused 0 but trapping effort for open traps was equivalent to the number of days in that occasion so that  $g0$  will vary linearly (on a link scale) with the time the trap was open (Efford et al. 2013). Density could vary among years ( $D \sim \text{session}$ ) while  $\sigma$  was assumed to be constant across years ( $\sigma \sim 1$ ). I used Akaike's information criterion for small samples (AICc) to compare models (Burnham and Anderson 2002). Models within 2  $\Delta\text{AICc}$  units of the top were incorporated into the model structure for the subsequent model comparison steps.

In the second step, I selected the best model for estimating detection probability parameters ( $g0$  and  $\sigma$ ). I used the usage structure identified in step one and again allowed density to vary among years while I compared models that included covariates thought to influence the baseline detection probability  $g0$ : Trap-type (type), occasion timing (time), sex, and the interactions among them ( $g0 \sim \text{type} * \text{sex}, \text{type} * \text{time}, \text{sex} * \text{time}$ ). Male grizzly bears usually have much larger home ranges than females resulting in a higher capture probability further from their activity centers, therefore, I included models with sex as a covariate for  $\sigma$  in the model selection process.

In the final step, I used the top detection model from step 2 to estimate the change in density across years ( $D \sim \text{year}$ ) by using session-number (in years) as a predictor. This fitted trend is linear on the link scale and corresponds to exponential growth or decline. Density is estimated as a function of year on the log-link scale, therefore the estimated  $\beta$  parameter is equivalent to  $r$  in the exponential growth curve  $D_t = D_{t-1}e^r$  where  $D_t$  is density at time  $t$  and  $D_{t-1}$  is density at time

$t-1$ . The finite rate of increase, or Pradel's lambda, is then  $\lambda = \exp(r)$ . The density trend model was compared to a model with density held constant across years ( $D \sim 1$ ) and a model where each session had unique densities without a trend ( $D \sim \text{session}$ ). If competing models were less than 2  $\Delta \text{AICc}$  units of the best model, I used AIC weights ( $\omega_i$ ) for each candidate model to obtain model-averaged mean and variance parameter estimates for density ( $\hat{D}$ ) and capture probability parameters  $g0$  and  $\sigma$  (Burnham and Anderson 2002).

### **2.3.3 Apparent survival and recruitment**

To identify the components of population change, I used the same data described in 2.2 and 2.3 in a Pradel robust design (PRD) framework. This approach allows estimation of demographic parameters in open populations (Pradel 1996, Nichols and Hines 2002) while using the Huggins conditional likelihood approach for estimating detection probabilities ( $p$ ) and recapture probabilities ( $c$ ) in closed populations (Huggins 1991). I parameterized the PRD model to estimate apparent survival ( $\phi$ ) and apparent recruitment ( $f$ ), capture probability ( $p$ ) and derive realized population growth ( $\lambda$ ) for both the NSN and MM populations. Apparent survival ( $\phi$ ) is the probability that an individual remains in the population and does not die or emigrate, and apparent recruitment ( $f$ ) is the rate of individuals entering the population through birth or immigration. These parameters are estimated between years and can be summed for each interval to produce the realized population growth ( $\lambda$ ). Analyses were conducted using the RMark package (White and Burnham 1999, Laake and Rexstad 2008) in program R v.3.4.0 (R Core Development Team 2017).

Like the SCR modeling in 2.3, I used a three-step model selection approach. In the first step, I allowed apparent survival ( $\phi$ ) and apparent recruitment ( $f$ ) to vary by sex and population in order to explore the effect of effort on detection probability  $p$ . Detection probability was constrained so that initial capture ( $p$ ) and recapture probabilities ( $c$ ) were the same. Effort was defined as either the number of traps open per occasion or, alternatively, the number of total trap nights for each occasion (number of traps x occasion length). The model with the lowest AICc score was used to define effort in the subsequent steps.

In the second step, covariates for capture probability ( $p$ ) included trap-type, sex, population, occasion specific time, effort, as determined from step one, and interactions between sex and trap-type, and time and trap-type. Trap-type is known to influence capture probability (Lamb et al. 2016); therefore captures at hair traps and rub trees were included as separate sequential sessions (e.g. Boulanger et al. 2008).

In the final step, I used the model structure for capture probability determined in the previous steps and modeled variation in demographic rates. I hypothesized that both apparent survival and apparent recruitment could vary between populations and sexes. I compared all combinations of sex and populations, with models keeping these rates constant, resulting in 16 models. I used the same model averaging techniques described in section 2.3 to obtain estimates of apparent survival and recruitment and their variances (Burnham and Anderson 2002). I derived estimates for population growth ( $\lambda$ ) from model-averaged estimates of apparent survival ( $\phi$ ) and recruitment ( $f$ ).

Population-specific estimates for apparent survival ( $\phi$ ) and recruitment ( $f$ ) were obtained by comparing models where one or both parameters could vary by population or be constant between populations. I used AICc weights from the four competing models to obtain model-

averaged estimates of apparent survival ( $\phi$ ) apparent recruitment ( $f$ ) and derived lambda ( $\lambda$ ) in each population.

## **2.4 Results**

Between 2005 and 2017, 78 (37 F, 41 M) grizzly bears were detected 479 times in the MM and 26 individuals (12 F, 14 M) were detected 176 times in the NSN (Table 2.1). Three male bears moved between populations: two from the NSN to the MM and one from the MM to the NSN. These individuals were handled as independent in each population. One additional adult male was known by his genetic structure to have NSN origin but was only captured in the MM. I did not detect any female movement between populations. In the last 4 years of monitoring, I marked an average of 9 new bears/year in the MM and but only 0.5 new bears/year in the similarly sized trap array over the NSN (Table 2.1).

**Table 2.1** Summary of capture statistics from DNA population monitoring in the McGillvary Mountains (MM) and North Stein Nahatlatch (NSN) grizzly bear populations in southwest British Columbia, Canada. Statistics calculated by year and population including the number of detections, the number of individual grizzly bears, the mean number of recaptures per bear, the maximum number of recaptures, the number of new individuals, the average distance between recaptures, and the maximum distance between recaptures.

Pop	Year	Detections	No. Individuals	Recaptures	Max. recaptures	New Individuals	Distance between recaptures (km)	
							Mean	Max
McGillvary Mountains	2006	53	24	2.21	8	24	4.47	20.19
	2010	31	16	1.92	7	8	7.43	21.03
	2011	68	26	2.62	10	10	6.46	25.02
	2012	70	31	2.23	8	8	6.83	24.72
	2013	76	25	3.04	11	8	5.81	16.81
	2014	69	33	2.09	8	11	6.40	43.10
	2016	112	39	2.87	11	9	6.63	34.26
North Stein-Nahatlatch	2005	31	13	2.2	7	13	9.93	21.07
	2010	13	9	1.44	3	6	12.84	26.81
	2011	15	9	1.67	4	1	11.54	20.36
	2012	28	13	2.15	6	4	5.63	12.75
	2013	26	8	3.25	6	0	6.48	18.88
	2014	25	8	3.13	8	1	9.05	32.67
	2015	24	8	3	8	1	9.33	28.36
	2017	14	6	2.5	4	0	3.90	16.02

### 2.5.1 Spatial Mark-Recapture Density Trends

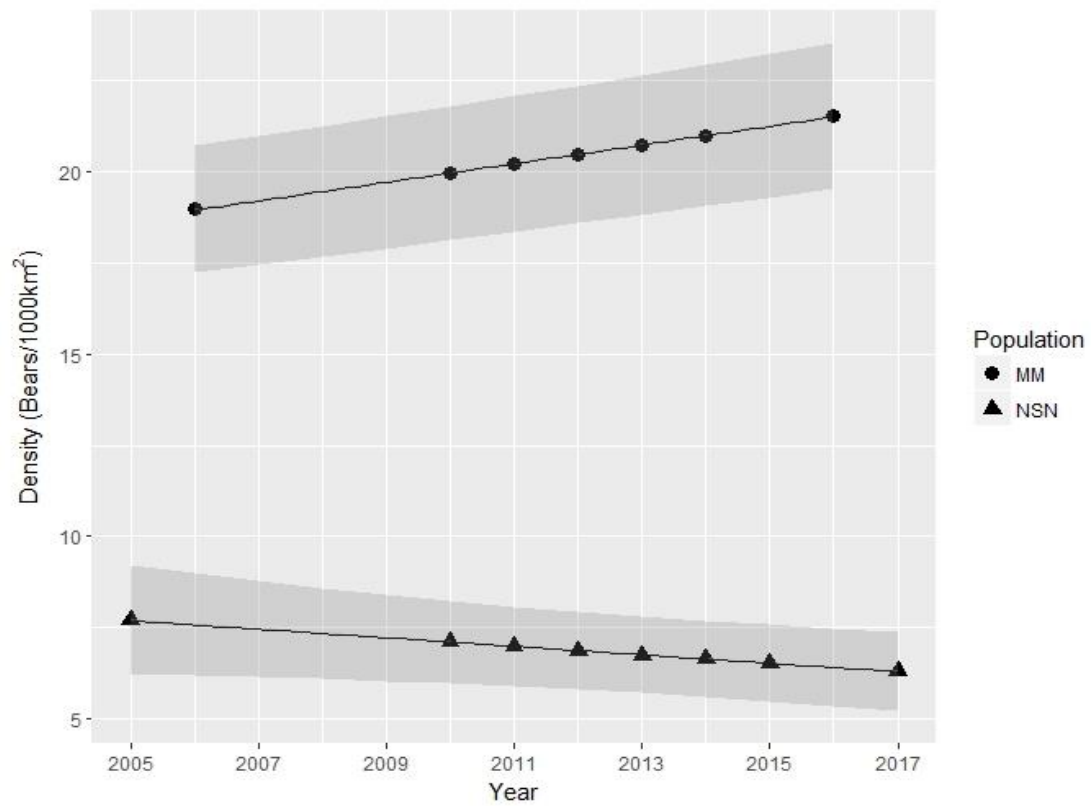
Grizzly bear population density and trend differed between the two populations. The top model for the MM population indicated that density was increasing ( $D \sim \text{year}$ ) with a growth rate of  $\lambda_{\text{secc}} = 1.01 \pm 4.6 \times 10^{-5}$  SE from 18.7 bears/1000km<sup>2</sup> in 2006 to 21.5 bears/1000km<sup>2</sup> in 2016 (Table 2.2, Figure 2.1). In the NSN population, the top two models for density were a model allowing density to change across years ( $D \sim \text{year}$ ) at a rate of  $\lambda_{\text{secc}} = 0.97 \pm 7.3 \times 10^{-5}$  SE and the null model, where density was constant across years (Table 2.2). Model-averaged results for density estimation and trend for the NSN population indicated that the population was either stable or slowly declining  $\lambda_{\text{secc}} = 0.98 \pm 0.02$  SE from 7.7 bears/1000km<sup>2</sup> in 2005 to 6.3 bears/1000km<sup>2</sup> in 2017 (Figure 2.1).

**Table 2.2** Spatial capture-recapture model selection for estimating trend in population density for the McGillvary Mountains (MM) and North Stein Nahatlatch (NSN) grizzly bear populations in southwest British Columbia, Canada. The null model ( $D \sim 1$ ), indicating no change in density between years, was compared to models where density was different among years ( $D \sim \text{session}$ ) and where density was changing as a linear function of time ( $D \sim \text{year}$ ) indicating population growth or decline. I included trap-type and sex as covariates for the probability of detection at the activity center of an individual ( $g0$ ) and sex as a covariate for the scale parameter of the detection function ( $\sigma$ ). See supplementary material table S.1 for model selection results for detection parameters.

Population	Density Model	K <sup>a</sup>	$\Delta\text{AICc}$ <sup>b</sup>	$\omega_i$ <sup>c</sup>
NSN	$D \sim \text{year}$	9	0.00	0.52
	$D \sim 1$	8	0.16	0.48
	$D \sim \text{session}$	15	10.49	0.00
MM	$D \sim \text{year}$	9	0.00	1.00
	$D \sim \text{session}$	14	10.18	0.00
	$D \sim 1$	8	10.34	0.00

<sup>a</sup> Number of model parameters  
<sup>b</sup> Difference between AICc of model and the AICc of the highest ranked model  
<sup>c</sup> Model weight





**Figure 2.1** Model average density estimates  $\pm$  SE (shaded) of annual density estimate over time from spatial capture-recapture models for the North Stein-Nahatlatch (NSN) and McGillvary Mountain (MM) portions of the South Chilcotin grizzly bear populations, British Columbia, Canada.

Top models for detection probability parameters,  $g0$  and  $\sigma$ , were the same for both populations. The best model for  $g0$  included sex, trap-type, and sex–trap-type interactions as covariates and the best model for  $\sigma$  included sex as a covariate (Supplementary material Figure S.1). Effort, defined as a binary variable indicating whether a trap was used or unused, performed better than models using the number of days to indicate usage (Supplementary material Table S.1).

Mean baseline detection probabilities  $g0$ , were similar for females in both populations but higher for males in the MM than in the NSN population (Table 2.3). Trap-type had little effect on the detection probability of males, but females were 6.4 and 3.7 times more likely to be detected at hair traps than rub trees in the NSN and MM population respectively (Table 2.3). Males had larger  $\sigma$  than females, and while  $\sigma$  for females was similar for both populations,  $\sigma$  for males was larger in the NSN (Table 2.3).

**Table 2.3** Model-averaged parameter estimates  $\pm$  SE from spatial capture-recapture models for the McGillvary Mountains (MM) and North Stein Nahatlatch (NSN) grizzly bear populations in southwest British Columbia, Canada. Detection probability for each population and sex at individual home range centre ( $g0$ ), scale parameter of the half-normal detection function ( $\sigma$ ) in km. See figure 2.1 and Supplementary Material Table S.2 for model structure.

Population	Density <sup>a</sup>	$\lambda$	Sex	$g0$		$\sigma$ (km)
				Hair trap	Rub tree	
NSN	$6.32 \pm 1.09$	$0.98 \pm 0.02$	F	$0.34 \pm 0.06$	$0.05 \pm 0.02$	$3.91 \pm 0.38$
			M	$0.13 \pm 0.03$	$0.15 \pm 0.03$	$11.48 \pm 1.41$
MM	$21.50 \pm 1.98$	$1.01 \pm 4.52 \times 10^{-5}$	F	$0.31 \pm 0.03$	$0.08 \pm 0.02$	$4.41 \pm 0.27$
			M	$0.22 \pm 0.03$	$0.21 \pm 0.03$	$7.91 \pm 0.47$

<sup>a</sup> Density (bears/1000km<sup>2</sup>) estimate for last year of sampling in each population.

### 2.5.2 Demographic components of trends

The top three models for estimating apparent survival ( $\phi$ ) and apparent recruitment ( $f$ ) had similar support and included sex or sex and population as covariates (Table 2.4). Model-averaged estimates of apparent survival ( $\phi$ ) were lower for males than females in both populations, and slightly lower for both males and females in the NSN than the MM (Figure 2.2 a, Supplementary material Table S.3). Apparent recruitment ( $f$ ) was higher for males than females in both populations and was lower for both sexes in the NSN than the MM (Figure 2.2 c). Model-averaged estimates of population growth by sex were  $\lambda_{\text{Female}} = 1.03 \pm 0.02$  SE and  $\lambda_{\text{Male}} = 1.01 \pm 0.02$  SE in the MM and  $\lambda_{\text{Female}} = 0.98 \pm 0.03$  SE and  $\lambda_{\text{Male}} = 0.92 \pm 0.04$  SE in the NSN (Figure 2.2 e).

When parameters were constrained to obtain estimates for each population independent of sex, apparent survival and apparent recruitment were higher in the MM than the NSN (Figure 2.2 b and c). Derived population growth ( $\lambda$ ) showed divergent population trends with the MM population growing ( $\lambda = 1.02 \pm 0.02$  SE) and the NSN population declining ( $\lambda = 0.95 \pm 0.03$  SE).

Top models for detection probability ( $p$ ) had the same model structure as the spatial mark-recapture analysis. The top model included sex, trap-type, sex \* trap-type interaction, and effort as covariates for  $p$ , where effort was the number of traps used each occasion (Supplementary material Table S.3).

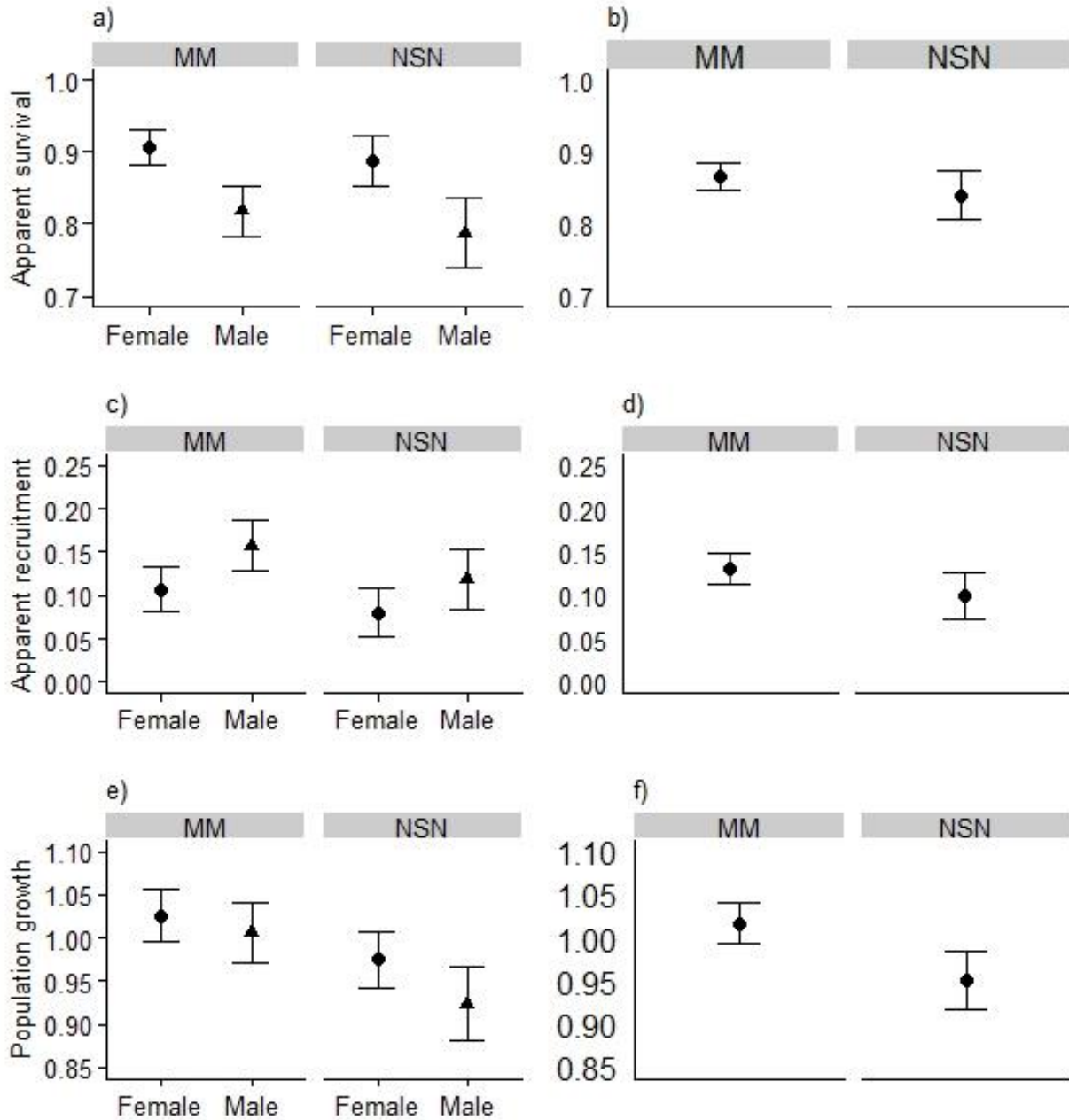
**Table 2.4** Pradel robust design models to estimate apparent survival ( $\phi$ ) and apparent recruitment ( $f$ ), for both the McGillvary Mountains (MM) part of the South Chilcotin and North Stein (NSN) part of the Stein-Nahatlatch grizzly bear populations in southwest British Canada. Models fit using common detection probability ( $p$ ) estimated in a prior analysis  $p(\sim \text{sex} + \text{type} + \text{effort} + (\text{sex} * \text{type}))$ . Effort refers to the number of traps per occasion and type refers to whether the trap was a hair trap or rub tree.

Model		$K^a$	$\Delta AICc^b$	$\omega_i^c$
$\phi(\sim \text{sex})$	$f(\sim \text{sex} + \text{pop})$	10	0.00	0.31
$\phi(\sim \text{sex} + \text{pop})$	$f(\sim \text{sex})$	10	1.09	0.18
$\phi(\sim \text{sex} + \text{pop})$	$f(\sim \text{sex} + \text{pop})$	11	1.38	0.16
$\phi(\sim \text{sex})$	$f(\sim \text{pop})$	9	2.68	0.08
$\phi(\sim \text{sex})$	$f(\sim \text{sex})$	9	2.70	0.08
$\phi(\sim \text{sex} + \text{pop})$	$f(\sim 1)$	9	3.55	0.05
$\phi(\sim \text{sex} + \text{pop})$	$f(\sim \text{pop})$	10	3.92	0.04

<sup>a</sup> Number of model parameters

<sup>b</sup> Difference between AICc of model and the AICc of the highest ranked model

<sup>c</sup> Model weight



**Figure 2.2** Pradel robust design model-averaged parameter estimates ( $\pm$ SE) for apparent survival ( $\phi$ ), apparent recruitment ( $f$ ) and population growth ( $\lambda$ ). Left panels (a,c,e) are model-averaged estimates where both sex and population were included as covariates. Right panel (b,d,f) model-averaged estimates for each population independent of sex.

## 2.5 Discussion

I identified different population densities and divergent population trends in 2 Threatened grizzly bear populations in British Columbia monitored from 5 to 17 years after the end of legal hunting. The MM population was growing and had 3.4 times the population density of the adjacent, and likely declining, NSN population (Figure 2.2). Both spatial and non-spatial estimates of population growth showed a similar trend, though non-spatial estimates were more divergent between populations with a more precipitous decline for the NSN population. Estimation of demographic parameters revealed that both apparent survival and recruitment were lower in the NSN, though the difference in apparent recruitment between the populations was consistently greater than that of apparent survival (Figure 2.2). The differences in the demographic components of population change between populations can be used to identify possible mechanisms of change as is necessary to facilitate recovery.

The increasing population trend in the MM population following the reduction of reported HCM is consistent with findings from the interior mountains of North America and Europe where populations have been recovering following a decline in HCM (Schwartz et al. 2006, Mace et al. 2012, Chapron et al. 2014). Although HCM, for reasons other than hunting, may eventually limit the MM population, the reduction of HCM following the end of hunting has been sufficient for the population to begin recovering. In contrast, despite the reduction in known HCM, the small, isolated NSN population is not growing, and the probable decline is mostly the result of low recruitment. Low recruitment in conjunction with slightly lower adult survival, is consistent with the hypothesis that other major limiting factors are affecting the NSN population, and reduction of HCM has been insufficient to recover this population.

Identifying the contribution of permanent migration to apparent survival and apparent recruitment increases my understanding of the mechanisms driving population change. Although I did not measure these movements directly, permanent migration rates and dispersal distances from natal home ranges, including differences between sexes, have been well documented for grizzly bears (Proctor et al. 2004, McLellan and Hovey 2011, Graves et al. 2014). Using this information and the genetic ancestry information from bears in the study populations, we can hypothesize the likely contribution of migration to apparent survival and recruitment. Female grizzlies are usually philopatric and remain in their natal population, while male grizzlies tend to disperse farther and have larger home ranges (McLellan and Hovey 2001, Proctor et al. 2004). I observed 3 events of permanent dispersal when 2 marked males emigrated from the NSN to the MM and 1 from the MM to the NSN. I did not detect any inter-population dispersal of females, nor did I capture any females with a genetic profile suggesting ancestry from a different population. Studies on captive brown bears show that birth rates are similar for both sexes (Tumanov 1995), therefore, if females are likely to remain in their natal home ranges, and males and females are born with equal probability, then it is likely that female apparent recruitment rate is near the actual recruitment rate of grizzlies at the age when they are more commonly caught in hair traps.

Several mechanisms could explain why recruitment rates were lower in the NSN than the MM. In other populations, habitat quality and, in particular, the abundance of high-energy foods has been shown to limit reproductive rates and population density (Schwartz et al. 2006, McLellan 2015). Perhaps poorer habitat quality in the NSN resulted in smaller litters, increased inter-birth intervals, delayed age of primiparity or high cub mortality. Lower reproductive output could also be due to a long period of population isolation leading to a genetic Allee effect (Keller

and Waller 2002, Laikre et al. 1996). The observed heterozygosity was  $H_o = 0.61$  for the MM and  $H_o = 0.51$  for the NSN (unpublished data); though both are below the average for North American populations ( $H_o = 0.65$ , Cronin and MacNeil 2012) heterozygosity is higher than that observed for other threatened and isolated brown bear populations (e.g. Gobi desert,  $H_o = 0.29$ , Tumendemberel et al. 2015; the Pyrenees before augmentation,  $H_o = 0.25$ , Taberlet et al. 1997). Finally, low reproductive success could also result from sexually selected infanticide exacerbated by small population demographic effects such as skewed sex ratio or years with no reproductively available females (Wielgus and Bunnell 1994).

In both populations I studied, females had higher apparent survival than males, and survival was slightly higher in the MM than the NSN (Figure 2.2); though standard errors of sex-specific estimates between populations overlapped. Male dispersal distances are larger than those of females (McLellan and Hovey 2001, Proctor et al. 2004) and loss due to emigration likely contributed to some of the differences in apparent survival between sexes. Mortality rates of male grizzlies, even in un-hunted populations, are often higher than for other cohorts (McLellan et al. 2007) and therefore would also contribute to reduced apparent survival for males. Apparent survival rates were higher in the MM and NSN populations than estimates from Banff National Park, Alberta, another un-hunted population sampled using similar methods. There, a high incidence of road and train kill is suspected to have decreased grizzly bear survival (Whittington and Sawaya 2015). The slightly lower apparent survival rates of grizzlies in the NSN than in the MM suggests that factors other than HCM may be affecting survival, however, identifying differences in causes of mortality would be required to test this hypothesis.

Although increasing, the density of grizzly bears in the MM (21.5 bears/1000 km<sup>2</sup>) is currently similar to the average (22.3 bears/1000 km<sup>2</sup>) of 75 populations in North America that



have little or no salmon in their diets (compiled by Mowat et al. 2013), but slightly lower than the average for British Columbia (27.4 bears/1000km<sup>2</sup>, n = 28). In contrast, the density of the NSN population (6.3 bears/1000 km<sup>2</sup>) is much lower than the average population density of areas with little or no salmon. Although lower bear densities have been recorded in parts of Alberta and the USA, only one of the 28 populations inventoried in British Columbia had a lower density estimate. Densities in the NSN are also lower than most small brown bear populations in Europe despite the latter having relatively high surrounding human density and modified habitats (e.g. 38 bears/1000 km<sup>2</sup> in the Italian Apennines, Ciucci et al. 2015; 21 bears/1000 km<sup>2</sup> in the Cantabrian mountains, Martin et al. 2012).

Population growth following the reduction of HCM has been recorded in many North American and European brown bear populations (e.g. Schwartz et al. 2006, Kendall et al. 2009, Kindberg et al. 2011, Mace et al. 2012, Pérez et al. 2014), indicating that reducing HCM may be sufficient to allow population recovery. However, if low-density populations become isolated, other factors may become important. For example, despite reductions in HCM the Pyrenean brown bear population continued to decline from low recruitment until augmentation reversed the trend in the central subpopulation while, in the absence of augmentation, the other subpopulation went functionally extinct (Chapron et al. 2009). Research from other grizzly bear populations suggests that changes in survival as small as 5% can result in negative population trends (Eberhardt et al. 2008). In the NSN, the difference between an increasing and stable population could thus be the fate of only one bear (derived population size of study area N≈16) highlighting the importance of stochastic events. Such a stochastic event in this population was that the only bear documented to have moved from the MM population to the NSN population was mistaken for a black bear and shot by a hunter. On the other hand, the only cubs known to

survive to maturity have been females. Managing for small populations thus requires additional attention to factors other than HCM.

Acquiring the necessary data from small populations to differentiate among multiple competing, and usually not mutually exclusive, hypotheses of population decline can be difficult because these species often occur at low densities, have long generation times, and low fecundity. Paradoxically, these characteristics predispose populations to extinction in rapidly changing environments (Caughley 1994, Purvis et al. 2000, Brook et al. 2008). My research highlights the importance of monitoring populations to understand the efficacy of management and other conservation actions. If a population is small and isolated, removing one major limiting factor, such as legal hunting, may be insufficient to ensure recovery.

## Chapter 3

# Vital rates underpinning trends of small and endangered large carnivore populations.

### 3.1 Abstract

Identifying the mechanisms causing population change is fundamental for conserving small and declining populations. Few studies have measured the demographic components of population change for mammal populations with fewer than 50 individuals. Substantial range contraction of brown bears (*Ursus arctos*) has resulted in a fragmented global population with many small isolates in need of conservation.

My goal was to understand population dynamics in two adjacent but genetically and geographically distinct, threatened grizzly bear populations in southwestern British Columbia, Canada following the cessation of hunting in that area. The larger population had approximately 45 resident bears and one-quarter of its perimeter was connected to other populations, while the smaller population had fewer than 25 individuals and was isolated.

I estimated population vital rates by monitoring the survival and reproduction of collared bears and their dependent offspring between 2005 and 2018. I measured large differences in adult female and cub survival. In the larger, more connected population, adult female survival was 0.96 (95% CI: 0.80-0.99) and cub survival was 0.85 (95% CI: 0.62-0.95) while in the smaller, isolated population adult female survival was 0.87 (95% CI: 0.69-0.95) and cub survival was 0.33 (95% CI: 0.11-0.67). Mean

litter sizes were similar between the MM (2.33, 95%CI: 1.89-2.78) and the NSN (2.25, 95%CI: 2.00-2.75). The stable reproductive state of the population indicated that the number of females with cubs of the year were similar for the MM (0.20, 95%CI: 0.12-0.29) and the NSN (0.17, 95%CI: 0.07-0.25). These differences projected population growth in the larger population ( $\lambda = 1.07$ , 95% CI: 1.04-1.12) and population decline in the smaller population ( $\lambda = 0.89$ , 95% CI: 0.78-0.99). Other vital rates, including mean litter size and stable reproductive state did not differ. Low female survival in the smaller population was a result of diverse mortality causes and may be indicative of demographic stochasticity. Low cub survival was indicative of small population effects or limited resources.

By comparing the vital rates from these two populations with those from other small brown and grizzly bear populations, I suggest that when populations are isolated, there is a tipping point at approximately 50 bears, below which population growth is rare and, even with intensive management, becomes prohibitive for population recovery.

### **3.2 Introduction**

Identifying mechanisms causing population change is essential for the conservation of small and declining populations (Caughley 1994, Peery et al. 2004, Bromaghin et al. 2015, Meyer et al. 2015, Duangchantrasiri et al. 2016). Differentiating between the effects of population smallness and the independent or synergistic causes of decline are difficult, but, in many cases necessary for successful population recovery (Brook et al. 2008). For widely distributed species occurring at a low density that have long generation times and low fecundity, estimating demographic parameters with sufficient precision to infer mechanisms requires large

sample sizes that often take years to collect, even from large populations (e.g. Gough and Kerley 2006, Schwartz et al. 2006, Matkin et al. 2014, McLellan 2015, Regehr et al. 2018).

Understanding the mechanisms of population change of these species in small, isolated populations is much more urgent but the sample sizes required for strong inferences are improbable (Mosnier et al. 2015, Zipkin and Saunders 2018). Identifying the common process of decline among small populations may highlight the realized effects of population smallness and provide insight for their conservation.

Brown bears (*Ursus arctos*) are a large-bodied, long-lived omnivore with low reproductive potential. Females are predominantly philopatric and therefore do not rapidly colonize neighbouring habitats or provide demographic rescue to small populations while males will often disperse outside of their natal home range (McLellan and Hovey 2011, Proctor et al. 2004). Substantial range contraction of this species has resulted in a fragmented global population with many small isolates in need of conservation (Mattson and Merrill 2002, McLellan et al. 2016). There have been significant efforts to recover populations, and some have been successful. In the 1930s, as few as 130 brown bears (*Ursus arctos arctos*) remained in Sweden but following a reduction in human-caused mortality (HCM), the population grew to over 700 by the mid-1990s (Swenson et al. 1995) and then to over 3200 bears by 2008 (Kindberg et al. 2011). In the United States, grizzly bear (*Ursus arctos horribilis*) populations in both the Yellowstone Ecosystem and in northern Montana grew at up to 7.6% annually for over twenty years (Mace et al. 2012, van Manen et al. 2015) to > 700 bears in each population (Kendall et al. 2009, Haroldson et al. 2014) following the reduction of HCM. Similarly, the Canadian Flathead population, grew by 7% annually throughout the 1980s and 1990s following a reduction in HCM, despite continued legal hunting (McLellan 2015).

Despite similar efforts to reduce adult bear mortality from HCM in other populations, recovery has not been universal. While the South Selkirk grizzly population with about 80 grizzly bears appears to be growing ( $\lambda = 1.02$ , Proctor et al. 2012, Wakkinen and Kasworm 2004), the neighbouring, isolated Cabinet Mountains population, which consists of 22 to 24 bears (Kendall et al. 2016), has shown limited growth, despite substantial efforts to recover the population over the past 30 years via a reduction in HCM and augmentation with 15 (11F, 4M) bears (Kasworm et al. 2014, Kendall et al. 2016). Likewise, the western Cantabrian brown bear population in Spain increased from approximately 60 bears in the 1990s to over 200 in 2014 (Pérez et al. 2014). In contrast, the eastern Cantabrian population increased slightly from 14 to ~19 bears over the same period following comparable recovery efforts (Pérez et al. 2014), although recent immigration of males from the western population may be increasing the population (Gonzalez et al. 2016). In the Pyrenees, brown bear populations declined to < 10 individuals in 1990, and, despite efforts to reduce adult mortality, by 1995 only 5 individuals remained in the western part of the range and the central population required reintroduction with bears from Slovenia (Chapron et al. 2003). While the western population became functionally extinct by 2004, the central population appears to be slowly recovering following reintroduction in the mid-1990s (Chapron et al. 2009). The success of population recovery via reduced HCM thus appears to be more successful in larger or connected populations.

Here, I investigate the vital rates in two adjacent but distinct populations of grizzly bears in southwestern British Columbia, Canada, following efforts to reduce adult mortality primarily by ending legal hunting in 2000. Genetic mark-recapture monitoring of these populations suggested population growth in the McGillivray Mountain (MM) population but a decline in the North Stein Nahatlatch (NSN) population. The MM population had approximately 43 bears (21.5

bears/1000km<sup>2</sup>) in the monitoring area, however, it is geographically and genetically connected to the large, unfragmented populations further north. The NSN population had approximately 20 bears (6.3 bears/1000km<sup>2</sup>) and has been genetically isolated likely for decades (Apps et al. 2014, McLellan et al. 2019). Based on open population models (Pradel 1996, Nichols and Hines 2002) identified lower apparent recruitment and slightly lower apparent survival in the NSN indicating that these differences were responsible for the divergent trends in the smaller, isolated population (McLellan et al. 2019). To further investigate why the two populations had different and opposite growth trends, I used 17 years of telemetry monitoring data of collared bears in these two populations to estimate vital rates to understand the demographic causes of population change and identify impediments to recovery specific to small populations.

### **3.3Methods**

#### **3.3.1 Bear Capture and Monitoring**

With other researchers I captured, collared and monitored from 2005 to 2018. Except for two males captured in foot snares, bears were immobilized by darting from a helicopter. Capture was carried out in the spring, shortly after den emergence when bears were feeding in avalanche chutes and open alpine meadows, or early autumn, when they fed on huckleberries. Spring capture was conducted when snow melt was sufficient for feeding in avalanche chutes (green-up) but before shrubs had leaf growth (leaf-out). This window of time where there is sufficient green-up but before leaf-out is usually around 10 days long and occurs once each year. The timing varies among years, usually occurring between mid-May and early July. Once

immobilized, bears over 2 years old were weighed, measured, and fitted with either GPS or VHF collars (Lotek Inc., Ontario, Canada). Tissue samples were obtained for genetic identification and a vestigial pre-molar for measuring age via cementum annuli. I classified two to five-year-old bears as subadults and those six years and older as adults because, retrospectively, this was the youngest observed age of primiparity. All collars had canvas spacers to ensure that the collar would drop off and the canvas was cut on the collars of young bears to ensure they dropped in about one year. The Animal Care Committee of the British Columbia Fish and Wildlife Management Branch approved and permitted all the capture and handling protocols. GPS collars were programmed to obtain a location once every three hours or every hour depending on the collar model.

Capture effort, defined as the time spent searching for bears, was evenly distributed between the study populations until 2014 when it had become apparent that the NSN population was not only small but had an unusually high incidence of adult female mortality. Although no bears had been injured or killed in this research program, the risk of additional female mortality due to capture in the small NSN population was deemed too high, so efforts from 2015-2018 were limited to the MM population. I continued to monitor the vital rates of all collared bears in both populations until 2018.

Throughout the first part of the study (2005-2008), I located collared bears by fixed-wing aircraft every two weeks from May to November. On each flight, I downloaded GPS location data and attempted to visually locate each bear and to count the dependent offspring of females. If I did not find a bear for more than eight consecutive weeks, I censored them from the sample at the time of their last known status. Because the populations were also monitored using genetic capture-recapture (chapter 2), there were no collared female bears with unknown fates. In the



second part of the study (May 2010 - October 2018), some recaptured females were fit with VHF collars because these small collars were preferable for long-term monitoring. Collared bears were located and observed from a helicopter at least once each spring (May or early June depending on snowmelt) and then again in summer (July and August) and fall (late September and October). I often located bears from the ground between aerial attempts and although these attempts did not follow a schedule, they increased the sightings of family groups and cub counts. Offspring age was determined by size for cubs in their birth year and yearlings in their second year. I grouped attendant offspring that were two years of age and older because they were not consistently indistinguishable if the previous year's status was unknown.

All collars were programmed to signal if the collar had not moved in 24 hours, and these mortality signals were investigated as soon as possible after detection. Whenever I found a dropped collar with rotted canvas, I assumed the bear was still alive. If a bear was found dead, I performed an investigation and necropsy in the field to determine the cause of death. Human involvement was suspected if the collar was cut. Because I was simultaneously conducting an annual DNA based capture-recapture monitoring program (McLellan et al. 2019), I was able to use this information in the interpretation of uncertain fates.

### **3.3.2 Survival Analysis**

I estimated the annual survival rates of adult and subadult bears using a staggered entry design for the Kaplan-Meier estimator (Pollock et al. 1989). I used months as the monitoring interval from April to October when most bears were active. I amalgamated November through March into one monitoring interval because monthly mortality would not be distinguishable

when bears were hibernating, and the model structure was parameterized accordingly for annual estimates. I considered population (S~Pop), sex (S~Sex) and age class (S~Age) as individual covariates in candidate models along with the null model (S~1) assuming no differences among class. I used RMark v.2.25 (Laake and Rexstad 2008, White 2008) to construct, analyze and obtain model-averaged survival estimates for each class. I had insufficient data to investigate interactions among groups without the drastic loss of estimate precision. I used AIC based model averaging to obtain survival estimates for each sex and age class (Burnham and Anderson 2002).

All collared bears in these populations entered a den during the winter season. Female den entrance varied from October 20<sup>th</sup> to November 12<sup>th</sup> and emergence varied from April 24<sup>th</sup> to May 20<sup>th</sup>. I located collared bears from a fixed-wing aircraft or a helicopter within 4 weeks of den emergence. If bears were not located within a month of den emergence they were censored from the cub survival data. I estimated cub survival by observing the number of cubs for each collared female shortly after den emergence and again throughout the same year. I assumed cub mortality if they were not seen with their mothers, and I censored them from analysis if their mothers dropped their collars or were not visually located again that year. Due to a possible lack of independence of survival of cubs within a litter (Swenson et al. 2001, Mace et al. 2012), I first compared cub survival for individual cubs and then within litters using an ANOVA. For each population, I resampled with replacement (bootstrapped) cub survival data 1000 times to obtain mean survival and 95% confidence intervals (McLellan 2015). I used the same method to estimate survival of yearlings. Analyses were conducted using PopTools (Hood 2011).

### **3.3.3 Age of primiparity and Litter size**

I estimated the average litter size of collared females located in the spring shortly after den emergence and only when females and their cubs were observed clearly. Litter sizes were bootstrapped 1000 times to obtain means and 95% confidence intervals.

I determined the average age of primiparity using the techniques described by Garshelis et al. (2008). This method includes all females observed before parturition even if they were not monitored until they reproduced. Means and confidence intervals were obtained for each population by bootstrapping the original sample 1000 times using PopTools (Hood 2011).

### **3.3.4 Reproductive Rate and State Transition**

The stable reproductive state distribution (SRSD) describes the proportion of the adult female population in each possible reproductive state (Schwartz and White 2008). To obtain an estimate of each population's SRSD, I first estimated the probability that a female will transition from one reproductive state to another. I defined the reproductive state of a female by the presence and age of dependent offspring. Females were classified as alone (A), with cubs (C), with yearlings (Y), or with older offspring (T). I observed a transition for any adult female monitored for two or more consecutive years. I considered ten biologically possible transitions (Table 3.1). A female alone could either remain alone or have cubs the following year. A female with cubs could lose her cubs and transition to being alone, lose her cubs and transition to having cubs, or transition to have yearlings. A female with yearlings or two-year-olds could either transition to be alone, to have cubs or to having offspring a year older. I used the multi-state

model in RMark (Laake and Rexstad 2008) to estimate the probability of transition from one state to another. Survival and recapture probability were constrained to 1.0 as they are a prerequisite for observing a transition. The resulting transition matrix was multiplied by a hypothetical starting state matrix (e.g. all alone) to obtain the reproductive state distribution after one transition (Eq. 1).

$$t2 = \begin{bmatrix} 1 & 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} AA & AC & 0 & 0 \\ CA & CC & CY & 0 \\ YA & YC & 0 & YT \\ TA & TC & 0 & 0 \end{bmatrix} \quad (Eq. 1)$$

I iteratively multiplied the resulting age distribution by the transition probability matrix in a Markov chain until it reached the asymptotic stable reproductive state distribution. For this analysis, I used markovchain package v. 0.6.9.15 (Spedicato et al. 2014) in program R (v.3.6.1: R Core Team, 2019). I resampled the data with replacement and bootstrapped estimates of the stable reproductive state distribution 1000 times to estimate means and 95%CI's for each population. I did not have a sufficient sample size to include female age as a covariate for transition probabilities.

**Table 3.1** Possible reproductive state transitions for adult female brown bears. Reproductive states are defined by the presence and age of accompanying offspring.

<u>From State</u>	<u>Transfer to State</u>			
	Alone	Cubs	Yearling	Twos
Alone	A → A	A → C		
Cubs	C → A	C → C	C → Y	
Yearling	Y → A	Y → C		Y → T
Twos	T → A	T → C		

Reproductive rate ( $m_x$ ), defined as the number of female cubs/year/female, was estimated for each population by multiplying the estimated number of female cubs per litter by the stable reproductive state proportion of females with cubs of the year (Schwartz and White 2008). The number of female cubs would be half the mean litter size assuming a 1:1 sex ratio (Tumanov 1995). This method for estimating the reproductive rate assumes no change in the stable state distribution over time but is more robust to sampling bias from capture and variability in monitoring duration than estimating SRSD by simply using the proportion of monitored individuals (Schwartz and White 2008).

### **3.3.5 Population Growth and Stable Age Distribution**

To estimate the asymptotic finite population growth rate ( $\lambda$ ), I estimated the net reproductive rate, defined as the estimated number of female cubs a female will produce in her lifetime, and the mean generation time for the MM and NSN populations. I estimated these latent variables by constructing an age-structured matrix population (Leslie matrix) model using repeated random samplings (Monte Carlo estimation) from the bootstrapped distributions of age-specific survival and reproduction for each population (Mace et al. 2012). I considered the age of last reproduction as 24 years (Schwartz et al. 2003, McLellan, 2015). For each iteration, I solved for the dominant eigenvalue which is the population growth rate ( $\lambda$ ), the net reproductive rate ( $R_0$ ) and average generation time (GenT) using popbio v.2.2.4 package (Stubben and Milligan 2007) in program R (R Core Team 2019). I repeated this process 1000 times for each population to estimate mean and variance for each variable.

I estimated the stable age distribution of each population by converting the age-structured matrix population model into a stage-structured population model. Because vital rates were estimated for age groups, only transition rates required calculation. The transition rate is the expected proportion of individuals transitioning from one life stage to the next and is conditional on individual survival and the population growth rate (Caswell 2001, Fujiwara and Diaz-Lopez 2017). I applied a conditional age group-transition rate described in Caswell 2001 where the probability that an individual will transition from one age group to the next ( $P_{j,i}$ ) is:

$$P_{j,i} = \frac{\lambda^{-(x_j - x_i - 1)} l(x_{j-1})}{\sum_{x=x_i}^{x_{j-1}} \lambda^{-(x - x_i)} l(x)} \quad (\text{Eq. 2})$$

and  $\lambda$  is the population specific growth rate,  $x_i$  is the first age in stage  $i$  and  $x_j$  is the first age in stage  $j = i + 1$  and  $l(x)$  is the survivorship at time  $x$ . I repeated this process for all the 1000 bootstrapped Leslie matrices from the preceding analysis to estimate the confidence interval around each population stable age class outcome (Mace et al. 2012).

### 3.4 Results

In the MM and NSN, respectively, 26 (18F, 8M) and 16 (9 F, 7M) bears were collared between 2005 and 2018. An additional three subadult males (2 MM, 1 NSN) were captured, aged, genetically identified, measured and weighed but not collared. I limited my survival analyses of independent (i.e. subadult and adult) bears to females but report causes of mortality for both females and males.

### **3.4.1 Causes of mortality**

None of the collared females and one collared male died in the MM while 5 collared females and no collared males died in the NSN population. The mortality of the male bear in the MM population was a result of repeated human-wildlife conflict. The causes of mortality for NSN females were diverse. One adult with an unknown reproductive state was killed in the early spring by another bear. Two nulliparous females (aged seven and eight) were suspected to have been illegally killed by humans; one collar had been cut off the bear and smashed into many pieces while the other collar was still intact but prematurely lost < 10 m from a road. This female had been genetically tagged in the concurrent DNA monitoring program each year since her birth but was never again tagged over the four following years. One subadult died in her den and was severely emaciated and showing severe gelatinous bone marrow transformation indicating starvation (Raglus et al. 2019), and one old bear died late in the fall with no sign of trauma (suspected natural senescence).

### **3.4.2 Survival of independent females**

Survival of independent female bears was determined from 42 and 26 bear-years (cumulative number of years sampled for all bears) of monitoring in the MM and NSN, respectively. The top model indicated that survival differed between populations (Table 3.2) but there was no measurable difference between sex or among age class of females, although sampling of subadults and males was limited, and the analysis lacked power (Table 3.2). Model averaged estimates of annual independent survival was 0.96 (95% CI: 0.80-0.99) in the MM and

0.87 (95% CI: 0.69-0.95) SN population (Table 3.3) when both suspected mortalities are included. Because survival estimates used to derive population growth using a projection matrix should only include females of reproductive age and one mortality was of an old bear, excluding her death the resulting adult female survival in the NSN was 0.91 (95% CI: 0.73-0.98).

**Table 3.2** Model Selection results for Kaplan-Meier estimates independent bear survival from collared grizzly bears in McGillvary mountains and the North Stein Nahatlatch populations. Age is subadults from 2 to 5 years and adult bears are  $\geq 6$  years.

Model	n <sup>a</sup>	AICc <sup>c</sup>	$\Delta$ AICc <sup>b</sup>	$\omega^c$
S (~Pop)	2	68.577	0.000	0.678
S (~1)	1	71.308	2.731	0.173
S (~Age)	2	72.767	4.190	0.083
S (~Sex)	2	73.229	4.652	0.066

<sup>a</sup> Number of model parameters

<sup>b</sup> Difference between AICc of the model and the AICc of the highest-ranked model

<sup>c</sup> Model weight

### 3.4.3 Age of primiparity and Litter size

I monitored six nulliparous females in the MM; three did not reproduce by six, seven and eight years old when they were censored because they had lost their collars. One reproduced for the first time at age 11 and the remaining two had first surviving litters at age eight and nine. However, both of these females were not observed for one year immediately prior so could have had non-surviving cubs at ages seven and eight, respectively and lost them. Two more females were first captured at age seven with cubs of the year. The estimated mean age of primiparity following Garshelis and Noyce (2008) was 7.4 years (95% CI: 3.0-11.0, where lower confidence limit was increased to three years to reflect the minimum age of primiparity possible for the species). If I include possible surviving litters of females that may have had non-surviving litters



the previous year, the age of primiparity was 8.2 years (95% CI: 4.8-10.0). In the NSN the age of first surviving litter was observed for one bear at 12 years, and two nulliparous females died at ages seven and eight years old. The mean estimate of primiparity for the NSN was 8.0 years (95% CI: 3.0-11). I was unable to obtain estimates of primiparity with sufficient precision to compare populations.

**Table 3.3** Vital rates estimated using Kaplan-Meier estimator from monitoring collared grizzly bears in the McGillvary mountains (MM) and North Stein Nahatlatch (NSN) populations. Reproductive rates estimated based on monitoring females with cubs.

	MM	NSN	p value
<b><u>Survival</u></b>			
Cubs	0.85 (0.62–0.95)	0.33 (0.11–0.67)	0.004
Yearling	1.00	1.00	
Adult female	0.96 (0.81–0.99)	0.88 (0.67–0.99)	0.002
Adult female*		0.91 (0.73–0.98) *	
<b><u>Reproduction</u></b>			
Litter size	2.33 (1.89–2.78)	2.25 (2.00–2.75)	0.837
SRSD with cubs	0.22 (0.116–0.287)	0.17 (0.07–0.25)	0.625
Mx	0.26 (0.15–0.38)	0.20 (0.093–0.310)	

\* Excluding female that died of old age

I monitored eight litters to weaning, six were two-year-old offspring, two were three-year-old offspring and one was four-year-old. I observed a female nursing her 2 ½-year-old cubs. I observed six interbirth intervals for three females, in the MM and four interbirth intervals for three females in the NSN. The resulting bootstrapped estimates of interbirth interval were 4.2 years (95% CI: 4.0-4.5) and 4.3 years (95% CI: 4.0-4.8) for the MM and NSN, respectively.

Litter sizes were estimated from 21 cubs in nine litters ( $\bar{x}$ = 2.33, 95% CI: 1.9-2.78) in the MM and nine cubs in four litters ( $\bar{x}$ = 2.25, 95% CI: 2.0-2.75) in the NSN (Table 3.3).

#### **3.4.4 Survival of dependent offspring**

I estimated the survival rates of cubs (first year of life) and yearlings (one year old) as well as the reproductive rates of adult females from the reproductive events of 22 adult females (15 MM, 7 NSN) that produced 20 cubs in eight litters in the MM and nine cubs in four litters in the NSN. Cub survival in the MM was 0.85 (95% CI: 0.62-0.95), and 0.33 (95% CI: 0.11-0.67) in the NSN. Cub survival was independent of litter membership ( $p = 0.97$ ); in the MM three cubs were lost from two litters (3 of 3 and 1 of 2) while all other six litters survived. In the NSN, one litter of three was entirely lost, and three other litters lost one of two cubs each. No litters in the NSN had all cubs survive (Table 3.3). No cub mortalities were attributed to maternal mortality in either population. I monitored the fate of 26 yearlings (20 MM, 6 NSN) and observed no mortalities.

#### **3.4.5 Stable reproductive state distribution (SRSD)**

I observed 38 reproductive state transitions in the MM (13 bears) and 30 in the NSN (6 bears). The resulting non-parametric bootstrapped estimates for the stable reproductive state distribution predicted similar proportions of females with cubs in each population; 0.20 (95% CI: 0.12-0.29) in the MM and 0.17 (95% CI: 0.07-0.25) in the NSN. The largest difference between the SRSD of the two populations was the proportion of adult females alone estimated as 0.41 (95% CI: 0.00-0.65) in the MM and 0.55 (95% CI: 0.38-0.84) in the NSN (Table 3.4, Figure 3.2a).

**Table 3.4** Reproductive state transition rates estimated using multi-state models on reproductive data from collared adult female grizzly bears ( $\geq 6$  years) in the McGillvary Mountain and North Stein Nahatlatch populations in southwestern British Columbia, Canada.

Population	From State	Transfer to State			
		Alone	Cubs	Yearling	Twos
MM	Alone	0.63	0.38		
	Cubs	0.00	0.00	1.00	
	Yearling	0.00	0.00		1.00
	Twos	0.75	0.25		
NSN	Alone	0.67	0.33		
	Cubs	0.17	0.00	0.83	
	Yearling	0.00	0.00		1.00
	Twos	1.00	0.00		

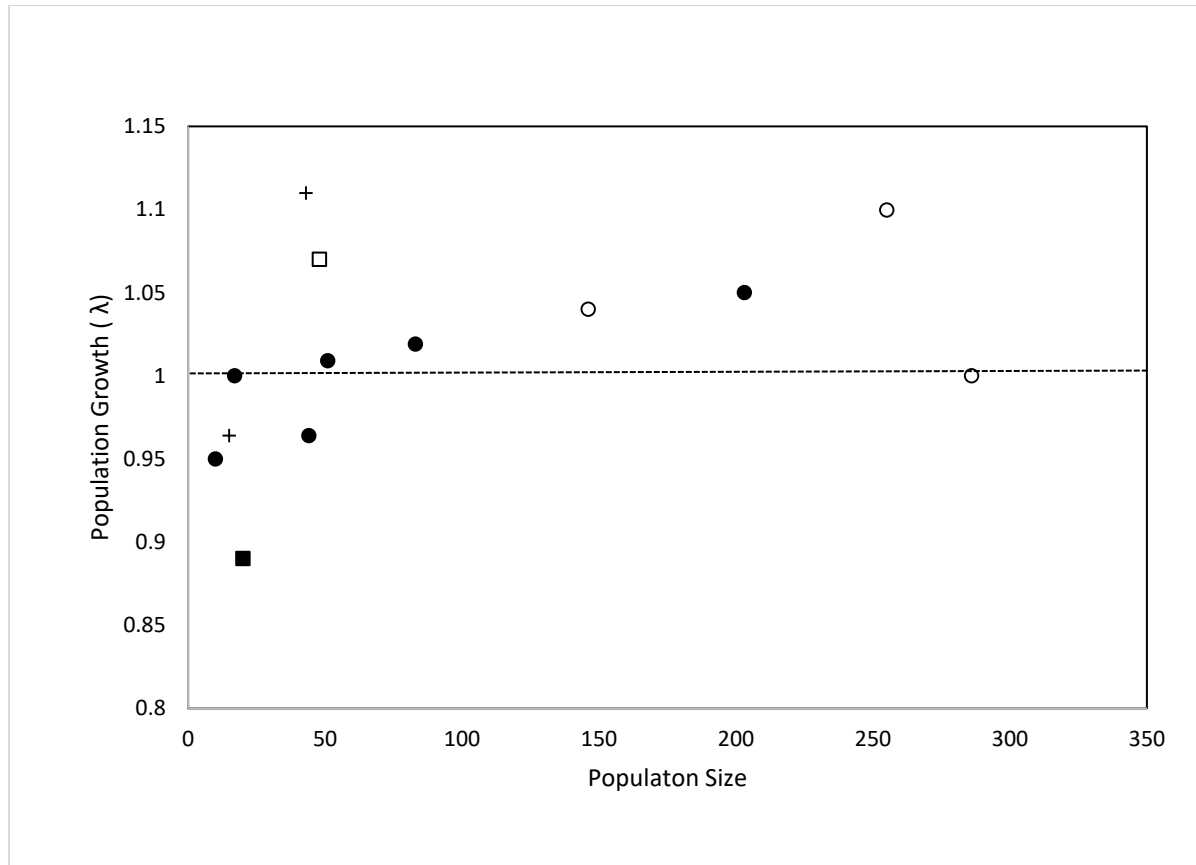
### 3.4.6 Population growth

Mean estimates of projected population growth rate ( $\lambda$ ) indicated that given the stable reproductive state and demographic rates observed, the MM population was growing with a  $\lambda = 1.07$  (95% CI: 1.04-1.12) while the NSN population was declining with  $\lambda = 0.89$  (95% CI: 0.78-0.99, Table 3.5). The mean estimated generation time was approximately 12.5 years in both populations with broader variance in the MM (Table 3.5). In contrast, the net reproductive rate,  $R_0$  (the average number of female cubs an adult female will produce in her lifetime given the age-specific survival and reproductive rates) was seven times higher in the MM (2.38, 95% CI: 1.14-4.03), than in NSN (0.31, 95% CI: 0.04-0.82) (Table 3.5).

**Table 3.5** Latent variables derived from bootstrapped vital rates estimated with age-structured population matrix for collared grizzly bears in the McGillvary Mountains (MM) and North Stein Nahatlatch (NSN) populations in southwestern British Columbia, Canada.

Variable		MM	NSN
Asymptotic Population Growth	$\lambda$	1.07 (1.045-1.119)	0.89 (0.78-0.99)
Net Reproductive Rate	$R_o$	2.376 (1.12 -4.03)	0.305 (0.31 -0.82)
Generation Time	GenT	12.55 (10.32-14.94)	12.51 (11.40-13.52)

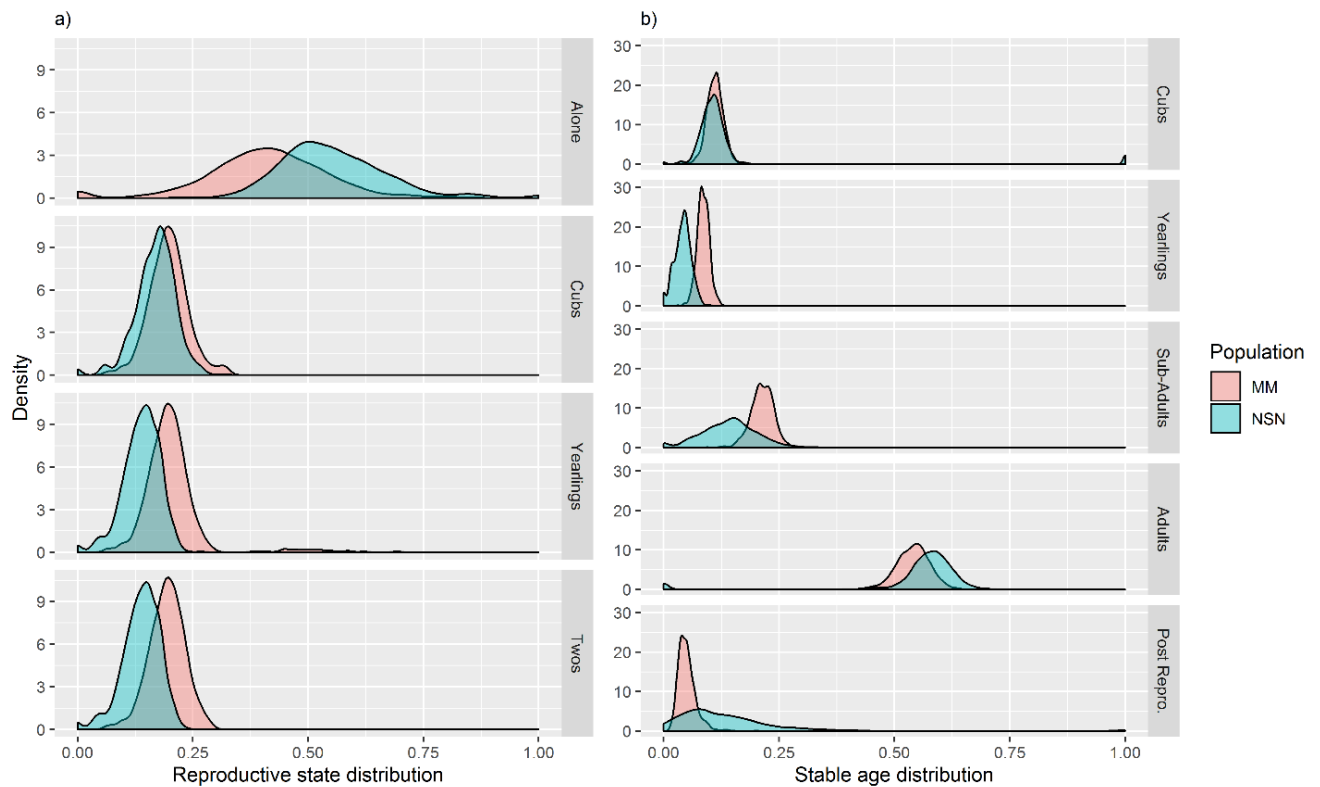
Comparing population size and associated projected population growth rate of the MM and NSN populations with other brown and grizzly bear populations with available data showed that growth in the MM population was similar to other connected populations (Figure 3.1). In contrast, the projected population decline in the NSN was similar to other small and isolated populations.



**Figure 3.1:** The relationship between population growth rate ( $\lambda$ ) and population size from this research and other populations highlighting that connected, or larger populations are more likely to be growing than smaller, isolated populations. The isolated North Stein Nahatlatch population (■) and other isolated populations (●); the connected McGillvary Mountain population (□) and other connected populations (○); augmented populations (+) (Clevenger et al. 1987, Wakkinen and Kasworm 2004, Garshelis et al. 2005, Palomero et al. 2007, Chapron et al. 2009, Kindberg et al. 2011, Proctor et al. 2012, Pérez et al. 2014, Gervasi et al. 2017).

### 3.4.7 Stable age distribution

The difference in survival probabilities resulted in differences in the stable age distribution of each population (Figure 3.2b). The MM had a higher proportion of yearling and subadult bears, whereas the NSN had proportionately more adults and older bears because of the relatively low cub survival rates in that population (Figure 3.2b).



**Figure 3.2** Density plots of **a)** the stable reproductive state distribution estimated using in multistate transition models on reproductive data from collared adult female grizzly bears ( $\geq 6$  years). **b)** bootstrapped estimates of the stable age distribution estimated from vital rates for grizzly bears in the McGillivary Mountain and North Stein Nahatlatch populations in southwestern British Columbia, Canada.

### 3.5 Discussion

Despite similar management efforts to recover by reducing HCM, vital rates of grizzly bears in the smaller NSN population indicated that it was declining while the larger MM population was growing. I identified both cub and adult female survival as factors most likely driving population decline in the small and endangered NSN population while the adjacent but genetically distinct and larger MM population had much higher cub and adult female survival rates and was growing. Both populations showed slightly lower reproductive rates than those in other populations despite having larger litters. Considering my findings and those from other small populations of brown and grizzly bears, I suggest that below a threshold of approximately 50 individuals, may not respond to recovery actions that reduce adult mortality as well as larger populations (Figure 3.1, Chapron et al. 2009, Proctor et al. 2012, Gonzalez et al. 2016, Kendall et al. 2016).

The vital rates I recorded in the MM were consistent with estimates from other un-hunted grizzly bear populations in North America (Garshelis et al. 2005, Schwartz et al. 2006, Mace et al. 2012). For example, at 0.96, adult female survival rates in the MM were the same as in both Banff (Garshelis et al. 2005) and Yellowstone (Schwartz et al. 2006) ecosystems, and very similar to the 0.95 recorded in Northern Montana (Mace et al. 2012) and 0.97 in Denali, Alaska (Keay et al. 2018). The reproductive rate in the MM of 0.26 was lower than other rapidly growing populations (e.g. 0.32 in Yellowstone (Schwartz et al. 2006); 0.41 in Sustina River, Alaska (Miller 1997); 0.33 in northern Montana (Mace et al. 2012); 0.42 in the first 15 years of study in the Flathead drainage of British Columbia (Hovey and McLellan 1996)) but similar to the 0.24 recorded in Banff where  $\lambda = 1.04$  (Garshelis et al. 2005). Litter sizes in the MM (2.33

cubs/litter) were larger than the average of 2.04 cubs/litter (range 1.8-2.3) in North American brown bear populations where females do not eat salmon (Zedrosser et al. 2011).

The difference in reproductive rate between the MM and other expanding populations was due to a relatively low proportion of females being with cubs compared to other reproductive states such as being alone or with older offspring. The stable reproductive state for adult females in the MM that are either alone or with three-year-old or older offspring was 0.34, which is higher than some other populations, such as 0.26 in northern Montana (Mace et al. 2012) and 0.10 in the Canadian Flathead while the population was growing (McLellan 2015). This difference appears to be due to a combination of an older age of primiparity, longer interbirth intervals and, possibly a high proportion of younger adult females for which the expected per-capita reproductive rate is lower (Schwartz et al. 2006, McLellan 2015). The coarse estimates suggest that these populations have among the oldest documented age of primiparity (Garshelis et al. 2005). Despite a low reproductive rate, cub survival in the MM was high ( $S_c = 0.85$ ) and complete litter losses were not observed. Large litter sizes and high cub survival are contributing to overall populating growth rate showing that this population is recovering.

Despite a probable reduction of adult mortality following the cessation of hunting in the NSN in 2000, the population appears to be declining mostly due to low adult female and cub survival. The prominence of natural adult mortality in the NSN population is notable; three natural deaths of independent females occurred in 26 bear-years of monitoring (0.12 mortalities/bear-year). By comparison, natural mortalities of female bears are rare in other populations. In the Yellowstone Ecosystem Schwartz et al. (2006) reported  $< 0.005$  natural mortalities/bear-year over 198 bear-years; McLellan (2015) found 0.018 natural mortalities/bear-year based on 227 bear-years of monitoring in the Canadian Flathead, and (Mace et al. 2012)



reported 0.008 mortalities/bear year in 122.6 bear-years of monitoring in northern Montana. Even in Denali, where the population was thought to be at carrying capacity, only three females died of natural causes and none due to HCM in 146.5 bear-years of monitoring (0.020 mortalities/bear-year, Keay 2018).

The rate of HCM of independent females in the NSN (0.08/bear-year) was also high and, although my sample size was limited, it appears to be more than double that of other un-hunted North American populations. For example, the rate of HCM for females was 0.033-0.057/bear-year in Montana (Mace et al. 2012), 0.025-0.0350 in Yellowstone (Schwartz et al. 2006), and 0.037 in Banff (Garshelis et al. 2005). At 0.048 human-caused deaths per bear-year of monitoring, even the heavily hunted Flathead drainage in British Columbia (McLellan 2015), has a lower female HCM rate than the un-hunted NSN.

The diversity of causes of death of NSN female bears suggests that there is no a single, systematic factor influencing the population trajectory but more likely stochastic events that have often been suggested to impact small populations (Lande 1988, Foley 1994, Ovaskainen and Meerson 2010). Although not as low as the 0.87 female survival rate I found in the NSN, other small, isolated populations that were intensively managed for recovery also had relatively low female survival: 0.91 in the west Pyrenean population just prior to functional extinction with 10 bears left (Chapron et al. 2009); 0.92 in the isolated Italian Apennine population (Gervasi et al. 2017) of about 51 bears (Ciucci et al. 2015); and 0.93 in the isolated Cabinet mountains, U.S.A., when the population was approximately 15 to 23 bears until the 1990s (Wakkinen and Kasworm 2004, Kendall et al. 2016). Even with extreme conservation efforts, these rates are lower than the 0.94 estimated from the heavily hunted Canadian Flathead population and similar to the 0.91 in the Susitna drainage of Alaska when the management goal was to reduce bear numbers with

heavy hunting pressure (Miller et al. 1997). Population dynamics in the small West Pyrenean, Apennine, Cabinet Mountains and NSN populations suggest that adult female mortality, even with intensive management, may not permit population recovery.

In addition to low female survival, low cub survival in the NSN also affected population growth. Annual cub survival of 0.33 in the NSN was similar to the lowest rate recorded for this species of 0.34 in both Denali and Katmai National Parks, Alaska. These were both un-hunted populations in remote, protected areas that are thought to be at carrying capacity (Sellers et al. 1999, Keay et al. 2018). Unlike in Denali where the grizzly bear reproductive rate remained comparable to expanding populations, reproductive rates in the NSN were low (0.20) even when compared to other declining populations. A combination of late average age of primiparity, (> 8 years old) and high inter-birth intervals (4.3 years) results in a low proportion of females with cubs. Like the MM, litter size in the NSN (2.45 cubs) is also higher than average for North American populations (Zedrosser et al. 2011).

Because they were not radio-collared, I did not determine the specific causes of cub mortality, however, there are several possibilities for their low survival in the NSN. The NSN population could be at a low-density carrying capacity and limited by food. The amount of body fat of mothers strongly influences the body size of cubs at den emergence (Robbins et al. 2012) and in Denali, females that lost cubs had lower body fat than those that did not lose cubs (Keay et al. 2018). Cub survival also declined by about 20% in years of limited food availability in the Canadian Flathead population (McLellan 2015). That a subadult bear in the NSN died of starvation, which is very rare for this species, does suggest that food may be limiting for this population, at least in some years. In a food limited population, however, I would also predict small litter sizes (Robbins et al. 2012) which was not the case in the NSN population.

Infanticide by adult males may also have contributed to high cub mortality (McLellan 1994). Sexually selected infanticide has been documented in brown bears in Sweden (Swenson et al. 2001) and it may be exacerbated when the adult sex ratio favours males (McLellan 2005, Chapron et al. 2009). Having more males in a population not only increases the probable encounter rate between males and mothers with cubs but there is also an increased probability each male is not the father of a litter and, therefore, more likely to be infanticidal. Also, there would be fewer breeding opportunities per male so fewer would be encumbered with receptive mates (McLellan 2005). In small populations with few adult females and long interbirth intervals, there will often be years when all adult females are encumbered with cubs, yearlings or older offspring and none are reproductively available (e.g. Gonzalez et al. 2016), likely increasing the risk of infanticide as a component Allee effect.

Low cub and adult survival may also be indicative of a genetic Allee effect. The isolation of the NSN population and, to a lesser extent, the MM population, has resulted in lower than average observed heterozygosity (MM  $H_o = 0.61$  and NSN  $H_o = 0.51$ ; Bellemain et al. 2007, Paetkau et al. 1998) and several bears are the product of full-sibling and parent-offspring mating (unpublished data). Studies of brown bears in zoo populations identified a decrease in litter size as a result of inbreeding depression (Laikre et al. 1996). In a study of multiple mammal species, Ralls et al. (1988) found an average 33% reduction in survival of offspring resulting from parent-offspring or full sibling mating. In other mammals, the lifetime breeding success can drop by as much as 70% from the equivalent of half-sibling mating and the reduction is often manifesting as increased age of primiparity (Huisman et al. 2016). Population recovery or persistence has been documented following population augmentation or natural immigration of un-related individuals (Åkesson et al. 2016, Quinn et al. 2019).

Comparing the relationship between the population growth rate and the size of isolated brown bear populations suggests that there is a threshold of around 50 bears below which reduction of human-caused mortality alone is insufficient to promote recovery (Chapron et al. 2009, Pérez et al. 2014). Studies on other species have shown that in the absence of immigration, small populations are unlikely to persist and the variation in population persistence can be explained by stochastic events and environmental catastrophes (Stacey and Mark 1992, Aresu et al. 2020). Although there are few examples from small populations that highlight the demographic components of population decline, our results support the suggestions that bad luck can be a critical factor limiting the recovery of small, isolated populations.

## Chapter 4

# **The influence of habitat on the trend of two threatened grizzly bear populations & ground testing habitat selection models.**

### **4.1 Abstract**

For grizzly bears (*Ursus arctos*) in areas with low human-caused mortality, the quantity, quality and distribution of food and other habitat features may become more important for individual fitness. The objective of this chapter is to identify whether the large differences in population density and growth rate between two threatened grizzly bear populations in southwestern British Columbia reflect a difference in the availability of seasonal food sources.

Grizzly bear habitat selection is seasonally dependent, and as different foods become available, grizzly bear diet composition changes accordingly. Here I use seasonally specific resource selection functions (RSFs) to predict seasonal habitat selection within individual home ranges. Then I use the resulting models to estimate the relative abundance of seasonally specific high-quality habitats in two adjacent but distinct grizzly bear populations. For this analysis, I consider four seasons: the spring-early summer season when bears feed predominantly on herbaceous plants and dig for bulbs; the early fruit season, where they feed on low elevation berries and cherries; the huckleberry season, when bears feed almost exclusively on black huckleberries (*Vaccinium membranaceum*); and the post berry season, when foraging behaviours are most diverse but whitebark pine seeds are a relatively common food source.

Projected models indicated similar habitat quality between populations for the spring and summer herb-bulb season, and the early fruit season (< 2% difference). High-quality huckleberry

habitat covered 11% to 14% of the larger (21.5 bears/1000km<sup>2</sup>), and growing (projected  $\lambda = 1.07$ ), MM population while the same quality habitat accounted for only 2%-3% of the area in the smaller (6.3 bears/1000km<sup>2</sup>) and declining (projected  $\lambda = 0.89$ ) NSN population. Although it is difficult to assess whether this difference is responsible for the differences in observed density, the difference suggests that there is likely a difference in carrying capacity for the two populations. While the post-berry habitat model also indicated a higher prevalence of good quality late season habitat in the MM than the NSN population, the model had a much lower predictive ability and therefore less robust for inferring meaningful differences in habitat quality at the population scale.

To confirm the utility of using resource selection models for inferring food availability, I also assessed the predictive capacity of the resulting huckleberry season RSF models by using generalized additive models to compare RSF model scores with huckleberry abundance measured in field plots. My results show that berry specific models did predict plant cover, the proportion of plants with fruit and overall berry abundance, but the mass (g) of berries picked in 10 minutes, controlled for the picker, was the measure of fruit abundance most accurately predicted by the huckleberry RSF model; adjusted  $R^2 = 0.48$  ( $p < 0.0001$ ).

## **4.2 Introduction**

The distribution of most large carnivore species is the result of continental-scale climate patterns and persecution by humans (Woodroffe 2000, Mattson and Merrill 2002, Wolf and Ripple 2017). The resulting pattern of occupancy is for persistence where human density is relatively low, and extirpation where human density is high (Wolf and Ripple 2017). Human-caused mortality of large carnivores has been such a dominant limiting factor that its reduction is

often the only action required to successfully recover declining populations (Schwartz et al. 2006, Lopez-Bao 2015, Proctor et al. 2018a). In areas with low human-caused mortality, additional limiting factors become more important and individual fitness depends upon the quantity, quality, and distribution of food and other habitat features (Mowat et al. 2013). Although the top-down effects of human-caused mortality may still limit the broad-scale distribution of large carnivore species (Nielsen et al. 2004a), fine-scale variation in population density and distribution may reflect the spatial and temporal variability of habitat quality (Rettie and Messier 2000, Mayor et al. 2009, Boyce et al. 2016).

For each individual there is a hierarchy of factors that limit, or potentially limit, its fitness, and the coarser the scale of selection, the more important the factor (Rettie and Messier 2000). Therefore, to understand the relationships between habitat characteristics and individual fitness, habitat quality must be estimated at the appropriate scale (Garshelis 2000). When a population is at carrying capacity and limited by bottom-up factors, animal abundance should reflect the quality of available habitat (Boyce et al. 2016). Even though species distribution at the large scale may be limited by current or historical HCM, finer scale habitat selection for food sources within home ranges will still reflect which habitats are important to individuals at that scale and the ubiquity of these habitats will affect the density of individuals there.

Estimating the abundance of high-quality habitat first requires identifying selected habitats and then quantifying their availability for individuals, or populations. Resource selection functions (RSFs) are commonly used statistical techniques for quantifying habitat selection. RSFs often compare multiple environmental correlates at locations used by animals to random locations considered to be available to the animals (Manly et al. 2002, Nielsen et al. 2002). The correlates are rarely mechanistic but most often they are derived from satellite imagery and

landscape mapping that are assumed to correlate to food sources or attributes for behaviours such as resting or avoiding predators and conspecifics (Boyce and McDonald 1999). The applicability and ecological understanding gained from the resulting models is often limited because they are based on surrogate, non-mechanistic variables (Nielsen et al. 2006). However, by carefully classifying animal use according to specific behaviours, such as seasonally specific foraging, and by removing locations for confounding activities such as sleeping, more mechanistic selection models can be built. The predictive ability of these models may be improved by choosing covariates that are thought to affect the production of a specific food, then the resulting RSFs should describe a more mechanistic pattern of selection to a specific food type. Because the resulting models are food-specific they are more useful for understanding bottom-up impacts on species distribution and abundance.

Grizzly bears (*Ursus arctos*), are large-bodied omnivores that inefficiently digest plant material (Pritchard and Robbins 2008) yet hibernate for almost half a year (Nelson et al. 2007). When active, they have very high caloric requirements and spend much of their time feeding (MacHutchon et al. 1998, McLellan 2011, McLellan and McLellan 2015). Grizzly and brown bears live in temperate climates and have dramatically shifting diets as the seasons progress and different foods become available. Consequently, the habitats grizzly bears use also change seasonally as different foods become available and they change what they eat (McLellan and Hovey 1995, Munro et al. 2006).

The specific foods consumed by grizzly bears varies among ecosystems, but there is a similar seasonal pattern among many populations. In the interior mountains of British Columbia, Alberta, and Montana, grizzly bears consistently select for avalanche chutes (Waller and Mace 1997, Munro 1999, Ramcharita 2000, McLellan and Hovey 2001, Serrouya et al. 2011) or



riparian areas (McLellan and Hovey 2001, Munro et al. 2006) during spring and early summer (May-July). Although these habitats are structurally different, avalanche chutes and riparian areas contain many of the same bear foods that flourish in wet sites (McLellan and Hovey 2001, Munro et al. 2006), and, for bears, they are functionally similar (McLellan and Hovey 2001). In the summer, when high-energy foods become available, bears will switch their diet to one that consists almost entirely of the specific food type and display hyperphagic behaviour by increasing the time they spend feeding (McLellan and McLellan 2015) to deposit the fat needed for hibernation and reproduction (McLellan 2011).

In many populations huckleberries (*Vaccinium membranaceum*) are the primary high-energy food source for grizzly bears in late summer (McLellan and Hovey 1995, Munro et al. 2006, McLellan 2007, Costello et al. 2014, Lamb et al. 2017) and grizzlies will often spend several weeks feeding on them (McLellan 2007, McLellan and McLellan 2015). In other populations, such as the Greater Yellowstone Ecosystem, grizzly bears eat whitebark pine (*Pinus albicaulis*) seeds in late summer (Mattson et al. 1991). The transition between dominant food sources results in spatially and temporally variable habitat selection patterns making food-based definitions of habitat fitting for this species.

The distribution of many plant species, including primary bear foods, is well documented and mapped but occurrence does not adequately describe the value to foragers. In particular, huckleberry is the primary understory shrub in many forest types in British Columbia (MacKenzie 2012), but it has highly variable fruit production. Variable production renders vegetative plant-based models ineffective for predicting habitat value because grizzly bears only eat the fruit. Additional environmental factors are necessary to produce models that describe and predict the occurrence of this grizzly bear food source. Despite the challenges for predicting the

occurrence and abundance of some high-energy food sources, their importance as drivers for grizzly bear reproduction and population density have been well documented (McLellan 2015, van Manen et al. 2015).

In the interior mountains of North America, dozens of research projects have monitored thousands of radio-collared grizzly bears and have produced hundreds of research papers that have helped managers enhance populations and improve the long-term security of these bears (McLellan 1989, Johnson et al. 2006, Eberhardt et al. 2008, Kendall et al. 2009, Laikre et al. 2010). In stark comparison, very little is known of the ecology of grizzly bears living in the southern Coastal Mountain Ranges. Despite stopping the legal grizzly bear hunt in this area two decades ago, recovery is inconsistent among populations and some remain critically endangered (Romain-Bondi et al. 2004, Apps et al. 2014, McLellan et al. 2017b, Morgan et al. 2019). Two of these threatened populations are geographically adjacent to one another and have similar ecosystem characteristics but remain genetically isolated from one another and have divergent population trends. The more northern McGillivray Mountains (MM) population has been increasing while the other, the North Stein Nahatlatch (NSN), has a much lower density of bears and is slowly declining to where it has been classified as critically endangered by the IUCN (McLellan et al. 2019, McLellan et al. 2016). The difference in population growth rates is the result of large differences in both adult female and cub survival (chapter 3). Because high energy foods are so important for bears in other populations (McLellan and Hovey 1995, Hilderbrand et al. 1999, MacHutchon and Wellwood 2003, Munro et al. 2006) one hypothesis for the ultimate cause of high cub and adult female mortality is that the population is near carrying capacity and limited by food resources.

In this chapter, I quantify seasonal habitat selection by grizzly bears in the MM and NSN populations to test the hypothesis that habitat quality is contributing to the difference in density and trend observed in the populations. I first delineate among seasons to differentiate between the availability of different seasonal food types. I expect that if food abundance is limiting population growth in the NSN population, then there will be proportionately less food available than in the MM population. In particular, I expect that habitats used by bears for eating high-energy foods during the summer and early autumn, or the season of hyperphagia, are more common in the MM than the NSN. I attempted to develop selection models that predict seasonally specific food types by delineating among seasonal foraging behaviours and diel activity for each individual. This further limits the variability introduced by inconsistencies among individuals and years. My second objective is to measure how well the resulting spatially extrapolated RSF berry season model predicts huckleberry abundance during the season when bears feed almost exclusively on this fruit. By measuring huckleberry production independent of bear use, I test the ability of RSF models to predict food abundance. This result will quantify the efficacy of using seasonal food-specific RSFs to further understand potential food-related mechanisms of population regulation of small, isolated populations.

## **4.2 Methods**

### **4.2.1 Capture and Collaring**

Between 2005 and 2018, grizzly bears in the McGillvary Mountain (MM) and North Stein Nahatlatch (NSN) populations were captured and collared. Bears  $\geq 3$  years of age were fit with GPS telemetry collars (Lotek Inc. Ontario, Canada) programmed to obtain either 8 or 24

locations per day depending on the size of the collar. Except for two adult males that were caught in foot snares, all bears were immobilized from a helicopter using a combination of tiletamine and zolazepam (Telazol®) administered with a projectile. Capture was done in both spring and autumn. Depending on the collar model, I downloaded locations bimonthly from a fixed-wing aircraft using a remote device or obtained locations via satellite upload. All collars were fit with a canvass spacer that rotted so all collars dropped off.

#### **4.2.2 Seasonal Delineation**

I defined four distinct seasons based on the dominant foods consumed by collared grizzlies in this study (McLellan 2007, McLellan and McLellan 2015). To account for the interannual variation of seasonal onsets, I defined seasons for each individual and year depending on observed foraging behaviours and large-scale movement patterns that characterize switching among patches (McLellan and McLellan 2015).

All collared bears in this study fed on herbs and bulbs following den emergence (April-May) and lasting until mid-summer (July) for bears that had early fruiting species in their home range, or until mid or late August when bears either switched to huckleberries or the herbaceous foods senesced. Diet during the herb-bulb season consisted of herbs, grasses, bulbs and corms. There was very little variability among individual diet compositions during this season.

The early fruit season followed the herb-bulb season and lasted from mid-July until early or mid-August. Food species selected during the early-fruit season were lower elevation fruiting shrubs including Saskatoon berries (*Amelanchier alnifolia*) and, to a lesser extent, pin (*Prunus pensylvanica*) and choke (*Prunus virginiana*) cherries. No bears in the NSN population and about ¼ of the bears in the MM population had early-fruit shrubs available in their home ranges.

The huckleberry season for most years occurred from mid-August until late September when grizzlies fed almost exclusively on this fruit. In years when the berry bushes were productive, all monitored bears in the MM fed on huckleberries, but some bears in the NSN population were never known to feed on huckleberries or had much shorter seasons. All observations of huckleberry foraging occurred in sites previously disturbed by wildfire, forest harvest or both.

The post-berry season diet was the most variable among individual bears and years and therefore the most difficult to define temporally. I defined it as after the end of the huckleberry season or, in the absence of the huckleberry season, the senescence of herbaceous forage. The dominant foods during the post-berry season were whitebark pine seeds, glacier lily bulbs (*Erythronium grandiflorum*) and one collared individual fed on salmon (*Oncorhynchus spp.*). In many areas, whitebark pine and glacier lilies grow adjacent to each other within the scale of selection (grain) measurable by the RSF. In years when huckleberries were scarce and bears did not feed on them, the change from the herb-bulb or early fruit season to the post berry season was defined as September 1<sup>st</sup> because this is when, according to site investigations, bears would begin to feed on whitebark pine cones of that year (McLellan 2007, McLellan and McLellan 2015).

#### **4.2.3 RSF Model Development**

I developed separate resource selection functions for the herb-bulb, early-fruit, huckleberry and post-berry seasons using mixed-effects logistic regression with individual bear as the random effect (Gillies et al. 2006). Availability was defined as features within the minimum convex polygon (MCP) annual home range for each individual. Only bears monitored

for a full year were included in the analysis to not bias seasonal selection patterns. Likewise, only seasons with complete data for a bear in a year were included to reduce the effects of partial seasons. For example, if a bear was collared for more than one year, but only half of the second year, only the complete seasons of the second year were included in the analysis.

I was interested in modelling habitats specific to foraging behaviours, therefore, I excluded all night-time locations between evening and morning civil twilight when bears are usually inactive (Nielsen et al. 2010, McLellan and McLellan 2015). Because bear site investigations indicated that grizzlies in this population only foraged for berries in previously disturbed sites, I developed an additional model for the huckleberry season where the sampling area was constrained to previously disturbed sites within an individual's home range. Comparisons between the reduced area huckleberry habitat model and the full home range model would indicate whether excluding large areas unused for foraging improved the model.

Model building included several steps. First, I tested predictor variables for multicollinearity which can decrease the precision of the model and possibly create erroneous results (Graham 2003). If predictor variables were considered highly correlated by having Pearson correlation coefficient of  $> 0.6$  (Nielsen et al. 2009), I conducted a separate logistic regression for each covariate and retained the variable with the lowest AIC score (Boyce et al. 2002, Burnham and Anderson 2002) and the highest pseudo- $R^2$  values for subsequent steps of model building.

The remaining environmental covariates were ordered by their explanatory power, measured by pseudo- $R^2$  value, and were sequentially added to create a multivariate model. If the inclusion of a covariate increased model performance by  $> 5\%$  or its exclusion changed the  $\beta$  parameter by more than 20%, it was retained in the final model (Bursac et al. 2008). Any

removed parameters were then re-added in reverse order to ensure that the order did not confound results (Proctor et al. 2015).

To assess whether it was appropriate to combine bears from the two populations into one model, the top model was compared to a model with population included as an additional random variable fit using maximum likelihood estimation and compared using AIC to the model with individual as the only random variable. Fixed variables were not changed for this comparison allowing the use of information-theoretic approaches to model comparison. Model building used lme4 (V.1.1-14, Bates and Mächler 2016), pscl (V.1.5.2, Jackman 2017) and MASS (7.3-49) packages in program R (v.3.6.2, R Core Team 2019).

I evaluated model performance using repeated k-fold cross-validation (Boyce et al. 2002). First, I randomly partitioned the data into  $k = 5$  groups and, in sequence, each group of 20% were withheld for model testing while the remaining 80% of the data were used to fit an RSF model as described above. The resulting model scores were partitioned into ten ranked quantile bins and predictions were evaluated based on the proportion of bear use and random locations in each bin. Spearman's rank correlation coefficient was used to assess the goodness-of-fit between bin RSF scores and the proportion of bear use-locations in each bin; high positive values indicating good predictive capacity. The entire process was repeated 10 times to estimate variance among validation measures. I also calculated the area under the receiver operating characteristic curve (ROC) to assess the predictive ability of the resulting RSFs. The area under the ROC may be biased slightly low for use-availability data but because the data set is large, the statistic is useful for understanding the accuracy of the fit model. ROC was calculated using pROC package (V.1.11.0, Robin et al. 2015) and the K-fold estimate function was developed in R.

#### 4.2.4 Environmental Variables

I considered environmental covariates for model development that, based on field observations and the literature, were hypothesized to affect habitat selection or food-specific productivity. These covariates included eight general types: climate, soil, terrain, greenness, landscape cover, whitebark pine cover, disturbance history, and road density (Table 4.1). Specifically, I included climate variables known for their influence on berry production and vegetation growth such as average seasonal rainfall, some seasonal temperature covariates, the number of frost-free days and the number of days above or below 18 °C (Selås 2000, Barnuud et al. 2014, Wang et al. 2016). Soil types were based on their unconsolidated mineral and organic materials mapped at a 100 m resolution (Bulmer et al. 2016).

I used a digital elevation model at a 25 m resolution (ESRI 2010, GEO BC 2011) to derive terrain variables previously shown to influence grizzly bear habitat selection and possibly affecting the growth and fruiting of food types (Proctor et al. 2015, Nielsen et al. 2004b). These included elevation, slope, aspect, solar radiation, compound topographic index (CTI) as a surrogate for terrain wetness (Rho 2002), and terrain ruggedness index (Evans 2004). Using the aspect layer, I calculated indices of southerliness (SOUTH) and westerliness (WEST) that each range from 0 to 1 where values close to 0 indicate north or easterly aspects respectively.

Southerliness ( $S$ ) is defined by:

$$S = 1 - \frac{|A-180|}{180} \quad (Eq. 1)$$

where  $A$  is aspect (1-360°). Westerliness ( $W$ ) is computed in two steps: first, if aspect ( $A$ )  $\leq 90^\circ$ , then  $a = A + 360^\circ$ , if aspect  $> 90^\circ$  then  $a = A$ , and westerliness ( $W$ ) is then:

$$W = 1 - \frac{|a-270|}{180} \quad (Eq. 2)$$



Normalized difference vegetation index (NDVI), commonly called greenness, is a measure of the density of green wavelengths of light reflected by plants and is an index of vegetative productivity. I mosaiced imagery collected from Landsat 8 satellite during the last week of July (2014-2018) when there was < 3% cloud cover (NASA Land Processes Distributed Active Archive Center Products 2014) to calculate greenness using the tasselled-cap transformation (Baig et al. 2014). I restricted imagery to late July for consistency across the study area and before plants began to senesce in the alpine.

Landscape cover was defined to be one of 13 discrete functional habitat units believed to be identifiable by both bears and humans and likely differentially selected by grizzly bears. I based polygon boundaries on those delineated in the Vegetation Composite Polygon Spatial layer (VRI) created by the BC Ministry of Forests (Ministry of Forests 2013). First, I classified each polygon using the British Columbia Land Cover Classification Scheme levels 1 through 5 to delineate among rock, ice, water, wetland, grassland, forested, herbaceous, and heather dominated habitats. Forests were classified by dominant tree species commonly delineated as separate biogeoclimatic zones (BEC) described in the VRI (MacKenzie 2012). Forest types in the study area included coastal western hemlock (CWH), Engelmann spruce and subalpine fir (ESSF), interior Douglas fir (IDF), mountain hemlock (MH), montane spruce (MS), and ponderosa pine (PP). For model parsimony and convergence reasons, I grouped ponderosa pine forests (< 1% of the study area) with IDF forests. PP is always adjacent to IDF in this region and have many understory plant species in common.

Unforested areas were divided into vegetated and non-vegetated. For alpine, the VRI base-map boundaries were often incorrect. I used the NDVI layer to differentiate among rock, ice and vegetated areas, where, on a scale from 1-10, 1 and 2 are ice and rock. This scale was

developed by examining the relative greenness in areas that had been visited on the ground and where vegetation plots had been recorded (see McLellan 2007).

Avalanche chutes are habitats kept in a perpetual sub-seral state because sliding snow frequently removes larger shrubs and trees. Each avalanche chute polygon was manually digitized from orthophotos and delineated into different avalanche chute types including herbaceous, krummholz, rock, and shrub-dominated. To differentiate the uppermost portions of avalanche chutes from alpine, I used VRI to identify treeline and above that was alpine (Ministry of Forests 2013). Alpine areas were classified as herb dominated, heather dominated, rock and ice. The percent of whitebark pine cover and overall canopy cover in a polygon were each included as additional continuous variables. Polygons dominated by human use such as homes, farms, schools, and towns were classified as anthropogenic. Landscape disturbance history was classified into disturbance type: fire, timber harvest, both or none; and the time since the last disturbance; > 30 years, 10 to 30 years, old and < 10 years. Preliminary analysis showed sharp increases in bear use of disturbed sites older than ~10 years but newer than ~30 years old. Categorical variables were used because the relationship between disturbance age and selection was not linear.

Road density has been correlated to grizzly bear mortality in several other populations (McLellan et al. 1999, Lamb et al. 2018, Proctor et al. 2018b). I estimated road density (km of road/km<sup>2</sup>) across the study area. First, I amalgamated digital road layers from the provincial database, Ainsworth Forest Company, and manually digitizing new roads. I then removed overgrown or reclaimed roads that were no longer navigable by a vehicle during the snow-free seasons. I then calculated road length within a circle with a 1.0 km<sup>2</sup> area to obtain the density of

roads surrounding each pixel. All data were organized and overlaid in a geographic information system (ArcMap V.10.4).

#### **4.2.5 Comparing seasonal habitats between the populations.**

I tested the hypothesis that highly selected habitats were more common in the MM than the NSN, and in particular, had proportionately more high-quality huckleberry habitat by comparing the proportion of the study areas in each RSF equal-area bin for the top model for each season.

#### **4.2.6 Bear foraging sites**

To test RSF model accuracy I estimated food abundance where bears were feeding and compared it to areas predicted by the RSF to have high-quality habitat. To quantify site-specific food abundance, I visited locations downloaded from collared grizzly bears within two weeks of the bear's being at the site. At each site I conducted a 100 m<sup>2</sup> plot in which I measured terrain attributes, disturbance history, canopy closure, and percent cover of all plant species. For fruiting bear foods, I recorded the percent of stems with berries, the phenological and generative state of the plant and berry load; Low = 0-5 berries/stem, Medium 6-15 berries/stem, and High > 15 berries/stem. I recorded evidence of bear behaviours such as bedding, berry feeding, herbaceous feeding, travelling, and whitebark pine feeding. Specific locations were randomly chosen, but if a heavily used area had been investigated several times, I gave preference to unfamiliar areas to

**Table 4.1** Spatial covariates used for seasonal RSF model development for grizzly bear habitat in southwestern British Columbia, Canada.

<b>Covariates</b>	<b>Code</b>	<b>Description</b>	<b>Data Type</b>
Climate Covariates	dd_0	Degree-days below 0°C	Continuous
	dd_18	Degree-days below 18°C	Continuous
	dd18	Degree-days above 18°C	Continuous
	dd5	Degree-days above 5°C	Continuous
	nffd_sp	Spring number of frost-free days	Continuous
	dd_0_sp	Spring degree-days below 0°C	Continuous
	dd18_sm	Summer degree-days above 18°C	Continuous
	dd5_sp	Spring degree-days above 5°C	Continuous
	map	Mean annual precipitation (mm)	Continuous
	ppt_at	Autumn precipitation (mm)	Continuous
	ppt_sp	Spring precipitation (mm)	Continuous
	ppt_wt	Winter precipitation (mm)	Continuous
	ppt_su	Summer precipitation (mm)	Continuous
	pas_wt	Winter precipitation as snow (mm)	Continuous
NDVI	green	Greenness	Continuous
Topographical	south	Southerliness	Continuous 0 to 1
	west	Westerliness	Continuous 0 to 1
	sol_rad	Solar Radiation	Continuous
	cti	Wettness	Continuous
	tri	Ruggedness	Continuous
	slope	Slope	Continuous
Crown Closure	canopy	Crown Closure	Continuous %
Whitebark pine	WBP	Whitebark pine cover	Continuous %
Open road density	OR_dens	Road density in km/km <sup>2</sup>	Continuous

Table continued on next page.

**Table 4.1** Continued.

<b>Covariates</b>	<b>Code</b>	<b>Description</b>	<b>Data Type</b>
Disturbance History (DIST) **	F_less10	Fire less than 10 years old	0 or 1
	F_10to30	Fire 10 to 30 yrs	0 or 1
	F_over30	Fire over 30 yrs	0 or 1
	H_less10	Harvest less 10 yrs	0 or 1
	H_10to30	Harvest 10 to 30 yrs	0 or 1
	H_over30	Harvest over 30 yrs	0 or 1
	None	None recorded	0 or 1
Landscape Cover (HAB_COV)	CWH	Cedar-Western Hemlock	0 or 1
	ESSF	Engelmann-Spruce-Subalpine Fir	0 or 1
	IDFPP	Interior Douglas Fir -Ponderosa Pine	0 or 1
	MH	Mountain Hemlock	0 or 1
	MS	Montane Spruce	0 or 1
	AVY	Herb dominated avalanche chutes	0 or 1
	ALP	Herb dominated alpine	0 or 1
	SHRUB_AVY	Shrub-dominated avalanche chutes	0 or 1
	HEATHER	Heather dominated alpine	0 or 1
	KRUM	Krumholtz	0 or 1
	WETLAND	Wetland	0 or 1
	ROCKI	Rock and Ice	0 or 1
	ANTH	Anthropogenically modified	0 or 1
Soil Parent Material (Soil)	GF	Glaciofluvial	0 or 1
	FL	Fluvial	0 or 1
	LA	Lacustrine	0 or 1
	CO	Colluvium	0 or 1
	TI	Till	0 or 1
	BR	BedRock	0 or 1
	GL	Glaciolacustrine	0 or 1
	O	Organic	0 or 1

\*\* For berry models estimated for disturbed sites only; disturbance was categorized into DIST\_AGE and DIST\_TYPE for better model function.

increase the documentation of habitat use across the study area. For each bear use plot, I matched a random plot where I collected the same information. These were at a random distance ( $< 350$  m) and direction but within the same habitat type (see HAB COV for RSF model development) but not overlapping the bear use plot.

To measure the site attributes specific to the huckleberry season I analyzed only locations where bears were feeding on this fruit and the associated random plots where bears were not feeding on it. I estimated the mean, variance and 95% confidence intervals for site attributes at used and random plots by bootstrapping 1000 times. I defined berry abundance as the product of overall huckleberry plant coverage, the percent of stems with berries, and the average berry load. Because areas where foraging had occurred would be biased low for berry load due to depletion by the bear, I also included berry cover, defined to be the same as berry abundance but excluding berry load.

#### **4.2.7 Huckleberry productivity plots**

To test the efficacy of the RSF huckleberry models for predicting fruit abundance, berry plot data were also measured independent of bear locations. Data were obtained from two separate sampling programs with the same objective of quantifying berry production and based on the site investigation methods described above.

In the first program, researchers conducted a series of  $100 \text{ m}^2$  plots every 50 m along 200 m transects. At each plot, site-specific characteristics were collected as well as the information on huckleberry plants and the fruit load as described above. Researchers also measured the mass of berries picked in 10 minutes beginning at a random point along the transect. The researcher was instructed to pick as fast as they could, and the person picking was recorded. Finally, for 5

random berries picked, researchers measured the sweetness in degrees Brix, using an Atago 3810 digital refractometer and averaged the measurements for the plot value.

The second program was conducted by a Fish and Wildlife Compensation Program project (FWCP, Hobbs et al. 2013) that collected data along 136 transects to estimate huckleberry abundance in areas where huckleberry fruit was expected and in adjacent areas where huckleberry plants were expected but fruit production was uncertain. Huckleberry plant coverage and the proportion of stems with berries were recorded along 100 m transects (Hobbs et al. 2013). The transects done by the FWCP did not estimate berry load in the same way so they were excluded from that analysis. I also included the previously described matched random plots for testing. Although these data may be slightly positively biased because plots were close to grizzly bear locations used to create the RSF models, the precise nature of the sampling methods will allow inference at the pixel scale.

#### **4.2.8 Huckleberry Season Model Testing Analysis**

I used the data collected from the huckleberry productivity transects to compare the predictive ability of four huckleberry specific RSF models. One was the top model for the season excluding interactions (BTOP) and the second was the top model including covariate interactions (BINT), increasing the statistical measures for model fit, but also increasing model complexity. Two other models (DTOP and DINT) were developed following the same rules except that use and availability were limited to previously disturbed sites within individual home ranges. DTOP is the top model from disturbed sites only, and DINT is the top model for disturbed sites including interactions.

The four berry season RSF models were projected across the study area using the equation

$$\hat{w} = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots \beta_n x_n) \quad (Eq. 3)$$

where  $\beta_1$  through  $\beta_n$  were the coefficients of selection estimated for each covariate in the RSF and values  $x_1$  through to  $x_n$  were the covariate values in that pixel (Nielsen et al. 2009). To scale the models, they were binned into 100 equal-area quantiles across the study area (Boyce and McDonald 1999, Morris et al. 2016). The RSF model values and their binned quantile values were extracted at each use location and to each test huckleberry plot point location. The expected number of locations according to bin size, assuming no selection, was compared to the number of locations in each bin with a chi-squared test. As a comparative control for the effects of binning on model accuracy, the BTOP model was projected and limited to previously disturbed sites to match the extent of the disturbance only models and expressed using equal area quantiles (BDTOP).

The efficacy of RSF models to predict food abundance was evaluated by comparing RSF values to the huckleberry abundance and productivity data measured in the transect plots. In the first step of quantifying the predictive ability of the RSFs, the possible non-linearity in the relationship between the RSF model and huckleberry measure variables (e.g. % stems with berries) were explored by comparing the fit of the linear mixed-effects regression with generalized additive mixed models (GAMMs, Crawley 2005). Then, using the most accurate technique from step one, each berry model variable was related to each RSF model independently because of collinearity and lack of independence among RSFs and the various measures of huckleberry productivity. Project and transect were included as random variables for both linear and non-parametric GAMMs to control for the lack of independence among plots



along a transect. Likewise, for measures of grams of fruit picked in 10 minutes, the picker was included as a random variable to control for differences among pickers. Linear regression and GAMMs were carried out using the lme4 (v. 1.1-21, Bates et al. 2019) and gamm4 (v.0.2-5, Wood and Scheipl 2017) packages in R.

The success of RSFs to predict huckleberry abundance that was comparable to berry abundance at sites used by bears was also evaluated. For this evaluation, I estimated each RSF model's accuracy, precision, specificity, sensitivity, and the F1 statistic that enumerates the trade-off between model precision and sensitivity (Fawcett 2006, Powers 2007). Model accuracy is the proportion of predictions that are true, or, the sum of true positives and true negatives divided by the sum of all model predictions. Precision is the correctly labelled positive values, defined as the number of true positives divided by the sum of both true and false positives. Sensitivity is the ratio of the true positives (e.g. huckleberry cover equal to or higher than at bear use sites) to the sum of true positives and false negatives, or, how accurate the models are for assessing good habitat quality. These statistics describe model performance by comparing model-predicted values to “true” values and therefore require the truth to be known or defined. I used cut-off points determined from bear use plots to define whether the estimate was “positive” or “negative”. For example, if the mean huckleberry plant cover at sites selected by bears when foraging on berries was 20%, then “positive” selection was for all plots with huckleberry cover as 20% and above, and all plots with less than 20% cover were considered “negative”. Whether an observation was true or not was defined for all bins, grouped in 5% increments and for a single point estimate for bins  $\geq 95$  together. The assessment across bins allows identification of variability in model performance across bins. While the point estimate for high bin values

describes the utility of the model for predicting good berry habitat in a way that is commonly used by researchers and managers (Morris et al. 2016).

## **4.3 Results**

### **4.3.1 Capture and Collaring**

Between 2005 and 2018, 45 grizzly bears were captured and collared in the McGillvary Mountain (18F; 10M) and North Stein Nahatlatch populations (9F; 8M) resulting in 81,027, high accuracy (3D) bear locations. After excluding nighttime locations when bears were inactive and incomplete seasons, I retained 58,305 (39,523 MM; 18,782 NSN) daytime locations for RSF model development.

### **4.3.2 Seasonal RSF Models**

Including the population (MM or NSN) as a random effect did not improve model performance during any season therefore I only retained individual bear as a random effect for subsequent analyses (Table 4.2).

Of the collared bears, 26 (20 F; 6 M) had data for at least one entire spring and early summer (herb-bulb season) and their locations were used in model development. The top RSF model for the herb-bulb season showed that bears selected highly productive south and west-facing avalanche chutes as well as herbaceous alpine meadows, particularly those in recent burns (Table 4.3). Areas used by humans were very strongly avoided. Grizzlies selected areas with low canopy cover, relatively high whitebark pine cover, a relatively high number of spring days above freezing and low previous autumn precipitation. Organic soil types were selected over

**Table 4.2** Model selection for the inclusion of continuous modifying covariates on habitat covariates or disturbance covariates in seasonal resource selection functions for grizzly bears in southwestern British Columbia, Canada.

Model	Models	k	$\Delta AIC$	$\omega_i$
Herb-Bulb	HERB + (HAB_COV * ppt_at)	49	0	1
	HERB + (HAB_COV * dd_0_sp)	49	576.1	0
	HERB + (HAB_COV * green)	49	699.6	0
	HERB + (HAB_COV * OR_Dens)	49	843.2	0
	HERB	37	917.6	0
Early Fruit	EARLY + (HAB_COV * pas_wt )	40	0	1
	EARLY + (HAB_COV * green)	40	39.889	0
	EARLY	30	110.614	0
	EARLY + (DIST_AGE_T) * pas_wt)	32	110.809	0
	EARLY + (DIST * green)	32	111.72	0
Huckleberry	BTOP + (HAB_COV * green)	49	0	1
	BTOP + (HAB_COV * ppt_sp)	49	61.2	0
	BTOP + (DIST AGE_T * dd_0)	43	282.5	0
	BTOP + (DIST AGE_T * green)	43	286.3	0
	BTOP	37	298.4	0
Disturbance – Berry**	DTOP + (ORI_FOR * DIST_AGE)	34	0	1
	DTOP + (ORI_FOR * DIST_TYPE)	34	94.6	0
	DTOP + (ORI_FOR * ppt_sp )	34	126.7	0
	DTOP + (DIST_TYPE * Soil_P)	39	136.6	0
	DTOP + (ORI_FOR * green)	30	142.1	0
	DTOP	26	153.3	0
Post-Berry	POST + (HAB_COV * green)	49	0	1
	POST + (HAB_COV * dd18_sm)	49	303.2	0
	POST + (HAB_COV * ppt_su)	49	462.8	0
	POST	37	743.0	0

\*\* Use and availability from previously disturbed sites only

**Top univariate resource selection functions estimated using stepwise model development**

HERB = dd\_0\_sp + ppt\_at + green + south + west + tri + canopy + WBP + OR\_Dens + DIST + HAB\_COV + Soil

EARLY = dd5\_sp + ppt\_sp + green + south + west + slope + canopy + OR\_Dens + DIST\_TYPE + DIST\_AGE + ORI\_FOR + Soil

BTOP = dd\_0 + ppt\_sp + green + south + west + cti + tri + canopy + OR\_Dens + DIST + HAB\_COV + Soil

DTOP = dd5\_sp + ppt\_sp + green + south + west + slope + canopy + OR\_Dens + DIST + DIST\_AGE + ORI\_FOR + Soil

POST = dd18\_sm + ppt\_su + green + sol\_rad + west + cti + slope + WBP + OR\_Dens + DIST + HAB\_COV + Soil

other types and there was a small effect suggesting selection for areas with higher open-road densities (Table 4.3). Interaction effects improved model fit and indicated that increased autumn precipitation negatively affected selection for avalanche chutes but increased selection for most forested areas regardless of disturbance (Table 4.2).

Early-fruit foraging was documented for 6 (5F; 1M) bears collared for the duration of the season. This behaviour was only observed for approximately  $\frac{1}{4}$  of the collared bears in the MM population. The top RSF model for the early-fruit season showed selection for areas with lower winter snowfall and relatively high greenness. Selected areas were less rugged (tri) and collected more moisture (cti) than available habitats (Table 4.3). In contrast to all other seasons, grizzlies selected habitats in the Interior Douglas Fir zone with a fire disturbance over 30 years old but like other seasons organic soils were selected (Table 4.3). Areas with high open road density were avoided during this season. Including interactions between the amount of precipitation as snowfall and habitat cover improved model fit, particularly for IDF and ESSF zones (Table 4.2).

I monitored 20 bears (15 F; 5M) for at least one complete huckleberry season. The top huckleberry models for each of the four availability and interaction criteria all showed strong selection for areas with relatively high spring precipitation (Table 4.4). For the models where all areas within their home ranges were considered available (BTOP and BINT), models predicted selection areas with fewer days below freezing, but when limited to disturbed areas only (DTOP and DINT), selection was more specifically for spring days above 5 °C (Table 4.4). When all areas were included, bears avoided forests as expected but also avoided recently harvested, and, to a lesser extent, recently burned areas. Greenness increased the probability of selection for both entire home range models and disturbed areas only models, however, its importance was reduced in the disturbed only models (Table 4.4). Overall, bears avoided rugged areas during the

huckleberry season but selected for steeper slopes within previously disturbed sites. Grizzlies also avoided high road density areas but more so when only disturbed sites were considered. Sites with organic soils were selected above other soil types. Repeated k-fold cross-validation for the berry season RSF was 0.979 (SD = 0.016) and 0.983 (SD = 0.018) with interactions. The area under the ROC curve was 0.938 (95%CI: 0.936-0.941) and 0.940 (95%CI: 0.938-0.942) for the model including interactions.

The huckleberry season top models for both availability grouping methods included covariate interactions (Table 4.2). Within home range selection the moderation of habitat cover type by greenness improved model fit the most. At the more focused, disturbance only scale, including the interactions between the disturbance age and forest type improved model fit most (Table 4.2, Table 4.4). Specifically, an increase in greenness increased selection for IDF forests and ESSF forests including disturbed areas within that forest type. A bear was 10.2 and 3.3 times more likely to select a site where the time since disturbance was between 10 and 30 years than a site with older or newer disturbance in these two forest types respectively. However, the moderating effect of disturbance age varied among other forest types. For example, disturbance > 30 years old was more strongly avoided in MS and harvest < 10 years old was more strongly avoided in ESSF forests than MS, MH and CWH forests (Table 4.4). The bootstrapped mean Spearman's rank correlation coefficient for repeated k-fold cross-validation indicated that all berry season models performed well and including interactions resulted in minor improvements in model performance (Table 4.4).

In the post-berry season, when grizzly bears no longer fed on huckleberries, they selected areas with high summer precipitation and a high number of days above 18 °C (Table 4.3). Other factors that increased the odds of selection were increased greenness, west-facing aspects and

areas with high solar radiation. WBP cover also was selected for as were areas with low road density. Bears selected for areas burned less than 10 years previously more than any other areas disturbed by fire or forest harvest. Areas without prior disturbance were preferred to disturbance over 30 years old. High elevation habitat types were selected including avalanche chutes, alpine herbaceous meadows, and even rock, presumably because bears were digging dens during this season (McLoughlin et al. 2002). In contrast, the IDF zone was also selected over all other forested zones and one male did feed on salmon in this zone until December. Greenness modified the selection of habitat types, particularly by drastically increasing the selection of IDF, and to a lesser extent, increasing the selection of avalanche chutes and rock, the latter is likely an error due to model grain by including multiple, adjacent, habitat types in a pixel.

Overlaying bear locations with the resulting RSF map from the model development area indicated that 50.5 % of spring-early summer bear locations were within 6% of the overall area (bins 95-100) and 20.1% were inside 1% of the area. Less than 10% of all locations were in the lower 50% of the RSF bins (Figure 4.1). The early fruit models were similarly predictive with over 50% of all early fruit locations within 6% of the available habitats and 25% inside 1% of the available habitat. The BTOP model and BINT model respectively captured 68% and 86% of berry season locations in 6% of the available habitat. Habitat selection was more diffuse in the post berry season. Only 30% of bear locations were in the top 6% of habitat types and 8% inside the top 1% of habitat (Figure 4.1).

**Table 4.3** Estimated scaled coefficients  $\pm$  SE for the top seasonal RSF models estimating resource selection by grizzly bears in southwest British Columbia, Canada. See table 4.4 for huckleberry season models. P values in parentheses ( $\alpha = 0.05$ ).

Covariates	Code	$\beta \pm$ SE (p value)		
		HERB	EARLY	POST BERRY
Intercept		-0.61 $\pm$ 0.29 (0.038)	-2.44 $\pm$ 0.45 (<0.001)	-0.36 $\pm$ 0.24 (0.15)
Climate	pas_wt		-1.31 $\pm$ 0.19 (<0.001)	
	dd_0_sp	-0.28 $\pm$ 0.02 (< 0.001)		
	dd18_sm			0.36 $\pm$ 0.03 (< 0.001)
	ppt_at	-0.68 $\pm$ 0.04 (<0.001)		
	ppt_su			0.63 $\pm$ 0.03 (< 0.001)
NDVI	Green	1.34 $\pm$ 0.02 (<0.001)	0.86 $\pm$ 0.05 (< 0.001)	1.00 $\pm$ 0.05 (< 0.001)
Topo	South	0.24 $\pm$ 0.01 (<0.001)	-0.07 $\pm$ 0.04 (0.070)	
	West	0.14 $\pm$ 0.01 (<0.001)	-0.19 $\pm$ 0.04 (< 0.001)	0.14 $\pm$ 0.02 (< 0.001)
	Sol_rad			0.15 $\pm$ 0.02 (< 0.001)
	cti		0.12 $\pm$ 0.03 (<0.001)	0.06 $\pm$ 0.02 (< 0.001)
	tri	-0.06 $\pm$ 0.02 (<0.001)	-0.19 $\pm$ 0.06 (0.003)	
	slope			-0.03 $\pm$ 0.02 (0.156)
	canopy	-0.32 $\pm$ 0.02 (<0.001)	-0.66 $\pm$ 0.07 (< 0.001)	
WBP	WBP	0.30 $\pm$ 0.04 (<0.001)		0.25 $\pm$ 0.07 (< 0.001)
Road Density	OR_dens	0.05 $\pm$ 0.01 (<0.001)	-0.26 $\pm$ 0.04 (< 0.001)	-0.17 $\pm$ 0.02 (< 0.001)
DIST	F_less10	1.30 $\pm$ 0.09 (<0.001)		0.48 $\pm$ 0.13 (< 0.001)
	F_10 to 30	REF	REF	REF
	F_over30	0.05 $\pm$ 0.11 (0.649)	-	-3.94 $\pm$ 0.28 (< 0.001)
	H_less10	-0.14 $\pm$ 0.13 (0.268)	-1.23 $\pm$ 1.13 (0.376)	-1.27 $\pm$ 0.24 (< 0.001)
	H_10to30	-0.32 $\pm$ 0.09 (<0.001)	0.33 $\pm$ 0.17 (0.050)	-1.50 $\pm$ 0.13 (< 0.001)
	H_over30	-0.28 $\pm$ 0.10 (0.006)	-1.27 $\pm$ 0.44 (0.004)	-2.87 $\pm$ 0.23 (< 0.001)
	None	0.05 $\pm$ 0.08 (0.535)	-1 $\pm$ 0.16 (0.001)	-1.71 $\pm$ 0.10 (< 0.001)
	CWH	-0.31 $\pm$ 0.06 (<0.001)	-	-0.74 $\pm$ 0.16 (< 0.001)
HAB COV	ESSF	-0.30 $\pm$ 0.05 (<0.001)	-0.30 $\pm$ 0.20 (0.168)	-0.33 $\pm$ 0.10 (< 0.001)
	IDF_PP	-0.96 $\pm$ 0.05 (<0.001)	-0.31 $\pm$ 0.39 (0.418)	-3.08 $\pm$ 0.28 (0.985)
	MH	0.00 $\pm$ 0.13 (0.988)	-	-0.42 $\pm$ 0.23 (0.062)
	MS	0.21 $\pm$ 0.07 (0.006)	0.29 $\pm$ 0.28 (0.297)	-1.48 $\pm$ 0.18 (< 0.001)
	AVY	0.14 $\pm$ 0.05 (<0.001)	-0.43 $\pm$ 0.17 (0.013)	0.22 $\pm$ 0.12 (0.068)
	ALP	REF	REF	REF
	SH_AVY	-0.53 $\pm$ 0.19 (0.005)	-0.74 $\pm$ 0.25 (0.004)	-0.01 $\pm$ 0.25 (< 0.957)

Table Continued on next page

<b>Table 4.3 Continued</b>				
<b>Covariates</b>	<b>Code</b>	<b><math>\beta \pm SE</math> (p value)</b>		
		<b>HERB</b>	<b>EARLY</b>	<b>POST BERRY</b>
HAB COV	HEATHER	-0.97 $\pm$ 0.06 (<0.001)	-0.08 $\pm$ 0.33 (0.801)	0.21 $\pm$ 0.13 (0.090)
	KRUM	-0.93 $\pm$ 0.05 (<0.001)	-0.33 $\pm$ 0.19 (0.077)	-0.15 $\pm$ 0.12 (0.208)
	ROCKI	-0.69 $\pm$ 0.06 (<0.001)	-0.18 $\pm$ 0.19 (0.033)	0.25 $\pm$ 0.10 (0.010)
	ANTH	-3.22 $\pm$ 0.26 (<0.001)	-	-
SOIL	GF	-0.29 $\pm$ 0.11 (0.010)	0.07 $\pm$ 0.28 (0.806)	-0.76 $\pm$ 0.30 (0.013)
	FL	0.28 $\pm$ 0.07 (<0.001)	0.98 $\pm$ 0.22 (< 0.001)	0.04 $\pm$ 0.14 (0.783)
	LA	0.13 $\pm$ 0.15 (0.406)	0.48 $\pm$ 0.31 (0.123)	-1.69 $\pm$ 0.51 (0.001)
	CO	0.52 $\pm$ 0.03 (0.080)	-0.13 $\pm$ 0.12 (0.291)	-0.27 $\pm$ 0.04 (< 0.001)
	TI	-0.23 $\pm$ 0.04 (<0.001)	-0.17 $\pm$ 0.14 (0.205)	-0.41 $\pm$ 0.05 (< 0.001)
	BR	REF	REF	REF
	GL	-1.12 $\pm$ 0.20 (<0.001)	-0.88 $\pm$ 0.39 (0.023)	-1.19 $\pm$ 0.45 (0.008)
	O	0.79 $\pm$ 0.11 (<0.001)	1.02 $\pm$ 0.27 (<0.001)	-0.56 $\pm$ 0.25 (0.023)
<b>Interaction Parameter</b>		<b>ppt_at</b>	<b>pas_wt</b>	<b>green</b>
HAB COV*	CWH	1.21 $\pm$ 0.06 (<0.001)	-	-0.08 $\pm$ 0.14 (<0.562)
	ESSF	0.56 $\pm$ 0.04 (<0.001)	0.26 $\pm$ 0.26 (0.325)	0.16 $\pm$ 0.07 (0.023)
	IDF_PP	0.66 $\pm$ 0.04 (<0.001)	0.23 $\pm$ 0.25 (0.360)	3.31 $\pm$ 0.21 (< 0.001)
	MH	-0.04 $\pm$ 0.18 (0.840)	-	-0.13 $\pm$ 0.32 (0.680)
	MS	1.32 $\pm$ 0.06 (<0.001)	1.03 $\pm$ 0.27 (<0.001)	-1.10 $\pm$ 0.25 (< 0.001)
	AVY	0.14 $\pm$ 0.05 (<0.001)	1.50 $\pm$ 0.28 (<0.001)	-0.04 $\pm$ 0.07 (0.561)
	ALP	REF	REF	REF
	SH_AVY	0.70 $\pm$ 0.10 (0.005)	1.39 $\pm$ 0.66 (0.034)	-1.04 $\pm$ 0.17 (< 0.001)
	HEATHER	0.30 $\pm$ 0.06 (<0.001)	1.54 $\pm$ 0.47 (0.001)	-0.59 $\pm$ 0.11 (< 0.001)
	KRUM	0.54 $\pm$ 0.05 (<0.001)	2.18 $\pm$ 0.29 (<0.001)	-0.56 $\pm$ 0.11 (< 0.001)
	ROCKI	0.51 $\pm$ 0.07 (<0.001)	0.61 $\pm$ 0.24 (0.011)	0.47 $\pm$ 0.07 (< 0.001)
	ANTH	-0.55 $\pm$ 0.13 (<0.001)	-	-
k-fold r2 (SE)		0.999 (0.001)	0.919 (0.03)	0.994 (0.006)
Area under ROC curve (95% CI)		0.905 (0.903-0.906)	0.907 (0.900-0.914.)	0.870 (0.866-0.874)



**Table 4.4** Model comparison for the top huckleberry models to highlight model variability due to increased model complexity with interaction terms and to examine the effects of defining non-habitat for model development. BTOP is the top huckleberry season model without interaction and (BINT) is the top model overall, with interactions. DTOP is the model constructed from the same data but only considering locations and availability within disturbance sites. DINT is DTOP with interaction term.

		BTOP	BINT	DTOP	DINT
Covariate	Code	$\beta \pm SE$ (p value)			
Intercept		$-2.07 \pm 0.34$ (< 0.001)	$-1.29 \pm 0.34$ (< 0.001)	$-0.47 \pm 0.51$ (0.362)	$-0.09 \pm 0.57$ (0.880)
	dd_0	$-1.05 \pm 0.04$ (< 0.001)	$-1.00 \pm 0.04$ (< 0.001)		
Climate	dd5_sp			$0.37 \pm 0.08$ (< 0.001)	$0.35 \pm 0.09$ (< 0.001)
	ppt_sp	$1.45 \pm 0.03$ (< 0.001)	$1.43 \pm 0.03$ (< 0.001)	$2.45 \pm 0.11$ (< 0.001)	$2.53 \pm 0.12$ (< 0.001)
NDVI	green	$0.96 \pm 0.03$ (< 0.001)	$0.52 \pm 0.06$ (< 0.001)	$0.37 \pm 0.05$ (< 0.001)	$0.37 \pm 0.05$ (< 0.001)
	south	$-0.31 \pm 0.02$ (< 0.001)	$-0.31 \pm 0.02$ (< 0.001)	$-0.38 \pm 0.04$ (< 0.001)	$-0.41 \pm 0.04$ (< 0.001)
	west	$-0.11 \pm 0.02$ (< 0.001)	$-0.10 \pm 0.02$ (< 0.001)	$-0.17 \pm 0.04$ (< 0.001)	$-0.15 \pm 0.04$ (< 0.001)
Topo	cti	$0.01 \pm 0.02$ (0.508)	$0.01 \pm 0.02$ (0.488)		
	tri	$-0.31 \pm 0.03$ (< 0.001)	$-0.30 \pm 0.03$ (< 0.001)		
	slope			$0.27 \pm 0.05$ (< 0.001)	$0.23 \pm 0.05$ (< 0.001)
Canopy	canopy	$-0.91 \pm 0.03$ (< 0.001)	$-0.84 \pm 0.03$ (< 0.001)	$-0.32 \pm 0.05$ (< 0.001)	$-0.33 \pm 0.05$ (< 0.001)
Roads	OR_dens	$-0.05 \pm 0.02$ (< 0.001)	$-0.07 \pm 0.02$ (< 0.001)	$-0.34 \pm 0.05$ (< 0.001)	$-0.34 \pm 0.05$ (< 0.001)
	F_less10	$-1.36 \pm 0.31$ (< 0.001)	$-1.42 \pm 0.31$ (< 0.001)		
	F_10 to 30	REF	REF		
	F_over30	-	-		
Disturbance	H_less10	$-2.47 \pm 1.27$ (0.052)	$-2.27 \pm 1.25$ (0.070)		
	H_10to30	$-0.74 \pm 0.36$ (< 0.042)	$-0.74 \pm 0.36$ (< 0.042)		
	H_over30	-	-		
	None	$-1.61 \pm 0.16$ (< 0.001)	$-1.68 \pm 0.16$ (< 0.001)		

Table Continued on next page

**Table 4.4** Continued

		<b>BTOP</b>	<b>BINT</b>	<b>DTOP</b>	<b>DINT</b>
<b>Covariate</b>	<b>Code</b>	<b><math>\beta \pm \text{SE}</math> (p value)</b>			
Dist Type	Both			REF	REF
	Fire			$-0.57 \pm 0.17$ (<0.001)	$-0.32 \pm 0.18$ (0.070)
	Harv			$-0.65 \pm 0.16$ (< 0.001)	$0.45 \pm 0.18$ (0.009)
Dist Age	<10 yr			REF	REF
	>30 yr			$1.19 \pm 0.18$ (< 0.001)	$1.05 \pm 0.39$ (0.007)
	10 to 30			$2.32 \pm 0.12$ (< 0.001)	$2.02 \pm 0.28$ (< 0.001)
Land Cover	OTHER*			$-2.05 \pm 0.22$ (< 0.001)	$-3.62 \pm 0.68$ (< 0.001)
	CWH*	$1.44 \pm 0.1$ (< 0.001)	$0.83 \pm 0.14$ (< 0.001)	REF	REF
	ESSF*	$1.47 \pm 0.07$ (< 0.001)	$0.54 \pm 0.17$ (< 0.001)	$-0.51 \pm 0.15$ (<0.001)	$-1.48 \pm 0.31$ (<0.001)
	MH*	$3.05 \pm 0.13$ (< 0.001)	$2.34 \pm 0.16$ (< 0.001)	$0.58 \pm 0.23$ (0.013)	$0.97 \pm 0.69$ (0.160)
	MS*	$0.54 \pm 0.12$ (< 0.001)	$0.09 \pm 0.18$ (0.634)	$-0.73 \pm 0.18$ (< 0.001)	$0.37 \pm 0.37$ (0.324)
	IDF_PP	$-0.34 \pm 0.21$ (0.058)	$-2.16 \pm 0.34$ (< 0.001)		
	AVY	$0.09 \pm 0.08$ (0.259)	$-0.45 \pm 0.14$ (0.001)		
	ALP	REF	REF		
	SH_AVY	$-0.88 \pm 0.14$ (< 0.001)	$-0.02 \pm 0.23$ (< 0.923)		
	HEATHER	$-0.36 \pm 0.09$ (< 0.001)	$-0.77 \pm 0.15$ (< 0.001)		
	KRUM	$-0.19 \pm 0.09$ (0.040)	$-0.62 \pm 0.13$ (< 0.001)		
	WETLAND	$-0.16 \pm 0.18$ (0.385)	$-0.33 \pm 0.25$ (0.193)		
	ROCKI	$-0.06 \pm 0.08$ (0.498)	$-0.61 \pm 0.11$ (< 0.001)		
Soil	GF	$-0.49 \pm 0.36$ (0.172)	$-0.55 \pm 0.37$ (0.132)	$0.59 \pm 0.57$ (0.300)	$0.61 \pm 0.58$ (0.292)
	FL	$0.53 \pm 0.13$ (< 0.001)	$0.49 \pm 0.13$ (< 0.001)	$0.74 \pm 0.31$ (0.015)	$0.49 \pm 0.32$ (0.121)
	LA	$0.39 \pm 0.32$ (0.218)	$0.52 \pm 0.32$ (0.107)	-	-

Table Continued on next page

**Table 4.4** Continued

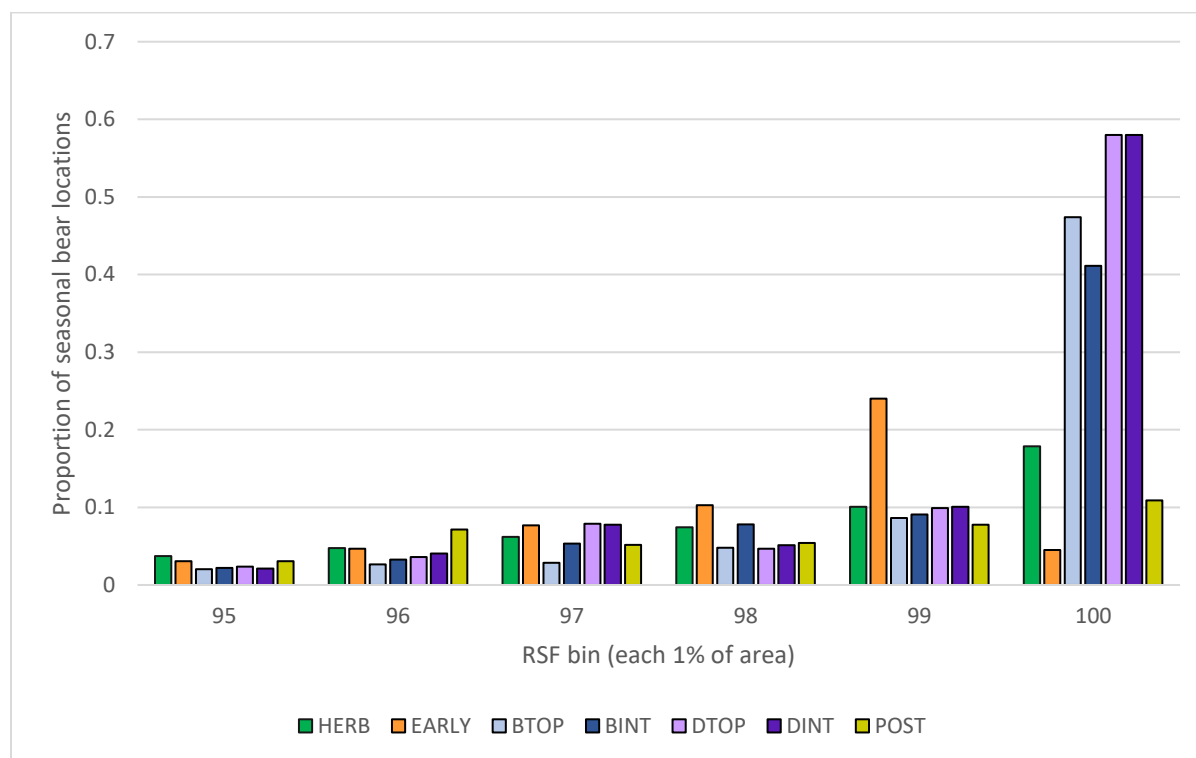
		<b>BTOP</b>	<b>BINT</b>	<b>DTOP</b>	<b>DINT</b>
<b>Covariate</b>	<b>Code</b>	<b><math>\beta \pm SE</math> (p value)</b>			
Soil	CO	0.34 $\pm$ 0.06 (< 0.001)	0.34 $\pm$ 0.06 (< 0.001)	0.63 $\pm$ 0.24 (0.008)	0.41 $\pm$ 0.25 (0.104)
	TI	0.38 $\pm$ 0.07 (< 0.001)	0.35 $\pm$ 0.07 (< 0.001)	0.62 $\pm$ 0.25 (0.015)	0.43 $\pm$ 0.27 (0.109)
	BR	REF	REF	REF	REF
	GL	-0.61 $\pm$ 0.39 (0.118)	-0.55 $\pm$ 0.39 (0.157)	0.71 $\pm$ 0.61 (0.243)	-0.12 $\pm$ 0.63 (0.844)
	O	0.63 $\pm$ 0.16 (<0.001)	0.34 $\pm$ 0.07 (<0.001)	1.21 $\pm$ 0.39 (0.002)	0.97 $\pm$ 0.40 (0.016)
<b>Interactions BINT</b>		<b>HAB_COV*green</b>		<b>Interactions DINT</b>	<b>HAB_COV *DIST</b>
Interactions	CWH *green	0.32 $\pm$ 0.09 (< 0.001)		CWH * (Age > 30)	REF
	ESSF*green	0.89 $\pm$ 0.07 (< 0.001)		ESSF * (Age > 30)	1.45 $\pm$ 0.44 (<0.001)
	IDF_PP*green	1.73 $\pm$ 0.32(< 0.001)		MH * (Age > 30)	-
	MH*green	0.47 $\pm$ 0.24 (0.044)		MS * (Age > 30)	-2.52 $\pm$ 0.79 (0.001)
	MS*green	0.42 $\pm$ 0.15 (0.005)		OTHER * (Age > 30)	2.54 $\pm$ 0.73 (0.001)
	AVY*green	0.37 $\pm$ 0.08 (<0.001)		CWH * (Age 10 – 30)	REF
	ALP*green	REF		ESSF * (Age 10 – 30)	0.94 $\pm$ 0.33 (0.004)
	SH_AVY*green	-0.59 $\pm$ 0.14 (<0.001)		MH * 10 -30	-0.29 $\pm$ 0.74 (0.697)
	HEATHER*green	0.09 $\pm$ 0.13 (0.507)		MS * 10 -30	-1.46 $\pm$ 0.41 (<0.001)
	KRUM*green	0.03 $\pm$ 0.12 (<0.820)		OTHER * 10 -30	2.54 $\pm$ 0.73 (<0.001)
	ROCKI*green	0.70 $\pm$ 0.08 (<0.001)			
k-fold r2 (SE)		0.980 (0.002)	0.984 (0.018)	0.960 (0.015)	0.949 (0.02)
AUC ROC (95% CI)		0.938 (0.936 – 0.941)	0.940 (0.938-0.942)	0.947 (0.942 – 0.952)	0.949 (0.945-0.954)

-Indicates that the parameter was considered in model building as it was part of a factorial variable but there was insufficient data to estimate selection usually resulting from complete avoidance.

### 4.3.3 Habitat distribution among populations

Differences in the availability of high-quality habitats between the MM and NSN populations were largest for the huckleberry and post-berry seasonal habitats while early fruit season and the herb bulb season models had similar availability in both populations (Figure 4.2). By definition each bin represents 1% of the total area in the model development area, therefore we expect that if habitat quality is equal between populations than both will have 6% of their population area in the top 6 bins representing the most highly selected habitats. The top herbaceous feeding model (HERB) indicated that 7% of the MM and 6% of the NSN areas were high-quality habitats. Similarly, the top model for the early fruit season, predicted 7% and 5% of the MM and NSN respectively, to be in the top 6 bins. In the huckleberry season, however, the top model (BINT) indicated that the top 6 RSF bins covered 11% of the MM area but only 3% of the NSN area. With the huckleberry models restricted to disturbed areas (DINT), the difference between populations was larger; the model estimated that 14% and 2% in the MM and NSN populations respectively were considered high-quality (> bin 95) huckleberry habitat (Figure 4.2).

For the post-berry season (POST), the model predicted that 9% of the MM and 3% of the NSN population areas were in good habitat however this model had a much lower proportion of bear use locations in the top 6% of bins than the other habitat selection models. As a result, the RSF model for the post berry season is less indicative of good habitat and therefore less reliable for comparing habitat availability between populations (Figure 4.1).



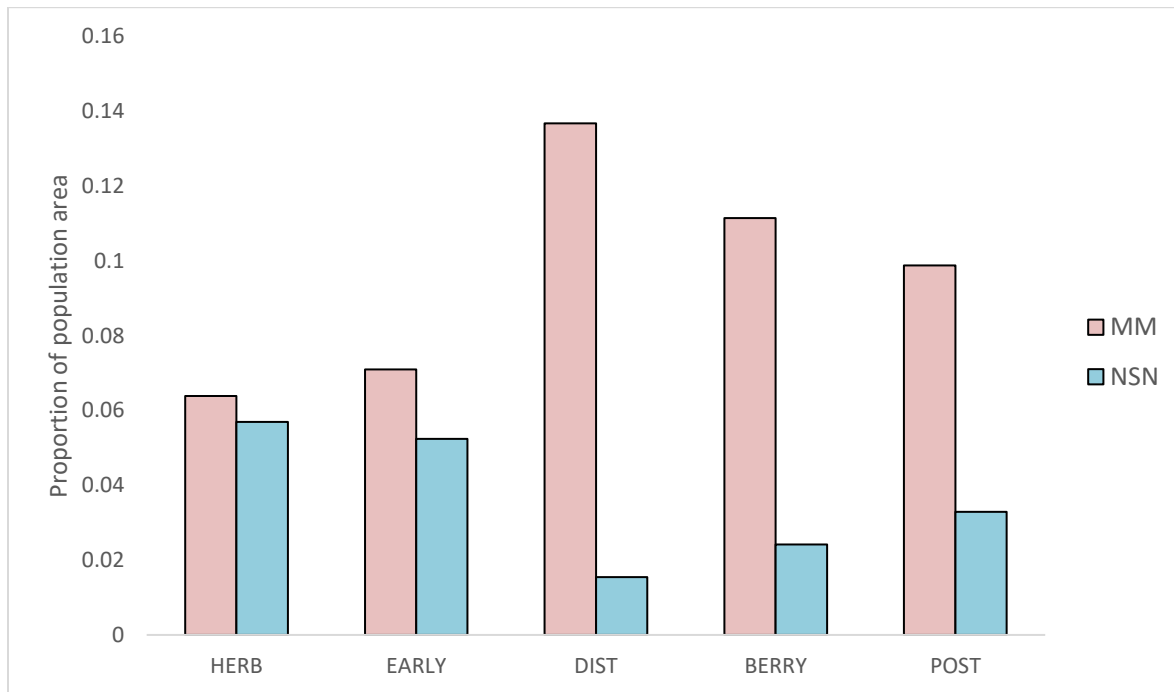
**Figure 4.1** Proportion of bear use locations in the top 6 RSF bins where each bin represents 1% of available habitat in the model construction area. All models are projected across the population areas. HERB (May-early July) season diet is dominated by herbaceous forage, roots and bulbs. EARLY fruit (July-mid Aug.) diets are dominated by fruit from tall shrub species (see text). DTOP & DINT (mid-Aug.- late Sept.) without and with interactions respectively, these models predict diet consists almost entirely of huckleberries; this model only considers selection in previously disturbed sites. BTOP & BINT (mid-Aug - late Sept) without and with interactions respectively, these models predict habitat selection for huckleberry foraging but consider use and availability within the home range including undisturbed sites. POST (Sept.-Oct.) follows the huckleberry season and includes many food types. All models scored highly in Spearman's rank correlation coefficient >90%.

#### 4.3.4 Berry Foraging Site Attributes

I measured attributes at 70 sites where bears (N = 17) had fed on huckleberries and 111 random sites within 350 m of a bear use site and the same habitat cover type (as described in the RSF as HAB COV). All of these feeding sites were in habitats that had previously been disturbed by wildfire, logging or both. Sites used by bears and random sites differed for all measures of huckleberry presence and productivity ( $p < 0.0001$  Table 4.5). Mean huckleberry plant cover was 20.1% (95% CI: 17.0-23.6) at use sites and 4.6% (95% CI: 2.8-6.1) at random sites. The proportion of stems with berries was 52.9% (95% CI: 45.6-60.3) at used sites while at random sites only 13.9% (95% CI: 7.9-19.2,  $p < 0.0001$ ) of stems had berries. Berry cover, defined as the product of huckleberry plant cover and percent stems with berries was, at 0.12 (95% CI: 0.10-0.15), an order of magnitude higher at use sites than the 0.013% (95% CI: 0.01-0.02) at random sites. Finally, berry abundance, measured as the product of berry cover and average berry load, was 1.75 (95% CI: 1.25-2.35) in bear use sites but only 0.14 (95% CI: 0.06-0.25) in random sites even though bears would have depleted the fruit at used sites before I measured it (Table 4.5).

**Table 4.5** Huckleberry (*Vaccinium membranaceum*; VM) abundance attributes measured in 100m<sup>2</sup> plots at sites where grizzly bears had fed on huckleberries and at random 100m<sup>2</sup> plots sites in the southern Coast Ranges of British Columbia. F-statistic and p values are from ANOVA for comparison of measures at use and random plots.

Variable	Bear Use	mean	variance	95% CI	df	F	p-value
VM % cover	Radnom	4.32	0.71	2.83-6.06	177	84.12	< 0.0001
	Use	20.11	2.81	16.90-23.62			
VM % stem berry	Radnom	13.92	7.90	8.67-19.23	161	72.69	< 0.0001
	Use	52.93	15.12	45.61-60.25			
VM berry cover	Radnom	0.014	$1.5 \times 10^{-5}$	0.007-0.022	158	78.93	< 0.0001
	Use	0.121	$1.7 \times 10^{-4}$	0.097-0.147			
VM berry abundance	Radnom	0.139	0.002	0.061-0.244	177	46.81	< 0.0001
	Use	1.752	0.091	1.185-2.404			



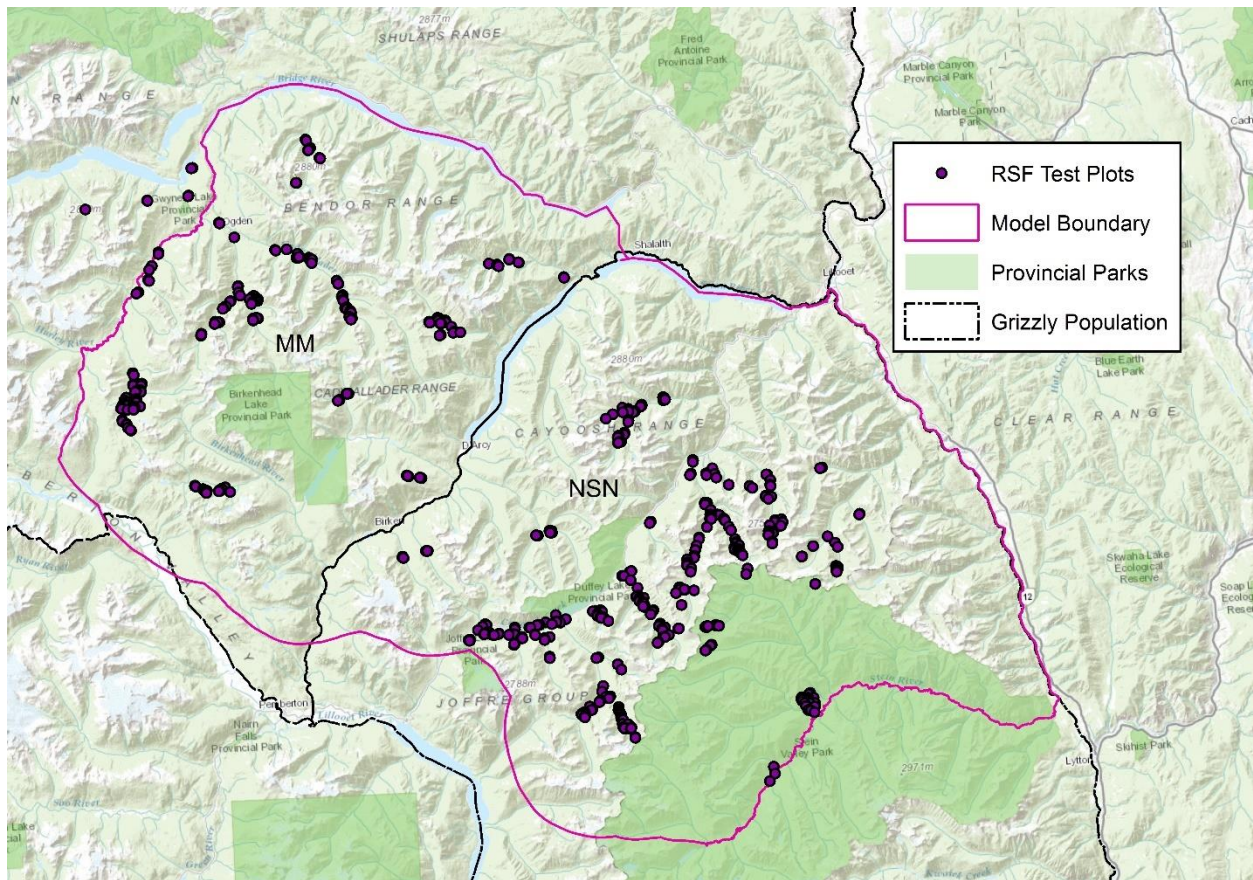
**Figure 4.2** The proportion of habitat that is high-quality ( $\geq$  RSF bin 95) for each foraging season in the McGillivray Mountain (MM) and North Stein Nahatlatch (NSN) grizzly bear populations. HERB (May-early July) season diet is dominated by herbaceous forage, roots and bulbs. EARLY fruit (July-mid Aug.) diets are dominated by fruit from tall shrub species (see text). DIST (mid-Aug.– late Sept.) diet consists almost entirely of huckleberries; this model only considers selection in previously disturbed sites. BERRY predicts habitat selection for huckleberry foraging but considers use and availability within the home range including undisturbed sites. POST (Sept.-Oct.) follows the huckleberry season and includes many food types.

#### 4.3.5 Test Plots and RSF Predictions

I visited 505 sites predicted to have huckleberry fruit by the BTOP and BINT models, 300 of which were nested in transects (Figure 4.3). The disturbance models (DTOP and DINT) had reduced sample sizes ( $N = 442$ ). Of all models tested huckleberry plant height and mean degrees Brix had insignificant splines and therefore fit better with a linear relationship (Table 4.6).

Except for berry degrees Brix, all measures of huckleberry production measured in the model testing plots correlated with the huckleberry season RSF model values (Table 4.6). For all models, RSF score correlated most strongly with the mass of berries picked in a 10-minute session (controlled for picker) with adjusted  $R^2$  value ranging from 0.28 for the DINT model to 0.48 for both the BTOP and BINT models. Other measures explained less of the variation in RSF model scores (Figure 4.4, Supplementary material Figures: S.2, S.3, S.4). The BINT model performed best for predicting huckleberry metrics when comparing the models with AIC (Table 4.6, Figure 4.4). When models were compared using the adjusted  $R^2$  statistic from the GAMM models, BINT performed consistently better except for percent stems with berries and berry cover (Table 4.6).





**Figure 4.3** Huckleberry season RSF model testing plot locations in the McGillivray Mountain (MM) and the North Stein Nahatlatch (NSN) grizzly populations in the south Coast Ranges of British Columbia, Canada. RSF model development area (pink outline) included both populations and all test plots were in sites previously disturbed by wildfire or forest harvest.

**Table 4.6** RSF model testing comparisons for four different model parameterizations (see text for details) using test plots measures of different huckleberry abundance parameters. Results show model comparison using generalized additive models.

Variable	RSF	$\beta$	F**	p-value	R-sq.(adj)	$\Delta$ AIC	Best Model
Huckleberry % cover	BINT	3.816	8.303	< 0.0001	0.089	0	† *
	BTOP	3.565	6.832	< 0.0001	0.069	7.5	
	DINT	2.902	5.996	0.0010	0.073	364.0	
	DTOP	2.889	5.525	0.0019	0.071	466.8	
Percent stems with berries	BINT	2.966	18.410	< 0.0001	0.103	0	†
	BTOP	2.705	20.910	< 0.0001	0.102	17.8	
	DINT	2.130	24.050	< 0.0001	0.132	347.6	
	DTOP	2.528	22.180	< 0.0001	0.144	494.8	*
Plant height (cm)**	BINT	0.019	2.655	0.0085	0.100	0	† *
	BTOP	0.018	2.325	0.0210	0.088	22.2	
	DINT	0.022	2.320	0.0213	0.060	153.2	
	DTOP	0.035	2.80	0.0056	0.072	252.17	
Berry cover	BINT	4.365	7.886	< 0.0001	0.097	0	†
	BTOP	4.216	7.044	< 0.0001	0.083	7.558	
	DINT	3.282	9.565	< 0.0001	0.095	356.4	
	DTOP	3.233	8.556	< 0.0001	0.101	462.9	*
Berry abundance	BINT	3.528	6.062	0.0002	0.065	0	† *
	BTOP	3.576	5.723	0.0002	0.061	20.5	
	DINT	2.461	3.730	0.0383	0.039	241.0	
	DTOP	2.429	4.102	0.0266	0.049	339.8	
Berries picked (gram)	BINT	6.206	6.886	< 0.0001	0.483	0	† *
	BTOP	6.448	6.636	< 0.0001	0.484	15.1	
	DINT	3.492	5.814	0.0007	0.279	54.9	
	DTOP	3.986	7.740	< 0.0001	0.360	73.4	
Mean °Bx	BINT	1.929	1.023	0.3900	0.038	0	†
	BTOP	1.784	0.743	0.5180	0.018	4.7	
	DINT	3.944	1.030	0.3500	0.082	24.8	*
	DTOP	4.529	1.310	0.3260	0.042	42.8	

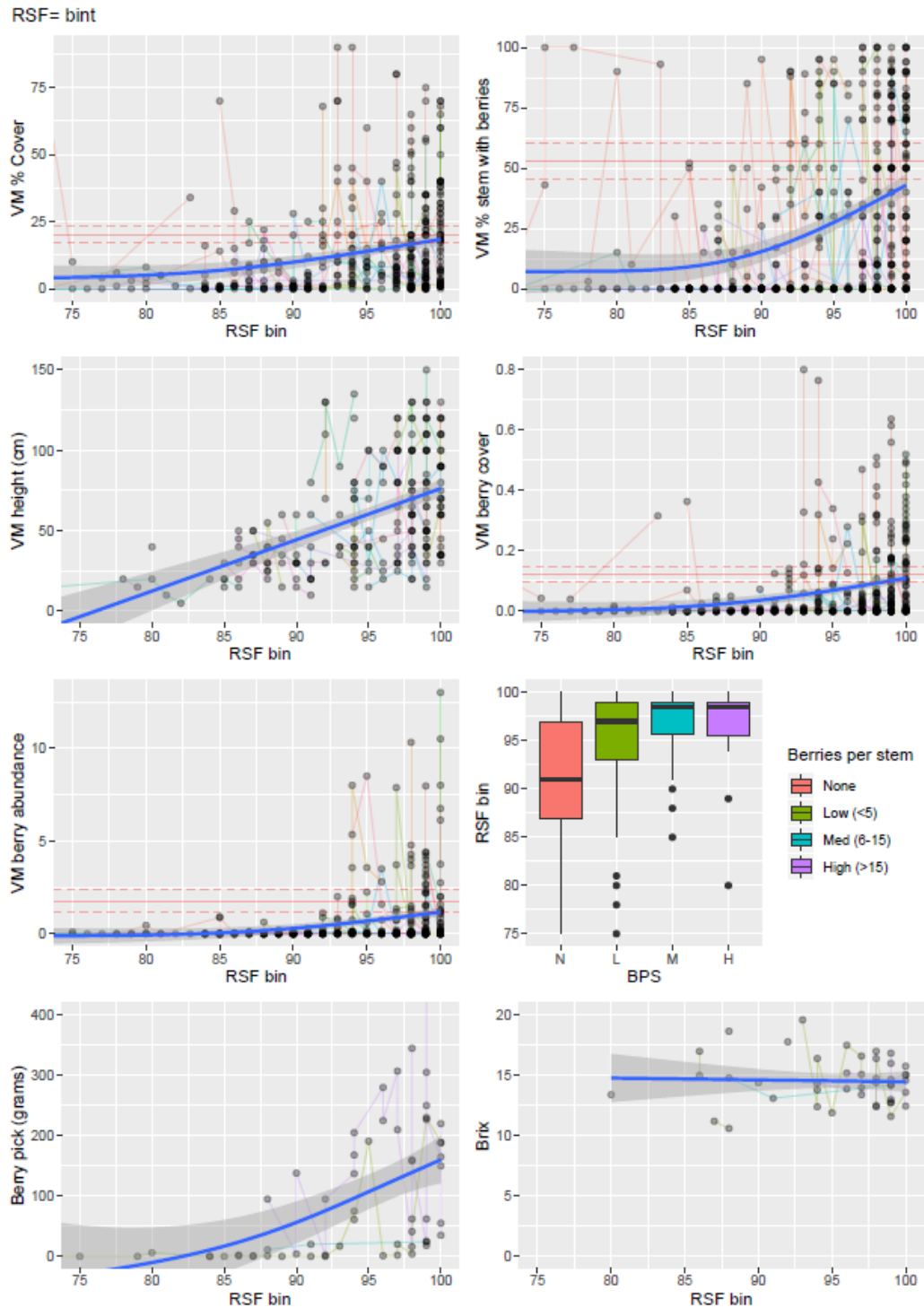
† Best model based on the lowest AIC score using the reduced data set.

\* Best model based on adjusted R-squared value

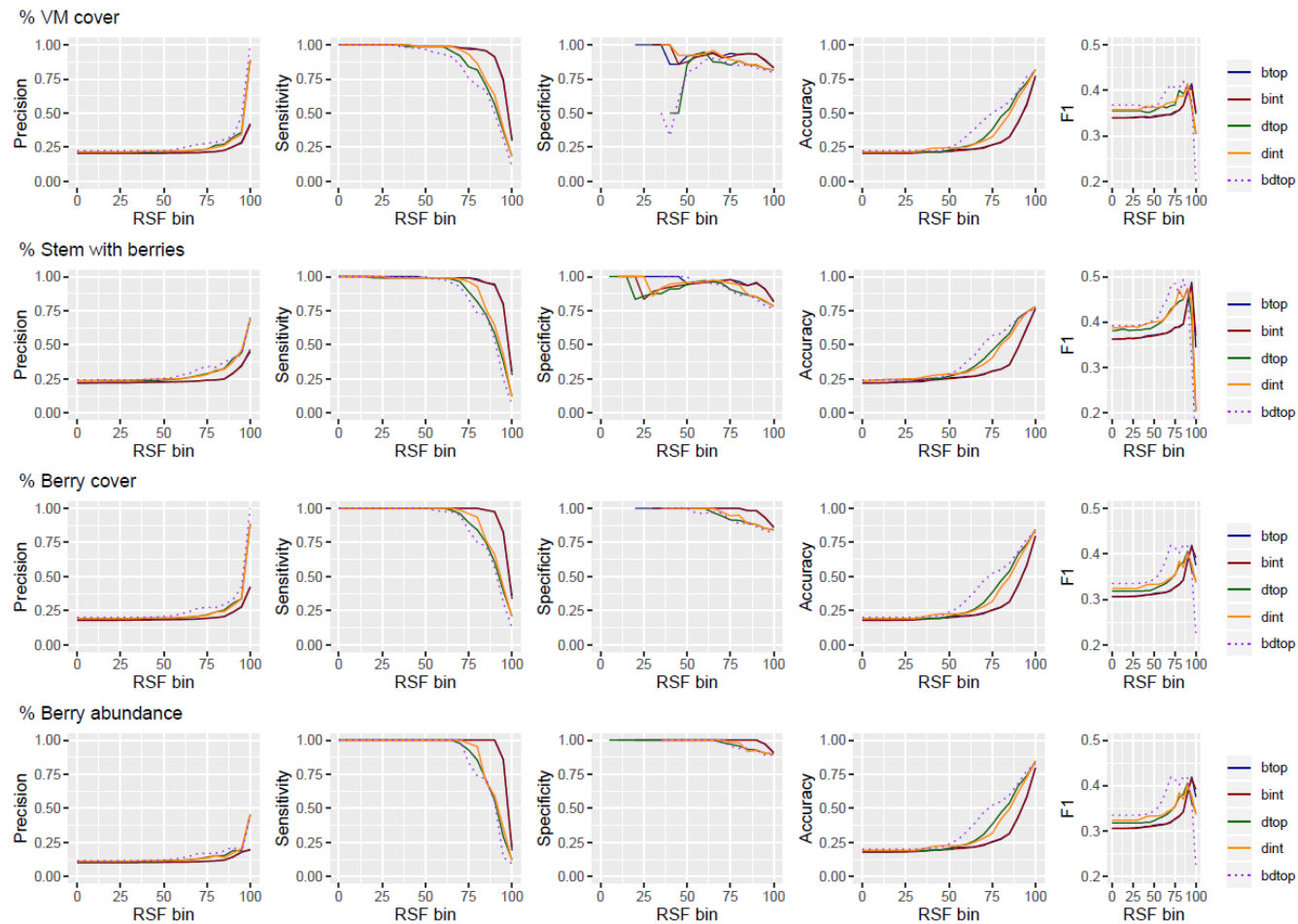
\*\* Linear mixed-effects model, t -statistic is reported in place of the F-statistic.

The way a model was binned had the greatest effect on the relationship between model accuracy, precision, sensitivity and specificity. For individual plots, I defined predictive accuracy to be when the model predicted values matched or was greater than the mean values measured at bear use sites. To highlight the effects of binning on model performance (Figure 4.5), I included a reference model for bin effects (BDTOP) which is the BTOP model structure, binned only in disturbed sites thereby allowing separation of model accuracy from the effects of binning shown by the similarity between the BDTOP (dashed line) and both disturbance-only models (Figure 4.5). Model accuracy was highest for the disturbance only models regardless of binning (Figure 4.5).

The percent of stems with berries was the huckleberry productivity measure most precisely estimated by all huckleberry season RSFs, and of those, the disturbance only models had highest precision (0.98% and 0.95%) for bin 95 and over. But the overall precision of models for bin 95 and above was below 50% indicating a high number of false positives. These models, however, had much lower sensitivities indicating that many true positives were not correctly identified (Figure 4.5) and perhaps bin cut off for good habitat should be lowered. The highest F1 score (harmonic mean of precision and sensitivity), was for either BINT or BTOP in all huckleberry measures. Specificity was also highest for BINT and BTOP above the 95 bin but the difference with the other models was much lower (Figure 4.5).



**Figure 4.4** Non-linear relationships estimated using generalized additive models between the predicted top huckleberry RSF model (BINT) and huckleberry (VM) metrics measured at model test plots across the McGillvary Mountain and North Stein Nahatlatch grizzly bear populations. See text for abundance definitions and supplementary material Figures S.2, S.3, S.4 for other RSF model comparisons.



**Figure 4.5** Bin specific estimates of model performance metrics including precision, sensitivity, specificity, accuracy and F1 score for four RSF huckleberry habitat selection models developed from seasonally specific bear locations. BTOP and BINT predict within home range habitat selection across all available habitats while DTOP and DINT are limited to disturbed sites based on the a priori exclusion of all others. BDTOP is the BTOP model binned within disturbed sites like DTOP and DNT, but only as a reference for comparison between the effects of binning and model structure.

## 4.4 Discussion

This chapter had two objectives. One was to predict grizzly bear habitat selection during four seasons defined by major foods bears consumed. Using these habitat models, I tested the hypothesis that the MM, where bear density was higher and the population increasing, would have more highly selected habitats, and in particular more high-quality huckleberry habitat, than in the NSN where the population density is low and in decline. The second objective was to assess the accuracy of the resulting RSF models for predicting huckleberry presence and abundance measured in field plots.

Consistent with habitat selection patterns in other grizzly populations, the habitat selection analyses in the MM and NSN populations identified differing, and sometimes opposite, selection patterns among seasons. During spring and early summer, when bears were predominantly feeding on herbaceous plants, roots and bulbs and sometimes marmots, they selected open areas in alpine herbaceous meadows and avalanche chutes on south or west-facing slopes with relatively few days below freezing. This pattern is consistent with many other populations (Waller and Mace 1997, Munro 1999, McLellan and Hovey 2001, Serrouya et al. 2011) but differs from areas where some bears also selected riparian habitat to feed on similar plant species but in low-elevation valleys without human settlement (McLellan and Hovey 2001). The resulting RSF projected across the study area showed that the proportion of the two areas that were high-quality spring habitat was slightly (5% vs 7%) higher in the MM than the NSN. But, with a much lower density of bears in the NSN, there would be more spring habitat per bear than in the MM and therefore less spring habitat was unlikely a major cause of the difference in population density and trend between these two populations (McLellan et al. 2019).

Early fruit foraging was only observed in the MM population when bears were feeding primarily on Saskatoon berries, pin and chokecherries at lower elevations in

relatively dry, hot environments (McLellan and McLellan 2015). These food types have not been identified as primary food types for grizzly bears in other areas in North America although similar early fruit seasons exist for buffalo berries (*Shepherdia canadensis*) elsewhere (McLellan and Hovey 1995, Nielsen et al. 2010, Denny et al. 2018). In the early fruit season, grizzlies selected areas with little winter precipitation as snow, in previously disturbed, or perpetually disturbed (electrical transmission lines) habitats. Although human settlement is generally closer to these habitat types than others because they are at low elevations, bears avoided higher road densities.

Interestingly no bears in the NSN population were observed feeding on early fruiting species, despite that the resulting RSF model predicts a relatively high abundance of this habitat type in the NSN area. This result may be a legacy of historic mortality restricting home ranges to higher elevations where this habitat type is not encountered. If this is the case, these habitats may provide foraging opportunities for dispersing bears, however, the efficacy of the RSF for predicting these food species across the area would be necessary to confirm this. Although the use of early fruit was likely a factor influencing the favourable population status in the MM compared to the NSN, only about a quarter of the population used this food source. Because most bears did not, early fruit habitat was unlikely to be a major factor causing the differences in population density and trend.

Habitat selection models developed for the huckleberry season, when grizzly bears fed almost exclusively on this species, were similar regardless of whether availability included entire home ranges or was restricted to previously disturbed sites. Differences were mostly in the effect size of variables, reflecting the change in the range of values associated with limiting what was defined as available. For example, the avoidance of high canopy cover was much higher in the model that included closed forests as available habitats than the model limited to disturbed sites where average canopy closure was much lower (Table 4.4).



Interestingly, selection for previously burned areas was higher than for previously harvested areas but the highest was where they overlapped. Disturbance age was also important and at the disturbance site scale, the importance of age was moderated by the original forest type. One explanation is that forest regeneration rates differ among forest types therefore likely affect berry production in a disturbed site over time. Understanding this relationship could be important for the application of habitat management efforts and specifically for berry production.

Regardless of whether the huckleberry specific RSF was projected across the landscape, or if the analysis was limited to previously disturbed sites, the proportion of high-quality huckleberry habitat was 5 to 7 times more abundant in the MM than in the NSN. This result supports the hypothesis developed elsewhere in Canada (McLellan 2015, Proctor et al. 2017) and Scandinavia (Hertel et al. 2018), that the difference in the availability of high-quality huckleberry habitat has contributed to bottom-up effects resulting in a higher density and positive trend of the grizzly bear population in the MM compared the population in the NSN. The mechanism is consistent with other research indicating that bears rapidly deposit fat needed for hibernation and reproduction while feeding on this high-energy food (Welch et al. 1997, McLellan 2011). In addition to the amount, the distribution and patch size of high-quality habitats (Serrouya et al. 2011) may also influence the bottom-up effects on population density.

As has been reported in other areas (Waller and Mace 1997, McLellan and Hovey 2001) habitat selection was much more variable among individuals in the post-berry season and this resulted in a less predictive model. This model's lack of precision is likely due to the inclusion of multiple behaviours by and among individuals and therefore varying selection patterns. When huckleberry fruit shrivels and senesces near the end of summer, no single food or food group becomes dominant (McLellan and Hovey 1995, Munro et al. 2006)



enough to concentrate bears into a few habitats as in previous seasons. Bears also become much less active as days shorten in the autumn (McLellan and McLellan 2015) and inactivity is likely less habitat-specific than foraging.

The implication of individual variability on the accuracy and interpretation has been highlighted in other research (Nielsen et al. 2002, Gaillard et al. 2010) and I expect the inclusion of multiple behaviours by individuals to have a similar effect on resource selection models. Including a random slope for individuals in the habitat selection models would increase our understanding if the variability of habitat selection was mostly between individuals (Gaillard et al. 2010). Increasing model predictive ability by further delineating among feeding behaviours for this season would be necessary to use post-berry season models for bottom-up comparisons among populations. Their current variability makes the post berry season model insufficient for making confident inferences.

The second objective of this chapter was to assess the utility of season-specific RSF models for predicting huckleberry presence and abundance measured in field plots. Results indicate that these models were highly accurate using conventional methods of model assessment including k-fold cross-validation, ROC and Spearman's Rank correlation coefficient on the allocation of used sites to model quantile bins (Boyce et al. 2002, Johnson et al. 2006, Morris et al. 2016). The strongest predictive relationship was between RSF score and the amount (g) of berries picked ( $R^2 = 48\%$ ), controlled for the individual picker. Even though human picking was used as a surrogate for bear foraging and the difference among people was sufficient to make the actual amount collected uninformative, the relationship between RSF value and berry foraging indicates that if picking followed a type II functional response, then the RSF best predicts areas where the largest number of berries per unit time can be picked. The models also correlated with various measures of berry abundance,

particularly for the higher values of the model, but data were fairly dispersed and the coefficient of determination ( $R^2$ ) ranged between 5% and 11%.

The cut-off points for estimating whether an RSF was true or not were the average values measured at sites where bears were feeding, therefore, by definition, many of the sites selected by bears had lower huckleberry cover and abundance than what were considered to be “true” sites. This would have the effect of decreasing measures of model precision and overrating the proportion of false positives and also possibly reducing model accuracy. Foraging bears would likely affect some of the berry abundance estimates. We can assume that at the bear use plots measure of abundance and berry load were higher when the bear selected the plot, though plant cover and height would remain unchanged, this would increase the mean berry abundance. Therefore, we would expect that the actual measures for areas used by bears to be higher than those observed, and that for test plots, the density of bears using the area may bias measures low.

Increasing model complexity by including covariate interactions increased model fit using information-theoretic approach during model development, only slightly improved other model performance measures by less than 1% (k-fold, ROC) and improved model predictive ability for huckleberry cover, percent stems with berries, overall berry cover and abundance in the top 5% of model bins (Figure 4.5, Table 4.6). Despite the concern for overfitting a model by increasing complexity, the huckleberry test plots suggest that the more complex models improved model predictive ability for huckleberries across the study area, albeit sometimes only slightly (Table 4.5).

Model quantile or equal area binning is commonly applied to RSFs for spatial inferences of habitat selection, comparative analysis among models, and for habitat management applications (Nielsen et al. 2004a, Johnson et al. 2006). My analysis using selection estimated from bear use areas confirms predictions by Morris et al. (2016) that

estimated model accuracy depends on how results are binned. This investigation into the accuracy of RSF models for predicting huckleberry production at test sites highlighted the importance of how RSF models are binned after they are estimated and that the trade-off between model precision and sensitivity at different levels should be considered. Identifying the requirements of model application will aid in the identification of appropriate bins, particularly when making management decisions based on habitat modelling.

My results show that berry specific models did predict berry abundance in previously disturbed sites though varied in accuracy depending on how the models were depicted or binned across the landscape. Further delineation of foraging behaviours for late-season behaviours would likely increase model precision and utility for this time of year. Interestingly, RSF predicted the amount(g) of berries picked in 10 minutes better than any other measure of VM abundance indicating that the plot sizes used for the other measures were not at the appropriate scale for inference of selection. Finally, the differences in the overall availability of high-quality habitats for different food types between populations suggests that season-specific bottom-up effects may account for some differences in population densities and warrants further investigation.

## Chapter 5

# Estimating the role of bottom-up processes in the recovery of endangered populations of a large carnivore.

### 5.1 Abstract

Where populations are limited primarily by bottom-up factors it is expected that population density will vary across the landscape in proportion to resource availability, and if there is a food source more important than others, then density will correlate more strongly with it.

In this chapter, I investigate the hypotheses that bottom-up effects are responsible for the difference in observed density and trend between two adjacent and threatened grizzly bear (*Ursus arctos*) populations in southwestern British Columbia, Canada. I use spatial capture-recapture techniques with projected seasonal Resource Selection Function models, open road density and whitebark pine (*Pinus albicaulis*) abundance, to test whether the density of grizzly bears across both study areas can be explained by seasonal food type availability or road density as a surrogate for mortality risk.

Using an information-theoretic approach I found that population density is most strongly connected to habitats selected during a season when bears fed on huckleberries as well as a large baseline difference between populations. The abundance of high-quality huckleberry habitat appears to an important factor enabling the recovery of the larger, genetically connected population. The adjacent, smaller and genetically isolated population is not growing and the relatively low abundance of high-quality berry habitat in this population may be contributing to the slow growth of the population. However, in the isolated

population, the lack of association between the current distribution of individuals on the landscape with extant huckleberry patches caused by overall low density in this population, indicates that the population is unlikely at carrying capacity. It is possible that the legacy of historic mortality and current stochastic effects, inbreeding effects, or other Allee effects, are also contributing to the continued low density observed on the landscape. While these small population effects may be more challenging to overcome, it appears that the landscape can accommodate a higher population density than that currently observed.

## **5.2 Introduction**

The population dynamics for most mammals, whether driven by top-down or bottom-up forces, are spatial processes (Gripengberg and Roslin 2007). Landscapes are heterogeneous. Therefore, the strength and importance of top-down and bottom-up forces vary across space. We expect that where populations are limited primarily by bottom-up factors, population density will vary across the landscape in proportion to resource availability (Boyce et al. 2016). Likewise, for populations limited by top-down processes, we expect the association between population density and habitat quality to be weakened while spatial patterns associated with top-down limitation become more influential (Rettie and Messier 2000, Nielsen et al. 2004a, Boulanger et al. 2018).

Unlike point estimates of population size, spatial variation in population density enables the investigation of the covariation of density with landscape attributes such as habitat quality and mortality risk. Resource selection is also a spatial process resulting from the selective movements of individuals in an attempt to maximize their fitness. The widespread availability of spatial data, (e.g. satellite imagery, landscape cover, digital elevation models) coupled with accurate locations from GPS tracking devices enables the

estimation and subsequent prediction of resource selection at different scales (Boyce and McDonald 1999, Apps et al. 2001, Boyce 2006, Nielsen et al. 2006, Ciarniello et al. 2007). Most commonly, resource selection functions (RSF) compare habitats used by a species to those available to estimate the relative probability that a habitat type will be used. Fitness is usually related to habitat suitability (Boyce et al. 2016) and density (McLoughlin et al. 2006), but with exceptions such as attractive sink dynamics (Nielsen 2011). Due to the seasonality of physiological demands as well as food quality and availability, a correlation between habitat selection and individual fitness cannot be assumed (Nielsen et al. 2013, Greene and Stamps 2017). Therefore, it is expected that some habitat types during some seasons correlate more strongly with density than others.

Spatial capture-recapture models (SCR) allow for robust estimates of population size and density while accounting for imperfect individual detection as well as individual movement and resulting exposure to sampling effort (Efford 2004). SCR also allows for the estimation of spatial variation in density or capture probability by including spatial covariates (Royle et al. 2013, Efford 2014, Proffitt et al. 2015). By modelling local density as a function of a spatial covariate, associations between landscape variables and density can be inferred. Therefore, by including time and space-specific resource selection models with spatial capture-recapture models facilitates direct inferences on the effects of habitat on population densities (Boulanger et al. 2018).

The McGillvary Mountain (MM) and North Stein-Nahatlatch (NSN) grizzly bear (*Ursus arctos*) populations are adjacent but genetically distinct populations in southwestern British Columbia, Canada. Both populations are considered threatened with the NSN critically endangered due to its small size and degree of genetic isolation (McLellan et al. 2017b). Like grizzly bears across most of their southern distribution, both populations experienced substantial human-caused mortality (HCM) for at least a century before a recent

reduction in HCM resulting from both the cessation of legal hunting and the gradual change in human attitudes towards large carnivores and conservation in general. Despite a similar history, the MM population is growing and recovering while the NSN population remains at a low density and is likely slowly declining (McLellan et al. 2019).

In chapter 4, I used GPS telemetry data and landscape covariates to develop seasonal resource selection functions (RSFs) where seasons were temporally defined by changing diet composition. The RSFs predicted habitat selection within home ranges where habitat selection was thought to reflect bottom-up processes (Johnson 1980, Rettie and Messier 2000). The herb-bulb season, the early fruit season, and the huckleberry season RSF models performed well and predicted between 50 and 95% of all seasonal locations within 6% of the available landscape (chapter 4). Seasonal habitat selection models for the short post-berry season were less reliable due to the high variability of foraging and pre-denning behaviours. However, the most common food source for this season was whitebark pine seeds, and, unlike the main foods for other seasons, whitebark pine distribution has been mapped and delineated according to abundance. Using the seasonal RSFs, I compared the proportion of the MM and NSN that consisted of seasonally selected habitats and determined that, there was much more high-quality huckleberry habitat in the MM than the NSN suggesting a possible bottom-up mechanism for differences in density between populations.

In this chapter, I further investigate the hypotheses that bottom-up factors are responsible for the difference in observed density and trend between the MM population and the adjacent NSN population (McLellan et al. 2019). If food is limiting and the NSN population is at, or near carrying capacity, and thus responsible for the difference in density, then I predict that population density within the study area will be spatially correlated with high-energy food abundance. In contrast, if contemporary top-down effects are the major factor limiting population density, I expect that either bear densities are negatively associated

with human use of the landscape, or that high-quality habitat and human use overlap creating an attractive sink phenomenon (Nielsen et al. 2006, Gripenberg and Roslin 2007).

I use season-specific RSFs, whitebark pine occurrence, and road density as spatial covariates in SCR models of the MM and NSN. The degree of correlation between the resulting bear density surface each covariate indicates if differences in density can be explained by top-down (i.e road density) or bottom-up process and the season and thus food types most likely responsible for differences in density.

## **5.3 Methods**

### **5.3.1 DNA Capture-Recapture**

Capture-recapture data was collected from 74 detectors, including hair traps and rub trees distributed across the 6528 km<sup>2</sup> study area spanning both grizzly bear populations (See chapter 2). Hair traps were distributed so that each drainage had a hair trap and larger drainages had two. Rub trees were common along roads and trails throughout the study area but their distribution was uneven, and there were often multiple trees along one linear feature. Hair traps consisted of one barbed wire strand tightly strung between trees, approximately 50 cm above the ground, forming a small corral around a pile of debris and scent lure (Woods et al. 1999). Grizzly bear hair samples were collected every four weeks for five intervals of similar duration (see chapter 2 for details) between the end of June and the end of September 2014; spanning all feeding seasons for these populations. Wildlife Genetics International (Nelson, British Columbia) screened the hair samples, extracted DNA, carried out genotyping to 22 microsatellite loci, and identified individuals following established techniques (Paetkau 2003).

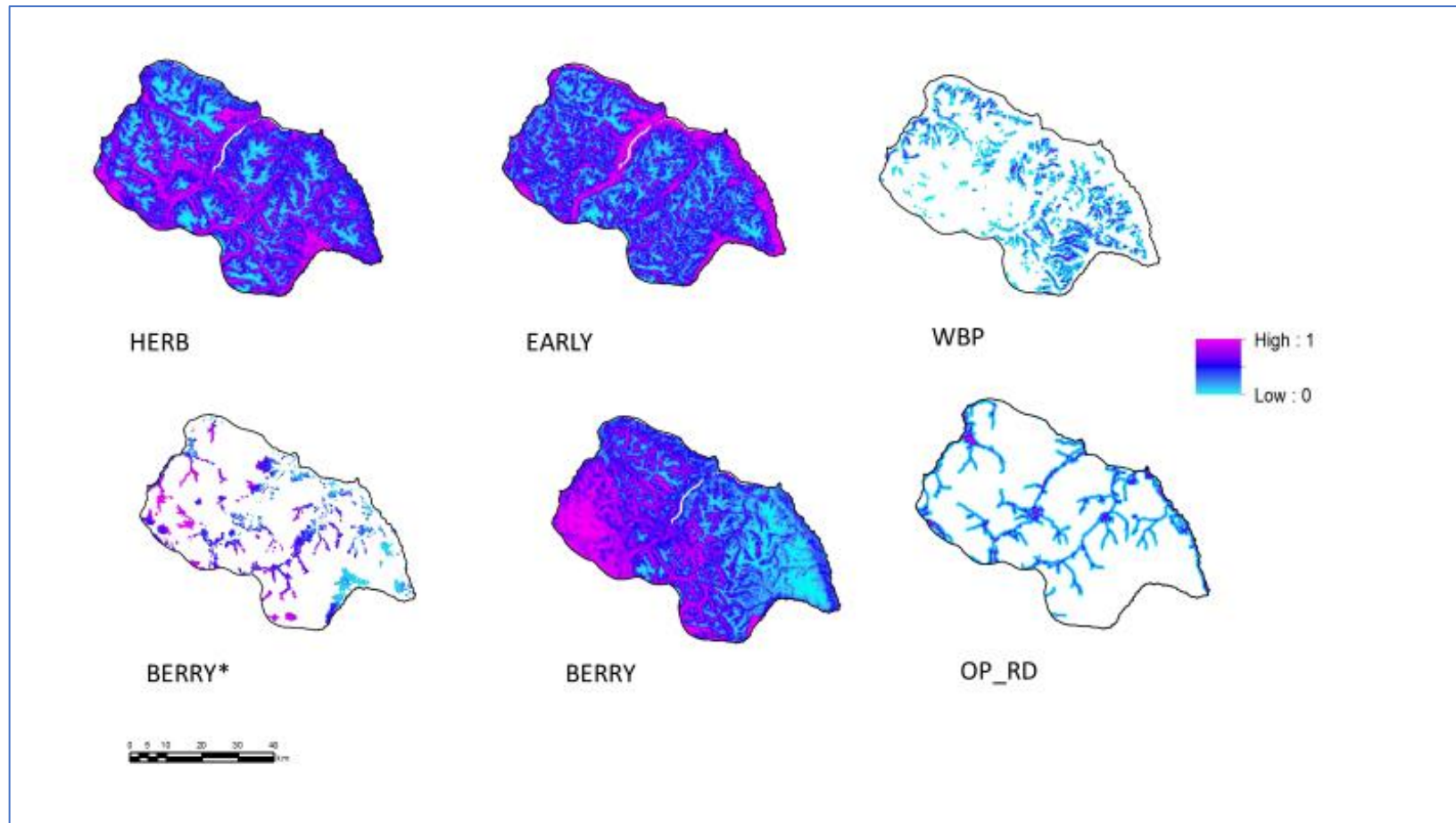


### 5.3.2 Habitat and road density covariates

Grizzly bears are generalist omnivores and their diets vary among populations or even among individuals within a population, however predictable seasonal shifts in diet and resource selection are common for the species (McLellan and Hovey 1995, 2001, Munro et al. 2006). Grizzly bear diet predictably changes due to shifts in the availability of foods resulting in seasons characterized by dominant foods in their diet. The clustering of food resources into habitat types allows us to observe seasonal shifts in resource use. In the MM and NSN, four major seasons can be distinguished from one another by bear movement between habitat types in which different foods dominate their diet. I defined these as the herb-bulb season (HERB) that begins shortly after den emergence and is characterized by foraging primarily on herbaceous plants and bulbs in the spring and early summer; in some years, when berries were scarce, this season would extend through the summer. The early fruit season (EARLY) occurs in the early to mid-summer when bears forage on Saskatoon berries (*Amelanchier alnifolia*), and pin (*Prunus pensylvanica*) and choke (*P. virginiana*) cherries. This feeding pattern was only observed in the MM but RSF modelling indicated that this habitat type may be available in locations scattered throughout the study area. The huckleberry season (BERRY) usually begins in mid-August and lasts until early-October, depending on the year, when bears fed almost exclusively on black huckleberries (*Vaccinium membranaceum*). The post-berry season (POST) is the least well defined of the foraging season due to a relatively high diversity of bear behaviours and associated habitat selection: some bears returned to digging bulbs in similar habitats to the HERB season, others fed on whitebark pine seeds (*Pinus albicaulis*), and some went directly from huckleberry feeding to den sites; one bear, and perhaps a second, fished for salmon.

In the previous chapter, I outlined how I used seasonally delimited location data from 45 bears to model seasonal habitat selection across both the MM and NSN populations (McLellan and McLellan 2015). Most of the variation in habitat selection between populations was in the presence and duration of a specific season so populations were pooled (chapter 3). For this analysis, I used the projected seasonal RSFs for the herb-bulb, early-fruit and huckleberry seasons (Figure 5.1). Due to the high variability of foraging and pre-denning behaviours, the post-berry season RSF lacked sufficient precision to be used as an informative covariate. However, if bears remained active, the most common food source for this season was whitebark pine seeds. Unlike the main foods for other seasons, whitebark pine distribution has been mapped and delineated according to abundance (Crone et al. 2011), and consequently, could be included as a measure of whitebark pine (WBP) availability (VRI-2017) (Figure 5.1).

Because they are an apex predator, and by far the largest carnivore in the region, the only top-down effects for adult grizzly bears is human-caused mortality (Garshelis et al. 2005, McLellan et al. 2018, Proctor et al. 2018b). Grizzly mortality has been correlated with road density in many areas which, as a result, is suggested to be a useful surrogate for negative effects of human use on grizzly bear populations (McLellan and Shackleton 1988, Lamb et al. 2018, McLellan et al. 2018, Proctor et al. 2018b). Road density quantifies ephemeral human presence and landscape use such as forest harvest, tourism, hunting, and recreation. In this analysis, I use open road density (OP\_RD) as a surrogate for the effects of human use on bear populations (Figure 5.1).



**Figure 5.1:** Seasonal food-based habitat and open road density maps for grizzly bears in southwest British Columbia, Canada. Units are scaled habitat quality from binned resource selection functions for HERB, EARLY fruit, BERRY seasons. Whitebark pine cover is percent cover (WBP) and open road density (OP\_RD) in km/ km<sup>2</sup> models is a surrogate for increased mortality risk. The BERRY \*depicts shows the footprint of potential black huckleberry patches in disturbed sites while BERRY reflects the RSF model projected across the landscape. The boundary between the MM and NSN follows the most centre line of increased road density crossing the study area noticeable on the OP\_RD panel.

### 5.3.3 Analysis methods

I used spatially explicit capture-recapture methods (Borchers and Efford 2008) to estimate the effects of habitat quality on grizzly bear population density across the study area using density surfaces (Borchers and Efford 2008). Spatial capture-recapture models require the definition of an area that encompasses all individuals possibly exposed to sampling, called the state-space. Masks are a spatial component of *secr* that can be used to define the boundaries of the area of integration and populated with spatial covariates to represent spatial variation in habitat quality. The state-space for this analysis was limited geographically to the west by a large lake and human settlement, and to the east by human settlement and the Fraser River. Population-specific masks were used to limit the state space of each to the common population boundary that genetically and geographically separates the two populations. Bear populations are continuous to the north and south, and these perimeters were determined by estimating the minimum effective sampling area necessary to estimate density with minimal bias (Borchers and Efford 2008). Predicted density declines asymptotically as the area of integration increases until the area is large enough to eliminate sampling area bias (Borchers and Efford 2008). The effective sampling area was estimated in program *secr* based on previous analyses and confirmed by plotting the effective sampling area curve *post hoc* for fitted models using the *esa.plot* tool in *secr*.

I used a multi-step approach to estimate the effects of habitat variability on population density to simplify the model selection process. For analysis, the MM and NSN were considered separate sessions so that the effective sampling area could be limited according to population boundaries and to allow for population-specific inference and account for variation in parameters between populations during model development. All spatial capture-

recapture analyses were conducted using *secr* v. 3.2.1 (Efford 2019) in program R v.3.6.1 (R Core Team 2019).

#### 5.3.4 Detection parameters

The objective of the first model selection step was to select the best model for estimating detection probability parameters. I used maximum-likelihood estimation in program *secr* to estimate the probability of detection at the activity centre ( $g_0$ ) and the rate of decline following a half normal curve according to the movement scale ( $\sigma$ ). Allowing density to vary by population, I compared models including covariates thought to influence the baseline detection probability ( $g_0$ ) including sex, trap-type, learned response (b), animal-specific and site-specific response (bk) and time (t). I also investigated the variation in detection probability due to the quality of habitat surrounding detectors (Royle et al. 2014). I used the same habitat covariates hypothesized to affect density except in this case habitat covariates were the average scaled RSF score or whitebark pine coverage in a 500-m radius around each trap which is approximately the average daily distance moved for females in this study area (unpublished data). Habitat covariates included seasonal spring habitat ( $g_0 \sim \text{herb}$ ), early fruit habitat ( $g_0 \sim \text{early}$ ), huckleberry habitat ( $g_0 \sim \text{berry}$ ) and whitebark pine habitat ( $g_0 \sim \text{wbp}$ ). Home range size varies by sex (Proctor et al. 2004, McLellan and Hovey 2011, chapter 2) so sex was included as a possible covariate for  $\sigma$  and compared to a null model where sigma was unaffected by sex. Relative support for each detection model, and the null model, was compared using Akaike information criterion corrected for small samples (AICc) (Burnham and Anderson 2002) and the top detection model was retained for subsequent density surface modelling. Home range centres were predicted using the most supported detection and scale movement model and the summed probability densities of the home range

centres were projected as an initial investigation of the distribution of home range centres across the study area (Royle et al. 2014).

### 5.3.5 Density surfaces

Before fitting spatial models of density, centroids of the cells making up the state space were populated with resource values and risk covariates derived from seasonal RSF models, whitebark pine cover or from road density layers to form a habitat mask. Habitat values were averaged for each 1.5 km<sup>2</sup> area and scaled for comparison among covariates. Following a series of iterative models investigating the effects of centroid spacing from 1km to 3km on density estimation, the spacing of mask centroids was set at 3.0 km in the *secr* mask to optimize computation time without affecting density estimates (Boulanger et al 2018).

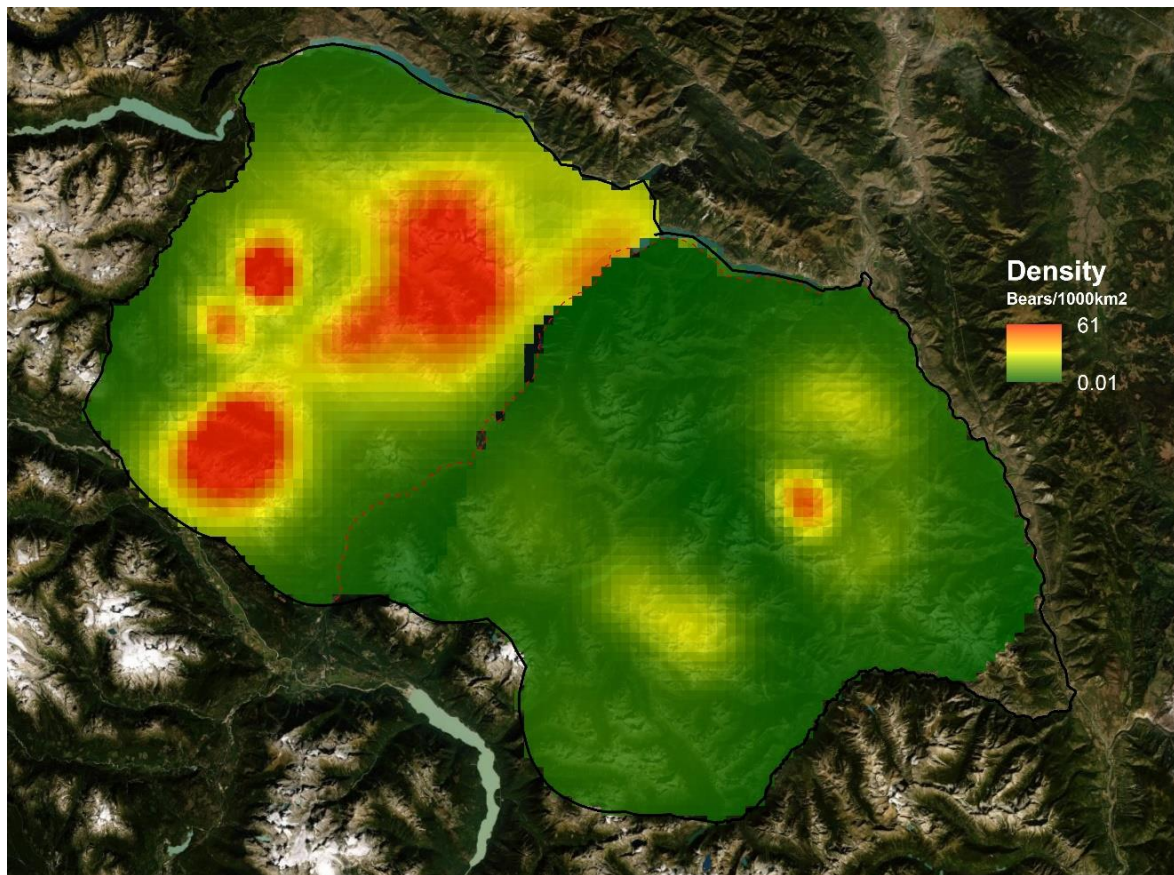
To investigate seasonal habitat quality and top-down human effects on bear density I fit density surface models,  $D(x,\phi)$ , that constrained density for each mask point ( $x$ ) to be a linear function of population identity, a seasonal habitat covariate or open road density ( $\phi$ ), or the additive or interactive effect between population and habitat (Borchers and Efford 2008, Boulanger et al. 2018). This method tests hypotheses that the density gradient observed in the region can be explained by bottom-up effects and specifically, which food season is the strongest predictor of local bear density. To differentiate them from the covariates used in detection modelling, seasonal density covariates are in uppercase letters (e.g. HERB, EARLY, BERRY, WBP and OP\_RD). Density surface models were compared using Akaike Information Criterion corrected for small samples (AIC<sub>c</sub>) (Burnham and Anderson 2002). I used back-transformed model estimates to predict density as a correlate of huckleberry

habitat. Errors for predicted density were calculated using the delta method with the msm package (v.1.6.7) (Jackson 2019).

## **5.4 Results**

In 2014, 41 grizzlies (22 F; 19 M) were detected 94 times over five sampling occasions. In the MM population 33 (18F; 15 M) individuals were detected 69 times and in the NSN 8 (4F; 4M) individuals were detected 25 times.

The top model for detection parameters included an interaction between sex and trap type and the spatial scale of detection varied by sex (Table 5.1). Habitat quality surrounding the detector did not affect detection probability enough to improve the detection model. The summed probability density functions estimated from the top detection model and predicted across the study area indicated pockets of high density in two parts of the MM and small and relatively low-density pockets in the NSN (Figure 5.2). There is a low-density area at the northern end of the NSN, adjacent to the MM populations, with very few detections. The predicted number of home range centres in the MM portion of the study area was 46.59 (95%CI: 36.21-62.88) and 7.48 (95%CI: 3.00-12.04) in the NSN. The regional abundance of individuals in the NSN is lower than the number of actual bears captured because the expected home range centre may not be within the study area.



**Figure 5.2:** Probability densities of home range centres for detected individuals using the top detection model for density estimation of grizzly bears in the MM and NSN populations in southwestern British Columbia Canada. The projected densities are limited to the study area boundary to reduce edge bias in density estimates resulting from increased distance from trap location. Red dash marks the boundary between the populations delineated along the highway and settled areas.



**Table 5.1** Model selection results for covariates influencing grizzly bear encounter rate ( $g0$ ), and movement scale ( $\sigma$ ) and density ( $D$ ) without density surface integration. See text for covariate definitions. Only the top 4 models are shown, all models are included in supplementary material Table S.4.

$D$	$g0$	$\sigma$	$K^a$	$\Delta AICc^b$	$\omega_i^c$
$D \sim \text{pop}$	$g0 \sim (\text{trap-type} * \text{sex})$	$\sigma \sim (\text{sex})$	8	0	0.82
	$g0 \sim (\text{trap-type} + \text{sex})$	$\sigma \sim (\text{sex})$	7	3.47	0.15
	$g0 \sim (\text{trap-type})$	$\sigma \sim (.)$	5	6.55	0.03
	$g0 \sim (\text{sex})$	$\sigma \sim (\text{sex})$	6	11.71	0

<sup>a</sup> Number of model parameters  
<sup>b</sup> Difference to the AICc of the highest-ranked model  
<sup>c</sup> Model weight

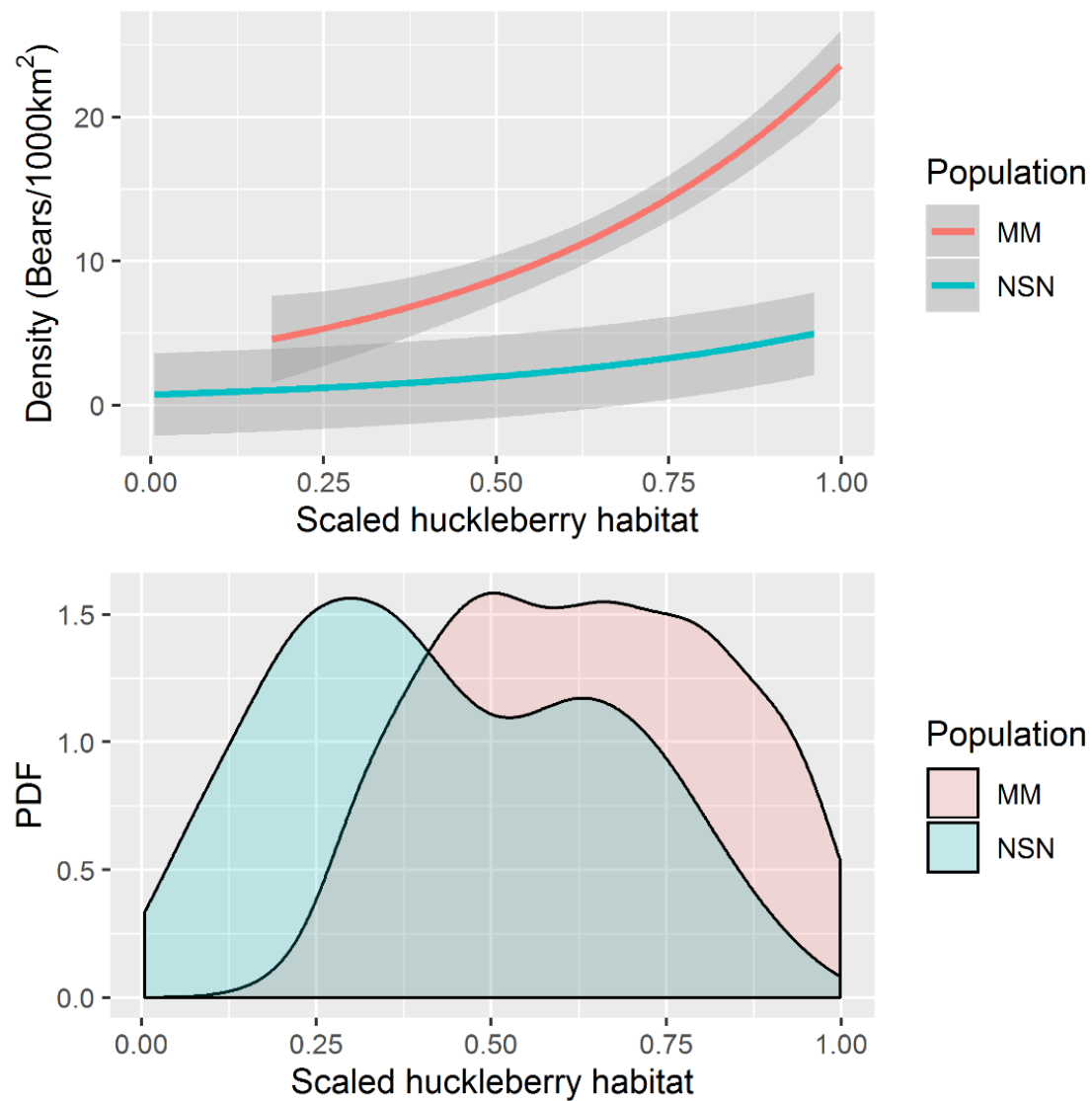
The top density surface model included density as a function of the additive effects of huckleberry habitat and population identity. This model was slightly better than the model with only population as a predictor for variation in density (Table 5.2). This result suggests that although there is a positive relationship between density and huckleberry habitat, other population-specific effects are contributing to the density differences between populations. The effects of other habitat types and road density on grizzly bear density were weak (Table 5.2).

**Table 5.2** Model selection results comparing density surfaces including habitat and road density covariates as well as population. Detection parameters were consistently defined for all models  $g0$  (trap-type \* sex)  $\sigma(\text{sex})$ .

Density surface model	$K^a$	$\Delta AICc^b$	$\omega_i^c$
$D \sim \text{BERRY} + \text{pop}$	9	0	0.3429
$D \sim \text{pop}$	8	0.215	0.3079
$D \sim \text{WBP} + \text{pop}$	9	2.917	0.0798
$D \sim \text{BERRY} * \text{pop}$	10	3.269	0.0669
$D \sim \text{HERB} + \text{pop}$	9	3.346	0.0644
$D \sim \text{EARLY} + \text{pop}$	9	3.468	0.0605
$D \sim \text{OP\_RD} * \text{pop}$	10	4.501	0.0361
$D \sim \text{WBP} * \text{pop}$	10	5.812	0.0188
$D \sim \text{EARLY} * \text{pop}$	10	6.752	0.0117
$D \sim \text{HERB} * \text{pop}$	10	6.874	0.011

<sup>a</sup> Number of model parameters  
<sup>b</sup> Difference to the AICc of the highest-ranked model  
<sup>c</sup> Model weight

Predicting density as a function of population and huckleberry habitat illustrates its positive relationship with huckleberries (Figure 5.3, top panel). Because the density-huckleberry relationship is modelled on the log-scale, the lower intercept of the back-transformed curve for the NSN (i.e., the population effect on density) causes the relationship to be flatter across the possible huckleberry habitat values than for the same habitat values in the MM. In addition, the proportion of good habitat is much higher in the MM than in the NSN, as demonstrated by the probability density functions for huckleberry habitat quality in each population (Figure 5.3, bottom panel).



**Figure 5.3** Relationship between density and scaled huckleberry habitat estimated from the top density surface model for the McGillvary MM and NSN grizzly bear populations in southwestern British Columbia, Canada. Lower panel is the probability density function for the scaled huckleberry habitat in each population. Huckleberry habitat quality is the scaled output of foraging specific resource selection functions projected across the populations where 0 is low quality habitat and 1 is high-quality habitat. Most selection for huckleberries occurs between 0.75 and 1.0 (see chapter 4 for details).

## 5.5 Discussion

This analysis supports the hypothesis that bottom-up effects are contributing to the difference in recovery dynamics observed in the MM and NSN populations. At a continental scale, the relationship between bear density and high energy food has been well documented (Hilderbrand et al. 1999, Mowat et al. 2013). Within populations, the implications of high energy foods on local density has been less frequently shown (McLellan 2015). Interestingly, my results show that density is so low in the NSN that variation in density with resources is limited, the broader span of densities in the MM allows for the comparison of density to habitat quality and the population density is likely affected by huckleberry availability.

The abundance of high-quality huckleberry habitat appears to an important factor enabling the recovery of the MM populations. While the NSN population is unlikely to achieve densities observed in the MM population, the lack of association between the current distribution of individuals on the landscape with extant huckleberry patches in the NSN, caused by overall low density in this population, indicates that the population is unlikely at carrying capacity. Thus, other factors are contributing to the absence of recovery. It is possible that the legacy of historic mortality and current stochastic effects (chapter 3), inbreeding effects or Allee effects are also contributing to the continued low density observed on the landscape. While these small population effects may be more challenging to overcome, it appears that the landscape can accommodate a higher population density than that currently observed.

Density was not linked to habitat types highly selected for during other seasons. All bears monitored in this study fed on herbaceous plants and bulbs in the spring; the fact that this habitat type was not linked to density across the study area or in relation to a specific population indicates that, despite its possible importance due to its ubiquity (chapter 4), this

habitat type was not limiting or driving population density. Likewise, the relationship between whitebark pine and density was also weak even though this food source is commonly used by bears in both populations. Furthermore, seeds from this conifer is a major component of the diet for grizzlies in the NSN where huckleberries are relatively rare. Roughly a quarter of the collared bears in the MM fed on early fruit while no collared bears in the NSN did (chapter 4), despite the availability of early fruit at lower elevations for both populations.

In contrast to other research, road density, which has been frequently linked to bear density (Lamb et al. 2018), behavioural changes (Northrup et al. 2012), and mortality (McLellan et al. 2007, Schwartz et al. 2010, Boulanger et al. 2014), did not correlate to grizzly density in this study area. Due to the rugged topography, and short life-span of roads in this area, their density is relatively low throughout the study area, between 0 and 7.63 km/km<sup>2</sup>, with a few areas with higher road density near human settlements or road junctions. As a result, there is seldomly more than one resource road per drainage, resulting in large areas of secure habitat with no roads at all (Figure 5.1). As a result, the road density across the study area has a similar pattern of a single road, sometimes with a few spurs, separated from one another by of between 4 to 8 km. of wilderness. Despite the lack of effect of roads on density, the present analysis does not test for the potential effect of roads on bear mortality and a more detailed study on this topic would be necessary before concluding that they play no role for population recovery.

One caveat of this study is that by building the *secr* model based on output from an RSF model, there is no propagation of error from the RSF to the density surface. Ignoring the uncertainty in RSF scores may have biased estimates of coefficients and/or cause us to underestimate coefficient uncertainty. However, the accuracy of all habitat models, when tested using k-fold cross validation (Boyce et al. 2002), was found to be over 90%. Thus,

effects on *secr* estimates of ignoring RSF error should be comparable across the different models we fit and should not affect our conclusions about huckleberries being the most important RSF-type predictor of bear density. Methods for directly integrating RSF and SCR into one analysis have been developed and implemented in other research (Linden et al. 2018), however the models do not use the resulting habitat selection estimates as predictors of density.

Spatial capture recapture analysis assumes that home range centres are stationary during sampling (Royle et al. 2016) however estimates of density are very robust to transience and dispersal. This capture-recapture program spanned an entire active season, this allows for individuals to use habitats throughout their home range within the capture time and may lead to more accurate estimates of sigma and home range than sampling in a single season. However, we can expect differences in  $\sigma$  to arise from transience and therefore sampling duration should be considered when comparing detection parameters among studies. It should also be noted that although each resource is important in a different season, this analysis only looks at the effects of resources across all seasons. This may mask effects on density on smaller temporal scales. As a result, only habitats that are important enough for their effects to be evident across all seasons will be identified in this analysis. The distribution of herbaceous foods, bulbs and pine nuts may affect bear distribution, but perhaps only in their respective season.

The relationship between habitat selection and animal density or abundance is of fundamental interest to ecologists. Until recently, predicting abundance across space from habitat use models predicated on the assumption that a population was at, or near, carrying capacity (Boyce and McDonald 1999, Boyce et al. 2016), otherwise comparisons were made with point estimates of one or both parameters, excluding spatial variation. The integration of spatial mark recapture and resource selection functions allow incorporation of the spatial

nature of both approaches (Borchers and Efford 2008, Royle et al. 2013, Linden et al. 2018) therefore eliminating some otherwise key assumptions. Specifically, in this analysis I used resource selection functions within a spatial-mark recapture framework and found that population density is most strongly connected to habitats selected during a season when bears fed on huckleberries as well as a large baseline difference between populations.

# Chapter 6

## General Discussion

### 6.1 Discussion

At the beginning of this research, I set out to identify the rates and causes of population change in two grizzly bear populations that the Province of British Columbia had classified as threatened. I developed three competing hypotheses that, when used in conjunction, would estimate the bear densities and current population trends for each population, but most importantly, provide a mechanism explaining the trends. While I fully appreciated that this task would be difficult for small populations, particularly if they were declining, I did not understand how unique an opportunity it was to describe, in detail, what the demographic components of decline looked like for a very small population; the manifestation of stochastic processes on individuals, in space and time, and how the negative results of stochastic processes or other small population effects, can then be used as an opportunity for recovery.

Identifying the current status for the MM population ended up being relatively easy; whether evaluated using population vital rates from collared individuals (chapter 3) or population wide DNA capture-recapture (chapter 2), the consensus was that the population was growing. The research pointed to a mechanism that, following the reduction in HCM, there was both high adult survival and high cub survival. The increasing density was associated with the selection of high energy foods, which provided fuel for the observed recovery (chapter 4 and 5). This was the successful outcome of management action, and it matched similar outcomes from similar efforts elsewhere (Kindberg et al. 2011, Mace et al. 2012, van Manen et al. 2015).



What I observed in the NSN population is more nebulous. What is now known, is that the population is small and not growing. My first hypothesis was that top-down limitation was still too high and as a result, the population was not recovering. What I found was that top-down limitation was higher than estimated for MM and other populations. However, the second prediction for this hypothesis, that reproductive rates would be high because the population was far below carrying capacity and therefore not limited by resources, was not supported. I found the reproductive rates of bears in the NSN were among the lowest observed for any grizzly population (chapter 3). From these results, I concluded that, while there is room for improvement as far as reducing top-down mortality, it does not appear to be the only factor.

My second hypothesis was that there are insufficient resources to support population growth and densities comparable to the MM population. Predictions in support of this hypothesis are relatively high adult survival, as is common in grizzly populations near carrying capacity (Garshelis et al. 2005, Keay et al. 2018), but low reproductive rates. This hypothesis thus appears to be supported and a plausible explanation for the absence of growth in the NSN and may be partially responsible for the continued lack of population recovery. In chapter 4, I showed that there was proportionally (by area) much less habitat with high-energy food in the NSN than in the MM, and in chapter 5, I established a relationship, albeit, somewhat weak, for the NSN, between population density and huckleberry abundance. Both of these analyses suggest that the carrying capacity for the NSN is likely lower than for the MM, but because the MM population has not yet reached carrying capacity, quantitative comparisons remain somewhat speculative.

Bottom-up limitation for grizzly bears results in predictable demographic responses including low reproductive rates while maintaining relatively high adult survival rates (Garshelis et al. 2005, Keay et al. 2018, McLellan 2015). Recruitment rates in the NSN were

much lower than in the MM primarily as a result of much higher cub mortality. In comparison, reproductive rates were not significantly lower and mean litter sizes in both populations were among the largest recorded for any population (Zedrosser et al. 2011). Low cub survival has been correlated to poor habitat conditions but often in conjunction with small litters (Robbins et al. 2012). Neither of these observations supports a lack of fitness due to bottom-up population limitation alone.

In addition, over the years of monitoring, two of the adult females that died (one by another bear and one a suspected HCM) left vacant home ranges, one in 2012 and another in 2014. No females were genetically detected in their home ranges after. Despite confirmed huckleberry fields in the western portion of the NSN (chapter 4), these females were the only ones monitored that had significant berry fields within their home range. Compiling the demographic and habitat modelling evidence, I suggest that while it is likely that the carrying capacity of the NSN is lower than the MM, the remaining NSN population is still below the carrying capacity and there is sufficient habitat for greater recovery.

Finally, we are left with the third hypothesis, which is, that small population effects are dominating the observed demographics of the NSN. Some scientists have proposed that even in the absence of evidence, all small, genetically isolated populations should be considered to be at least potentially suffering from inbreeding effects because such effects have been well documented (Frankham 2005, Laikre et al. 2010). Although I agree with exercising the precautionary principle, I think that highlighting the observations that are indicative of small populations and potential ones that are of special concern for small populations of grizzly bears is worthwhile. One hypothesis, that would be challenging to manage and possibly specific to few taxa including grizzly bears, is that small populations have higher occurrences of mating seasons in which there are no females available to mate, thus increasing the incentive for sexually selected infanticide by adult males (chapter 3). This

hypothesis is supported by the low observed cub survival. However, because the cause of cub deaths is unknown, it remains untested.

Other predictions from the small population hypothesis are that inbred individuals would have low population heterozygosity (Chapron et al. 2003, Kenney et al. 2014) and as a result of inevitable inbreeding, cub survival and recruitment rates would also be low. While the population heterozygosity was lower than average, some other small populations were even lower (Taberlet et al. 1997, Tumendemberel et al. 2015). It seems likely that some of the observed low cub survival, high interbirth intervals and late primiparity are all, at least partially, outcomes of inbreeding effects.

The consistency among this population and other small brown bear populations discussed in chapter 3 highlights that, like so many other species, grizzly bears may also have a small population threshold, below which adult female and cub survival are low, and intervention is necessary to curb extirpation. If this threshold is true for grizzly bears than a similar threshold is likely also true for other mammal species, particularly those with similar life histories.

My research exposes several opportunities for recovery including organic genetic and demographic rescue, or an assisted rescue by population augmentation. Organic rescue would require population connectivity between the NSN and neighbouring populations. As the MM population continues to grow, this becomes more likely however, management efforts that conserve habitat connectivity between populations, without the development of a source sink dynamic, will be necessary. In the short term, population augmentation by moving female bears from other populations into the NSN, would simultaneously increase the breeding population and introduce genetic variability to the population. There is evidence of small population recovery following augmentation or demographic rescue from neighbouring

populations, although the mechanism, whether it is increased reproduction or survival, has not been identified (Chapron et al. 2009, Gonzalez et al. 2016, Kendall et al. 2016).

Each chapter in this thesis is a continuation of the previous ones. Together they identify the mechanisms behind population recovery or lack of recovery. The unique details of what is contributing to population change in these populations are important for their recovery. However, the details of the process by which they were uncovered are likely of interest and utility for understanding the dynamics of other small and possibly declining populations. This study is an example of combining the small and declining population paradigms described by Caughley (1994) and understanding where they overlap. In this case, the overlapping effects of limited bottom-up resources and small population effects appear to be responsible for the lack of population recovery. By examining the population dynamics of small populations in this framework I have accomplished what I set out to do: find out why this population is small and declining and what can be done about it.

## **6.2 Applications in Conservation Biology**

Whether a population is trending or stationary is one of the most commonly asked questions by conservation biologists and managers. It is also one of the criteria used by the IUCN (International Union for the Conservation of Nature 2020) to define the degree of threat faced by a population. However, estimating trend and direction, much less the mechanisms causing an observed trend, is complicated and full of practical and theoretical challenges. My research is an example of using a multiple competing hypotheses approach to differentiate among several possible causes of population decline. In my research I estimated population density and trends; population vital rates, including survival, reproductive rates and their components. Each rate was considered in light of possible causes. Independently, each analysis in this dissertation is useful for the management of these grizzly bear

populations, however the real strength results from their amalgamation. By putting them together to compare among multiple plausible hypotheses, and systematically identify corroborating or contradicting evidence, it is possible to make inferences greater than the sum of each part.

The multiple competing hypothesis framework, its components, and how they are used to decipher among possible mechanisms driving population change, are independent of species or even discipline (Peery et al. 2004, Betini et al. 2017). For each taxon there is a list of potential causes threatening population stability and persistence—whether this is pollution and habitat degradation commonly faced by amphibians and reptiles (Gibbon et al. 2000), or invasive species and climate change threatening freshwater fish populations (Jelks et al. 2008). The need to decipher among multiple agents of decline in order to implement effective conservation actions remains the same. My research is an example of the implementation of the multiple competing hypothesis framework that has potential for much broader application in conservation biology.

Another common issue faced by conservation biologists is necessarily drawing inferences from small sample sizes. Appropriate conservation actions are needed on small populations but it is impossible to obtain a large sample size needed for statistical rigour when there are very few animals available to measure. Even though there may be other quantifiable reasons the population is small, limited sample sizes is enough to cast doubt on any metric that is estimated. As a result, there arises an awkward balance between the lack of statistical confidence due to a small sample that is implicit to small populations yet urgent need to act to conserve small populations, particularly if they are declining.

One of the reasons I was able to obtain meaningful estimates from a small population because of the long study duration (13 years) and by having another population in my study from which to draw comparisons. The benefits of long-term research in ecology and

conservation have been shown for many species, including Bearded Vulture (*Gypaetus barbatus*) in the Pyrenees (Margalida 2017), African savanna elephants (*Loxodonta africana*) (Fritz 2017), and chimpanzees (*Pan troglodytes*) in Gombe National Park (Pusey et al. 2007). However, studies that have successfully estimated vital rates for mammal populations with fewer than 25 individuals are extremely rare (e.g. Wittmer et al. 2005). The degree to which the vital rates differed from large populations should be of comparative value for anyone studying a small population. Though long-term initiatives are impractical for many researchers, my research reiterates the importance of long-term and comparative studies, especially for small populations.

Another aspect of my dissertation research that is likely widely applicable in ecology and conservation science is the amalgamation of fine-scale habitat selection analysis to identify food-specific foraging, with broad-scale habitat selection models that utilize available spatial data. The importance of food to the density and distribution of animals is fundamental to ecology yet estimating the availability and abundance of food and how it relates to population density is surprisingly complicated. At fine scales, identifying food specific resource selection requires observing where and what animals eat, and how this compares to what is available to them (e.g. Denryter et al. 2017). However, this method alone is limited to small-scale patterns of selection and food availability is not always easily expanded to the home range or population scale. At broader scales, Resource Selection Functions (RSFs), have been commonly used to predict habitat selection. RSFs use widely available spatial data (e.g. satellite, digital elevation models, climate models) for predicting resource selection patterns, but due to the nature of the input variables, they are usually devoid of a mechanistic link between resource selection and population level attributes such as density and abundance (Gillies et al. 2006, Johnson et al. 2006, Fieberg et al. 2010, Apps et al. 2016). The resulting models have often not produced substantial advances for

understanding habitat or managing bottom-up processes because they are based on multiple behaviours predicted by a group of surrogate habitat variables.

The disassociation between RSF model outputs and food is largely the result of the integration of multiple behaviours, that are food independent (e.g. predator avoidance, movement, sleeping), into estimates of resource selection (chapter 4, Nielsen et al. 2010, Bose et al. 2018). To further obscure matters, interannual variation in selection that often arises from environmental fluctuations, is inadequately accounted for by assuming that calendar dates are sufficient to account for seasonal variations. Much of this variability manifests as variability among individuals in their selection patterns. Gillingham and Parker (2008) showed that when individual moose (*Alces alces*) were pooled into one RSF, there were no individuals that had the selection pattern estimated by the resulting RSF. Likewise, Elk (*Cervus elphus*), a highly gregarious species, also showed large individual variability in time specific habitat selection independent from age and sex class (Montgomery et al. 2018). The resulting resource selection models thus inaccurately predict forging specific habitat selection and by extension, the abundance of specific food types.

By building resource selection models based on behaviour-specific data, in this case food specific foraging, I was able to spatially identify habitat patches and determine the relative quality of habitat across a landscape-based resources. The models were still largely based on spatial surrogates, however because models were behaviourally specific and animal locations were categorized based on use-site visits that determined behaviour, they accurately predicted food specific selection patterns, and resource availability. The resulting highly accurate and resource specific habitat map is important for management and conservation decisions as well as for hypothesis testing at the population scale (chapter 5). Because management often involves trade offs for securing habitat, it is easy to see why understanding the mechanisms for habitat selection, would be beneficial for many species.

Accurately estimating food resource distribution and availability allows for mechanistic approaches to understanding the density and distribution of individuals on a landscape. As a result, providing a mechanistic link between habitat selection and food abundance extends the utility of RSFs as they can be used to test among hypotheses across multiple scales without a suite of potentially confounding assumptions (Boyce et al. 2016). Although grizzly bears are particularly well suited for food based RSFs due to their seasonally predictable, omnivorous diet, this technique could be used to estimate food specific habitat abundance for, many other species with similar life histories or large differences in seasonal or diel habitat selection patterns. For example, the Peruvian spider monkey (*Ateles chamek*), is an arboreal primate that is mostly frugivorous and displays behavioural differences in seasonal and daily habitat selection patterns (Felton et al. 2009). There is some indication of bottom-up limitation in this species where food specific foraging patterns shift with varying availability of fruit, but, like grizzly bears, this monkey's range distribution appears to be limited by top-down HCM (Wallace et al. 2008). Applying foraging specific resource selection modeling would likely contribute to the understanding of how top-down and specific bottom-up factors affect the large-scale distribution of this species.

In order to exploit the rapidly increasing availability of remotely sensed data and technological advances in GIS and spatial statistics, ecologists and conservation biologist will need to find ways to integrate these data in ways that are meaningful to the ecologically relevant patterns and processes at the individual and population levels. We want to have confidence that all the pretty maps we make, actually mean something to the animals and ecosystems.



## **6.2 Project Legacy**

This research program did not exclusively culminate in this dissertation. As a result of the information gathered, the NSN has received a new IUCN and provincial species at risk classification. Local First Nations have come together, in the first multi-nation collaborative project in the region, to continue monitoring the entire NSN population and are committed to supporting recovery. The provincial government has also passed legal orders on land use to limit human access to sensitive areas within the population. Provincial park managers are now consulting with researchers when producing visitor management plans and local and international NGOs are playing an integral role in recovery initiatives by serving as organizers, motivators and funders. Finally, together we have developed an augmentation program that is set to begin in 2020.

## Literature Cited

- Åkesson, M., O. Liberg, H. Sand, P. Wabakken, S. Bensch, and Ø. Flagstad. 2016. Genetic rescue in a severely inbred wolf population. *Molecular ecology* 25:4745–4756.
- Apps, C. D., B. N. McLellan, T. A. Kinley, and J. P. Flaa. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. *The Journal of Wildlife Management* 65:65.
- Apps, C. D., B. N. McLellan, M. F. Proctor, G. B. Stenhouse, and C. Servheen. 2016. Predicting spatial variation in grizzly bear abundance to inform conservation. *Journal of Wildlife Management* 80:396–413.
- Apps, C., D. Paetkau, and B. Bateman. 2007. Grizzly Bear population density and distribution in the southern Coast Ranges of British Columbia: Year 3 progress & data summary. Victoria B.C.
- Apps, C., D. Paetkau, S. Rochetta, B. McLellan, A. Hamilton, and B. Bateman. 2014. Grizzly bear population abundance, distribution & connectivity across British Columbia's southern Coast Ranges. Report V.2.0. Victoria B.C.
- Aresu, M., A. Rotta, A. Fozzi, A. Campus, M. Muzzeddu, D. Secci, I. Fozzi, D. D. E. Rosa, and F. Berlinguer. 2020. Assessing the effects of different management scenarios on the conservation of small island vulture populations. *Bird Conservation International*:1–18.
- Baig, M. H. A., L. Zhang, T. Shuai, and Q. Tong. 2014. Derivation of a tasselled cap transformation based on Landsat 8 at-satellite reflectance. *Remote Sensing Letters* 5:423–431.
- Barnuud, N. N., A. Zerihun, M. Gibberd, and B. Bates. 2014. Berry composition and climate: responses and empirical models. *International Journal of Biometeorology* 58:1207–1223.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Bellemain, E., M. A. Nawaz, A. Valentini, J. E. Swenson, and P. Taberlet. 2007. Genetic tracking of the brown bear in northern Pakistan and implications for conservation. *Biological Conservation* 134:537–547.

- Berec, L., E. Angulo, and F. Courchamp. 2007. Multiple Allee effects and population management. *Trends in Ecology and Evolution* 22:185–191.
- Betini, G. S., T. Avgar, and J. M. Fryxell. 2017. Why are we not evaluating multiple competing hypotheses in ecology and evolution? *Royal Society Open Science* 4:160756.
- Borchers, D. L., and M. G. Efford. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. *Biometrics* 64:377–385.
- Bose, S., T. D. Forrester, D. S. Casady, and H. U. Wittmer. 2018. Effect of activity states on habitat selection by black-tailed deer. *Journal of Wildlife Management* 82:1711–1724.
- Boulanger, J., K. C. Kendall, J. B. Stetz, D. a Roon, L. P. Waits, and D. Paetkau. 2008. Multiple data sources improve DNA-based mark-recapture population estimates of grizzly bears. *Ecological Applications* 18:577–589.
- Boulanger, J., and B. McLellan. 2001. Closure violation in DNA-based mark-recapture estimation of grizzly bear populations. *Canadian Journal of Zoology* 79:642–651.
- Boulanger, J., S. E. Nielsen, and G. B. Stenhouse. 2018. Using spatial mark-recapture for conservation monitoring of grizzly bear populations in Alberta. *Scientific Reports* 8:1–15.
- Boulanger, J., G. B. Stenhouse, and A. Margalida. 2014. The impact of roads on the demography of grizzly bears in Alberta. *PLoS ONE* 9:e115535.
- Boyce, M. S. 2006. Scale for resource selection functions. *Diversity and Distributions* 12:269–276.
- Boyce, M. S., C. J. Johnson, E. H. Merrill, S. E. Nielsen, E. J. Solberg, and B. van Moorter. 2016. Can habitat selection predict abundance? *Journal of Animal Ecology* 85:11–20.
- Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution* 14:268–272.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Bromaghin, J. F., T. L. McDonald, I. Stirling, A. E. Derocher, E. S. Richardson, E. V. Regehr, D. C. Douglas, G. M. Durner, T. Atwood, and S. C. Amstrup. 2015. Polar bear population dynamics in the southern Beaufort Sea during a period of sea ice decline. *Ecological Applications* 25:634–651.

- Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers under global change. *Trends in Ecology and Evolution* 23:453–460.
- Bulmer, C., M. G. Schmidt, B. Heung, C. Scarpone, J. Zhang, D. Filatow, M. Finvers, S. Berch, and S. Smith. 2016. Improved soil mapping in British Columbia, Canada, with legacy soil data and random forest. Pages 291–303 *in* G. Zhang, D. Brus, F. Liu, X.-D. Song, and P. Lagacherie, editors. *Digital Soil Mapping Across Paradigms, Scales and Boundaries*. Springer Science and Business Media, Singapore.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edition. Springer, New York.
- Bursac, Z., C. H. Gauss, D. K. Williams, and D. W. Hosmer. 2008. Purposeful selection of variables in logistic regression. *Source Code for Biology and Medicine* 3:1–8.
- Caswell, H. 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. Second, illustr edition. Sinauer Associates, Sunderland, Massachusetts.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215–244.
- Chapron, G., P. Kaczensky, J. D. C. Linnell, M. von Arx, D. Huber, H. Andrén, J. V. López-Bao, M. Adamec, F. Álvares, O. Anders, L. Balčiauskas, V. Balys, P. Bedő, F. Bego, J. C. Blanco, U. Breitenmoser, H. Brøseth, L. Bufka, R. Bunikyte, P. Ciucci, A. Dutsov, T. Engleder, C. Fuxjäger, C. Groff, K. Holmala, B. Hoxha, Y. Iliopoulos, O. Ionescu, J. Jeremić, K. Jerina, G. Kluth, F. Knauer, I. Kojola, I. Kos, M. Krofel, J. Kubala, S. Kunovac, J. Kusak, M. Kutal, O. Liberg, A. Majić, P. Männil, R. Manz, E. Marboutin, F. Marucco, D. Melovski, K. Mersini, Y. Mertzanis, R. W. Mysłajek, S. Nowak, J. Odden, J. Ozolins, G. Palomero, M. Paunović, J. Persson, H. Potočnik, P.-Y. Quenette, G. Rauer, I. Reinhardt, R. Rigg, A. Ryser, V. Salvatori, T. Skrbinšek, A. Stojanov, J. E. Swenson, L. Szemethy, A. Trajçe, E. Tsingarska-Sedefcheva, M. Váňa, R. Veeroja, P. Wabakken, M. Wölfl, S. Wölfl, F. Zimmermann, D. Zlatanova, and L. Boitani. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346:1517–1519.
- Chapron, G., P.-Y. Quenette, S. Legendre, and J. Clobert. 2003. Which future for the French Pyrenean brown bear (*Ursus arctos*) population? An approach using stage-structured deterministic and stochastic models. *Comptes Rendus - Biologies* 326:S174–S182.

- Chapron, G., R. Wielgus, P. Y. Quenette, and J. J. Camarra. 2009. Diagnosing mechanisms of decline and planning for recovery of an endangered brown bear (*Ursus arctos*) population. PLoS ONE 4:e7568.
- Charlesworth, D., and J. H. Willis. 2009. The genetics of inbreeding depression. Nature reviews. Genetics 10:783–96.
- Ciarniello, L. M., M. S. Boyce, D. R. Seip, and D. C. Heard. 2007. Grizzly bear habitat selection is scale dependent. Ecological Applications 17:1424–1440.
- Ciucci, P., V. Gervasi, L. Boitani, J. Boulanger, D. Paetkau, R. Prive, and E. Tosoni. 2015. Estimating abundance of the remnant Apennine brown bear population using multiple noninvasive genetic data sources. Journal of Mammalogy 96:206–220.
- Clevenger, A. P., F. J. Purroy, M. S. De Buruaga, F. Purdoy, and M. S. De Burguaga. 1987. Status of the brown bear in the Cantabrian Mountains, Spain. Bears: Their Biology and Management 7:1–8.
- Costello, C. M., F. T. van Manen, M. A. Haroldson, M. R. Ebinger, S. L. Cain, K. A. Gunther, and D. D. Bjornlie. 2014. Influence of whitebark pine decline on fall habitat use and movements of grizzly bears in the Greater Yellowstone Ecosystem. Ecology and Evolution 4:2004–2018.
- Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. Trends in Ecology & Evolution 14:405–410.
- Crawley, M. J. 2005. Statistics An Introduction using R. John Wiley And Sons, Ltd., West Sussex.
- Crone, E. E., E. J. B. McIntire, and J. Brodie. 2011. What defines mast seeding? Spatio-temporal patterns of cone production by whitebark pine. Journal of Ecology 99:438–444.
- Cronin, M. A., and M. D. MacNeil. 2012. Genetic relationships of extant brown bears (*Ursus arctos*) and polar bears (*Ursus maritimus*). Journal of Heredity 103:873–881.
- Curry-Lindahl, K. 1972. The brown bear (*Ursus arctos*) in Europe: decline, present distribution, biology and ecology. Bears: Their Biology and Management 2:74–80.
- Denny, C. K., G. B. Stenhouse, and S. E. Nielsen. 2018. Scales of selection and perception: landscape heterogeneity of an important food resource influences habitat use by a large

- omnivore. *Wildlife Biology*:1–10.
- Denryter, K. A., R. C. Cook, J. G. Cook, and K. L. Parker. 2017. Straight from the caribou's (*Rangifer tarandus*) mouth: detailed observations of tame caribou reveal new insights into summer-autumn diets. *Canadian Journal of Zoology* 95:81–94.
- Duangchantrasiri, S., M. Umponjan, S. Simcharoen, A. Pattanavibool, S. Chaiwattana, S. Maneerat, N. S. Kumar, D. Jathanna, A. Srivathsa, and K. U. Karanth. 2016. Dynamics of a low-density tiger population in Southeast Asia in the context of improved law enforcement. *Conservation Biology* 30:639–648.
- Eberhardt, L. L., B. M. Blanchard, and R. R. Knight. 2008. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. *Canadian Journal of Zoology* 72:360–363.
- Efford, M. 2004. Density estimation in live-trapping studies. *Oikos* 106:598–610.
- Efford, M. 2018. secr 3.1.0 spatially explicit capture–recapture in R. [www.otago.ac.nz/density](http://www.otago.ac.nz/density)
- Efford, M. 2019. secr 3.6.1 spatially explicit capture-recapture in R. [www.otago.ac.nz/density](http://www.otago.ac.nz/density)
- Efford, M. G. 2014. Bias from heterogeneous usage of space in spatially explicit capture-recapture analyses. *Methods in Ecology and Evolution* 5:599–602.
- Efford, M. G., D. L. Borchers, and G. Mowat. 2013. Varying effort in capture-recapture studies. *Methods in Ecology and Evolution* 4:629–636.
- ESRI. 2010. ArcMap 10. [www.esri.com](http://www.esri.com)
- Evans, J. 2004. Topographic ruggedness index. AML <http://arcscripsts.esri.com/details.asp?dbid=11863>
- Fawcett, T. 2006. An introduction to ROC analysis. *Pattern Recognition Letters* 27:861–874.
- Felton, A. M., A. Felton, D. Raubenheimer, S. J. Simpson, W. J. Foley, J. T. Wood, I. R. Wallis, and D. B. Lindenmayer. 2009. Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behavioral Ecology* 20:685–690.
- Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M. S. Boyce, and J. L. Frair. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical Transactions of the Royal Society B* 365:2233–2244.

- Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. *Conservation Biology* 8:124–137.
- Frankham, R. 2005. Genetics and extinction. *Biological Conservation* 126:131–140.
- Fritz, H. 2017. Long-term field studies of elephants: understanding the ecology and conservation of a long-lived ecosystem engineer. *Journal of Mammalogy* 98:603–611.
- Fujiwara, M., and J. Diaz-Lopez. 2017. Constructing stage-structured matrix population models from life tables: comparison of methods. *PeerJ* 5:e3971.
- Gaillard, J. M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B* 365:2255–2265.
- Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Columbia University Press, New York, pp. 111–164. Page *in* L. Boitani and T. K. Fuller, editors. *Research Techniques in Animal Ecology: Controversies and Consequences*. Columbia University Press, New York.
- Garshelis, D. L., M. L. Gibeau, and S. Herrero. 2005. Grizzly bear demographics in and around Banff National Park and Kananaskis Country, Alberta. *Journal of Wildlife Management* 69:277–297.
- Garshelis, D. L., K. V. Noyce, and P. L. Coy. 2008. Calculating the average age of first reproduction free of the biases prevalent in bear studies. *Ursus* 10:437–447.
- GEO BC. 2011. Digital Elevation Model. Government of British Columbia Data Catalogue. [www.data.gov.bc.ca](http://www.data.gov.bc.ca)
- Gervasi, V., L. Boitani, D. Paetkau, M. Posillico, E. Randi, and P. Ciucci. 2017. Estimating survival in the Apennine brown bear accounting for uncertainty in age classification. *Population Ecology* 59:119–130.
- Gibbon, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and C. T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. *BioScience* 50:653.
- Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75:887–898.

- Gillingham, M. P., and K. L. Parker. 2008. The importance of individual variation in defining habitat. *Alces* 44:7–20.
- Gonzalez, E. G., J. C. Blanco, F. Ballesteros, L. Alcaraz, G. Palomero, and I. Doadrio. 2016. Genetic and demographic recovery of an isolated population of brown bear *Ursus arctos* L., 1758. *PeerJ* 4:e1928.
- Gough, K. F., and G. I. H. Kerley. 2006. Demography and population dynamics in the elephants *Loxodonta africana* of Addo Elephant National Park, South Africa: Is there evidence of density dependent regulation? *Oryx* 40:434–441.
- Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809–2815.
- Graves, T., R. B. Chandler, J. A. Royle, P. Beier, and K. C. Kendall. 2014. Estimating landscape resistance to dispersal. *Landscape Ecology* 29:1201–1211.
- Greene, C. M., and J. A. Stamps. 2017. Habitat selection at low population densities. *Ecology* 82:2091–2100.
- Gripenberg, S., and T. Roslin. 2007. Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. *Oikos* 116:181–188.
- Haroldson, M. A., F. T. van Manen, M. R. Ebinger, M. D. Higgs, D. D. Bjornlie, K. A. Gunther, K. L. Frey, S. L. Cain, and B. C. Aber. 2014. Trends in causes and distribution, and effects of whitebark pine decline on grizzly bear mortality in the Greater Yellowstone Ecosystem. *Intermountain Journal of Sciences* 20:59715.
- Hayden, B., and J. M. Ryder. 1991. Prehistoric cultural collapse in the Lillooet area. *American Antiquity* 56:50–65.
- Henschel, P., L. Coad, C. Burton, B. Chataigner, A. Dunn, D. MacDonald, Y. Saidu, and L. T. B. Hunter. 2014. The lion in West Africa is critically endangered. *PLoS ONE* 9:e83500.
- Hertel, A. G., R. Bischof, O. Langval, A. Mysterud, J. Kindberg, J. E. Swenson, and A. Zedrosser. 2018. Berry production drives bottom-up effects on body mass and reproductive success in an omnivore. *Oikos* 127:197–207.
- Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999. The importance of meat, particularly salmon, to body size,



- population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77:132–138.
- Hobbs, J., F. Iredale, S. Keightley, and C. McLean. 2013. Grizzly Bear Habitat Management in the Bridge River Restoration Area: 2011 & 2012 Final Report.
- Hood, G. 2011. PopTools v.3.2.5.
- Hovey, F. W., and B. N. McLellan. 1996. Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. *Canadian Journal of Zoology* 74:1409–1416.
- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47:725–732.
- Huisman, J., L. E. B. Kruuk, P. A. Ellis, T. Clutton-Brock, and J. M. Pemberton. 2016. Inbreeding depression across the lifespan in a wild mammal population. *Proceedings of the National Academy of Sciences* 113:3585–3590.
- IUCN. 2015. IUCN Red List of Threatened Species. <https://www.iucn.org>
- IUCN Red List of Threatened Species. 2020. <https://www.iucn.org/resources/conservation-tools/iucn-red-list-threatened-species>.
- Jackman, S. 2017. Political science computational laboratory. 1.5.2.
- Jackson, C. H. 2011. Multi-State Models for Panel Data: The msm Package for R. *The Journal of Statistical Software* 38:1–29.
- Jelks, H. L., S. J. Walsh, N. M. Burkhead, S. Contreras-balderas, E. Díaz-pardo, D. A. Hendrickson, J. Lyons, N. E. Mandrak, F. McCormick, J. S. Nelson, S. P. Platania, B. A. Porter, C. B. Renaud, J. J. Schmitter-soto, E. B. Taylor, and M. L. Warren. 2008. Imperiled North American freshwater and diadromous fishes. *Fisheries* 33:372–386.
- Johnson, C. J., E. Nielsen, Scott, H. Merrill, Evelyn, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use – availability data: theoretical motivation and evaluation methods. *The Journal of Wildlife Management* 70:347–357.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Kasworm, W. F., T. G. Radandt, J. E. Teisberg, and C. Servheen. 2014. Cabinet-Yaak grizzly bear recovery area 2013 research and monitoring progress report. Missoula, Montana.

- Keay, J. A., C. T. Robbins, and S. D. Farley. 2018. Characteristics of a naturally regulated grizzly bear population. *Journal of Wildlife Management* 82:789–801.
- Keller, L. F., and D. M. Waller. 2002. Inbreeding effects in wild populations. *Trends in Ecology and Evolution* 17:230–241.
- Kendall, K. C., A. C. Macleod, K. L. Boyd, J. Boulanger, J. A. Royle, W. F. Kasworm, D. Paetkau, M. F. Proctor, K. Annis, and T. A. Graves. 2016. Density, distribution, and genetic structure of grizzly bears in the Cabinet-Yaak Ecosystem. *Journal of Wildlife Management* 80:314–331.
- Kendall, K. C., J. B. Stetz, J. Boulanger, A. C. MacLeod, D. Paetkau, and G. C. White. 2009. Demography and genetic structure of a recovering brown bear population. *Journal of Wildlife Management* 73:3–17.
- Kenney, J., F. W. Allendorf, C. McDougal, and J. L. D. Smith. 2014. How much gene flow is needed to avoid inbreeding depression in wild tiger populations? *Proceedings of the Royal Society B: Biological Sciences* 281:1–8.
- Kindberg, J., J. E. Swenson, G. Ericsson, E. Bellemain, C. Miquel, and P. Taberlet. 2011. Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildlife Biology* 17:114–123.
- Laake, J. J., and E. Rexstad. 2008. RMark—an alternative approach to building linear models. Appendix C. Program MARK: a gentle introduction.:C1–C111.
- Laikre, L., F. W. Allendorf, L. C. Aroner, C. S. Baker, D. P. Gregovich, M. M. Hansen, J. A. Jackson, K. C. Kendall, K. McKelvey, M. C. Neel, I. Olivieri, N. Ryman, M. K. Schwartz, R. S. Bull, J. B. Stetz, D. A. Tallmon, B. L. Taylor, C. D. Vojta, D. M. Waller, and R. S. Waples. 2010. Neglect of genetic diversity in implementation of the convention on biological diversity: Conservation in practice and policy. *Conservation Biology* 24:86–88.
- Laikre, L., R. Andrén, H. O. Larsson, and N. Ryman. 1996. Inbreeding depression in brown bear *ursus arctos*. *Biological Conservation* 76:69–72.
- Laliberte, A. S., and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. *BioScience* 54:123–138.
- Lamb, C. T., G. Mowat, B. N. McLellan, S. E. Nielsen, and S. Boutin. 2017. Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore.

- Journal of Animal Ecology 86:55–65.
- Lamb, C. T., G. Mowat, A. Reid, L. Smit, M. Proctor, B. N. McLellan, S. E. Nielsen, and S. Boutin. 2018. Effects of habitat quality and access management on the density of a recovering grizzly bear population. *Journal of Applied Ecology* 00:1–12.
- Lamb, C. T., D. A. Walsh, and G. Mowat. 2016. Factors influencing detection of grizzly bears at genetic sampling sites. *Ursus* 27:31–44.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455–1460.
- Linden, D. W., A. P. K. K. Sirén, and P. J. Pekins. 2018. Integrating telemetry data into spatial capture–recapture modifies inferences on multi-scale resource selection. *Ecosphere* 9:1–14.
- Lopez-Bao, J. V. 2015. Carnivore coexistence : Wilderness not required. *Science* 348:871–872.
- Mace, R. D., D. W. Carney, T. Chilton-Radandt, S. A. Courville, M. A. Haroldson, R. B. Harris, J. Jonkel, B. N. McLellan, M. Madel, T. L. Manley, C. C. Schwartz, C. Servheen, G. Stenhouse, J. S. Waller, and E. Wenum. 2012. Grizzly bear population vital rates and trend in the Northern Continental Divide Ecosystem, Montana. *Journal of Wildlife Management* 76:119–128.
- MacHutchon, A. G., and D. W. Wellwood. 2003. Grizzly bear food habits in the northern Yukon, Canada. *Ursus* 14:225–235.
- MacHutchon, G. A., S. Himmer, H. Davis, and M. Gallagher. 1998. Temporal and spatial activity patterns among coastal bear populations. *Ursus* 10:539–546.
- MacKenzie, W. 2012. Biogeoclimatic ecosystem classification program of non-forested ecosystems in British Columbia. Province of British Columbia, Victoria BC.
- Malthus, T. 1798. *An Essay on the Priciple of Population*. London.
- van Manen, F. T., M. A. Haroldson, D. D. Bjornlie, M. R. Ebinger, C. M. Costello, and G. C. White. 2015. Density dependence, whitebark pine, and vital rates of grizzly bears. *The Journal of Wildlife Management* 80:1–14.
- Manly, B. F., L. McDonald, D. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource selection by animals: statistical design and analysis for field studies*. Second

- edition. Kluwer Academic Publishers, Dordrecht.
- Margalida, A. 2017. Importance of long-term studies to conservation practice: the case of the bearded vulture in the Pyrenees. Pages 519–553 in J. Catalan, J. M. Ninot, P. L. Chesson, and N. Huntly, editors. High mountain conservation in a changing world.
- Martin, J., E. Revilla, P. Y. Quenette, J. Naves, D. Allainé, and J. E. Swenson. 2012. Brown bear habitat suitability in the Pyrenees: Transferability across sites and linking scales to make the most of scarce data. *Journal of Applied Ecology* 49:621–631.
- Matkin, C. O., J. Ward Testa, G. M. Ellis, and E. L. Saulitis. 2014. Life history and population dynamics of southern Alaska resident killer whales (*Orcinus orca*). *Marine Mammal Science* 30:460–479.
- Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1991. Food habits of Yellowstone grizzly bears, 1977–1987. *Canadian Journal of Zoology* 69:1619–1629.
- Mattson, D. J., and T. Merrill. 2002. Extirpations of grizzly bears in the contiguous United States, 1850–2000. *Conservation Biology* 16:1123–1136.
- Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. *Écoscience* 16:238–247.
- McLellan, B. N. 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction I Density and age - sex composition. *Canadian Journal of Zoology* 67:1856–1860.
- McLellan, B. N. 1994. Density-dependent population regulation of brown bears. *Int. Conf. Bear Res. and Manage. Monogr. Series*:15–24.
- McLellan, B. N. 2005. Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. *Ursus* 16:141–156.
- McLellan, B. N. 2011. Implications of a high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. *Canadian Journal of Zoology* 558:546–558.
- McLellan, B. N. 2015. Some mechanisms underlying variation in vital rates of grizzly bears on a multiple use landscape. *Journal of Wildlife Management* 79:749–765.
- McLellan, B. N., and F. W. Hovey. 1995. The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. *Canadian Journal of Zoology* 73:704–712.

- McLellan, B. N., and F. W. Hovey. 2001. Habitats selected by grizzly bears in a multiple use landscape. *The Journal of Wildlife Management* 65:92–99.
- McLellan, B. N., and F. W. Hovey. 2011. Natal dispersal of grizzly bears. *Canadian Journal of Zoology* 79:838–844.
- McLellan, B. N., F. W. Hovey, R. D. Mace, J. G. Woods, D. W. Carney, M. L. Gibeau, W. L. Wakkinen, and W. F. Kasworm. 2007. Rates and causes of grizzly bear mortality in the Interior Mountains of British Columbia, Alberta, Montana, Washington, and Idaho. *The Journal of Wildlife Management* 63:911–920.
- McLellan, B. N., F. W. Hovey, and J. G. Woods. 1999. Rates and causes of grizzly bear mortality in the interior mountains of western North America. Pages 673–677 *Proc. Biology and Management of Species and Habitats at Risk*. Kamloops.
- McLellan, B. N., G. Mowat, T. Hamilton, and I. Hatter. 2017a. Sustainability of the grizzly bear hunt in British Columbia, Canada. *Journal of Wildlife Management* 81:218–229.
- McLellan, B. N., G. Mowat, and C. T. Lamb. 2018. Estimating unrecorded human-caused mortalities of grizzly bears in the Flathead Valley, British Columbia, Canada. *PeerJ* 6:e5781:1–12.
- McLellan, B. N., M. F. Proctor, D. Huber, and S. Michel. 2016a. *Ursus arctos*. The IUCN Red List of Threatened Species 2016: e.T41688A45034772.
- McLellan, B. N., M. F. Proctor, D. Huber, and S. Michel. 2016b. The IUCN Red List of Threatened Species 2016: Brown Bear.
- McLellan, B. N., M. F. Proctor, D. Huber, and S. Michel. 2017b. Brown Bear (*Ursus arctos*) (amended version of 2017 assessment). The IUCN Red List of Threatened Species 2017.
- McLellan, B. N., and D. M. Shackleton. 1988. Grizzly bears and resource -extraction industries: effects of roads on behaviour, habitat use and demography. *Journal of Applied Ecology* 25:451–460.
- McLellan, M. L. 2007. Ecological relationships between grizzly bears and forest management in the coast-interior transition of southern British Columbia: 2007 field season progress report. Page Southwest BC Grizzly Project. D’Arcy BC.
- McLellan, M. L., and B. N. McLellan. 2015. Effect of season and high ambient temperature on activity levels and patterns of grizzly bears (*Ursus arctos*). *PLoS ONE* 10:1–14.

- McLellan, M. L., B. N. McLellan, R. Sollmann, C. T. Lamb, C. D. Apps, and H. U. Wittmer. 2019. Divergent population trends following the cessation of legal grizzly bear hunting in southwestern British Columbia, Canada. *Biological Conservation* 233:247–254.
- McLoughlin, P. D., M. S. Boyce, T. Coulson, and T. Clutton-Brock. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B: Biological Sciences* 273:1449–1454.
- McLoughlin, P. D., R. L. Case, R. J. Gau, H. D. Cluff, R. Mulders, and F. Messier. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. *Oecologia* 132:102–108.
- Meyer, S., B. C. Robertson, B. L. Chilvers, and M. Krkošek. 2015. Population dynamics reveal conservation priorities of the threatened New Zealand sea lion *Phocarctos hookeri*. *Marine Biology* 162:1587–1596.
- Miller, S. D., R. A. Sellers, and J. A. Keay. 2003. Effects of hunting on brown bear cub survival and litter size in Alaska. *Ursus* 14:130–152.
- Miller, S. D., G. C. White, R. A. Sellers, H. V Reynolds, J. W. Schoen, K. Titus, V. G. Barnes, R. B. Smith, R. R. Nelson, W. B. Ballard, and C. C. Schwartz. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. *Wildlife Monographs*:3–55.
- Ministry of Forests, L. and N. R. O. 2013. Vegetation Composite Polygons. [www.data.bc.ca](http://www.data.bc.ca)
- Montgomery, R. A., K. M. Redilla, W. Ortiz, T. Smith, B. Keller, and J. J. Millspaugh. 2018. Evaluating the individuality of animal-habitat relationships. *Ecology and Evolution* 8:10893–10901.
- Morgan, D., M. Proctor, G. Mowat, B. McLellan, T. Hamilton, and L. Turney. 2019. Ranking the conservation ranking of grizzly bear population units. Victoria B.C.
- Morris, L. R., K. M. Proffitt, and J. K. Blackburn. 2016. Mapping resource selection functions in wildlife studies: Concerns and recommendations. *Applied Geography* 76:173–183.
- Mosnier, A., T. Doniol-Valcroze, J. F. Gosselin, V. Lesage, L. N. Measures, and M. O. Hammill. 2015. Insights into processes of population decline using an integrated population model: The case of the St. Lawrence Estuary beluga (*Delphinapterus leucas*). *Ecological Modelling* 314:15–31.

- Mowat, G., D. C. Heard, and C. J. Schwarz. 2013. Predicting grizzly bear density in western North America. *PLoS ONE* 8:13–17.
- Mowat, G., and C. Lamb. 2016. Population status of the South Rockies and Flathead grizzly bear populations in British Columbia, 2006-2014 Report.
- Munro, R. 1999. The impacts of transportation corridors on grizzly and black bear habitat use patterns near Golden, BC.
- Munro, R. H. M., S. E. Nielsen, M. H. Price, G. B. Stenhouse, and M. S. Boyce. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. *Journal of Mammalogy* 87:1112–1121.
- Myhrvold, N. P., E. Baldridge, B. Chan, D. Sivam, D. L. Freeman, and S. K. M. Ernest. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* 96:3109–000.
- NASA Land Processes Distributed Active Archive Center Products. 2014. LANDSAT 8 Imagery. US Geological Survey.
- Nelson, R. A., G. E. Folk, E. W. Pfeiffer, J. J. Craighead, C. J. Jonkel, and D. L. Steiger. 2007. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. *Bears: Their Biology and Management* 5:284–290.
- Nichols, J. D., and J. E. Hines. 2002. Approaches for the direct estimation of  $\lambda$ , and demographic contributions to  $\lambda$ , using capture-recapture data. *Journal of Applied Statistics* 29:539–568.
- Nichols, J. D., J. E. Hines, J. Lebreton, and R. Pradel. 2000. Estimation of contributions to population growth: a reverse-time capture-recapture approach. *Ecology* 81:3362–3376.
- Nielsen, S. 2011. Relationships between grizzly bear source-sink habitats and prioritized biodiversity sites in central British Columbia. *BC Journal of Ecosystems and Management* 12:136–147.
- Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. Munro. 2002. Modeling grizzly bear habitats in the Yellowhead Ecosystem of Alberta: taking autocorrelation seriously. *Ursus* 13104240:45–56.
- Nielsen, S. E., J. Cranston, and G. B. Stenhouse. 2009. Identification of priority areas for grizzly bear conservation and recovery in Alberta, Canada. *Journal of Conservation*

Planning 5:38–60.

- Nielsen, S. E., S. Herrero, M. S. Boyce, R. D. MacE, B. Benn, M. L. Gibeau, and S. Jevons. 2004a. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. *Biological Conservation* 120:101–113.
- Nielsen, S. E., G. McDermid, G. B. Stenhouse, and M. S. Boyce. 2010. Dynamic wildlife habitat models: Seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. *Biological Conservation* 143:1623–1634.
- Nielsen, S. E., R. H. M. Munro, E. L. Bainbridge, G. B. Stenhouse, and M. S. Boyce. 2004b. Grizzly bears and forestry: II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. *Forest Ecology and Management* 199:67–82.
- Nielsen, S. E., A. B. A. A. Shafer, M. S. Boyce, and G. B. Stenhouse. 2013. Does learning or instinct shape habitat selection? *PLoS ONE* 8:e53721.
- Nielsen, S. E., G. B. Stenhouse, and M. S. Boyce. 2006. A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation* 130:217–229.
- Northrup, J. M., J. Pitt, T. B. Muhly, G. B. Stenhouse, M. Musiani, and M. S. Boyce. 2012. Vehicle traffic shapes grizzly bear behaviour on a multiple-use landscape. *Journal of Applied Ecology* 49:1159–1167.
- van Oort, H., B. N. McLellan, and R. Serrouya. 2011. Fragmentation, dispersal and metapopulation function in remnant populations of endangered mountain caribou. *Animal Conservation* 14:215–224.
- Ovaskainen, O., and B. Meerson. 2010. Stochastic models of population extinction. *Trends in Ecology and Evolution* 25:643–652.
- Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. *Molecular Ecology* 12:1375–1387.
- Paetkau, D., L. P. Waits, P. L. Clarkson, L. Craighead, E. Vyse, R. Ward, and C. Strobeck. 1998. Variation in genetic diversity across the range of North American brown bears. *Conservation Biology* 12:418–429.
- Palomero, G., F. Ballesteros, C. Nores, J. C. Blanco, J. Herrero, and A. García-Serrano. 2007. Trends in Number and Distribution of Brown Bear Females with Cubs-of-the-year in the Cantabrian Mountains, Spain. *Ursus* 18:145–157.



- Peery, M. Z., S. R. Beissinger, S. H. Newman, E. B. Burkett, and T. D. Williams. 2004. Applying the declining population paradigm: diagnosing causes of poor reproduction in the marbled murrelet. *Conservation Biology* 18:1088–1098.
- Pérez, T., J. Naves, J. F. Vázquez, A. Fernández-Gil, J. Seijas, J. Albornoz, E. Revilla, M. Delibes, and A. Domínguez. 2014. Estimating the population size of the endangered Cantabrian brown bear through genetic sampling. *Wildlife Biology* 20:300–309.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. *The Journal of Wildlife Management* 53:7–15.
- Powers, D. M. W. 2007. Evaluation: from precision, recall and F-factor to ROC, informedness, markedness and correlation. Page School of Informatics and Engineering.
- Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709.
- Pritchard, G. T., and C. T. Robbins. 2008. Digestive and metabolic efficiencies of grizzly and black bears. *Canadian Journal of Zoology* 68:1645–1651.
- Proctor, M. F., W. F. Kasworm, K. M. Annis, A. G. MacHutchon, J. E. Teisberg, T. G. Radandt, and C. Servheen. 2018a. Conservation of threatened Canada-USA trans-border grizzly bears linked to comprehensive conflict reduction. *Human-Wildlife Interactions* 12:348–372.
- Proctor, M. F., B. N. McLellan, G. B. Stenhouse, G. Mowat, C. T. Lamb, and M. S. Boyce. 2018b. Resource Roads and Grizzly Bears in British Columbia and Alberta, Canada. Page Canadian Grizzly Bear Management Series.
- Proctor, M. F., B. N. McLellan, C. Strobeck, and R. M. . Barclay. 2004. Gender-specific dispersal distances of grizzly bears estimated by genetic analysis. *Canadian Journal of Zoology* 82:1108–1118.
- Proctor, M. F., B. N. McLellan, C. Strobeck, and R. M. R. Barclay. 2005. Genetic analysis reveals demographic fragmentation of grizzly bears yielding vulnerably small populations. *Proceedings of the Royal Society B: Biological Sciences* 272:2409–2416.
- Proctor, M. F., S. E. Nielsen, W. F. Kasworm, C. Servheen, T. G. Radandt, A. G. Machutchon, and M. S. Boyce. 2015. Grizzly bear connectivity mapping in the Canada-United States trans-border region. *Journal of Wildlife Management* 79:544–558.

- Proctor, M. F., D. Paetkau, B. N. McLellan, G. B. Stenhouse, K. C. Kendall, R. D. MacE, W. F. Kasworm, C. Servheen, C. L. Lausen, M. L. Gibeau, W. L. Wakkinen, M. A. Haroldson, G. Mowat, C. D. Apps, L. M. Ciarniello, R. M. R. Barclay, M. S. Boyce, C. C. Schwartz, and C. Strobeck. 2012. Population fragmentation and inter-ecosystem movements of grizzly bears in Western Canada and the Northern United States. *Wildlife Monographs* 180:1–46.
- Proctor, M., C. Lamb, and G. Machutchon. 2017. The grizzly dance between berries and bullets : relationships among bottom-up food resources and top-down mortality risk on grizzly bear populations in southeast British Columbia. Page Trans-border Grizzly Bear Project. Kaslo BC Canada.
- Proffitt, K. M., J. F. Goldberg, M. Hebblewhite, R. Russell, B. S. Jimenez, H. S. Robinson, K. Pilgrim, and M. K. Schwartz. 2015. Integrating resource selection into spatial capture-recapture models for large carnivores. *Ecosphere* 6:1–15.
- Province of British Columbia. 2012. Grizzly Bears- Environmental Reporting BC. [www.env.gov.bc.ca/soe/indicators/plants-and-animals/grizzly-bears.html](http://www.env.gov.bc.ca/soe/indicators/plants-and-animals/grizzly-bears.html).
- Purvis, A., J. L. Gittleman, G. Cowlshaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences* 267:1947–1952.
- Pusey, A. E., L. Pintea, M. L. Wilson, S. Kamenya, and J. Goodall. 2007. The contribution of long-term research at Gombe National Park to chimpanzee conservation. *Conservation Biology* 21:623–634.
- Quinn, C. B., P. B. Alden, and B. N. Sacks. 2019. Noninvasive sampling reveals short-term genetic rescue in an insular red fox population. *Journal of Heredity*:559–576.
- R Core Development Team. 2017. R foundation for statistical computing. R Development Core Team.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing., Vienna, Austria.
- Raglus, T. I., B. De Groef, S. Rochfort, G. Rawlin, and C. McCowan. 2019. Bone marrow fat analysis as a diagnostic tool to document ante-mortem starvation. *Veterinary Journal* 243:1–7.
- Ralls, K., J. D. Ballou, and A. Templeton. 1988. Estimates of lethal equivalents and the cost

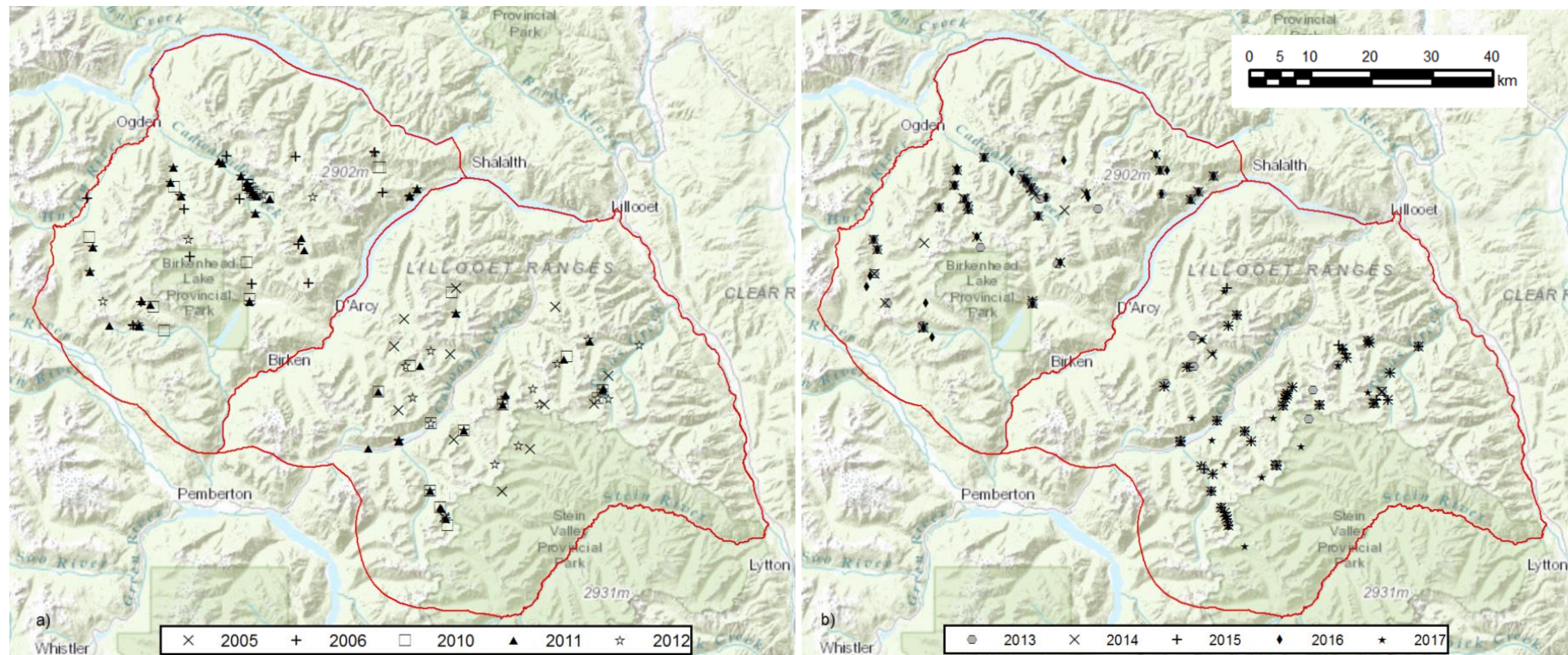
- of inbreeding in mammals. *Conservation Biology* 2:185–193.
- Ramcharita, R. K. 2000. Grizzly bear use of avalanche chutes in the Columbia Mountains, British Columbia. The University of British Columbia.
- Regehr, E. V., N. J. Hostetter, R. R. Wilson, K. D. Rode, M. S. Martin, and S. J. Converse. 2018. Integrated population modeling provides the first empirical estimates of vital rates and abundance for polar bears in the Chukchi Sea. *Scientific Reports* 8:1–12.
- Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: Its relationship to limiting factors. *Ecography* 23:466–478.
- Rho, P. 2002. Wetness: An Avenue Script for ArcView 3.2.
- Riley, S. J., G. M. Nessler, and B. A. Maurer. 2004. Dynamics of early wolf and cougar eradication efforts in Montana: Implications for conservation. *Biological Conservation* 119:575–579.
- Robbins, C. T., M. Ben-David, J. K. Fortin, and O. L. Nelson. 2012. Maternal condition determines birth date and growth of newborn bear cubs. *Journal of Mammalogy* 93:540–546.
- Robbins, C. T., C. C. Schwartz, K. A. Gunther, and C. Servheen. 2006. Grizzly bear nutrition and ecology studies in Yellowstone National Park. *Yellowstone Science* 14:19–26.
- Robin, A. X., N. Turck, A. Hainard, N. Tiberti, F. Lisacek, C. Sanchez, M. Müller, and M. X. Robin. 2015. pROC. CRAN.
- Romain-Bondi, K. A., R. B. Wielgus, L. Waits, W. F. Kasworm, M. Austin, and W. Wakkinen. 2004. Density and population size estimates for North Cascade grizzly bears using DNA hair-sampling techniques. *Biological Conservation* 117:417–428.
- Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2014. Spatial capture-recapture. Page Spatial Capture-recapture. 1st edition. Academic Press Elsevier Inc., Waltham, MA.
- Royle, J. A., R. B. Chandler, C. C. Sun, and A. K. Fuller. 2013. Integrating resource selection information with spatial capture-recapture. *Methods in Ecology and Evolution* 4:520–530.
- Royle, J. A., A. K. Fuller, and C. Sutherland. 2016. Spatial capture–recapture models allowing Markovian transience or dispersal. *Population Ecology* 58:53–62.

- Sawaya, M. A., J. B. Stetz, A. P. Clevenger, M. L. Gibeau, and S. T. Kalinowski. 2012. Estimating grizzly and black bear population abundance and trend in Banff National Park using noninvasive genetic sampling. *PLoS ONE* 7:e34777.
- Schwartz, C. C., M. A. Haroldson, and G. C. White. 2010. Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. *Journal of Wildlife Management* 74:654–667.
- Schwartz, C. C., M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161:1–68.
- Schwartz, C. C., S. D. Miller, and M. A. Haroldson. 2003. Grizzly Bear. Pages 556–586 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. *Wild Mammals of North America: Biology, Management, and Conservation*. 2nd edition. The Johns Hopkins University Press, Baltimore.
- Schwartz, C. C., and G. C. White. 2008. Estimating reproductive rates for female bears: proportions versus transition probabilities. *Ursus* 19:1–12.
- Selås, V. 2000. Seed production of a masting dwarf shrub, *Vaccinium myrtillus*, in relation to previous reproduction and weather. *Canadian Journal of Botany* 78:423–429.
- Sellers, R. A., S. D. Miller, T. S. Smith, and R. Potts. 1999. Population dynamics of a naturally regulated brown bear population on the coast of Katmai National Park and Preserve. Final Report. Anchorage.
- Serrouya, R., B. N. McLellan, G. D. Pavan, and C. D. Apps. 2011. Grizzly bear selection of avalanche chutes: testing the effectiveness of forest buffer retention. *Journal of Wildlife Management* 75:1597–1608.
- de Silva, S., and P. Leimgruber. 2019. Demographic tipping points as early indicators of vulnerability for slow-breeding megafaunal populations. *Frontiers in Ecology and Evolution* 7:1–13.
- Spedicato, G. A., T. S. Kang, S. B. Yalamanchi, and YadavDeepak. 2014. The markovchain Package: A Package for Easily Handling Discrete Markov Chains in R. [cran.rstudio.org](http://cran.rstudio.org).
- Stacey, P. B., and T. Mark. 1992. Environmental variation and the persistence of small populations. *Ecological Applications* 2:18–29.

- Stubben, C., and B. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* 22:1–23.
- Swenson, J. E., F. Sandegren, S. Brunberg, and P. Segerström. 2001. Factors associated with loss of brown bear cubs in Sweden. *Ursus* 12:69–80.
- Swenson, J. E., P. Wabakken, F. Sandegren, A. Bjärvall, R. Franzén, and A. Söderberg. 1995. The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildlife Biology* 1:11–25.
- Taberlet, P., J.-J. Camarra, S. Griffin, E. Uhres, O. Hanotte, L. P. Waits, C. Dubois-Paganon, T. Burke, and J. Bouvet. 1997. Noninvasive genetic tracking of the endangered Pyrenean brown bear population. *Molecular Ecology* 6:869–876.
- Tumanov, I. L. 1995. Reproductive characteristics of captive European brown bears and growth rates of their cubs in Russia. *Ursus* 10:63–65.
- Tumendemberel, O., M. Proctor, H. Reynolds, J. Boulanger, A. Luvsamjamba, T. Tserenbataa, M. Batmunkh, D. Craighead, N. Yanjin, and D. Paetkau. 2015. Gobi bear abundance and inter-oases movements, Gobi Desert, Mongolia. *Ursus* 26:129–142.
- VRI-Forest Vegetation Composite Polygons and Rand 1 Layer. 2017. . Ministry of Forests, Lands, Natural Resource Operations and Rural Development.  
<https://catalogue.data.gov.bc.ca/dataset/vri-forest-vegetation-composite-polygons-and-rank-1-layer>.
- Wakkinen, W. L., and W. F. Kasworm. 2004. Demographics and population trends of grizzly bears in the Cabinet–Yaak and Selkirk Ecosystems of British Columbia, Idaho, Montana, and Washington. *Ursus* 15:65–75.
- Wallace, R. B., R. A. Mittermeier, F. Cornejo, and J. P. Boubli. 2008. *Ateles chamek*. The IUCN Red List of threatened species.  
<https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T41547A10497375.en>.
- Waller, J. S., and R. D. Mace. 1997. Grizzly bear habitat selection in the Swan Mountains, Montana. *The Journal of Wildlife Management* 61:1032–1039.
- Wang, T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE* 11:1–17.

- Weber, W., and A. Rabinowitz. 1996. A global perspective on large carnivore conservation. *Conservation Biology* 10:1046–1054.
- Welch, C. A., J. Keay, K. C. Kendall, and C. T. Robbins. 1997. Constraints on frugivory by bears. *Ecology* 78:1105–1119.
- White, G. C. 2008. Closed population estimation models and their extensions in Program MARK. *Environmental and Ecological Statistics* 15:89–99.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Whittington, J., and M. A. Sawaya. 2015. A comparison of grizzly bear demographic parameters estimated from non-spatial and spatial open population capture-recapture models. *PLoS ONE* 10:1–17.
- Wielgus, R. B., and F. L. Bunnell. 1994. Sexual segregation and female grizzly bear avoidance of males. *The Journal of Wildlife Management* 58:405–413.
- Wittmer, H. U., B. N. McLellan, D. R. Seip, J. A. Young, T. A. Kinley, G. S. Watts, and D. Hamilton. 2005. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Canadian Journal of Zoology* 83:407–418.
- Wolf, C., and W. J. Ripple. 2017. Range contractions of the world’s large carnivores. *Royal Society Open Science* 4:1–11.
- Wood, S., and F. Scheipl. 2017. Generalized Additive Mixed Models using “mgcv” and “lme4.”
- Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3:165–173.
- Woods, J. G., D. Paetkau, D. Lewis, B. N. McLellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging of free-ranging black and brown bears. *Wildlife Society* 27:616–627.
- Zedrosser, A., S. M. J. G. Steyaert, H. Gossow, and J. E. Swenson. 2011. Brown bear conservation and the ghost of persecution past. *Biological Conservation* 144:2163–2170.
- Zipkin, E. F., and S. P. Saunders. 2018. Synthesizing multiple data types for biological conservation using integrated population models. *Biological Conservation* 217:240–250.

## **Supplementary Material**



**Figure S.1** Hair trap array for capture-recapture population monitoring in the North Stein Nahatlatch (NSN) and McGillvary Mountain (MM) grizzly populations in southwestern British Columbia, Canada, between **a)** 2005 and 2012 and **b)** 2013-2017. Panels are separated for clarity only. Red line shows the study area boundary and the search area for areal capture described in chapter 3.



**Table S.1** Model selection for detection parameters estimated using spatial capture-recapture methods in each the MM part of the South Chilcotin and NSN part of the Stein-Nahatlatch grizzly bear populations in southwest British Columbia, Canada, between 2005 and 2017. **a)** Step one: candidate models compare usage defined as the number of days a trap is open or closed per occasion (days) with usage defined as a binary indicating whether a trap was open or not during an occasion, while density could vary among years (D~ session). **b)** Step 2: candidate models for detection parameters ( $g_0$  and  $\sigma$ ) while density could vary among years (D~ session).

<b>a) Step 1</b>					
<b>Population</b>	<b>Model</b>		<b>K<sup>a</sup></b>	<b><math>\Delta AICc^b</math></b>	<b><math>\omega_i^c</math></b>
MM	$g_0(\sim 1)$ Usage: binary	$\sigma(\sim 1)$	10	0.00	1.00
	$g_0(\sim 1)$ Usage: days	$\sigma(\sim 1)$	10	61.89	0.00
NSN	$g_0(\sim 1)$ Usage: binary	$\sigma(\sim 1)$	11	0.00	1.00
	$g_0(\sim 1)$ Usage: days	$\sigma(\sim 1)$	11	50.53	0.00
<b>b) Step 2</b>					
<b>Population</b>	<b>Model</b>		<b>K<sup>a</sup></b>	<b><math>\Delta AICc^b</math></b>	<b><math>\omega_i^c</math></b>
MM	$g_0(\sim \text{type} + \text{sex} + (\text{type} * \text{sex}))$	$\sigma(\sim \text{sex})$	14	0.00	1.00
	$g_0(\sim \text{type})$	$\sigma(\sim \text{sex})$	12	30.98	0.00
	$g_0(\sim \text{type} + \text{sex})$	$\sigma(\sim \text{sex})$	13	33.09	0.00
	$g_0(\sim \text{type} + \text{time})$	$\sigma(\sim \text{sex})$	18	38.71	0.00
	$g_0(\sim \text{type} + \text{time} + (\text{type} * \text{time}))$	$\sigma(\sim \text{sex})$	24	47.94	0.00
	$g_0(\sim 1)$	$\sigma(\sim \text{sex})$	11	56.51	0.00
	$g_0(\sim \text{sex})$	$\sigma(\sim \text{sex})$	12	58.54	0.00
	$g_0(\sim \text{sex} + \text{time} + (\text{sex} * \text{time}))$	$\sigma(\sim \text{sex})$	24	63.79	0.00
	$g_0(\sim \text{time})$	$\sigma(\sim \text{sex})$	17	63.89	0.00
	$g_0(\sim \text{sex} + \text{time})$	$\sigma(\sim \text{sex})$	18	65.71	0.00
	$g_0(\sim 1)$	$\sigma(\sim 1)$	10	116.57	0.00
NSN	$g_0(\sim \text{type} + \text{sex} + (\text{type} * \text{sex}))$	$\sigma(\sim \text{sex})$	15	0.00	1.00
	$g_0(\sim \text{type})$	$\sigma(\sim \text{sex})$	13	19.74	0.00
	$g_0(\sim \text{type} + \text{sex})$	$\sigma(\sim \text{sex})$	14	20.42	0.00
	$g_0(\sim \text{sex})$	$\sigma(\sim \text{sex})$	13	23.25	0.00
	$g_0(\sim 1)$	$\sigma(\sim \text{sex})$	12	24.78	0.00
	$g_0(\sim \text{type} + \text{time})$	$\sigma(\sim \text{sex})$	18	30.98	0.00
	$g_0(\sim \text{sex} + \text{time})$	$\sigma(\sim \text{sex})$	18	33.35	0.00
	$g_0(\sim \text{time})$	$\sigma(\sim \text{sex})$	17	35.95	0.00
	$g_0(\sim \text{sex} + \text{time} + (\text{sex} * \text{time}))$	$\sigma(\sim \text{sex})$	23	46.92	0.00
	$g_0(\sim \text{type} + \text{time} + (\text{type} * \text{time}))$	$\sigma(\sim \text{sex})$	23	49.81	0.00
	$g_0(\sim 1)$	$\sigma(\sim 1)$	11	60.73	0.00

a No. model parameter

b Difference between AICc of model and the AICc of the highest ranked model

c Model weight

**Table S.2** Candidate models for detection probability ( $p$ ), estimated using Pradel robust design capture-recapture. Apparent survival ( $\phi$ ) and apparent recruitment ( $f$ ) could vary by sex and population,  $\phi$  ( $\sim$ sex+pop) and  $f$  ( $\sim$ sex +pop). Recapture probability ( $c$ ), was the same as  $p$ . **a)** Step one compared effort defined as the number of traps open per occasion ( $\sim$ effort) with the number of traps times length of the occasion in days ( $\sim$ both). **b)** Step two used the top model from step one to compare other covariates affecting capture probability  $p$ .

Model	K <sup>a</sup>	$\Delta$ AICc <sup>b</sup>	$\omega_i$ <sup>c</sup>
<b>a) Step one</b>			
$p$ ( $\sim$ effort)	8	0	1.00
$p$ ( $\sim$ both)	8	100.60	0.00
$p$ ( $\sim$ 1)	7	207.49	0.00
<b>b) Step two</b>			
$p$ ( $\sim$ sex + type + effort + (sex * type))		0.00	1.00
$p$ ( $\sim$ sex + type + effort)		28.18	0.00
$p$ ( $\sim$ sex + time + pop + type + effort)		45.03	0.00
$p$ ( $\sim$ type + effort)		48.22	0.00
$p$ ( $\sim$ pop + type + effort)		48.48	0.00
$p$ ( $\sim$ pop + type + effort + (pop * type))		50.49	0.00
$p$ ( $\sim$ time + type + effort)		65.21	0.00
$p$ ( $\sim$ time + effort)		78.92	0.00
$p$ ( $\sim$ time + type + effort + (time * type))		85.87	0.00
$p$ ( $\sim$ sex+ effort)		87.75	0.00
$p$ ( $\sim$ pop + effort)		106.50	0.00
$p$ ( $\sim$ effort)		107.38	0.00

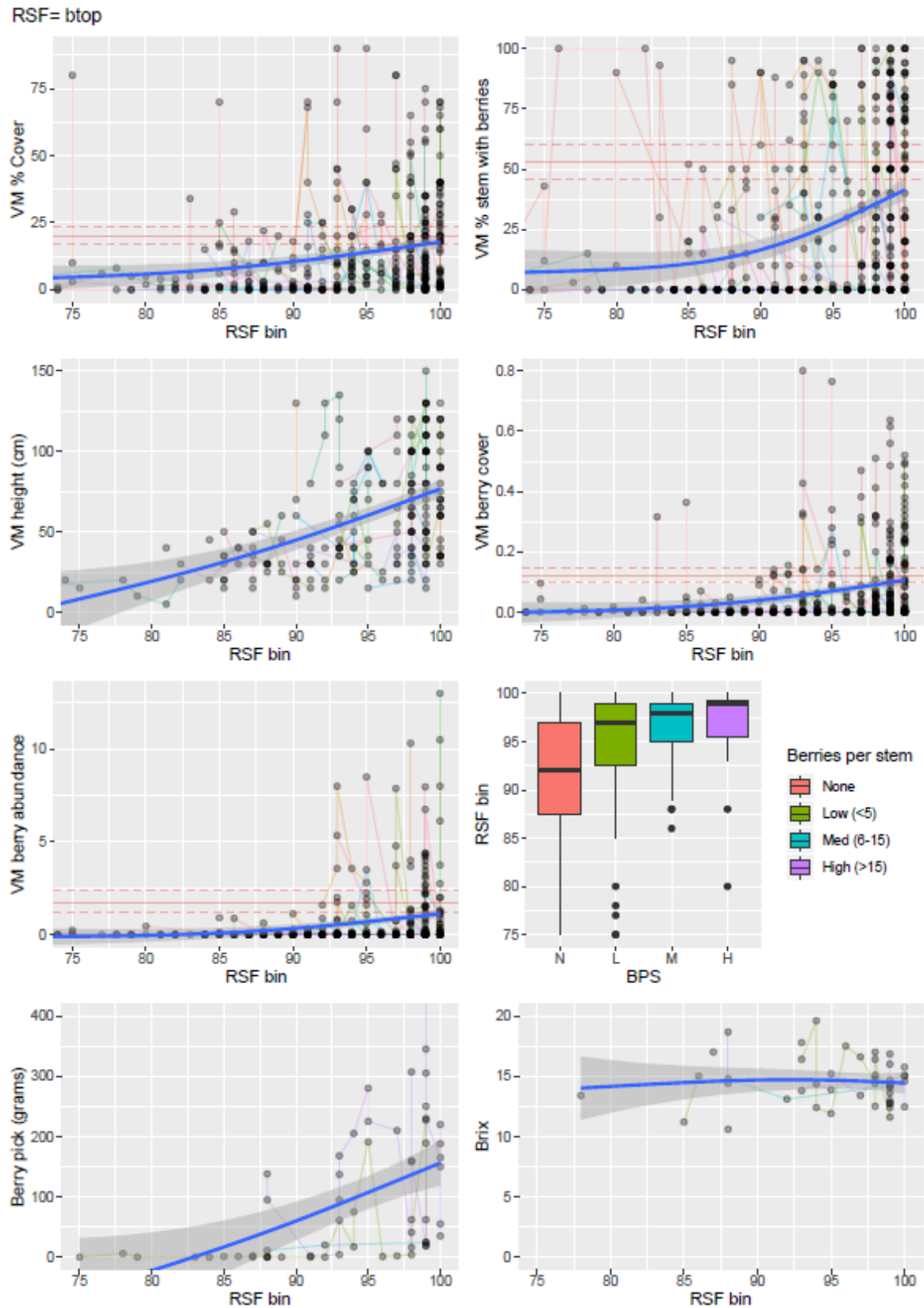
<sup>a</sup> No. model parameter

<sup>b</sup> Difference between AICc of model and the AICc of the highest ranked model

<sup>c</sup> Model weight

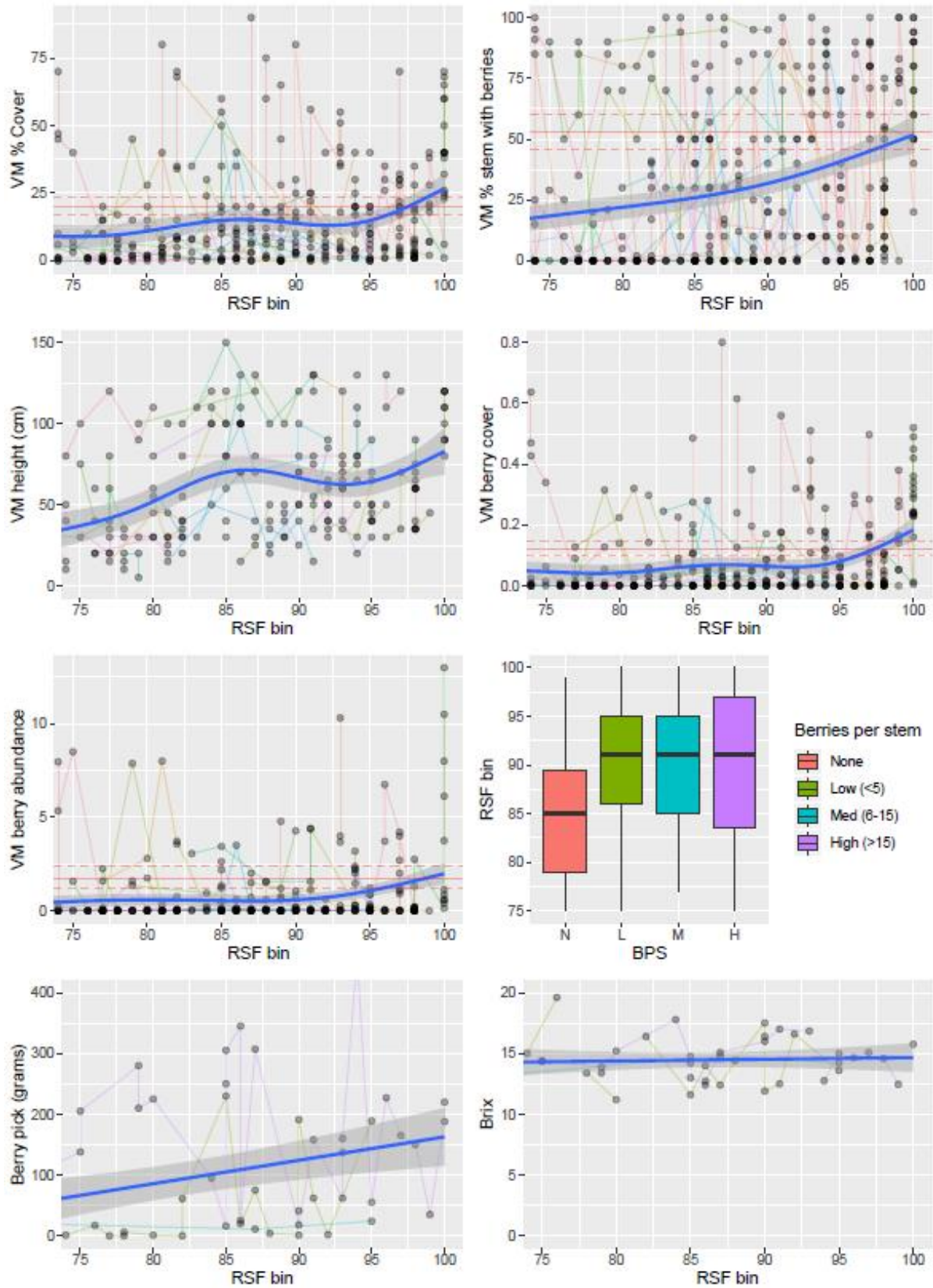
**Table S.3** Model coefficients for the top five Pradel robust design models to estimate apparent survival ( $\phi$ ) and apparent recruitment ( $f$ ) and derived population growth ( $\lambda$ ), for both the McGillvary Mountains (MM) part of the South Chilcotin and North Stein (NSN) part of the Stein-Nahatlatch grizzly bear populations in southwest British Columbia, Canada. Models fit using common detection probability ( $p$ ) estimated in a prior analysis  $p$  ( $\sim$ sex + type + effort + (sex\*type)). Effort refers to the number of traps per occasion and type refers to whether the trap was a hair trap or rub tree.

Model	AIC $\omega_i$	Sex	Pop	$f \pm SE$	$\phi \pm SE$	$\lambda \pm SE$
$\phi$ ( $\sim$ sex) $f$ ( $\sim$ sex + pop)	0.310	F	MM	$0.104 \pm 0.022$	$0.907 \pm 0.020$	$1.023 \pm 0.027$
		F	NSN	$0.060 \pm 0.019$	$0.907 \pm 0.020$	$0.972 \pm 0.024$
		M	MM	$0.176 \pm 0.026$	$0.800 \pm 0.030$	$1.014 \pm 0.034$
		M	NSN	$0.106 \pm 0.028$	$0.800 \pm 0.030$	$0.919 \pm 0.036$
$\phi$ ( $\sim$ sex + pop) $f$ ( $\sim$ sex)	0.180	F	MM	$0.091 \pm 0.020$	$0.919 \pm 0.019$	$1.019 \pm 0.024$
		F	NSN	$0.091 \pm 0.020$	$0.873 \pm 0.032$	$0.973 \pm 0.032$
		M	MM	$0.155 \pm 0.023$	$0.824 \pm 0.031$	$1.007 \pm 0.031$
		M	NSN	$0.155 \pm 0.023$	$0.738 \pm 0.047$	$0.922 \pm 0.043$
$\phi$ ( $\sim$ sex + pop) $f$ ( $\sim$ sex + pop)	0.156	F	MM	$0.100 \pm 0.022$	$0.914 \pm 0.020$	$1.026 \pm 0.026$
		F	NSN	$0.068 \pm 0.023$	$0.890 \pm 0.031$	$0.963 \pm 0.029$
		M	MM	$0.171 \pm 0.026$	$0.81 \pm 0.033$	$1.020 \pm 0.034$
		M	NSN	$0.118 \pm 0.033$	$0.770 \pm 0.049$	$0.904 \pm 0.042$
$\phi$ ( $\sim$ sex) $f$ ( $\sim$ pop)	0.081	F	MM	$0.140 \pm 0.018$	$0.893 \pm 0.021$	$1.055 \pm 0.028$
		F	NSN	$0.082 \pm 0.022$	$0.893 \pm 0.021$	$0.983 \pm 0.030$
		M	MM	$0.140 \pm 0.018$	$0.825 \pm 0.025$	$0.987 \pm 0.028$
		M	NSN	$0.082 \pm 0.022$	$0.825 \pm 0.025$	$0.915 \pm 0.031$
$\phi$ ( $\sim$ sex) $f$ ( $\sim$ sex)	0.081	F	MM	$0.140 \pm 0.018$	$0.893 \pm 0.021$	$1.055 \pm 0.028$
		F	NSN	$0.082 \pm 0.022$	$0.893 \pm 0.021$	$0.983 \pm 0.030$
		M	MM	$0.140 \pm 0.018$	$0.825 \pm 0.025$	$0.987 \pm 0.028$
		M	NSN	$0.082 \pm 0.022$	$0.825 \pm 0.025$	$0.915 \pm 0.031$

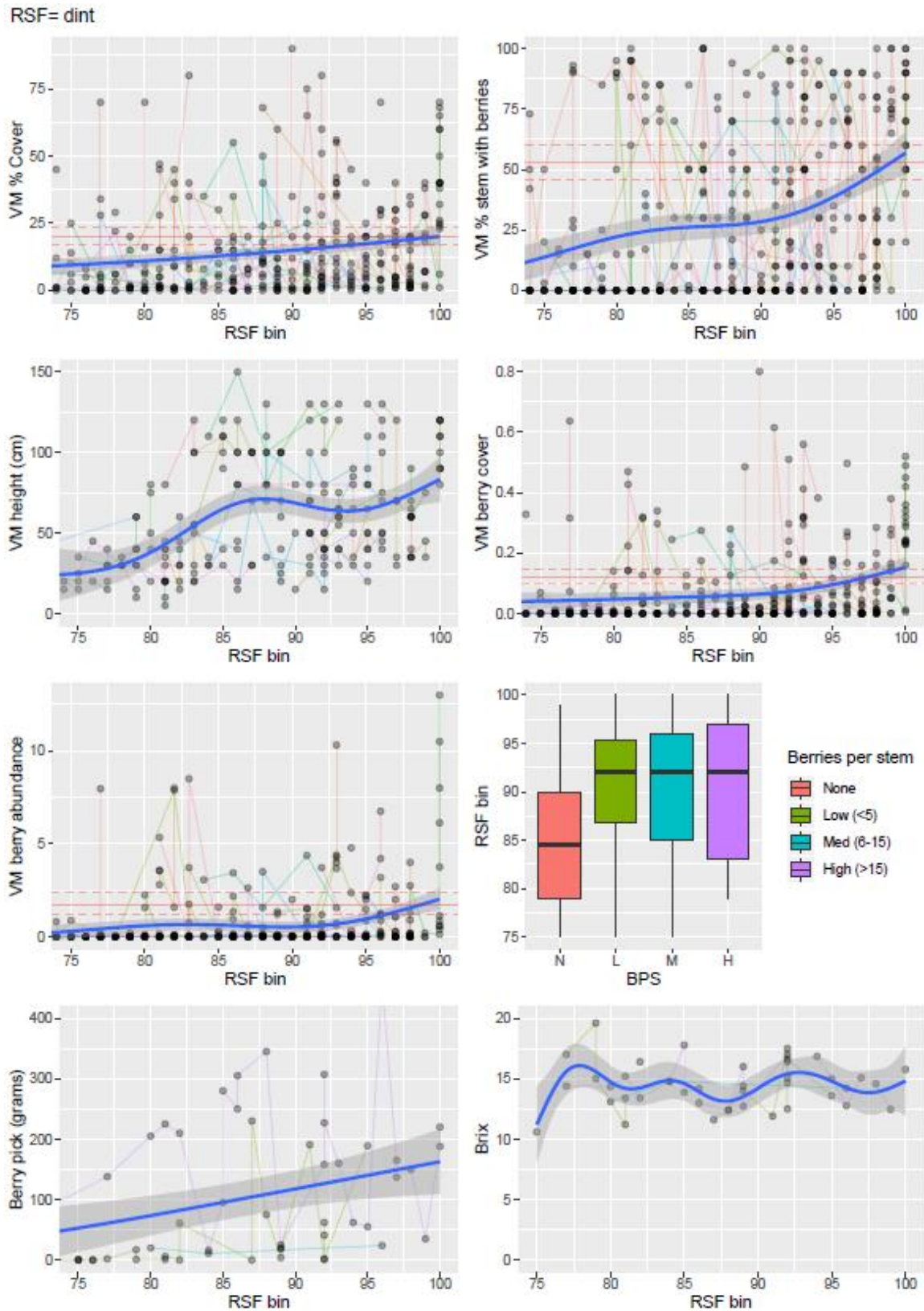


**Figure S.2** Non-linear relationships estimated using generalized additive models between the predicted top huckleberry RSF model (BTOP) and huckleberry (VM) metrics measured at model test plots across the McGillvary Mountain and North Stein Nahatlatch grizzly bear populations. See text for abundance definitions in section 4.3.5.

RSF= dtop



**Figure S.3** Non-linear relationships estimated using generalized additive models between the predicted top huckleberry RSF model (DTOP) and huckleberry (VM) metrics measured at model test plots across the McGillvary Mountain and North Stein Nahatlatch grizzly bear populations. See text for abundance definitions in section 4.3.5.



**Figure S.4** Non-linear relationships estimated using generalized additive models between the predicted top huckleberry RSF model (DINT) and huckleberry (VM) metrics measured at model test plots across the McGillvary Mountain and North Stein Nahatlatch grizzly bear populations. See text or abundance definitions in section 4.3.5.



**Table S.4** Model selection results for covariates influencing grizzly bear encounter rate ( $g0$ ), and movement scale ( $\sigma$ ) and density ( $D$ ) without density surface integration. See section 5.32 for covariate definitions.

$D$	$g0$	$\sigma$	K	$\Delta AICc$	$\omega_i$
$D(\text{pop})$	$g0(\text{trap-type} * \text{sex})$	$\sigma(\text{sex})$	8	0	0.82
	$g0(\text{trap-type} + \text{sex})$	$\sigma(\text{sex})$	7	3.47	0.15
	$g0(\text{trap-type})$	$\sigma(.)$	5	6.55	0.03
	$g0(\text{sex})$	$\sigma(\text{sex})$	6	11.71	0
	$g0(\text{herb})$	$\sigma(.)$	5	16.39	0
	$g0(\text{b})$	$\sigma(.)$	5	16.49	0
	$g0(\text{wbp})$	$\sigma(.)$	5	17.47	0
	$g0(.)$	$\sigma(.)$	4	18.21	0
	$g0(\text{early})$	$\sigma(.)$	5	19.49	0
	$g0(\text{bk})$	$\sigma(.)$	5	19.72	0
	$g0(\text{berry})$	$\sigma(.)$	5	19.88	0
	$g0 \sim 1$	$\sigma(.)$	5	20.60	0
	$g0 \sim t$	$\sigma(.)$	8	21.10	0
$D(.)$	$g0(.)$	$\sigma(.)$	3	36.36	0
$D(\text{sex})$	$g0(.)$	$\sigma(.)$	4	38.60	0

<sup>a</sup> No. model parameter

<sup>b</sup> Difference between AICc of model and the AICc of the highest ranked model

<sup>c</sup> Model weight