Grizzly bear population dynamics across productivity and human influence gradients

by

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Abstract

Coexistence with large carnivores is one of the greatest conservation challenges across the globe, in part because mechanisms of coexistence are unknown or contested. Large carnivores can be conflict-prone and pose real or perceived threats to human life and property. In North America, grizzly bears (*Ursus arctos*) typify the struggle to conserve and coexist with large carnivores amongst a matrix of competing land uses. Grizzly bears are a symbol of wildness to society, but the management of this species can divide communities, derail collaborative conservation initiatives, and are the focus of high-profile media coverage and lawsuits. At the center of this controversy is scientific uncertainty around population dynamics of the species, primarily relating to population size, limiting factors, and the ecology of conflict. The contemporary threats of wilderness loss, human population expansion, and climate change pose both a no-analog future for grizzly bears, but also opportunity. Leveraging novel ecological tools, and the ongoing human-induced landscape and climate change, considerable opportunity exists to investigate the mechanisms driving grizzly bear population dynamics and those promoting coexistence—enduring populations of wildlife in human-dominated landscapes. The goal of this dissertation was to test the factors limiting grizzly bear population dynamics across ecosystems, update local population estimates, and to identify the mechanisms promoting carnivore coexistence and those exacerbating it. Here I leverage 40 years of demographic data on grizzly bears collected across ecosystems to investigate hypotheses around grizzly bear population dynamics across productivity and human influence gradients in British Columbia (BC). This work provides multiple lines of evidence that grizzly bear populations purportedly coexisting in human-dominated landscapes are highly reliant on demographic rescue (immigration) from adjacent wilderness areas. This source-sink dynamic is exacerbated when attractive habitat decouples the link between habitat quality and fitness, resulting in an ecological trap. Human influences such as human population density and road density have the potential to create strong, top-down limiting forces on bear populations that dwarf bottom-up influences. However, much of British Columbia is not permanently occupied by people, and the majority of grizzly populations across the province are more strongly bottom-up limited. Considerable potential exists to ensure the conservation and coexistence of bears is a success if evidence-based mitigation is executed collaboratively and equitably. I provide insight into the response of bear density to mitigation measures for reducing road density and highlight several cases where evidence from this dissertation lead to meaningful conservation actions that will benefit bears, a variety of wildlife inhabiting similar areas, and people. Collectively, this dissertation provides strong inference into the spatial structure and drivers of grizzly bear population dynamics across ecosystems and suggests that data generated for applied problems can be leveraged to test theory while informing conservation at massive spatial extents.

Preface

This dissertation is an original work by Clayton Lamb. The grizzly bear telemetry research projects, of which this dissertation is a part, received research ethics approval from the University of Alberta Research Ethics Board, “Rates and causes of grizzly bear mortality”, No. AUP00002181, June 14, 2017. Ethical approval for the analyses of the genetic tagging data used here was provided by the University of Alberta Research Ethics Office, December 2014 (Category A, non-invasive).

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Three papers that support this dissertation were also published during Clayton Lamb’s PhD, but were not part of the core dissertation on population dynamics, and are not included in this document. The three papers can be found here:

Lamb, C.T., Festa-Bianchet, M., Boyce, M.S. 2018. Invest long term in Canada’s wilderness. *Science*. 359(6379) pp. 1002. **PDF**

Lamb, C.T., Walsh, D., Mowat, G. 2016. Factors influencing detection success of grizzly bears at genetic sampling sites. *Ursus.* 27(1): 31-44. **PDF**

Lamb, C.T., G. Mowat, S. Gilbert, B.M. McLellan, S.E. Nielson, S. Boutin. 2017. Density-dependent signaling: An alternative hypothesis on the function of chemical signaling in a non-territorial solitary carnivore. *PLoS ONE*. **PDF**

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1 Chapter 1: Introduction

1.1 Context

The conservation of large carnivores is one of the greatest, and defining, challenges of our time (Estes *et al.* 2011; Ripple *et al.* 2014). Large carnivores once roamed across 96% of the terrestrial globe (circa 1500), but today these intact large carnivore guilds cover a mere 36% of this same area (Wolf & Ripple 2017). Carnivore populations, and their ranges, have been historically reduced through direct persecution by people in response to real, and perceived, threats to human life and property (e.g. livestock, households, vehicles) (Ripple *et al.* 2014). In contrast to the threats posed by large carnivores, these animals can also provide tangible benefits to human safety and health (Gilbert *et al.* 2017; Braczkowski *et al.* 2018), profoundly influence ecosystems (Estes *et al.* 2011; Ford *et al.* 2014), and are featured heavily in many western (e.g. Kellog's Tony the Tiger) and indigenous cultures (e.g. the spirit bear); suggesting that conserving and coexisting with these species has high social, ecological, and cultural value. The contemporary threats of wilderness loss, human population expansion, and climate change, pose both a no-analog future for large carnivores, but also opportunity. Leveraging novel ecological tools (Schwartz, Luikart & Waples 2007; Kays *et al.* 2015), and the ongoing human-induced landscape and climate change, considerable opportunity exists to investigate the mechanisms driving large carnivore population dynamics and those promoting carnivore coexistence—enduring populations of wildlife in human-dominated landscapes—in the 21st century. Human influence on carnivore populations is expanding into the most remote areas of the globe (Potapov *et al.* 2017), however, governments and conservation professionals stand to make considerable progress in conserving large carnivores if armed with insightful and accurate evidence (Karanth & Chellam 2009; Hoffmann *et al.* 2010).

Three main questions structure the primary evidence required for large carnivore conservation: 1) what limits population density? 2) how do individuals and populations exist in human dominated areas that are highly lethal, yet support persisting populations, and 3) how can evidence from 1 and 2 be leveraged to conserve populations? Underlying these applied questions are fundamental questions in population and behavioral ecology that form the basis of evidence that informs action.

Identifying the processes limiting population density remains at the core of population ecology (Krebs *et al.* 1995; Sinclair & Krebs 2002). Population density and persistence are ultimately controlled by one or more of the following factors: top-down (predation) (Estes *et al.* 2011; Darimont *et al.* 2015; Hatton *et al.* 2015), competition (within and amongst species) (Coulson *et al.* 2001; Sibly 2005; Bonenfant & Gaillard 2009), and bottom-up (food resources) (Boutin 1990; Krebs *et al.* 1995). The cumulative influence of these factors on populations remains a source of considerable scientific debate and uncertainty (Krebs 2002a; Sutherland *et al.* 2013), especially for carnivores (Karanth & Chellam 2009; Karanth *et al.* 2013; Gilroy, Ordiz & Bischof 2015) despite their overrepresentation in scientific publications and funding (Martín-López *et al.* 2009). The wide ranging, low density, elusive, and dangerous nature of large carnivores has historically reduced their inclusion in mammalian population dynamic research, which was largely dominated by small mammal, avian, and ungulate research (Krebs *et al.* 1995; Gaillard *et al.* 2000; Coulson *et al.* 2001; Karanth & Chellam 2009). However, the recent advent and application of three technologies (genetic tagging, remote cameras, and GPS telemetry collars) to wildlife ecology in the late 1990s has provided means to study elusive and wide-ranging large carnivores at previously unattainable spatial extents. For example, using a combination of remote cameras and telemetry, Balme, Slotow & Hunter (2009) assessed the efficacy of conservation actions on leopard (*Panthera pardus*) demography in South Africa. Leopard survival and population density increased, and populations grew at 14-16% a year suggesting the conservation actions—reducing conflict and human-caused mortality—were successful and were a primary factor limiting this population. Identifying the factors limiting large carnivore populations forms a critical component of their conservation and is slowly filling a knowledge gap unlocked by new monitoring technologies.

A no-analog future of large carnivores purportedly coexisting in heavily human-dominated landscape is developing across the globe and challenging long-standing views of carnivore conservation (Carter *et al.* 2012; Gaynor *et al.* 2018; Perino *et al.* 2019). Range recolonization into, and across, human dominated areas have been documented in localized areas, in Asia (Karanth & Chellam 2009; Chapron *et al.* 2014), North America (LaRue *et al.* 2012; Morehouse & Boyce 2016), and Africa (Woodroffe 2011), suggesting that carnivore recovery amongst people is possible. However, a fundamental disagreement surrounds the mechanisms promoting carnivore coexistence in human dominated areas. The debate centers on whether behavioural adaptation of animals (e.g. nocturnality, or risk avoidance)(Carter *et al.* 2012; Tucker *et al.* 2018; Gaynor *et al.* 2018), and changing social values of people (Butler, Shanahan & Decker 2003; Chapron & López-Bao 2016; Bruskotter *et al.* 2017; Gaynor *et al.* 2018) are sufficient to create persisting landscapes of coexistence, or, if more secure source populations of carnivores in connected wilderness areas maintain coexistence landscapes through source-sink dynamics (Hanski 1998; Karanth *et al.* 2013; Gilroy *et al.* 2015). Protecting wilderness (land sparing) has long been a dominant strategy for conserving many large carnivore populations across the globe (Woodroffe & Ginsberg 1998; Karanth & Chellam 2009; Wikramanayake *et al.* 2011). However, recent observations of large carnivores recolonizing human-dominated areas in Europe, beyond the demographic reach of wilderness (Chapron *et al.* 2014; Lopez-Bao *et al.* 2015), and coexisting near people via nocturnal strategies (land sharing) (MacHutchon *et al.* 1998; Carter *et al.* 2012; Gaynor *et al.* 2018) has challenged the land sparing approach (Lopez-Bao *et al.* 2015). These observations of large carnivores recolonizing human-dominated areas, and subsequent assertions of coexistence, have since been criticized for lacking landscape-level demographic data to identify the density and vital rates of large carnivores in these areas and the potentially critical role source-sink dynamics might play in sustaining these populations (Karanth *et al.* 2013; Gilroy *et al.* 2015). With ongoing global efforts (i.e., United Nations Aichi Target 11)(Lamb, Festa-Bianchet & Boyce 2018a) to protect rapidly disappearing wilderness (Potapov *et al.* 2017), there is a need to resolve the uncertainty surrounding the role of wilderness in sustaining large carnivore populations as continuous metapopulations (Wiens 2007) across human influence gradients.

Taking evidence through to meaningful conservation action for wildlife populations is one of the central goals of conservation biology. There are generally four situations that typify the axes from evidence to action: 1) evidence was sufficient, was used, and had positive impacts on wildlife populations, 2) evidence was sufficient, was not used, 3) evidence was insufficient, was not used, and 4) evidence was insufficient, was used, and had either positive or negative impacts on wildlife populations—as the outcome of this would largely be left up to chance. Classic examples of #1 are found in most ecology textbooks and include saving the California condor (*Gymnogyps californianus*) from near extinction following the ban of toxic lead ammunition that was poisoning them (Finkelstein *et al.* 2012), or reintroducing wolves (*Canis lupis*) to Yellowstone, heralded as a global conservation success and restoration of an ecosystem (Ripple *et al.* 2014). Situations where evidence is abundant, but not used (#2) are unfortunately common in conservation biology and typically arise due to socioeconomic constraints on the actions that would benefit wildlife. Examples include the failure to restore threatened caribou (*Rangifer tarandus*) habitat in Canada, largely due to their habitat occurring in globally significant oil and gas reserves (Hebblewhite 2017), or the reduction of global road densities to benefit large carnivore populations, as the majority of the global roads support critical transportation of people, or resource extraction from rural and wilderness areas (Ceia-Hasse *et al.* 2017). Insufficient evidence creating apathy and no action (#3) is common, but does not mean these "data-deficient" species are not imperiled. Howard & Bickford (2014) assessed the likely extinction risk for data deficient amphibians by extrapolating risk from assessed species based on life history traits, environmental variables, and habitat loss. Their results suggested that data deficient species were at greater risk than their fully assessed, and more evidence-rich, conspecifics. Finally, unintended outcomes from conservation actions may arise when action is taken on insufficient or inappropriate evidence (#4, sensu (Ford *et al.* 2019)). For example, the removal of non-native sheep prior to the creation of Patagonia National Park substantially increased fawn predation of huemul deer (*Hippocamelus bisulcus*)—the species the park was designed to protect—precipitating population declines (Wittmer, Elbroch & Marshall 2013). Similarly, bans on trophy hunting that are based on opposition to the moral or ethical acts of trophy hunting, but lack appropriate evidence on the population-level processes or local community values surrounding trophy hunting, can at worst exacerbate biodiversity loss (Di Minin, Leader-Williams & Bradshaw 2016a), or at minimum erode the social and collaborative support required to conserve wildlfe (Naidoo *et al.* 2016; Angula *et al.* 2018). Taken together, these examples highlight the need for sufficient evidence, that can be used appropriately and collaboratively, to conserve wildlife.

Current levels of conservation efforts are predicted to be insufficent to conserve many of the world's large carnivores (Clark, Paquet & Curlee 2003; Hoffmann *et al.* 2010; Di Minin *et al.* 2016b). However, emerging technologies for coexstance, if applied in accordance with appropriate evidence on limiting factors, create considerable optimism for large carnivore conservation. Highways, railways, and associated human settlement can fracture population connectivity (Proctor *et al.* 2012), and contribute to carnivore mortaity (Gilhooly *et al.* 2019). Novel approaches such as highway fencing and wildlife overpasses (Ford, Barrueto & Clevenger 2017), or early warning systems to alert animals to oncoming trains (Backs, Nychka & St. Clair 2017) may reduce or completely remove the influence of these transportation corridors on carnivores. For example, (Sawaya, Kalinowski & Clevenger 2014) show that grizzly bear (*Ursus arctos)* genetic connectivity was rapidly re-established following highway fencing and the creation of wildlife overpasses, which directly reduced bear collisions and mortality in corridor sections (Gilhooly *et al.* 2019). Similarly, (Miller *et al.* 2016) highlight the effectiveness of electric fencing, fladry, and chemical deterrents in reduding livestock predation by multiple carnivore species. These results suggest that simple, evidence-based technologies, can contribute to carnivore conservation and coexistence.

With increasing pressures on the natural world and limited conservation funding, ecologists are increasingly required to conduct work with applied insights to inform mitigation of immediate conservation concern (Krebs 2018). This applied ecology needn't be free of theoretical insight and can instead create an avenue for testing theory which can then flow into applied outcomes for wildlife. Although potentially troublesome for wildlife, climate and habitat change present a natural experiment occurring at a global scale. There is substantial opportunity to use the large gradients of human influence and habitat quality across massive spatial scales to ask questions steeped in theoretical ecology, that create tangible, and actionable evidence. With mounting threats to wildlife populations and polarization around large carnivore management, there is an urgent need for scientists to generate insightful evidence that can be leveraged to effectively conserve populations (Karanth & Chellam 2009; Hoffmann *et al.* 2010).

1.2 Focal Species: Grizzly Bear

Large carnivores are characterized as low-density, wide-ranging and slow reproducing (Ripple *et al.* 2014). Large carnivores consume a variety of diet items. Two-thirds of the world's large carnivore species subsist off meat exclusively, and one-third are omnivores or vegetarian (Ripple *et al.* 2014). The large body and home range size of these animals create high energy demands, paired with low reproduction rates, making individuals and populations of large carnivores particularly susceptible to conflict with humans over food and space.

Here I focus on grizzly bears in North America, which typify large carnivores on the continent. Grizzly bears are apex omnivores that exist at low densities, can range over 1000s of km^2, and produce few offspring, which they do not produce until they are at least 5-7 years old. Further, this species hibernates during the winter, surviving (and females producing cubs) on fat reserves accumulated during their 5-7 active months of the year. This constrained active season, and the need to generate massive fat reserves makes this wide-ranging, large (200-1000 lbs) carnivore especially food motivated and conflict-prone.

The global *Ursus arctos* range decreased by >40% between 1500-2000, but recent evidence suggests it is now increasing, as seen in Europe (Chapron *et al.* 2014), Canada (Morehouse & Boyce 2016), and the United States (Bjornlie *et al.* 2014). Much of this expansion has been outward from secure wilderness areas, into more human-dominated landscapes. As a result, bear conflicts with, and attacks on, humans are increasing (Bombieri *et al.* 2019). Further, these dramatic conflicts between people and bears are high profile and generate more media coverage than those with any other terrestrial or aquatic predator (Bombieri *et al.* 2019). These animals are icons of wilderness and grandeur, yet can be conflict-prone and dangerous to humans, creating unique and challenging issues for managing and coexisting with this species.

The management of North America's grizzly bear populations is difficult and polarizing. Efforts to manage grizzly bears, regardless of whether the goal is to increase or decrease abundance, are often met with strong opposition, creating a challenging situation for resource managers. Numerous lawsuits surrounding grizzly bear management in USA and Canada have been filed and fought in court. The lawsuits range from opposition to the creation of a hunt (Christensen 2018), or cessation of hunting (Brooks 2019), and whether the species should be listed (Tallman 2011; Christensen 2018) or not (Anderson 2017) under the US Endangered Species Act. At the center of these debates is uncertainty around the population ecology of grizzly bears (Tallman 2011; Anderson 2017), including current population densities, and their trajectory under future changes in climate, human influence on the landscape, and management regimes (Pease & Mattson 1999; Artelle *et al.* 2013; Roberts, Nielsen & Stenhouse 2014; van Manen *et al.* 2015; McLellan *et al.* 2017; Darimont *et al.* 2018).

Considerable opportunity exists in leveraging the large gradient of habitat productivity and human influence across the grizzly bear range to test the environmental and anthropogenic influences structuring grizzly bear population dynamics across massive spatial extents. Resolving this uncertainty stands create mechanistic insight to increase the capacity for collaborative and effective conservation actions targeted towards this species.

1.3 Scope and Goals of this Dissertation

The unifying theme of this dissertation is that grizzly bear populations are heavily impacted by human influence, but the species' inherent dispersal ability, paired with connected wilderness areas and advances in mitigation technology are poised to create persisting coexistence landscapes. The mechanistic, large-extent, insight stemming from this dissertation were made possible due to recent advances in wildlife (genetic tagging and GPS collars), habitat monitoring technology (remote sensing), and a collaborative research framework facilitating the pooling of 1000s of monitored bears and vegetation plots. Throughout this dissertation I rely on multiple hypotheses, confronted with multiple lines of evidence, to make strong inference. I begin by reviewing the immense opportunity genetic tagging has created for population ecology across the globe (Chapter 2), then use these approaches to investigate the factors limiting grizzly population density: in a threatened population and test the influence of road density and mitigation strategies (Chapter 3), and across British Columbia (BC, Chapter 4). Following this I test the ecological trap hypothesis in southeast BC (Chapter 5) and the role of source-sink dynamics and behavioral adaptation in coexistence landscapes across BC (Chapter 6). Below I highlight the specific hypotheses and analyses used in my dissertation chapters

In Chapter 2, I review the potential for genetic tags—a unique sequence of DNA loci used to identify individuals, species, sex, and lineage—to answer the most pressing questions in ecology across the globe: (1) Why and how does population density change across space? (2) Why and how does population size change through time? (3) How and at what rate do organisms move between populations and across space? (4) How can negative interactions between people and wildlife be mitigated? I apply the approaches reviewed to a long-term genetic tagging dataset from the southern Canadian Rockies, to answer the four questions above and highlight the integrated, large-extent insight possible from a single genetic tagging dataset.

In Chapter 3, I quantify the influence of habitat quality, road density, and road closures on the density and distribution of a threatened grizzly bear population using genetic spatial capture recapture (SCR). Public concern about timber extraction and road densities in the Kettle-Granby Grizzly Bear Population Unit (GBPU), paired with government uncertainty about the population status prompted this work. A natural experiment was set up when roads in the area were closed to public access following the 1997 population inventory in the region, allowing me to partition out the influence of roads, and human use of the roads, on bear population density. I extend the inference from the SCR model to predict the likely range expansion of this range-edge population into the Okanagan Valley. This study highlights, for the first time, the role of road density, and public access on roads in limiting bear density and provides empirical predictions of the recolonization frontier for this species.

In Chapter 4, I compiled the majority of genetic tagging data for grizzly across BC (>1,900 animals) to assess the degree of bottom-up vs. top-down limitation acting on grizzly bear populations using spatial capture recapture. I provide an updated, spatially-explicit population estimate for grizzly bears across BC and quantify the number of bears that could potentially live in the Province without human influence. This work is the first fine-scale, large-extent analysis of limits to grizzly bear population density and reveals strong spatial structure in limiting factors across BC.

In Chapter 5, I test for the presence, and demographic effects of an ecological trap in an internationally significant grizzly bear population in Canada's southern Rocky Mountains. The ecological trap hypothesis posits that maladaptive habitat selection can occur when novel conditions decouple the link between habitat quality and fitness, a situation often linked to the rapid human-induced changes on the landscape. To date, there have been large carnivore studies that hint at the presence of an ecological trap, but none that generated sufficient evidence required to delineate an ecological trap: (i) individuals must show equal or greater selection for trap habitat relative to surrounding source habitats, (ii) the fitness of individuals using trap habitat must be lower than the fitness of individuals not using the trap, and (iii) to have persistent, population-level effects, animals must move from source habitats into the ecological trap. Evaluation of this hypothesis with the required evidence provides a robust test of the ecological trap hypothesis and the far-reaching effects of localized mortality on populations removed from the ecological trap.

In Chapter 6, I pool data from telemetry and genetic tagging projects conducted across BC since 1978, to quantify the demographic and bevioural mechanisms shaping coexistence landscapes for grizzly bears. I specifically quantify the response of grizzly bear population density, survival, reproduction, and immigration across a gradient of human influence, while controlling for habitat productivity. Further, I test for behavioral responses, either spatial or temporal avoidance, that mitigate the risks of living in human-dominated areas and contribute to coexistence. This study provides insight into the role of wilderness (areas with little to no human disturbance), connectivity, and carnivores as active participants in sustaining coexistence landscapes.

2 Chapter 2: Genetic tagging in the Anthropocene: scaling ecology from alleles to ecosystems

2.1 Introduction

The extent to which climate change and habitat loss will impact the density and distribution of wild populations in the future is one of the greatest sources of scientific uncertainty in modern ecology and conservation (Dirzo *et al.* 2014; Lewis & Maslin 2015; Ibisch *et al.* 2016; Newbold *et al.* 2016; Krebs 2018). Resolving this uncertainty requires a mechanistic approach to understand the processes that limit the distribution and abundance of organisms – ecology's central question. Equipped with a robust set of quantitative tools, investigators are in a strong position to derive new insights from environmental change to reveal the mechanisms driving population change. Currently, four broad questions structure this line of inquiry:

1) Why and how does population density change across space?
2) Why and how does population size change through time?
3) How and at what rate do organisms move between populations and across space?
4) How can negative interactions between people and wildlife be mitigated?

These questions form the basis of the heart of ecology and unanswered questions at its frontier (Sutherland *et al.* 2013). Further, questions 1-4 are not mutually exclusive, with clear feedback pathways between questions, e.g., decreased connectivity that drives population declines, or high animal density resulting in elevated human-wildlife conflict. Investigators can answer each question in isolation but uncovering the intricate, and often synergistic mechanisms driving observed patterns often requires answers to most or all of the questions. Currently, many methods used to answer these questions are expensive, invasive, or information-scarce (Figure 1, Hebblewhite & Haydon 2010; Burgar *et al.* 2018), limiting sampling effort and the strength of inference. For example, telemetry data can be used to monitor the rates and causes of mortality or to identify connectivity corridors but not to estimate population density unless a complete census is performed (McLellan 1989). Similarly, camera traps can, in some cases, be used to identify individuals and estimate density, but they provide limited connectivity information (Royle *et al.* 2014a) and are not currently a robust tool for estimating demographic parameters of unmarked animals (Chauvenet *et al.* 2017; Burgar *et al.* 2018).

A more efficient and information-rich approach to answering all four of the critical questions in ecology outlined above would adopt minimally-invasive approaches that are cost-effective to initiate over vast areas. Such methods would be further valuable if links could be identified between population density, trajectory, movement of individuals, and interactions between people and wildlife (Figure 2-1 & Figure 2-2). Genetic tags— a unique sequence of DNA loci used to identify individuals and their species, sex, and lineage—combined with modern analytical methods (e.g., spatial capture recapture [SCR], Royle *et al.* 2017) have emerged as one of the most promising approaches to meet these demands, particularly for ecological process distributed across large spatial extents and for large, elusive, sensitive, unmarked or low-density species (Taberlet, Waits & Luikart 1999; Lukacs & Burnham 2005; Schwartz *et al.* 2007; Proctor *et al.* 2010) (Figure 2-3). Genetic tags derived from spoors (e.g., scat, hair, feathers, saliva), which are used to genotype individuals, produce a unique, and immutable identification tag for each organism. Information from genetic tags can also include sex (Waits & Paetkau 2005; Lamb, Robson & Russello 2014), and for some material, such as hair, additional molecular and hormone analyses can provide age-class (Carroll *et al.* 2018; Cattet *et al.* 2018), reproductive status (Cattet *et al.* 2017), diet (Mowat, Curtis & Lafferty 2017a), and stress-level (Lafferty *et al.* 2015). These spoors can be collected using minimally-invasive methods (e.g. Piggott & Taylor (2003) or Henry & Russello (2011), also termed "non-invasive"), over vast areas, and by non-specialist participants like citizen scientists. For example, bears rub their bodies on trees, likely to signal occupancy to conspecifics (Lamb *et al.* 2017a). Researchers can identify these ‘rub trees’ and collect residual hair follicles left on the bark or on augmented hair collectors (e.g., barbed wired). The hair follicles are then used to extract DNA to identify individuals (Kendall *et al.* 2009). This approach has been used across the range of brown bears (*Ursus arctos*), including at least 4,795 trees in a single 31,410 km^2 study area (Kendall *et al.* 2009). Citizen scientists are now collecting hair from a network of bear rub trees in North America’s Rocky Mountains (Morehouse & Boyce 2016; Lamb *et al.* 2017a), stimulating public interest in wildlife conservation, while offering a powerful approach to democratize science in a widespread manner (Schuttler *et al.* 2018).

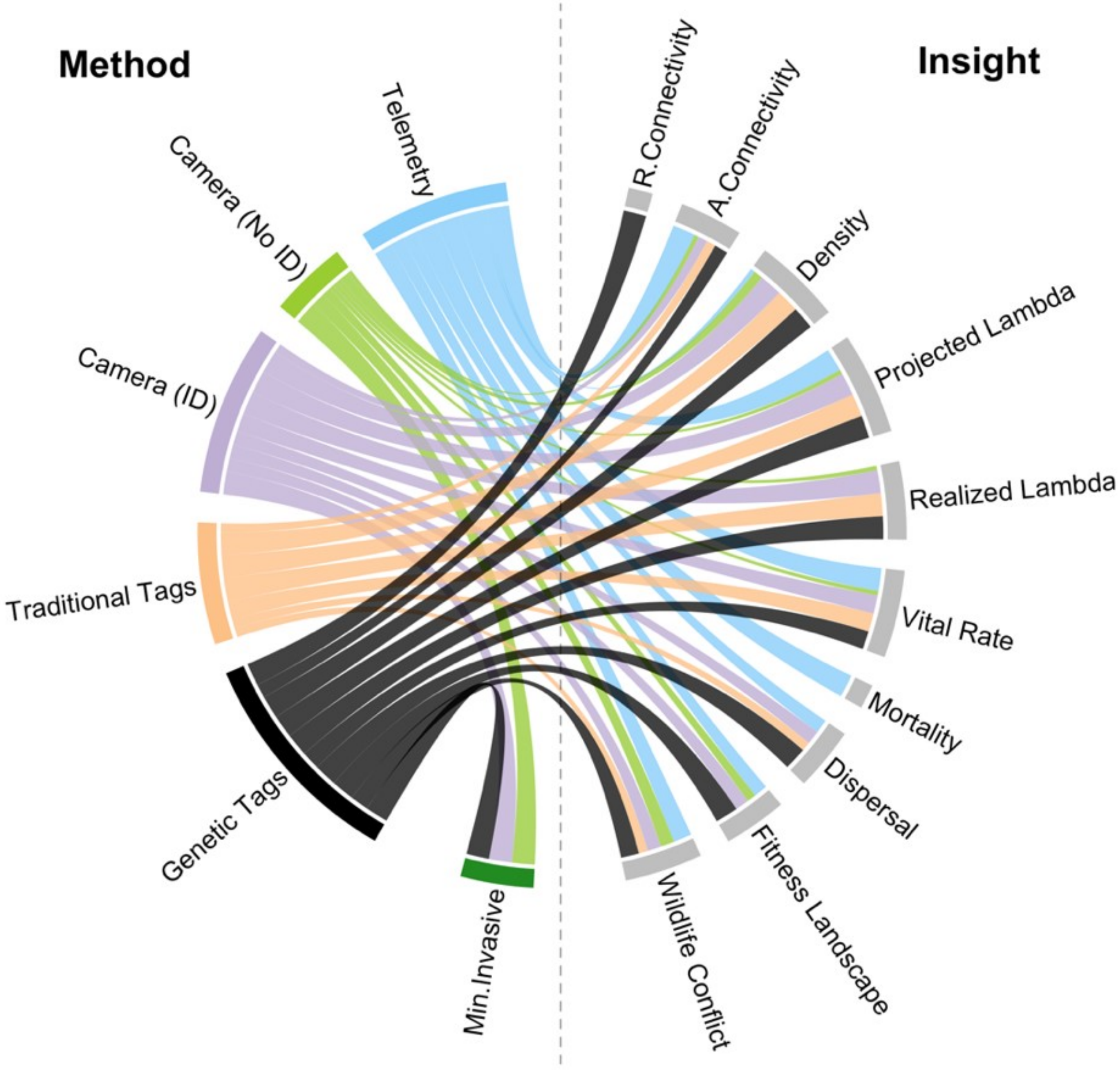


Figure 2-1. Subjective comparisons between methods for analysing parameters of interest for population and conservation insight. Width of bands represent ratings from 0-5, with 0 being not possible and 1-5 being increasingly suited. We rated each method on its ability to produce ecological insight into a variety of metrics and finally whether the method was minimally-invasive. (Definitions: Camera (No ID)= Camera trap with unmarked individuals, Camera (ID)= Camera trap with identifiable individuals, Min.Invasive=Minimally Invasive Sampling, A.Connectivity=Apparent connectivity, R.Connectivity=Realized connectivity).

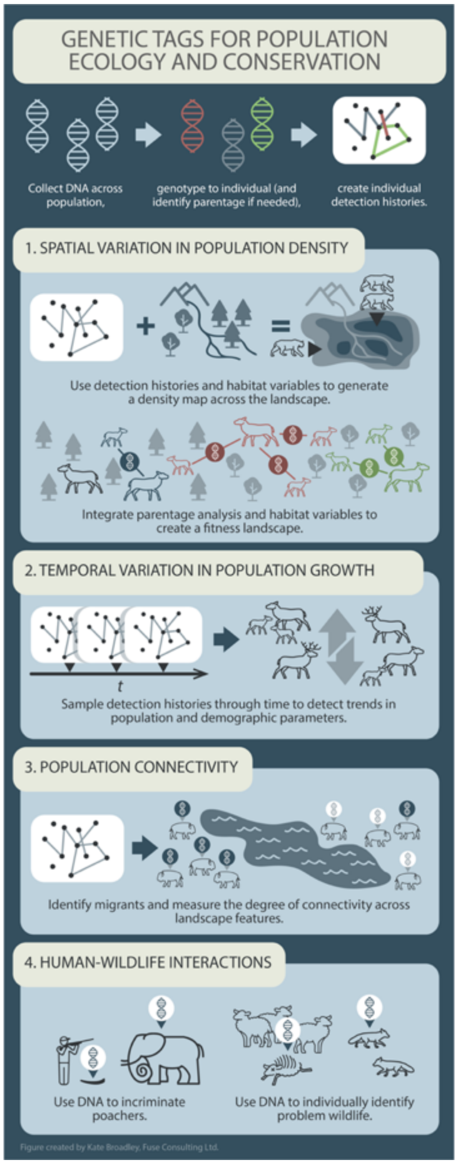


Figure 2-2. Visual schematic of the four main uses of genetic tags for population ecology and conservation insight. 1) Spatial variation in animal density can be determined by using a single genetic tagging survey and spatial capture-recapture to parameterize structural relationships between animal density and potential limiting ecological factors. Fitness landscapes can be estimated from genetic tagging surveys by reconstructing family triads and identifying individual offspring contributions and the ecological area the individual occupies. 2) Conducting multiple genetic tagging surveys allows investigation of population growth rates and individual demographic parameters (survival, recruitment, immigration, and emigration). 3) Population connectivity can be assessed with direct genetic methods or through the creation of movement resistance surfaces using individual capture histories. 4) Insight into human-wildlife interactions can be gleaned from genetic tags, e.g., forensically identifying poached individuals, using DNA to identify culprits in cases of livestock depredation, and testing hypotheses surrounding the causes of human-wildlife conflict and how to manage it.

To counter the defaunation that characterizes the Anthropocene, scientists need to gather evidence that can inform the impact of policy decisions on the density and distribution of organisms. Robust ecological inference can be generated by a number of approaches, such as telemetry (Metz *et al.* 2018), experimentation (Krebs *et al.* 1995; Ford *et al.* 2014), and field-based census (Boutin *et al.* 2006); here we show that genetic tagging provides additive and complementary ecological insight to these established methods. Genetic tagging provides a diverse toolkit to gather evidence that spans from allelic variation to population density, growth, and community composition; making this an ideal approach to address applied and theoretical ecological issues at previously unattainable spatial extents.

Our review focuses on the estimation of population parameters and processes based on the identification of individuals via unique genetic tags. The review first explores the application of genetic tags to 1) assess population density, fitness, and their habitat correlates 2) calculate population growth rates and its determinants: survival, recruitment, immigration and emigration, 3) assess many aspects of population connectivity: a) contemporary and historic connectivity and, b) realized (inter-population gene sharing) and apparent (inter-population movement) connectivity and, 4) infer causes of, and solutions to, human-wildlife interactions using forensic genetics. A case-study is then provided, using a long-term genetic tagging dataset of grizzly bears in the Canadian Rockies, to showcase possible ecological insights from these approaches, complete with reproducible code (see supplementary material). The rapid advancement in laboratory techniques, computing power, and statistics has made genetic tagging of wild populations more affordable and manageable, and facilitated critical ecological and conservation inference for wide-ranging, elusive, sensitive, and low-density species in the Anthropocene from samples that may be as limited as a clump of hairs (Figure 2-2).

2.1.1 Why and how does population density change across the landscape?

Explaining and predicting the abundance of animals is a central goal of ecology, and it underlies species conservation and wildlife management (Messier 1991; Krebs *et al.* 1995). Habitat loss is the primary driver of population decline for most species (Dirzo *et al.* 2014). As such, understanding density-habitat relationships is of critical importance to predicting ecological outcomes and informing conservation actions (Hodgson *et al.* 2009). The recent integration of spatial capture-recapture (SCR) methods, genetic tagging, and spatialization of predictor variables—revolutionized through remote sensing and advanced geographic information systems (Kwok 2018) —allows ecologists to quantify density-habitat relationships with unprecedented statistical rigour over large spatial scales.

Capture-recapture methods were developed in the late 1800s and required that individuals be physically captured and marked with unique identifiers, such as ear tags (Petersen 1896). This invasive approach carries a relatively high cost of data collection and logistical hurdles to ensure that animal welfare needs are met, thus limiting sampling efforts. In addition, until recently, most abundance analyses of tagging data required an assumption of population closure (Boulanger & McLellan 2001), which occurs when individuals do not leave or enter the sampled area. The closure assumption is often unrealistic in practice and can cause considerable biases in demographic estimates (Boulanger & McLellan 2001) that are difficult to correct. SCR methods overcome the closure assumption by explicitly accommodating spatial variation in detection probability as a result of the juxtaposition of individual home ranges with an array of traps, to produce unbiased estimates of population density (Borchers & Efford 2008; Royle *et al.* 2014a).

A key component of SCR is information on the timing and location of capture events for each individual in the study, which are easily generated in genetic tagging studies. The advent of

Polymerase Chain Reaction (PCR) methods in 1983 (Saiki *et al.* 2014) allowed ecologists to identify individuals using minimally-invasive genetic tags. At the turn of the 21st century, genetic capture-recapture was used, for the first time, to estimate the abundance of two wild populations: humpback whales (Palsbøll *et al.* 1997) and brown bears (Woods *et al.* 1999), and its use has grown rapidly since (Figure 2-3).

Figure 2-3. Selected species and locations for which genetic tagging for demographic insights into population density, growth rates, direct measures of connectivity, or human-wildlife conflict has been successfully applied. Projects using genetic tagging for these demographic insights have been conducted on every continent, except Antarctica, and have sampled a variety of taxa, using many different sources of DNA, but are biased towards mid-large sized mobile mammals. References to each study provided in supplementary information.

In spite of the widespread use of genetic tagging in SCR studies (Figure 2-3), a limited number of investigators have extended SCR methods beyond estimating population density to explore density-habitat relationships (Fuller *et al.* 2015; Linden *et al.* 2016; Lamb *et al.* 2017c; Boulanger, Nielsen & Stenhouse 2018; Sutherland *et al.* 2018). Recently, Sutherland et al. (2018) examined the link between contamination (PCB) and the population density of American mink (*Neovison vison*) using genetic-based SCR. Mink, often used as an indicator species for aquatic ecosystems, were found in much lower densities near a contaminated river system compared to those near a more pristine river; underscoring the value of pairing SCR methods with genetic tags to collect individual identities across multiple river systems to reveal cryptic ecological patterns. Similarly, Lamb *et al.* (2018) tested the effects of habitat and road density on the recovery of a threatened grizzly bear population using genetic tags. While grizzly bear density was lower in areas of high road densities, Lamb *et al.* (2018) showed that the creation of protected areas and road closures elevated bear density and mitigated the effects of roads, allowing the population to recover. Results of this work have already been incorporated into regional planning efforts to reduce road densities (Mowat *et al.* 2017b; Proctor *et al.* 2018c), highlighting the value of density-habitat links when immediate conservation action is required. Finally, Stetz *et al.* (2018) extend the density-habitat relationship to explore the effects of interspecific competition on population density, thus adding a community ecology dimension.

The integration of genetic tagging methods with the field of landscape ecology has provided an opportunity for investigators to link individual fitness—the currency of natural selection (Darwin 1859; Pelletier *et al.* 2007)—to the habitat individuals use; a key component missing in current habitat selection studies (Gaillard *et al.* 2010). Habitat selection studies derived from telemetry can provide insights on which landscape features are used, relative to their availability, but not how those features contribute to variation in reproductive success. For example, where genetic tags are intensively collected over large areas, or in small populations, reconstructing family triads (perfect complementary allele sharing between parents and offspring) allows for the explicit identification of individual offspring contributions, which can be matched to the ecological conditions experienced by the parents (Figure 2-2). Maps of fitness landscapes can be produced when such models are extrapolated with spatially continuous variables, such as those derived from remote sensing (Kwok 2018). Such fitness surfaces represent a link between landscape, population and evolutionary ecology, and represent a new frontier given that we were unable to find any published examples. Constructing family pedigrees is most practical in small, fragmented, or isolated populations (Proctor *et al.* 2018a), but that is where it can be very useful in understanding fitness correlates and monitoring the efficacy of connectivity management (Pemberton 2008; Ford *et al.* 2011; Proctor *et al.* 2018b). Further, Chandler *et al.* (2018), provide an innovative and complementary SCR approach to link survival and recruitment rates with landscape attributes and extrapolate results across space. Chandler *et al.* (2018) marked individuals with physical tags, but we highlight this important work here because it is the first analysis of its kind, that we are aware of, and could easily be applied to genetically tagged individuals. Quantifying relationships between density, fitness, and habitat is one of the most significant developments in modern applied ecology and conservation, with genetic tagging playing a leading role in this scientific advance. We urge investigators to, whenever possible, conduct manipulative or natural experiments, paired with genetic tags and SCR, to provide strong inference (Ford & Goheen 2015) into the factors driving spatial variation in population density.

2.1.2 Why and how does population size change over time?

Krebs *et al.* (1995, 2002, 2018) suggest that identifying the determinants of population change (hereafter λ), will have profound implications for effective conservation action. Conventional measures of λ (i.e., projected λ, Franklin 2001) can be estimated from recruitment (e.g. young:adult ratio) and survival (e.g. proportion of marked animals that are alive per year) data, which are commonly collected by wildlife management agencies via telemetry studies (Schwartz *et al.* 2006). Estimates of projected λ uncover whether the individuals in the population were able to replace themselves (Franklin 2001). While the data used to estimate projected λ are commonly available, this approach assumes a stable age distribution and equal immigration and emigration rates—given that only survival and recruitment are considered— assumptions that are rarely satisfied under variable conditions. Violation of any one of these assumptions can result in biased estimates of projected λ, casting doubt on its reliability (Koons *et al.* 2005). In contrast, realized λ makes no such assumptions and represents the observed change in population size over time. Estimates of realized λ help answer whether the individuals in the population are being replaced (through either surviving longer, emigrating less, or immigrating and reproducing more), a subtle, but important difference from projected λ making realized lambda a more accurate and reliable estimate of population change (Franklin 2001). Genetic tagging is well suited to produce measures of realized λ through successive density estimates or by tracking the net gain and loss of individuals in a population through time with demographically open models (Royle *et al.* 2014b; Efford 2018). The latter being the preferred and more robust approach (Nichols & Hines 2002).

Demographically open models can be used to estimate parameters for survival, recruitment, immigration, and emigration – the fundamental parameters driving changes in λ (Cooch & White 2006; Royle *et al.* 2014a). Combined, these parameters provide an explicit estimate of realized λ that is often more robust than the estimate of realized λ derived from comparing point estimates of density, especially for low-density populations and threatened species (Sibly & Hone 2002). Further, linking the demographic components of λ to habitat features presents a powerful opportunity to explore the influence of habitat on population dynamics (Chandler *et al.* 2018).

Some of the most rigorous examples of using genetic tags to link demographic parameters to the environment is through a series of studies conducted on black bears (*Ursus americanus*) (McCall *et al.* 2013), grizzly bears (Sawaya *et al.* 2012; Whittington & Sawaya 2015; Lamb *et al.* 2017b), and wolverines (*Gulo gulo*) (Brøseth *et al.* 2010; Efford & Boulanger 2018). For example, Brøseth *et al.* (2010) examined wolverine survival using genetically-tagged individuals sourced from scat collection covering 65,000 km^2 across Norway. Key insights from this work include detection of negative density-dependence in adult survival (a rarely observed demographic pattern), as well as additive mortality due to high harvest rates. Illuminating detailed demographic processes in a low-density, elusive carnivore, highlights the power of genetic tagging for ecological insight and information for conservation action. Similarly, a decade of monitoring wolverines in northern Canada revealed population declines exceeding 40%, a trend that would have been undetectable without the use of genetic tags and SCR (Efford & Boulanger 2018).

Immigration and emigration are fundamental aspects of λ and play key roles in meta-population dynamics, yet are notoriously hard to measure in wild populations, providing one reason why these processes are currently understudied in ecology (Kokko & López-Sepulcre 2006). Tracking λ with genetic tags provides an opportunity to estimate immigration and emigration rates explicitly using demographically open SCR (for example with R package, OpenPopSCR) or spatially-explicit integrated population models, both of which are active areas of development (Ergon & Gardner 2014; Royle *et al.* 2014b; Schaub & Royle 2014; Chandler *et al.* 2018). To ensure unbiased demographic estimates, the study area must be larger than the dispersal distance of the study animal, such that dispersal can be modelled (Ergon & Gardner 2014).

2.1.3 How and at what rate do organisms move between populations and across space?

Connectivity - the degree to which the landscape facilitates or impedes the movement of organisms (Taylor *et al.* 1993) – is a vital component of spatial and temporal population dynamics. The global road network provides an example of the human impacts on wildlife connectivity. The terrestrial world is currently divided by roads and human settlement into ~600,000 fragments, most of which are very small (<1 km^2, Ibisch *et al.* 2016), and roads can greatly reduce connectivity for many taxa (Holderegger & Di Giulio 2010; Bischof, Steyaert & Kindberg 2016). Researchers are seeking rapid and cost-effective approaches to quantify factors influencing animal movement and to identify ways to mitigate the negative effects of roads and other disturbances. Genetic tagging provides crucial information to support the estimation of apparent and realized connectivity (Proctor *et al.* 2012, 2015; Sawaya *et al.* 2014).

There are three general ways to assess connectivity between populations using genetic tags: capture-recapture methods (Lamb *et al.* 2017b; Cayuela *et al.* 2018), direct genetic methods (Paetkau *et al.* 2004; Proctor *et al.* 2005), and indirect genetic methods (Schwartz *et al.* 2007; R *et al.* 2015). Each of these methods produce a unique temporal signature of connectivity (contemporary vs historic) and inference on the type of connectivity detected (apparent [demographic/physically connected] vs realized [genetically connected]). Here we explore the utility and potential pitfalls of each approach.

Capture-recapture methods, like telemetry, provide a direct assessment of where and how animals are moving on the landscape. Connectivity between populations can be determined through the recapture of individuals between populations (Lamb *et al.* 2017b), or through the use of SCR methods to create models of connectivity based on landscape features and recapture distances (Royle *et al.* 2014c). Such approaches provide a contemporary look at apparent connectivity, i.e., they show who is moving where during the time of sampling and the degree to which populations are demographically connected, but do not reveal if that connectivity results in gene flow (realized connectivity). Although capture-recapture data do not provide the same resolution of movements as telemetry, the large sample size provided by pairing minimally-invasive genetic tagging with capture-recapture methods has provided many intriguing insights into the connectivity of wild populations. For example, Fuller *et al.* (2015) extended their SCR density-habitat model to estimate limits to mink connectivity, uncovering strong connectivity among stream networks and the negative impacts of human development. Similarly, Bischof *et al.* (2017) show that brown bears place home range centers in largely unroaded landscapes and resist using habitat that involves crossing a road. Bischof's results are especially striking due to increasing global road densities and the fragmentation of wilderness (Ibisch *et al.* 2016; Potapov *et al.* 2017). Measures of apparent connectivity using capture-recapture methods provide investigators with insight into the interaction between landscape features, animal movements, and the potential for barriers to movement affecting population demography and genetics.

Moreover, SCR methods permit the simultaneous integration of both density and connectivity into a single empirical inferential framework (Morin *et al.* 2017).

Direct genetic methods estimate connectivity through the detection and movement of individuals between genetically-distinct populations. Direct estimates of connectivity measure the movement of individuals over contemporary time periods and can provide insight into both apparent and realized connectivity. Compared to capture-recapture methods, direct genetic methods generally require less effort to identify dispersers in the population (McLellan & Hovey 2001a; Cayuela *et al.* 2018). Direct genetic methods leverage information on parentage and capture location to reveal dispersal using only a single sampling event, thus alleviating the need to catch individuals before and after they disperse (Figure 2-2, Proctor *et al.* 2004; Cayuela *et al.* 2018). Dispersing individuals have been identified using genetic tags in a number of species including capercaillies (Segelbacher, Höglund & Storch 2003), roe deer (Coulon *et al.* 2004), wolverines (Cegelski *et al.* 2006), black bears (Dixon *et al.* 2007; Sawaya *et al.* 2014), grizzly bears (Proctor *et al.* 2012; Sawaya *et al.* 2014), and rats (Paetkau *et al.* 2009). Dispersers can only be identified from populations with divergent genetic signatures, thus well connected populations with many dispersers will be poor candidates for direct genetic methods to estimate connectivity (Proctor *et al.* 2005). The use of family triads (or limited pedigrees) is an emerging direct genetic method that overcomes the inability to detect dispersers in well-mixed populations and allows the identification of both apparent and realized connectivity (Cosgrove *et al.* 2017; Cayuela *et al.* 2018; see Proctor *et al.* 2018a for an example). The use of family triads in connectivity studies will ultimately provide insight into the assumed link between apparent and realized connectivity (Cayuela *et al.* 2018), and perhaps more importantly, the efficacy of mitigation efforts (Sawaya *et al.* 2014), like sex-specific wildlife crossing structures across highways (Ford *et al.* 2017).

Direct genetic methods have allowed investigators to investigate sex-specific fragmentation, otherwise undetected with indirect methods (Proctor *et al.* 2005, 2012), and helped redefine how the IUCN assessed the conservation status of brown bear populations worldwide (Mclellan *et al.* 2016). In a few cases, direct methods have been applied to uncover continental-scale connectivity issues (Segelbacher *et al.* 2003; Proctor *et al.* 2012). In light of the burgeoning pulse of large landscape connectivity initiatives across the world (Pulsford *et al.* 2015; Travis Belote *et al.* 2016), direct genetic methods that link habitat loss with realized connectivity are an important opportunity for improved connectivity research (Cosgrove *et al.* 2017).

Indirect genetic methods use the distribution of alleles between populations as a signal to infer connectivity (Manel & Holderegger 2013). These methods measure the exchange of genes between populations over many generations and have provided crucial insights into the historical connectivity between populations. Indirect genetic methods have guided conservation efforts for endangered species and the *ex situ* preservation of genetic diversity (Russello & Amato 2004; Henry *et al.* 2009). However, ecological insight can be limited when using indirect methods for at least three reasons: 1) these methods assume that populations are in equilibrium between mutation rates, natural selection, genetic drift, and the natural migration rate (Hartl & Clark 1997); conditions that are rarely met in Anthropocene landscapes (Whitlock & McCauley 1999); 2) the genetic signatures detectable by such methods often require hundreds of generations to build up, potentially masking key and immediate variation caused by recent landscape change affecting individual movements (Tucker *et al.* 2018); and 3) these methods alone provide little information on demographic connectivity, despite results from such methods often being misconceived as providing such insights (Lowe & Allendorf 2010). Consequently, both Lowe &

Allendorf (2010) and Cayuela *et al.* (2018) recommend that investigators interested in population connectivity combine the inferences from indirect genetic methods with the direct measures of demographic connectivity discussed above to disentangle the effects of dispersal, gene flow, and barriers to connectivity on wild populations, a task that genetic tags are well suited to address.

2.1.4 How can negative interactions between people and wildlife be mitigated?

Conflict between humans and wildlife is a global issue occurring across many taxa (Dirzo *et al.* 2015; Ripple *et al.* 2016), especially carnivores (Can *et al.* 2014; Ripple *et al.* 2014). Localized human-wildlife conflict can have far-reaching, population-level effects (Lamb *et al.* 2017b). However, evidence-based conflict reduction can improve the conservation status of large carnivores. For example, Proctor *et al.(* 2018b) used evidence derived from genetic tags and a comprehensive conflict reduction program to increase the inter-population connectivity of an isolated grizzly bear population in a region where conflicts were the main cause of threatened status. Reduced mortality, and increased connectivity, were accompanied by an increase in the grizzly bear population, reversing a decade-long decline.

Many policies that reduce conflict (e.g., culls, translocations, and physical barriers) are applied broadly and sometimes to non-target individuals. Non-selective removal of individuals from conflict-prone species may apply unfavorable selective pressure on individuals that are able to coexist in human-dominated landscapes. Consequently, correctly identifying both conflict individuals and familial patterns can be an effective tool to facilitate coexistence (Caniglia *et al.* 2013; Morehouse *et al.* 2016). Genetic tagging is ideally suited to provide this knowledge. Identifying both the who and why of human-wildlife conflict are central to effective mitigation. As part of a large genetic capture-recapture project for brown bears, Morehouse et al. (2016)

collected hair samples from human-wildlife conflict sites, typically areas where bears were accessing anthropogenic food sources. Through parentage analysis, they found conflict prone animals follow matrilineal lines because mothers teach their young how and where to forage. Similar results have also been observed in black bears (Hopkins III 2013). The implications of these results are striking given that current policy protects females with cubs, a policy which may unintentionally exacerbate the problem. The research suggests that coexistence efforts shift to preventing initial conflicts and to removing individuals once a conflict occurs to prevent intergenerational transmission of conflict-prone behaviour.

Similarly, genetic tags have been used to confirm the identity of conflict tigers (*Panthera tigris*) in India (Singh *et al.* 2015). When a conflict arises (e.g., an attack on people or property), managers seek to find and remove the problem animal. Having a positive identification of the offending animal at the conflict scene forms a critical part of resource allocation for prevention, but efficacy of this method is dependent on rapid genotyping. Nevertheless, genetic tags can provide confirmation when a conflict animal has been removed, potentially reducing the chances that non-conflict individuals will be killed and increasing public safety.

Carnivores depredating livestock is a financially costly and socially-charged issue (Treves, Krofel & McManus 2016). Controversy surrounds which carnivores are responsible and whether livestock are predated by carnivores or simply observed consuming an animal that died for other reasons (Caniglia *et al.* 2013). Using genetic tags extracted from carnivore saliva on livestock carcasses, Caniglia et al. (2013) were able to identify the species, sex, and individuals responsible for predating livestock (Caniglia *et al.* 2013). They were also able to identify a female wolf who had been involved in depredation four years earlier, suggesting that studies of this nature could examine the spatio-temporal patterns of individual-level depredation events and better guide compensation and mitigation efforts (Caniglia *et al.* 2013).

Genetic tags have been used to prevent and convict poachers. Harper *et al.* (2018) document nine recent cases (since 2012) where genetic tags formed the foundation of evidence to prosecute poachers targeting rhinoceros (*Diceros bicornis* and *Ceratotherium simum*). Genetic tags were used to link confiscated horns with carcasses, leading to a cumulative 113 years of jail time across these cases. Such cases of successful prosecution are essential and urgently needed to reduce poaching in the Critically Endangered black rhinoceros population, which has declined from several hundred thousand to only 2,400 over the last two centuries. Similarly, African elephants (*Loxodonta africana*) have declined by 30% across the African continent in the last decade due to poaching, human-wildlife conflict, and habitat loss (Chase *et al.* 2016). Forensic genetic tags have been used extensively to incriminate ivory poachers, uncover transnational crime rings, and dissuade future events (Archie & Chiyo 2012; Wasser *et al.* 2018). Further, the most common human-wildlife conflict for elephants is crop raiding and genetic tags have been used to identify individual African elephants involved in crop-raiding, thus refining efforts to understand and mitigate conflict (Archie & Chiyo 2012). The extent to which genetic tagging can help promote coexistence with wildlife will depend on the rapid synthesis of genetic information with wildlife management and applied conservation efforts.

2.1.5 Limitations of genetic tagging and opportunities afforded by genomics

Two main challenges exist in genetic tagging free-ranging animals: 1) low quality and quantity of DNA available from minimally-invasive sampling (MIS) approaches, and 2) genotyping enough molecular markers to provide sufficient resolution for pedigree reconstruction. Fortunately, the rapid growth in the fields of genetics and genomics are helping to overcome some of these challenges (as predicted by Taberlet *et al.* (1999)), which we briefly review here.

MIS of genetic material – often scat or hair – is more likely to degrade or become contaminated by sampling procedures (Russello *et al.* 2015; Carroll *et al.* 2018). For example, hair follicles exposed to ultraviolet light and moisture may result in DNA broken into 100-500 base pair fragments; limiting the number and length of molecular markers that can be generated (Andrews *et al.* 2018). Conversely, more invasive sampling methods (e.g. taking a blood sample from a captured animal) enable greater control over the collection and preservation of DNA. Developing new means to counteract the drawbacks of MIS approaches can help address research costs and enhance the welfare of study animals (e.g., Stetz *et al.* 2015; Lamb *et al.* 2016). Investigators should remain aware of the increased genotyping errors possible from MIS and follow protocols that detect and minimize these errors (Paetkau 2003; Waits & Paetkau 2005).

The majority of studies reviewed here have relied on microsatellite loci to identify individuals and reconstruct family dyads and pedigrees. Due to the cost and time required to develop species and population-specific parameters from microsatellite loci there are a limited number of genetic markers available to create accurate pedigrees, reconstructing population-level parameter estimates, and inferring connectivity and gene flow (reviewed here: Andrews *et al.* 2018; Carroll *et al.* 2018). However, Russello *et al.* (2015) and others (Andrews *et al.* 2018; Carroll *et al.* 2018; Ekblom *et al.* 2018) provide new approaches to assess genome-wide data in wild populations using MIS approaches. Genomic approaches provide orders of magnitude more molecular markers than microsatellite approaches. As a result, the genomic era is poised to overcome many of the challenges previously faced with few markers.

2.2 An application of genetic tags to grizzly bear ecology and conservation in the Canadian Rocky Mountains

Grizzly bears are elusive, wide-ranging animals with a high conservation profile. The grizzly bear was the first terrestrial species for which abundance was estimated using genetic tags (Woods *et al.* 1999); and is a fitting species to illustrate the insights now possible with these type of data following 20 years of methodological development. Here we investigate factors driving population density, trajectory, connectivity, and conflict using the South Rockies Grizzly Bear Project data collected between 2006-2017 from the Rocky Mountains in southeastern British Columbia, Canada. Generally, this project uses systematic hair collection methods to genetically tag grizzly bears across an ~12,000 km^2 area. To date, the project has tracked 641 individual grizzly bears detected, via microsatellite genotyping, 2618 times (unique individual-site-occasion), during 64 sampling occassions between 2006-2017 (Figure 2-4). Further details on this project are provided in (Lamb *et al.* 2016b, 2017b). We illustrate the application and scope of possible insights from these approaches (R scripts in appendix) and point the reader to work where more complex analyses have been conducted on these data.

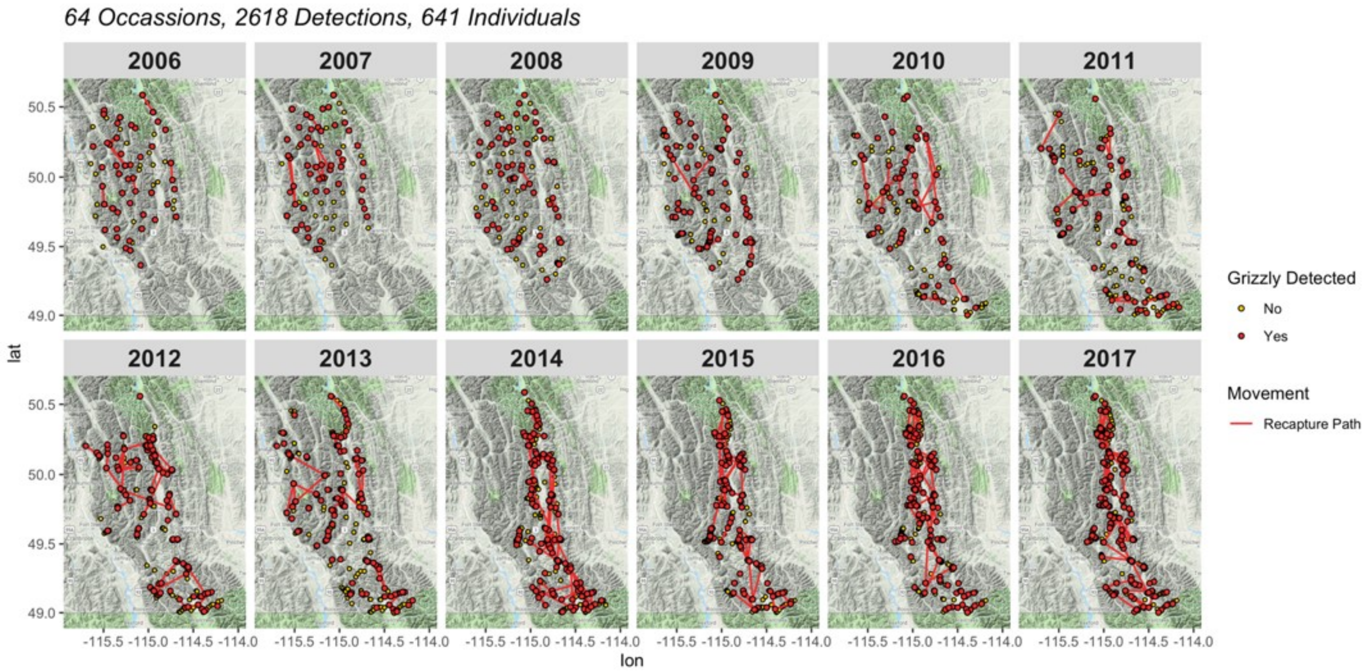


Figure 2-4. Annual sampling distribution of grizzly bears in the southern Rockies in British Columbia, Canada. In 2014 we reduced the extent of the study area to focus on the portion of the study area with the highest conservation risks, and subsequently increased sampling intensity.

2.2.1 Spatial Variation in Animal Density

We estimate the density, abundance, and limiting factors to grizzly bear population density using the 2014 genetic tagging data (Figure 2-4), composed of 145 individuals detected 295 times over 5 occasions. We fit SCR models to these data using the ‘secr’ package (Efford 2016) in program R, following the approach of Lamb *et al.* (2018) to correlate spatial covariates with population density. Generally, these models use the spatial recaptures of animals to estimate a spatial detection function, and animal density as a Poisson point process. These models are flexible: they are able to account for variation in detections across space and time, exclude non-habitat in density estimation, and include habitat variables as predictors of density.

Results suggest that there were 205 (95% CI: 165-254) grizzly bears occupying our larger region of study in 2014, or a density of 17.6 (95% CI: 14.2-21.8) individuals per 1000 km^2. Adding in spatial predictors of density increased model fit over the null model (delta AICc=10.1) and suggested that the density of roads (gravel resource roads, paved highway, and urban roads) had a strong negative effect on grizzly bear density (Figure 2-5). Although road effects on grizzly bear habitat use and survival have been well documented (McLellan & Shackleton 1988; Boulanger & Stenhouse 2014), linking the effects to reduced population density has been elusive, until genetic tagging and SCR methods were combined (Lamb *et al.* 2017c); providing a simple path to parameterizing such relationships.

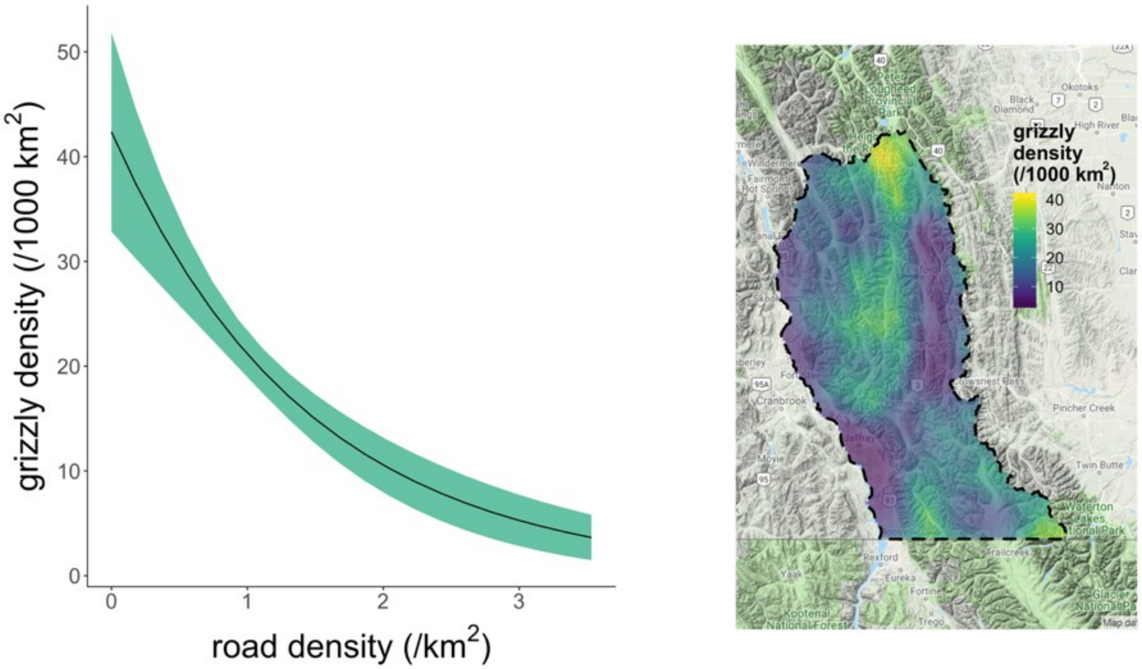


Figure 2-5. Relationship between grizzly bear population density and road density during spring-fall 2014 in the southern Rocky Mountains, British Columbia, predicted from top ‘secr’ model.

2.2.2 Population Growth, Demographic Parameters

We estimated population growth and survival of the Southern Rockies grizzly bear population by harnessing 12 years of genetic tagging and recently developed likelihood-based spatial open-population capture–recapture models (Efford 2018). We focus our analysis on the northern half of our study area where the highest mortality rates have resulted in population declines (Lamb *et al.* 2017b); we explore population growth and survival across two time periods (early: 2006-2012, and late: 2013-2017). Open-population capture–recapture models track individual animals through time to estimate the entrance (reproduction) and exit (mortality) parameters, while accounting for confounding effects of dispersal (immigration and emigration) and heterogeneous detections through the use of spatial detection data. We fit open-population SCR models to these data using the 'openCR' package (Efford 2018) in program R.

Consistent with previous, non-spatial analyses of these data (Lamb *et al.* 2017b), this population experienced a decline of approximately 3% per year between 2006-2012 (λ=0.97 [95% CI:0.94-1.00], Figure 2-6) and increased at 2% per year between 2013-2017 (λ=1.02 [95% CI:0.98-1.06]) . Survival was estimated at 0.85 (95% CI: 0.82-0.87) between 2006-2012, and 0.87 (95% CI: 0.83-0.90) between 2013-2017. If increasing this population to 2006 levels is a priority, we provide the evidence required for wildlife managers to implement the reduction of resource road densities and thus human access and bear mortality (Lamb *et al.* 2017c; Proctor *et al.* 2018c). Other options include reducing bear conflicts in town through the removal of attractants (e.g., roadkill carcass pits, fruit trees) as well reducing collisions with vehicles and trains, both of which are long-term, additive stressors on the population. Taking these steps proactively should dampen the magnitude of future population declines.

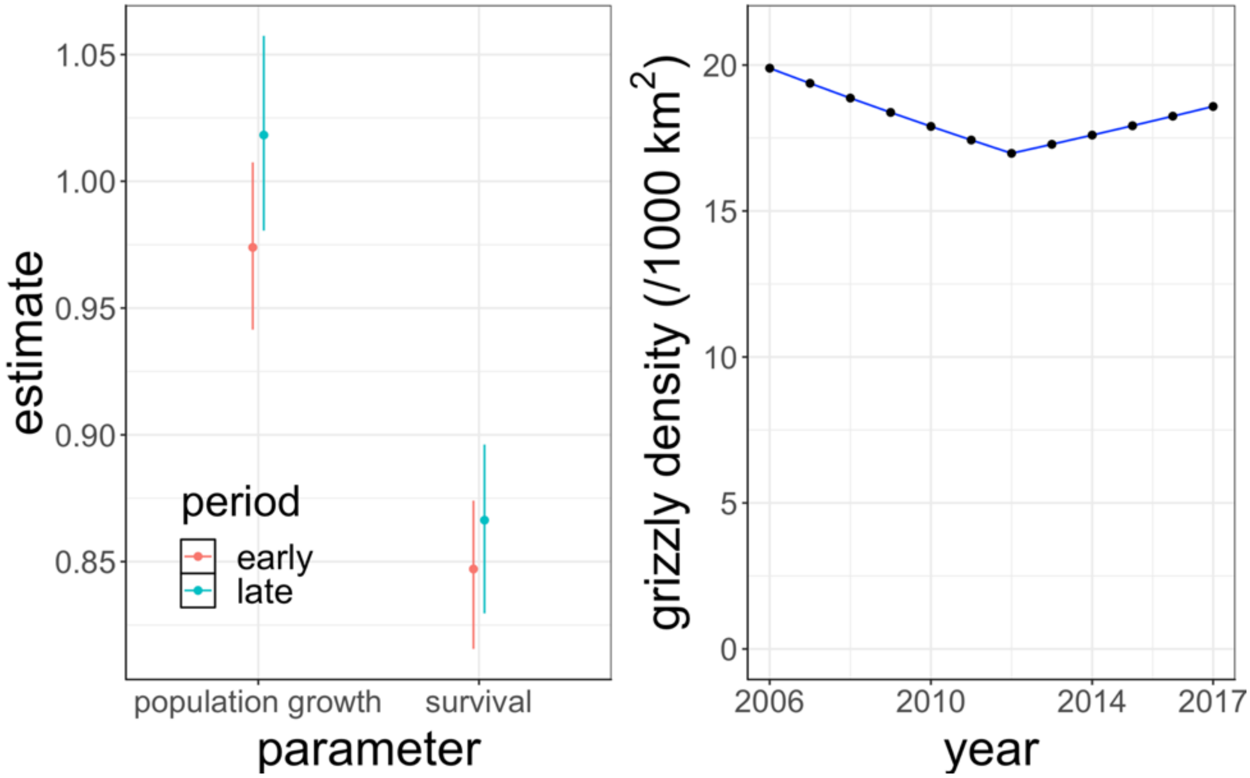


Figure 2-6. Estimated population growth rate, survival and population trajectory for grizzly bears in the southern British Columbia Rockies between 2006-2017 predicted from top 'openCR' model. Early period refers to 2006-2012, and late to 2013-2017. Annual density estimates generated using period-specific growth rates and the 2014 density estimate from the 'secr' analysis.

2.2.3 Population Connectivity

To examine the potential for a fracture to population connectivity across a highway corridor, we replicated the analysis of Proctor *et al.* (2005), but with additional animals detected since that time (2006-2016). We estimated genetic clustering for two groups of bears, one separated by a wide, natural valley (Figure 2-7, East and West), and another separated by a wide valley with human settlement including towns, a highway, and railway, where mortality is high and geneflow may be impeded (Proctor *et al.* 2012; Lamb *et al.* 2017b). We genotyped 9 loci to identify individuals in our project, but often included more loci if identities were uncertain or we were interested in population connectivity. For this analysis we included genotypes with at least 15 loci, leaving us with 295 individuals.

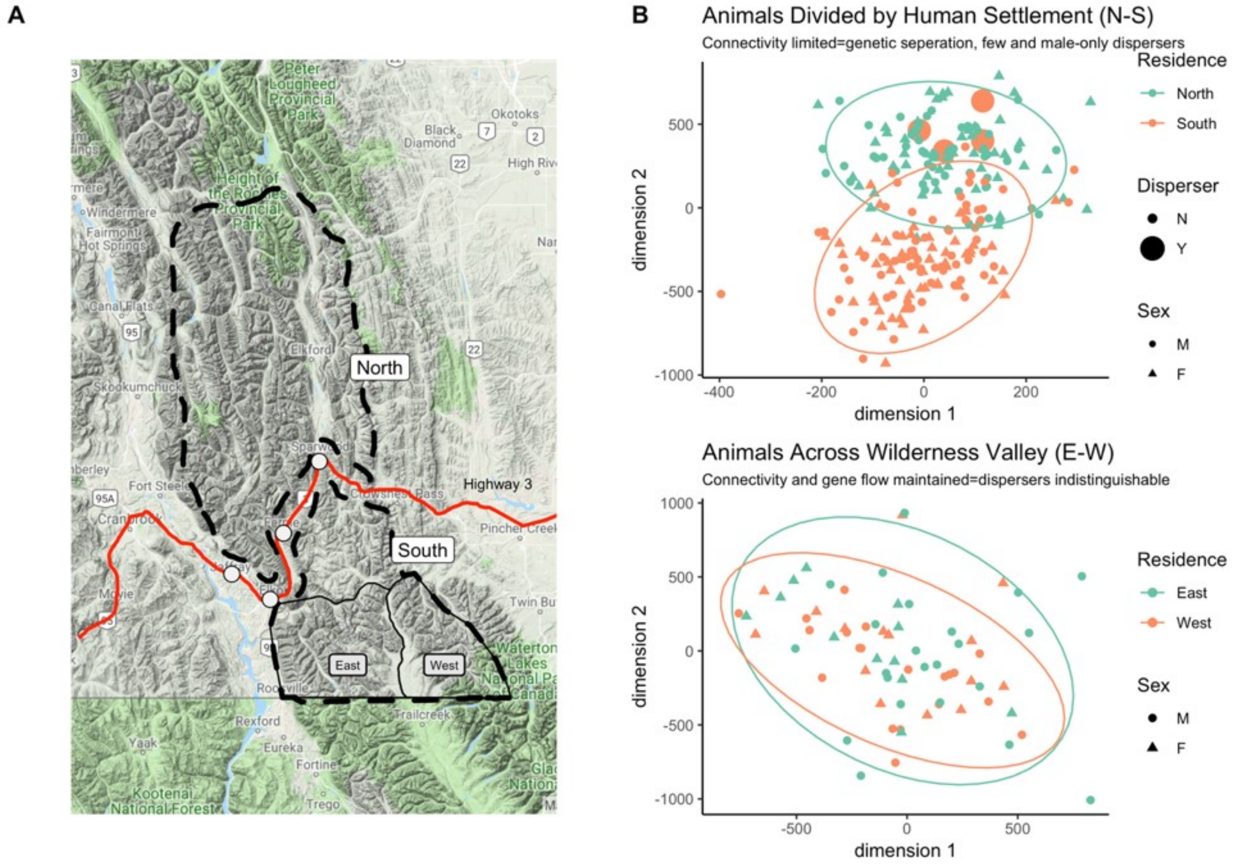


Figure 2-7. Grizzly bear connectivity analysis and identification of dispersers in fractured areas across a human-dominated (North-South) and wilderness valley (East-West) in the southern British Columbia Rockies between 2006-2016. Highway 3 shown in red and towns in the fracture zone shown as grey circles.

A two-step process was used to access connectivity, first we used the program GENETIX (Belkhir *et al.* 1999) to identify clusters of similar genotypes with no a priori assumptions of group membership following the approach by Proctor *et al.* (2012). If connectivity was hindered, we expected some degree of divergence in the clusters on each side of the valley. Second, if a fracture to connectivity was detected we looked for individuals that may have dispersed into the population using GeneClass (Piry *et al.* 2004) to assess recent patterns in inter-area movement and to explore any differences in movements between the sexes. GeneClass uses assignment tests (Paetkau *et al.* 2004) to calculate the probability of each individual's assignment to a particular area, allowing for the identification of dispersers.

Results suggested connectivity and geneflow were maintained across the wilderness valley but not across the human-settled valley. Dispersers were indistinguishable from residents in the wilderness valley because this group was well connected, and the genetic clusters from each side of the valley completely overlapped. In contrast, across the human-settled valley, we found that the only animals that had successfully dispersed across the valley were four male bears, giving rise to genetic separation between individuals separated by development in the valley floor. This result reinforces the need to mitigate the connectivity fracture in this valley to re-establish genetic and demographic connectivity.

Analyses similar to the example provided here have been integral for enacting conservation measures. For example, following the identification of barriers to connectivity (Proctor *et al.* 2012), approximately 13,000 hectares of conservation land have been protected in British Columbia through direct purchase or conservation easements valued at >$32M.

2.2.4 Human-wildlife interactions

We applied our genetic tagging data to inform a conservation issue faced by wildlife managers in our region. A farm has been suspected of attracting grizzly bears due to the presence of unsecured animal carcasses. Concerned residents began collecting bear hair samples off the barbed wire fences that border this farm. We genotyped these samples, enumerated the number of unique animals detected, and explored the spatial extent of their movements across the landscape. Similar analyses have been completed using parent-offspring relationships to investigate family patterns in conflict (Morehouse *et al.* 2016).

After only 1.5 years of citizen-scientists collecting hair, we were able to detect 5 animals accessing the farm, an abundance of bears accessing a 0.25 km^2 area, to feed on carcasses (Figure 2-8). When attractants, bears, and humans converge, the result is often dead bears, thus the spatial context of the potential demographic effects of localized mortality on populations is important (Morehouse *et al.* 2016; Lamb *et al.* 2017b). We previously detected each of these animals a number of times in our genetic tagging study, revealing the landscape context of this food source: attracting bears that range as far as 37 km away, with a total expanse of 65 kilometers between the two farthest detections. These data demonstrate the need to better control this attractant source and other carcass pits in the region.

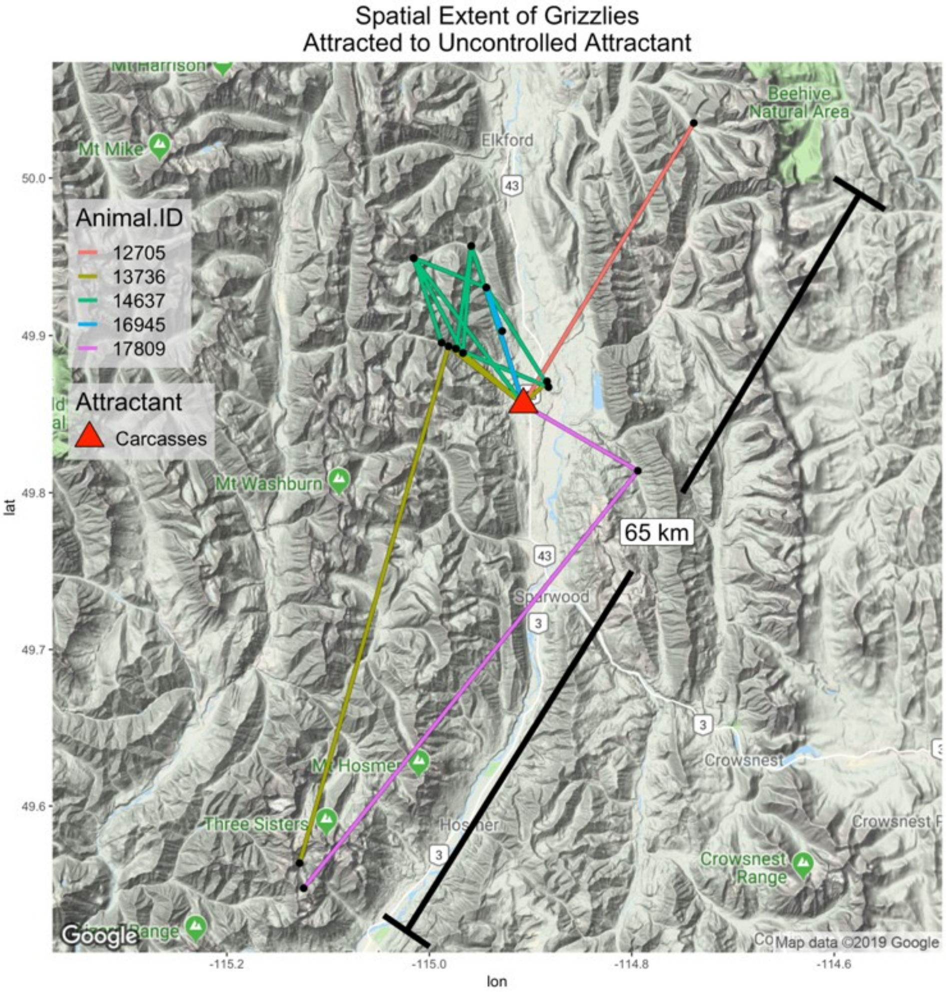


Figure 2-8. Spatial extent of detections of grizzly bears accessing a known and uncontrolled attractant (red triangle) in the southern British Columbia Rockies. Bears accessing this food have been detected as far as 37 km away, highlighting the far-reaching impacts of attractants and the value in landscape-level monitoring using genetic tags.

2.2.5 Case study summary

Here we applied recently developed analyical techniques to over a decade of genetic tagging data on grizzly bears in the Canadian Rockies. Results from this approach provided the 1) population density and influences from landscape correlates, 2) population trajectory and survival rate, 3) identification of connectivity fractures influenced by human-settled valleys and mortality, and finally, 4) insight into the spatial extent and demography of conflict. This collective inference provides an integrated picture of the drivers of the population, potential conservation concerns, and evidence to support immediate mitigation measures. We view these insights as critical information in population ecology and conservation and suggest that genetic tags provided us the means to easily ask and answer many pressing questions—both applied and theoretical—for this elusive, high-profile species across large spatial scales.

2.3 Conclusions

With increasing pressures on the natural world and limited conservation funding, ecologists require methods that are information-dense and efficient to collect. Krebs (2018) states: "*Two major empirical processes stare ecologists in the face at this time in history and should demand our attention – climate change and habitat loss … There is a pressing need to study immediate conservation and management problems*" (Krebs 2018). Genetic tags contribute significantly to satisfying these requirements and offer a compelling framework for addressing questions of ecological theory and conservation of species.

Possibly the most significant advance offered through genetic tagging is the underutilized ability to reveal how the most fundamental demographic mechanisms –population density, trajectory, and individual fitness- contribute to observed ecological processes (Figure 2). Linking demographic parameters to the mechanisms driving fitness allows for deep ecological understanding, and therefore effective mitigation of environmental change on wildlife populations, species, and ultimately ecological communities. Whenever possible, investigators should leverage natural experiments or conduct controlled manipulations to strengthen the inference possible with the approaches we outline here.

The depth and scale of ecological inference available from genetic tags is rapidly increasing. The future will likely see increased integration of population dynamics with population genetics for eco-evolutionary insights (Lowe, Kovach & Allendorf 2017), as well as community-level monitoring using genetic metabarcodes (Cristescu 2014), and eDNA (Pikitch 2018). Indeed, these approaches have recently been used to assess shark diversity (Bakker *et al.* 2017) and niche partitioning (Kartzinel *et al.* 2015), but challenges remain in using eDNA to infer abundance (Rice, Larson & Taylor 2018). Integrating these rapidly advancing community-level approaches with the population-level advances detailed here and the growing field of genomics (Carroll *et al.* 2018), presents further opportunity for ecological insight that scales from the allele to the ecosystem. With the rise of evidence-based policy under a rapidly changing environmental context, genetic tags are poised to advance the frontiers of ecology, conservation, and our understanding of the natural world in the Anthropocene.

2.4 Data Availability

Data and code are available on Figshare: **https://doi.org/10.6084/m9.figshare.7695620**

3 Chapter 3: The effect of habitat quality and access management on the density of a recovering grizzly bear population

3.1 Introduction

The world is becoming increasingly roaded, providing humans access to previously inaccessible areas (Ibisch *et al.* 2016). Wilderness across the globe is being lost (Watson *et al.* 2016) with wildlife incurring a high demographic cost (Fahrig & Rytwinski 2009; Benítez-López, Alkemade & Verweij 2010). Increasing human-carnivore overlap as humans gain access into the remaining wilderness is elevating the cumulative pressures on carnivore populations (Ceia-Hasse *et al.* 2017); however, large-scale carnivore recolonisation and human-carnivore coexistence are possible in human-dominated landscapes when targeted conservation efforts relieve human pressures on carnivores (Chapron *et al.* 2014). A landscape of global human-carnivore coexistence will require an understanding of the factors limiting carnivore populations and robust management actions to mitigate these factors.

Grizzly (brown) bears (*Ursus arctos*) have experienced drastic range contractions across the globe due to habitat loss and direct persecution (Ripple *et al.* 2014; McLellan *et al.* 2016). Globally, grizzly bear survival decreases in areas where humans and bears overlap, especially near roads (Falcucci *et al.* 2009; Schwartz, Haroldson & White 2010), even in unhunted populations (Nielsen *et al.* 2004a; Boulanger & Stenhouse 2014). Conservation of grizzly bears under increasing densities of humans and roads will require management of human access into bear habitat; this can be accomplished by either 1) reducing road densities, or 2) limiting public access to roads. Both of these management tools are currently used in North America, yet there is little empirical evidence to support their utility (but see Schwartz, Haroldson & White 2010;

Boulanger & Stenhouse 2014) and none testing the effect of these management actions on bear density.

Our study focused on a provincially threatened grizzly bear population, the Kettle-Granby Grizzly Bear Population Unit (GBPU; Fig 1), at the species' southern range margin in south-central British Columbia (BC). This population was designated as provincially threatened based on a 1997 population inventory [38 bears (95% CI: 23-53), Boulanger (2000) and Boulanger *et al.* (2002)] that estimated the population to be less than half the habitat-based carrying capacity (Gyug & Hamilton 2007). Both prior to and following the 1997 population inventory, land and wildlife managers in the area undertook management actions to recover grizzly bears and maintain wilderness in an increasingly industrialized landscape. As is typical in many management scenarios, multiple management actions were enacted. Grizzly bear hunting was closed in the Kettle-Granby GBPU in 1995 because the bear population was thought to be declining. Between 1985 and 2001, as road densities continued to increase due to forestry, three provincial parks (covering 14% of land area in the GBPU) and two access management areas (5% of the GBPU land area) were created. Provincial parks do not allow industrial activities and thus serve as a potential refuge from roads and associated human access. Access management areas were put in place to eliminate motorised vehicle access by the public into sensitive grizzly bear habitat that had been roaded. In spite of these efforts, active road densities (mean = 1.64 km of road per km^2 of area) currently exceed the long-term target of 0.6 km/km^2 outlined in the Government Action Regulation for grizzly bears for the Kettle-Granby GBPU (BC Regulation 582/2004; General Wildlife Measures #8-373), stimulating scrutiny of provincial management of road densities for grizzly bear conservation (Ng & Dhaliwal 2016; Forest Practices Board 2017).

In 2015, we conducted a DNA-based mark-recapture inventory of grizzly bears (Woods *et al.* 1999) in the Kettle-Granby GBPU to estimate the number of bears present following 20 years of management actions, and to investigate the ecological and anthropogenic factors that were influencing density. To accomplish this, we used spatially explicit capture-recapture (SECR) methods that incorporate covariates to examine the combined effects of road density, road closures, protected areas, and habitat quality on population density. Land and wildlife managers often have greater control over road densities and access restrictions than they do habitat quality, thus our primary goal was to test the effect of road density on grizzly bear density and to then examine the efficacy of mitigation strategies: road closures (access management) and road density thresholds. Second, we compared the 2015 and 1997 population estimates to assess population trend in response to the management actions implemented in the interim. Third, we crafted recommendations for land managers based on our data and presented these here and in a condensed report tailored to local managers (Mowat *et al.* 2017b). Finally, we used the density-landscape relationships from the Kettle-Granby GBPU to assess the potential for bears to recolonise adjacent extirpated areas. The approach outlined here provides a general framework and method for using mark-recapture information from any species to investigate potential limiting factors to population density and the effectiveness of management actions. Integration of spatial covariates with spatially explicit capture-recapture methods provides a substantial step forward in the testing of hypotheses pertaining to the management of wildlife populations.

3.2 Materials and methods

3.2.1 Study Area

In BC, Grizzly Bear Population Units (GBPUs) are used to group grizzly bears into jurisdictional units for management purposes (Figure 3-1). In southern BC, GBPU boundaries often follow natural and man-made barriers that bears infrequently cross or, less often, boundaries between genetically distinct populations (Proctor *et al.* 2012). The Kettle-Granby GBPU (6,581 km^2) extends from the United States-Canada international border, north to Highway 6, and is bounded by the Kettle River to the west and Lower Arrow Lake to the east. Logging occurs throughout the GBPU, except in provincial parks, and is the main motivation for backcountry road construction. Current road density in the Kettle-Granby GBPU is 1.64 km/km^2, and roads are used by industry to access cut blocks and by the public for recreation. Access management areas near Granby Provincial Park permit industry use but exclude the public, which nearly eliminates motorised traffic.

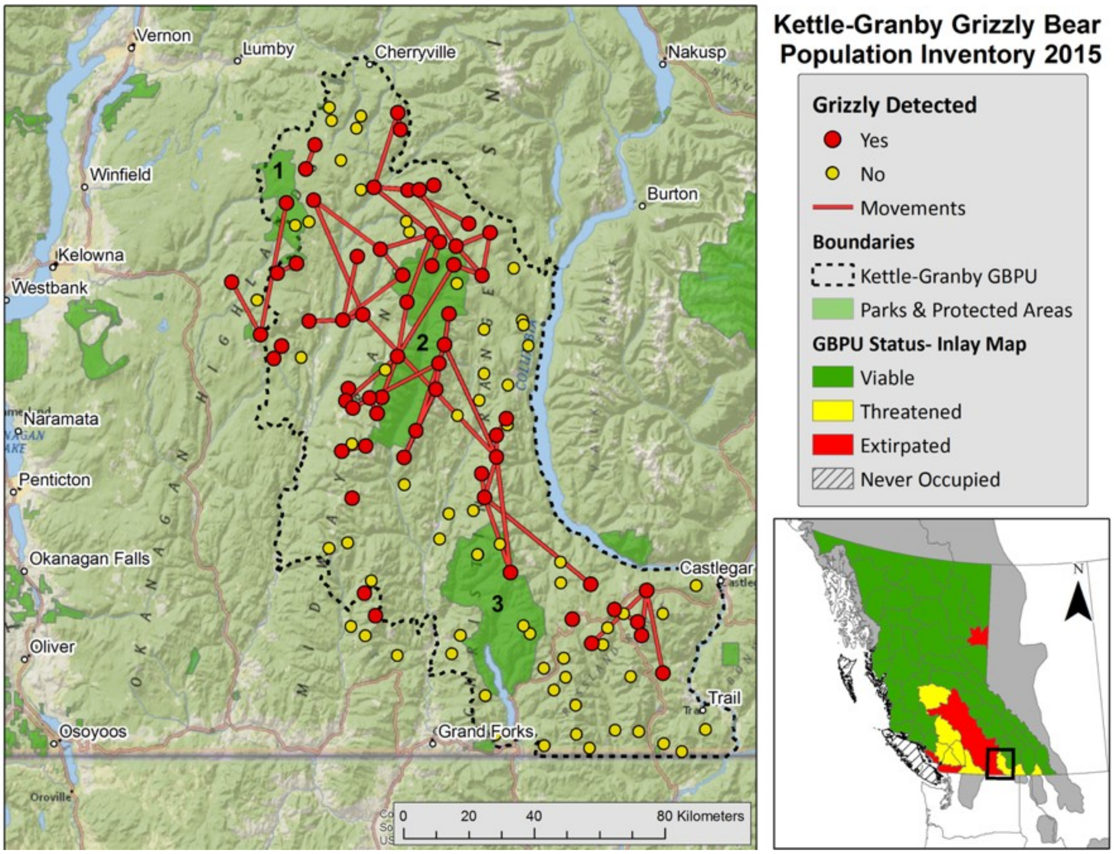


Figure 3-1. Study area for the 2015 grizzly bear population inventory of the threatened Kettle-Granby Grizzly Bear Population Unit (GBPU) in British Columbia, Canada. Grizzly bear sampling locations, detections, and between-site movements within the Kettle-Granby are shown on the left. Provincial Parks (> 100 km^2) within the unit include 1) Graystokes, 2) Granby, and 3) Gladstone. Provincial status of GBPUs is shown on the bottom right, with the southern distribution of grizzly bears outside British Columbia shown in grey (portion of Yellowstone population omitted along the bottom right).

Terrain is variable throughout the Kettle-Granby GBPU; high plateaus and rolling hills are common in the southern portion of the area, while the northern half is more mountainous. Subalpine parkland is common at high elevations, but alpine meadows and avalanche chutes are rare (Robertson 1999). Areas of lower elevation are usually heavily forested; however, dry, south-facing hillsides dominated by shrubs and grasses are common in the southern portion of the GBPU.

3.2.2 Inventory Design

We followed study design suggestions from Efford & Boulanger (2015) who conducted a simulation exercise specific to the Kettle-Granby population to evaluate various sampling designs based on the goal of maximising both cost efficiency and the precision of population estimates. This involved using 7x7 km cells to distribute trap effort and checking 125 scent-lured hair snag sites across four successive sessions to achieve the target precision of < 20% relative standard error. Efford & Boulanger (2015) found that moving sites between simulated sampling sessions did not improve precision and that small deviations from systematic site coverage did not cause bias or reduce precision.

3.2.3 Field and Genetic Methods

Between June 15 and August 19, 2015, we set scent-lured hair snag sites throughout the Kettle-Granby GBPU and checked them for hair samples four times at roughly two-week intervals. A total of 124 sites (96 ground and 28 helicopter access) were monitored throughout the summer (Figure 3-1). We used 3-4 litres of rotten cow blood and ½ litre of putrefied fish oil as a scent-lure at the sites. We used standard methods for site construction and sample collection (Woods *et al.* 1999; Kendall *et al.* 2008); further information can be found in Lamb, Walsh & Mowat (2016), and Mowat & Lamb (2016).

Genetic analysis was done at Wildlife Genetics International (Nelson, BC, Canada). We analysed 8 microsatellite loci and gender to assign individual identity with high confidence. Genotyping methods and subsampling procedures followed standard practices as detailed in Paetkau (2003), Mowat *et al.* (2005), and Lamb, Walsh & Mowat (2016).

3.2.4 Statistical Analysis

We used spatially explicit capture-recapture (SECR) models (Borchers 2012) to estimate the density and abundance of grizzly bears in the Kettle-Granby GBPU. We used the 'secr' package (Efford 2016), a likelihood-based approach accessed in program R (R Core Team 2016), to conduct our population analysis. A 'secr' model consists of two nested models, a detection model and a state model, which are fit to grizzly bear detection data. The detection model relates to the spatial detection of individuals, where the detection probability of a trap is related to the trap's proximity to an individual's home range centre, such that traps far from an individual's home range centre have reduced detection probability. The state model uses a latent Poisson point process to describe the distribution and density of home range centres within the region of analysis.

We fit spatially explicit capture-recapture models to the detection data using a hazard half-normal detection function, which is described by the detection model and controlled by the parameters λ (lambda) and δ (sigma). Lambda describes the per capita detection probability per unit effort. Sigma describes the spatial extent of an individual's use of the landscape, such that animals with large home ranges have large sigma values. The state model (hereafter, density model) allows a null, homogenous density surface (D) to be fit to the region of interest, or permits the user to input spatial covariates (Figure 3-2) to create a heterogeneous density surface that potentially distributes home range centres in a more ecologically meaningful way.

We used three groups of spatial covariates (Figure 3-2) to refine density estimates and further investigate the factors that affect demography in the region:

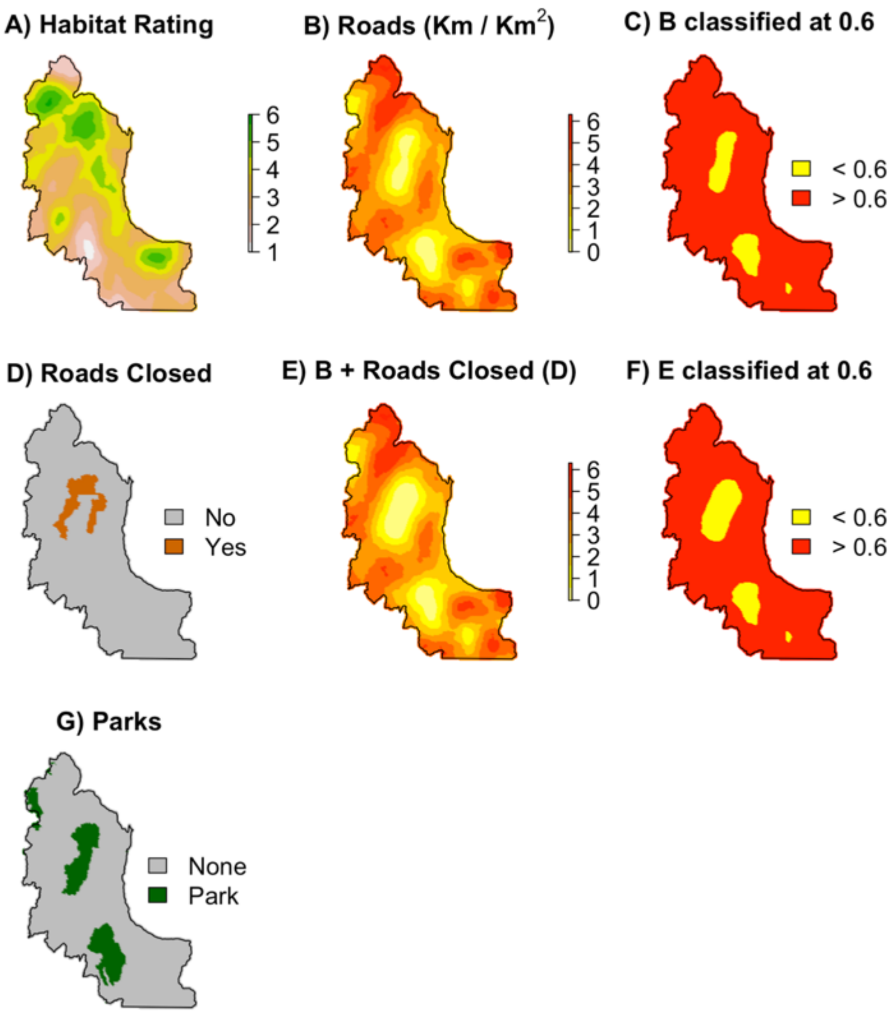


Figure 3-2. Spatial depiction of covariates hypothesised to influence grizzly bear density in the Kettle-Granby GBPU of south-central British Columbia in 2015.

1) Habitat (A): Maps of grizzly bear habitat suitability were created using Broad Ecosystem Units (~1,800 ha) from the provincial classification system (Resources Information Standards Committee 2006). Each unit was subjectively rated (from 1 to 6) by bear habitat experts based on descriptions of ecological factors (climate, geology, terrain, physiography, and vegetation), local grizzly bear research and inventory results, and local, experiential knowledge. The highest seasonal value for a unit was used for the annual map to best depict the habitat

quality as perceived by a wide-ranging animal that can move between habitats seasonally. The suitability maps represent vegetation food only and do not include salmon, ungulates, insects, or human foods and garbage.

2) Road density (B-F): We used a provincial road lines product from 2015 (Provincial Grizzly Bear Technical Working Group 2016), which is the most accurate and up-to-date provincial road layer available. We tested both road density (B, Road Dens) and a threshold road density covariate classified at 0.6 km/km^2 (C, Road Dens 0.6) based on proposed provincial road density standards (Provincial Grizzly Bear Technical Working Group 2016) and research suggesting grizzly bear females select home ranges with road densities below this threshold (Mace *et al.* 1996), or face survival consequences (Boulanger & Stenhouse 2014). Due to the potential negative effects of roads, managers in some jurisdictions close roads to motor vehicle traffic (D, Road Closures) to reduce human presence (some permitted industrial use is allowed) in grizzly bear habitat. We tested the effects of roads and road closures simultaneously by creating a road density variable that was based only on roads open to motor vehicles and compared models. We again tested a continuous measure of roads open to motor vehicles (E, Open Road Dens) and a threshold variable classified at 0.6 km/km^2 (F, Open Road Dens 0.6).

3) Protected areas (G, Parks): Protected areas can be sanctuaries for wildlife as these areas receive increased protection from development.

We summarised habitat and road density using an 8-km radius moving window analysis carried out in ArcGIS 10.3 (ESRI). We chose to use a moving window because the relationship between an individual’s home range centre and the surrounding habitat extends beyond the habitat characteristics directly adjacent to the home range centre, especially for wide-ranging animals. Annual home ranges for grizzly bears were between 200 and 1,250 km^2 (8-20 km radii) depending on sex, age, and habitat quality (Graham & Stenhouse 2014; McLellan 2015, M Proctor unpublished data), thus we used an 8-km radius (200 km^2) as an approximation of the area used by bears during our period of investigation (~2.5 months, or just under half of the non-denning season).

The area of density integration in our ‘secr’ model was constrained to a 20-km buffer around all traps, which represents the extreme edge of detection for the individuals in the sample. We bounded the area of integration using a polygon of non-habitat (see Fig. S1 in Supporting Information), which we defined using expert opinion and landscape features such as large lakes, habitat suitability, and large valleys settled by people. Using an area of integration that is too small can positively bias ‘secr’ density estimates, while too large an area does not, as density estimates asymptote with buffer width (Fig. S2).

We created *a priori* hypotheses pertaining to both the detection and density models and compared the fit of these models using Akaike’s Information Criterion [Table 1, (Akaike 1974; Burnham & Anderson 2002)]. Fitting complex ‘secr’ models can be computationally intensive, thus we first fit a series of detection models to the data using a homogenous density surface and used the top detection model in our subsequent runs of the density model. Covariates hypothesised to influence λ included session-specific detection (t, time) and behavioural response (bk, site-learned response). We fit only one model for δ, a null model where home range index was static through time and space because differences in home range size between the sexes have been shown to be compensatory with λ in other study areas (Efford & Mowat 2013). Following the identification of a top detection model, we fit this model to each sex separately to estimate sex-specific detection parameters (λ and δ), and to test whether the sum of our sex-specific abundances was similar to the model with both sexes included.

We also explored the road density threshold of 0.6 km/km^2 proposed by the province of BC (Provincial Grizzly Bear Technical Working Group 2016) and other jurisdictions [such as Alberta, Canada (Alberta Grizzly Bear Recovery Plan 2008-2013 2008) and the United States (Mace *et al.* 1996)] as a road density target above which grizzly bear conservation is a concern. We classified the open road density (Figure 3-2 E) using breakpoints between 0.1 and 3 km/km^2, fit 'secr' models while implicitly controlling for habitat quality by including the Habitat variable in our models, and finally computed log likelihoods and weights for each model. In this comparison, each model had the same number of parameters (k) and only differed in the breakpoint used to classify road density variables. Thus, we directly compared models with log likelihood, where the model with the maximum log likelihood characterised the optimal break point. In addition, we calculated cumulative model weights to identify the range of breakpoints with competing fit to the data.

Finally, we used the habitat-density relationships from the top 'secr' model to create a density surface within the Kettle-Granby GBPU and extrapolated these relationships into the west where grizzly bears are currently absent. Producing a density surface within the Kettle-Granby also allowed us to produce region-specific abundance estimates, such as estimates for protected areas, which are far too small to conduct a stand-alone mark-recapture study. We constrained density extrapolations to an area 50 km west of our sampling grid.

3.3 Results

3.3.1 *Hair Collection*

We identified 74 individual grizzly bears (38 males and 36 females) from 177 detection events (unique individual and session). We captured 36 of the 74 individuals, or approximately half of the total bears detected, during the first sampling occasion (Supplementary Fig S3).

3.3.2 *Population Estimate and Density*

Detection models fit the data best when λ varied by session and allowed different capture probabilities for bears caught the first time at a site compared to subsequent detections at that site (trap-specific behaviour variation, Table 3-1). Our 20-km buffer was sufficient to encompass home range centres of all bears detected in our sample (Supplementary Fig S1, S2).

Grizzly bear density across the Kettle-Granby GBPU was estimated as 13.2 (95% CI: 10.3-16.7) grizzly bears / 1000 km^2, with error below the 20% relative standard error threshold (RSE = 12.3%), suggesting a reasonably precise estimate. Sex-specific abundances (

Table 3-2) were 41 females (95% CI: 29-57) and 46 males (95% CI: 32-64). Summing sex-specific abundances [

Table 3-2, Female: 41 (95% CI: 29.3-57.4), Male: 45.7 (95% CI: 32.4-64.4)] resulted in an identical abundance (87 individuals, 95% CI: 66-108) as the combined-sex model. Detection parameters (

Table 3-2, lambda and sigma) were compensatory, as suggested by Efford & Mowat (2013), with males occupying a larger spatial extent than females, but having a lower per capita detection probability than females, due to their larger range. Sex ratios for the Kettle-Granby were nearly equal, at 0.90 females to every male.

Our top 'secr' model included a positive effect of habitat quality and a negative effect of road densities > 0.6 km/km^2 on grizzly bear density (Table 3-1 & Figure 3-3). Results suggest a second competing model because the top two models (differing only by the inclusion/exclusion of closed roads from the road density surface) have comparable support (AICc weight = 0.455 and 0.333). The spatial difference between the Road Dens 0.6 and Open Road Dens 0.6 variables (Figure 3-2 C & F) is minimal, and results from removing roads from the relatively small access management area (~400 km^2; 6% of study area); however, we felt the slight increase in model likelihood for Open Road Dens 0.6 represented a biologically meaningful signal, and we expect the gains in likelihood would be even greater had the access management area represented a larger portion of the study area. To investigate the biological effect of road closures, we estimated grizzly bear abundance inside the ~400 km^2 of road closures in the Kettle-Granby GBPU and contrasted this to abundance had the roads not been closed (by adding roads inside the road closures back into the surface). Results suggest 27% fewer grizzly bears (~4 individuals) in the ~400 km^2 of road closures had the roads not been closed [without access management: 11 bears (95% CI: 7.6-15.9), with access management: 15.1 bears (95% CI: 9.9-23.1]. Thus, we selected (D ~ Habitat + Open Road Dens 0.6) as the most supported model.

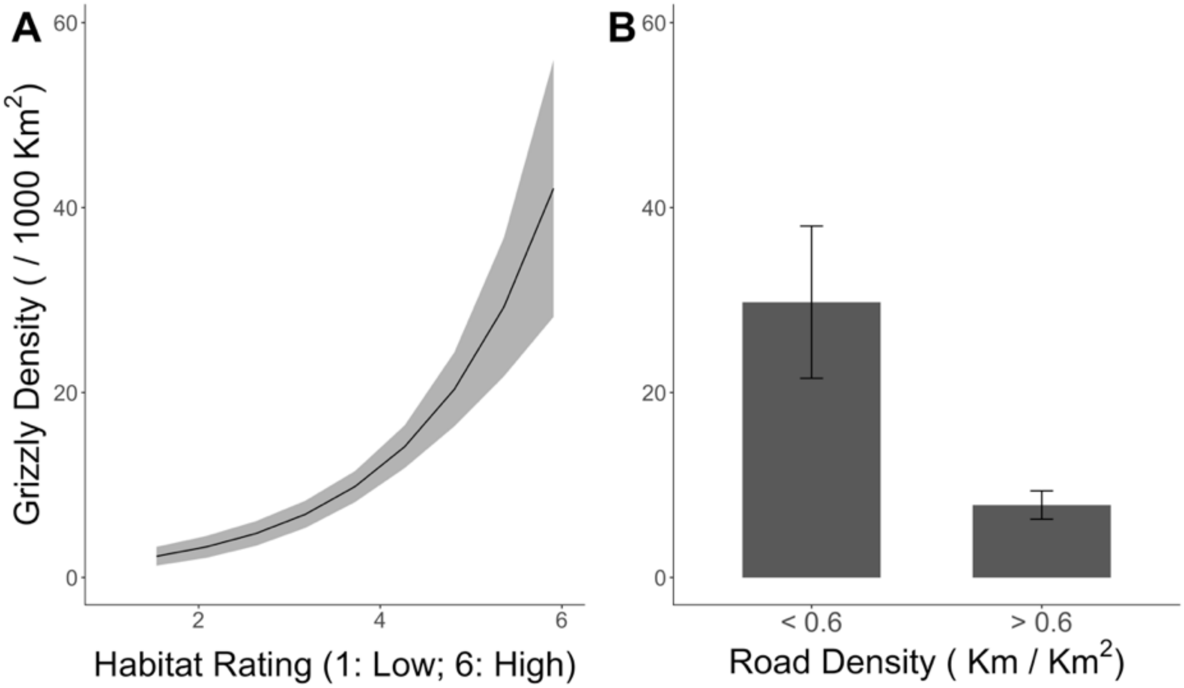


Figure 3-3. A) Predicted responses of the most supported model illustrating the positive relationship between habitat quality and grizzly bear density (with Road Density fixed to > 0.6 km/km^2, reflecting most of the landscape). B) Effect of road density threshold on grizzly bear density. Areas with road densities below 0.6 km/km^2 had much higher grizzly bear densities than areas with road densities above 0.6 km/km^2 (with Habitat Rating fixed at 3, which was median habitat quality).

Table 3-1. Model selection table for spatially explicit capture-recapture model implemented in ‘secr’. Detection model for all models below: lambda ~ t + bk, sigma ~ 1. See Materials and methods text for variable definitions. k = number of parameters in model.

Model	AICc	dAICc	AICc weight
D ~ Habitat + Open Road Dens 0.6	1246.599	0	0.455
D ~ Habitat + Road Dens 0.6	1247.225	0.626	0.333
D ~ Habitat + Open Road Dens	1249.745	3.146	0.094
D ~ Habitat + Park	1250.777	4.178	0.056
D ~ Habitat + Road Dens	1250.841	4.242	0.054
D ~ Habitat	1255.376	8.777	0.005
D ~ Open Road Dens 0.6 + Park	1266.298	19.699	0
D ~ 1	1272.986	26.387	0

Table 3-2. Parameter estimates from top ‘secr’ model. 95% confidence intervals shown in parentheses. Grizzly bear density is bears / 1000 km2 and sigma is in metres.

Sex	Abundance	Density	Lambda	Sigma
Total	86.6 (68.1 - 110.1)	13.2 (10.3 - 16.7)	0.149 (0.1 - 0.221)	5959.5 (5306.4 - 6692.9)
F	41 (29.3 - 57.4)	6.2 (4.5 - 8.7)	0.235 (0.137 - 0.402)	5121.6 (4383.5 - 5984.1)
M	45.7 (32.4 - 64.4)	6.9 (4.9 - 9.8)	0.097 (0.054 - 0.174)	6842.7 (5749.1 - 8144.5)

Grizzly bear density was heterogeneous across the landscape and structured towards areas of high habitat quality and low road densities (Figure 3-3 & Figure 3-4). Protected areas were characterised by generally low road densities, moderate to high habitat quality, and higher grizzly bear densities compared to non-protected areas (Table 3-3).

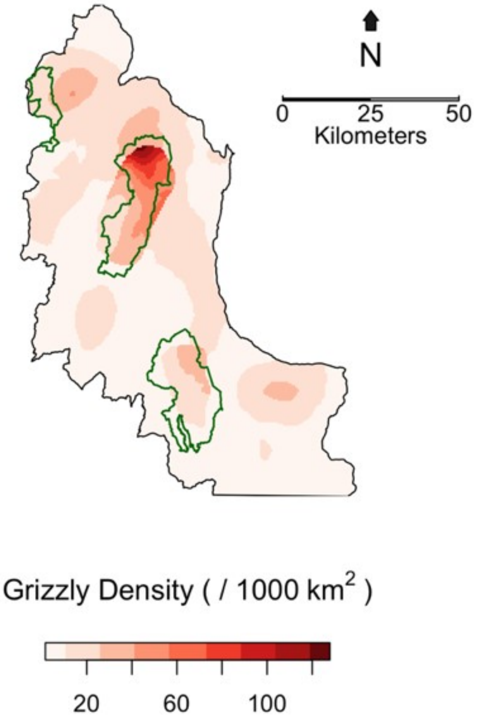


Figure 3-4. Grizzly bear densities (bears/1000 km^2) within the Kettle-Granby GBPU in 2015 as estimated by the best-fit spatial capture-recapture model. Provincial parks are outlined in green (top: Graystokes, middle: Granby, bottom: Gladstone).

Table 3-3. Region-specific abundance and density estimates, ranked from lowest to highest density, within the Kettle-Granby GBPU. 95% confidence intervals shown in parentheses.

Name	Area (km^2)	Density	Abundance
Outside Protected Area	5674	10.7 (8.1 - 14.1)	60.8 (46.1 - 80.1)
Gladstone Park	394.8	14.2 (8.4 - 23.6)	5.6 (3.3 - 9.3)
Graystokes Park	119.6	15.9 (11.7 - 22.6)	1.9 (1.4 - 2.7)
Granby Park	411.5	44.2 (27.9 - 70.2)	18.2 (11.5 - 28.9)

We tested for an optimal breakpoint in road density that best predicts the pattern of grizzly bear density observed in the Kettle-Granby GBPU. Results generally support the threshold of approximately 0.6 km of road per km^2 of area that is currently proposed or used in many jurisdictions (Figure 3-5). Our analyses demonstrated that 0.5 km/km^2 was the optimal threshold for the Kettle-Granby, with 0.6 a very close second. Values between 0.2 and 0.7 accounted for > 80% of cumulative model weight, suggesting that although 0.5 was the most likely breakpoint, a range of values (~ ± 0.2) on either side of 0.5 are also likely. We chose to keep 0.6 km/km^2 as our breakpoint to maintain consistency with the provincial cumulative effects analysis and proposed policy guidelines. Values higher than 0.6 quickly produced poorer model fit.

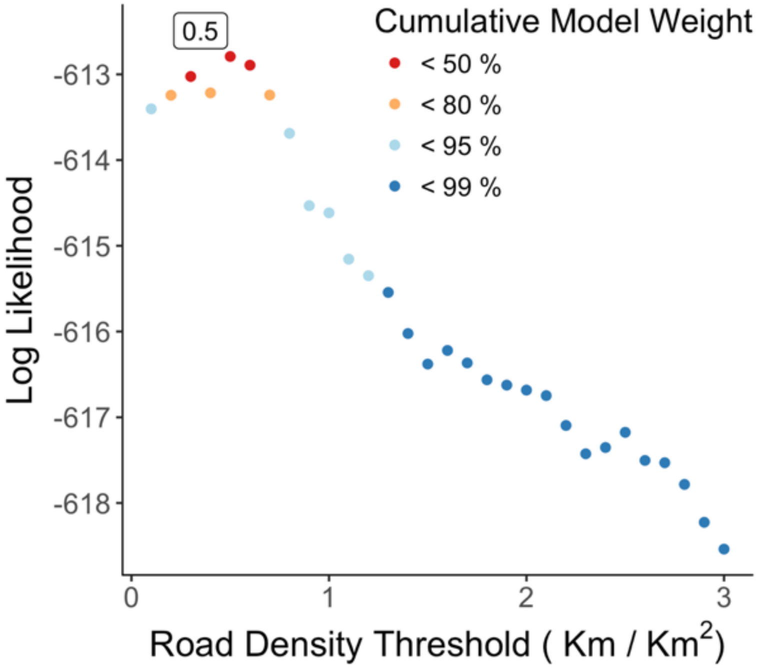


Figure 3-5. Distribution of log likelihood values and cumulative model weights used to find an optimal road density breakpoint for grizzly bear density in the Kettle-Granby GBPU of south-central British Columbia in 2015.

Although the Okanagan Valley to the west of our study area is characterised by high road densities and generally poor grizzly bear habitat, our model predicted local nodes of low to medium grizzly bear densities in the area, although these nodes were all in relatively close proximity to large human populations and several were isolated by wide expanses of low grizzly bear density (Figure 3-6).

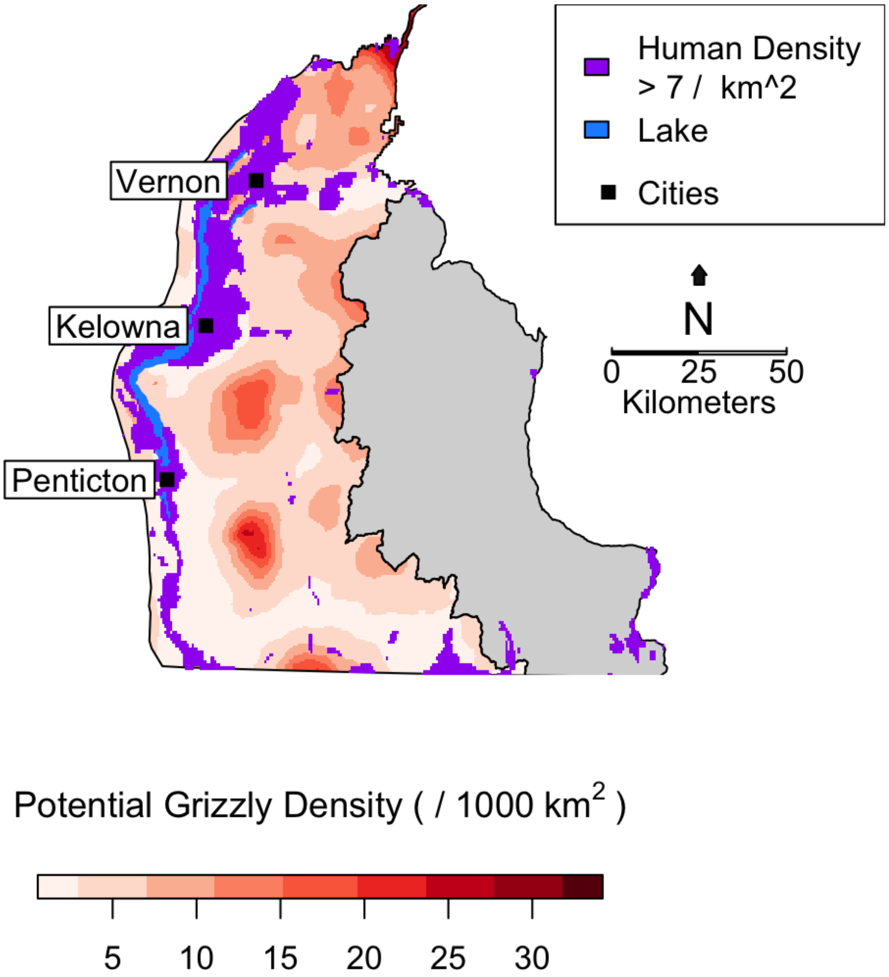


Figure 3-6. Predicted grizzly bear densities (bears/1000 km^2) in the southeast Okanagan region where grizzly bears are currently extirpated. Kettle-Granby GBPU shown in grey.

3.4 Discussion

We used recently developed spatially explicit capture-recapture methods that allow the inclusion of covariates to investigate factors correlated to the local density of a provincially threatened grizzly bear population. Grizzly bear density was highest in areas of high habitat quality and low road density. Increased human access into the backcountry, most often through resource extraction roads, increases human-bear conflict and thus increases bear mortality in both hunted and unhunted populations (McLellan & Shackleton 1988; Nielsen *et al.* 2004a; Falcucci *et al.* 2009; McLellan 2015). In addition to direct mortality near roads, perceived risks by bears may decrease foraging efficiency (Hertel *et al.* 2016), and alter activity patterns (McLellan & Shackleton 1989; Martin *et al.* 2010; Northrup *et al.* 2012a) and movements (Roever, Boyce & Stenhouse 2010; Bischof *et al.* 2016), thus potentially reducing habitat effectiveness.

Although roads produce myriad consequences to wildlife (Fahrig & Rytwinski 2009; Ibisch *et al.* 2016), management agencies have the ability to mitigate these negative effects by restricting access or limiting the creation of new roads. However, the efficacy of these methods to safeguard grizzly bear density has yet to be tested, which has hindered uptake by practitioners. A lack of empirical evidence linking road closures to reduced mortality or increased population density also exists for other large mammals (Rowland *et al.* 2004). Here we tested the generality of the 0.6 km/km^2 (0.6 km of road per km^2 of area) threshold—proposed by the Alberta Grizzly Bear Recovery Team (Alberta Grizzly Bear Recovery Plan 2008-2013 2008) and applied in the US Grizzly Bear Recovery Areas—in a small population of grizzly bears in southern BC. We found grizzly bear densities to be much higher in areas below the 0.6 threshold, even after controlling for habitat quality, and this threshold version of road density fit the data better than continuous road density. Furthermore, we assessed the sensitivity of this threshold by varying it from 0.1 to 3 and found greatest support for a threshold between 0.5 and 0.6, above which grizzly bear density was much lower. It should be noted there was decreasing but comparable model fit for threshold values on either side of the maximum (0.2 to 0.7) (Figure 3-5). Our results generally corroborate the 0.6 km/km^2 threshold and we suggest that managers, unless they have local empirical data on grizzly bear response to roads, use this as a target where grizzly bear conservation is a priority. Further investigation into the modifying effects of region-specific habitat productivity, grizzly bear population density, and traffic volume may uncover mechanisms that allow more locally relevant thresholds. For example, McLellan (2016) documented grizzly bear densities four times greater than found here, yet McLellan's study area had 0.74 km/km^2 of 2-wheel drive roads plus another 0.9 km/km^2 of smaller, more ephemeral roads. However, McLellan's study area was > 75 km from the nearest human settlement and had much higher habitat quality, including large huckleberry (*Vaccinium membranaceum*) fields, avalanche chutes, and riparian areas, which likely buffered some of the negative impacts of roads. McLellan (2016) suggested little impact of increasing road density in portions of that area because the number of people using the road network may not increase with more roads.

Although the 0.6 km/km^2 threshold is a useful road density target, this measure does not account for the spatial distribution of roads. In theory, a landscape with 0.6 km/km^2 of road could have 600 m of road in every km^2 of habitat, offering little sanctuary for wildlife. Schwartz, Haroldson & White (2010) found that the proportion of land > 500 m from open roads was important for grizzly bear conservation. Our results are consistent with this finding; many bears were captured, and had home range centres, in the largest tract of unroaded area: Granby Provincial Park. Consequently, in addition to keeping landscape-level road densities below 0.6

km/km^2, practitioners should strive to manage the areas of highest habitat quality for no open roads (i.e. secure habitat > 500 m from open roads) and reduce road densities in areas of intermediate habitat quality. Allowing higher road densities in low quality bear habitat and outside of movement corridors should have the least impact. In Mowat *et al.* (2017), we suggested a number of priority areas where reducing road densities would facilitate increased population connectivity and security.

There are many cases where grizzly bear conservation is a concern and the 0.6 km/km^2 road density threshold has already been exceeded; leaving practitioners little choice but to actively remove roads or restrict human access on roads to address grizzly bear conservation needs. In 1985, road closures were enacted in the Kettle-Granby to protect alpine environments, and in 1997, road closures specifically designed to support grizzly bear recovery were established on both sides of Granby Provincial Park, where road densities (0.9 km/km^2) were higher than proposed targets (0.6 km/km^2) and roads overlapped productive habitat. Our results suggest grizzly bear density would be 27% lower within these areas if access management had not been enacted. While the Kettle-Granby grizzly bear densities are concentrated and at relatively high levels in protected areas and adjacent areas with access controls (Table 3-3), our results suggest the potential exists to increase bear densities outside the protected areas and further recover this population through future access controls (Braid & Nielsen 2015; Mowat *et al.* 2017b).

We show that the provincially threatened grizzly bear population in the Kettle-Granby GBPU has increased since the previous estimate in 1997. Population estimates from the 1997 mark-recapture data have been generated using numerous approaches and consistent estimates of 7.8-8.5 grizzly bears / 1000 km^2 were obtained (Boulanger *et al.* 2002; Efford & Boulanger

2015; Apps *et al.* 2016). In 2015, we detected 74 individuals in our sampling and estimated the Kettle-Granby grizzly population at 87 individuals or a density of 13.2 grizzly bears / 1000 km^2; an ~ 55-69% increase in density from 1997. Although comparing two point estimates is a relatively weak measure of population trend, the 2015 data suggest the population density is higher than it was in 1997. If the population continues to increase, more bears may be forced to use more heavily roaded portions of our study area, and the 0.6 km/km^2 road density threshold proposed here may change.

It may be surprising that the grizzly bear population has increased in the Kettle-Granby GBPU given that logging and associated road construction have continually expanded into wilderness (unroaded) areas in the Kettle-Granby. However, parks and access management areas were created in the 1990s, human access into areas of high quality habitat was restricted, and hunting was stopped in 1995 which reduced human-caused mortality. Combined, these measures likely contributed to grizzly bear population recovery. Furthermore, increased early seral habitat from logging can also improve grizzly bear habitat (Nielsen *et al.* 2004b). Protected areas cover less than 20% of the GBPU, and they are all relatively small (Table 3-3), yet these areas of elevated protection and low road densities harboured the highest densities of grizzly bears; nearly as many individuals currently occupy these small areas as occupied the entire area in 1997. Small, but connected protected areas may thus serve as effective conservation options for umbrella species, especially in multi-use landscapes where large protected areas may be unrealistic.

Grizzly bears were legally hunted in the Kettle-Granby GBPU until 1995. Hunting plus other forms of human-caused mortality likely reduced bear numbers within our study area in the past. Like many populations monitored in greater detail over the past several decades (Garshelis, Gibeau & Herrero 2005; Schwartz *et al.* 2006; Mace *et al.* 2012; McLellan 2015), the Kettle-Granby population is likely expanding due, at least in part, to reduced human-caused mortality. Stopping the legal kill may have been a factor supporting recovery, but because more female bears appear to be killed for non-hunting causes in other areas (McLellan 2015; Mowat & Lamb 2016), limiting access to important habitat likely reduced the kill of female bears by people accessing high-quality habitat for other reasons (e.g., ungulate hunting, motorised recreation). In contrast to hunting mortalities, which are regulated, non-hunting mortalities are difficult to quantify and control (Lamb *et al.* 2017b). Since the cessation of the hunt in 1995, only 13 human-caused grizzly bear mortalities have been recorded in the Kettle-Granby GBPU (1995-2015), largely due to human-bear conflicts (61%) and poaching (31%). Unfortunately, the number of unreported mortalities is unknown, although they are often equal to or greater than the number of reported mortalities (McLellan *et al.* 1999; McLellan, Mowat & Lamb 2018).

The Kettle-Granby population is at the southwestern edge of the southern interior grizzly bear distribution in North America. Stent (2011) summarised the distribution of grizzly bears within and around the Kettle-Granby GBPU between 1980 and 2009 and noted an erosion of the western edge of the distribution, which effectively increased the size of the extirpated area in the Okanagan Valley. Our results suggest the population is now expanding westward, and there is potential for recolonization of at least part of the extirpated zone. Indeed, grizzly bear sightings and mortalities have been recorded in the extirpated zone since the Stent (2011) review, and our results suggest this area has the potential to support a low density grizzly bear population in areas removed from human settlements. However, recolonization is contingent on demographic rescue (immigration) from the Kettle-Granby population, which will require both sufficient connectivity between habitat patches and public acceptance of grizzly bears in these areas which are close to dense human populations.

Human use of natural areas for economic reasons is ubiquitous around the globe. Biodiversity loss and species extinctions are occurring through generally small, but successive disturbances (Laurance *et al.* 2014). The negative impacts of activities that disturb landscapes and ecosystems for economic prosperity can often be mitigated post-use for the benefit of biodiversity and ecological processes. We show here that road density is negatively related to grizzly bear density, but this undesirable effect can be ameliorated when access controls or road removal are implemented to limit human presence. Utilisation of natural resources and the disturbance associated with their extraction is currently non-negotiable; however, having protocols in place to reduce the negative impacts of resource extraction (i.e. limiting new road development or closing roads when work is finished) is an encouraged approach. We believe there is opportunity in research focused on understanding the key industry-related factors limiting biodiversity and suggest policymakers strive for a no-net increase, or reduction, in these factors where possible.

3.5 Management implications and wider relevance

Our density model allowed us to compare grizzly bear density, habitat quality, and road density to identify locales that could generate the greatest response in bear density with the lowest mitigation cost (Mowat *et al.* 2017b). Efforts to reduce or eliminate road density in areas of high habitat quality should generate the greatest increase in grizzly bear abundance. The population we studied was grouped in four partially isolated areas in summer, which suggested that greater connectivity of ranges would further reduce conservation risk. Our data demonstrated that bears moved among these locales during summer, which likely put those individuals at higher mortality risk as they crossed through heavily roaded valleys. With this in mind, we recommend reducing road densities in three areas of moderate road density to improve population connectivity at a modest overall cost (Mowat *et al.* 2017b). The spatial nature of the population model used here allowed the formulation of management options that went well beyond what was possible with non-spatial capture-recapture models.

Our analysis firmly links the negative effects of roads on grizzly bear density and suggests that access management is a viable mitigation strategy. Secondly, our results corroborate the 0.6 km/km^2 road density threshold currently in use by many management agencies. However, we do note that much of the work recommending this threshold (including our own) comes from recovering bear populations in medium quality habitat, and the degree to which population status, habitat quality, and ranging behaviour influences optimal road density thresholds remains unknown. Where possible, investigators should test and publish their thresholds to allow for an effective meta-analysis. If defensible, area-specific road density thresholds were available, generalised relationships could be extrapolated to areas where bear conservation is a priority but local research efforts are limited or non-existent. Finally, it bears repeating that a road density threshold does not incorporate the distribution of roads across the landscape, thus prudent management will also maintain a portion of the landscape > 500 m from roads [Mace *et al.* (1996) suggests 56%, preferably in high quality habitat; Schwartz, Haroldson & White (2010)], as was done in our study area where large protected areas were roadless.

We expect the benefit of access management to cascade beyond grizzly bears to other wildlife negatively affected by roads (Fahrig & Rytwinski 2009; Benítez-López *et al.* 2010; Ceia-Hasse *et al.* 2017). Many species are negatively affected by roads (Fahrig & Rytwinski

2009); African lions (*Panthera leo)*, wild dogs (*Lycaon pictus*), cats (*Felidae* spp.*s*), and apes (*Gorilla and Pan* spp.*)* are amongst the charismatic megafauna faced with increased roads and resulting demographic consequences (Walsh *et al.* 2003; Ceia-Hasse *et al.* 2017). Even for these species, despite their charismatic status and high conservation risk, dedicated habitat restoration and mortality reduction is required for long-term persistence (Stephens 2015). Mitigating the negative effect of roads on such species may require species-specific road density thresholds (Ceia-Hasse *et al.* 2017), which will vary by life-history and susceptibility to road mortality and disturbance. Nevertheless, we expect the reduction of road densities and human access in high quality habitat to have positive results for wildlife.

We demonstrate how spatial capture-recapture methods can be used to investigate factors that correlate spatially with animal density, and these methods have applications for many species that are surveyed using techniques that identify individuals. Many species are inventoried for immediate management needs such as assessing population status, investigating causes of decline, or managing harvest. Analyses similar to ours could be a value-added component to many inventories around the world because the link between top-down and bottom-up influences on animal density is a key ecological question (Nielsen *et al.* 2017), with many immediate applications.

3.6 Supporting information and data accessibility

Supporting information available at: https://besjournals.onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2F1365-2664.13056&file=jpe13056-sup-0001-FigS1-S3.docx. Data available from the Dryad Digital Repository **https://doi.org/10.5061/dryad.bk0rd** (Lamb *et al.* 2017c).

4 Chapter 4: Limits to grizzly bear population density across ecosystems

4.1 Introduction

Identifying the ecological mechanisms structuring population density is a central tenet of ecology (Krebs 2008). Focusing on population density allows investigators to overcome the potentially divergent or covarying signals between individual vital rates (survival, reproduction, immigration, and emigration) underlying population density and ecological mechanisms (Coulson *et al.* 2006). However, estimating population density is challenging for cryptic, wide-ranging, or low-density species due to imperfect detection. Recent advances in detection methods [camera traps (Mondol *et al.* 2009) or genetic tags (Woods *et al.* 1999)] and analytical approaches [spatial capture-recapture (SCR) (Borchers & Efford 2008; Royle *et al.* 2014a)] have facilitated the estimation of density and spatial correlates across massive spatial scales. As a result, the critical question of "why does animal density vary across the landscape?" can be addressed explicitly, even for cryptic, wide-ranging, or low-density species such as large carnivores.

The conservation of large carnivores poses a major societal challenge and is the focus of polarizing debate in the world's courts, media, and scientific literature (Karanth *et al.* 2013; Ripple *et al.* 2014; Gilroy *et al.* 2015; Fernández-Gil *et al.* 2016). The debate often centers around uncertainty in the ecological mechanisms limiting population density of large carnivore populations, and a disconnect between the relatively few rural people living with carnivores and the many people advocating for carnivore conservation that live in urban areas devoid of carnivores (i.e., the urban-rural divide). Grizzly bears (*Ursus arctos*) are at the center of this debate across North America. For example, State scientists suggested that grizzly bears had recovered in the continental USA and should be removed from the endangered species list. However, uncertainty around current and future population densities paired with ethical concerns around bear hunting if delisted. sparked intense debate and legal action in the country (Christensen 2018). Similarly, grizzly bear hunting in British Columbia, Canada (hereafter BC) has been the source of much debate in the Province with some scientists suggesting that "overmortality" (Artelle *et al.* 2013), as well as politically influenced population estimates and policy (Darimont *et al.* 2018), pose a realized threat to bear populations, while Provincial scientists suggest the hunt poses little risk (McLellan *et al.* 2017). Uncertainty in the ecological mechanisms limiting population density of large carnivores fuels polarizing and dissenting views. There is an immediate need to generate evidence to fill this knowledge gap and reduce the harmful effects of uncertainty on effective carnivore conservation, management, and collaboration.

Here we focus on grizzly bear populations in British Columbia, Canada. About half of Canada's grizzly bears reside in British Columbia (COSEWIC 2012), due to the Province's productive habitats relative to areas further north (Mowat, Heard & Schwarz 2013b). However, expanding road networks (10,000 km/year) (Auditor General 2017) threaten the security of wild bear habitats through increases in human presence and the increased mortality and disturbance that result (Proctor *et al.* 2018c). Further, BC's globally acclaimed wilderness, resource extraction, recreational opportunities, economy, and education, has attracted many new inhabitants, surging human populations densities in recent years. In 1871, there were 40,000 people in BC, half of which were Indigenous (Ministry of Environment 1995). By 2000 there were 3.8 million people (Ministry of Environment 1995), and only 19 years later in 2019 there are now 5.0 million people and the population continues to grow at >7 times the National average (Province of British Columbia 2019). With increasing human threats to the security of BC's bear habitat, there is a need to resolve the uncertainty around bear population sizes and limiting factors.

Genetic tags— a unique sequence of DNA loci used to identify individuals and their species, sex, and lineage—have provided ecologists with an information-rich, non-invasive approach for investigating limiting factors on population density that can be deployed across massive spatial scales (Lamb *et al.* 2019). Grizzly bears in British Columbia were the first terrestrial mammal to be genetically tagged for mark-recapture studies of population density (Woods *et al.* 1999), and the method has since been used across BC to calculate grizzly bear population density for the management of sustainable harvest rates (McLellan *et al.* 2017). These data have been used in isolation to estimate population size, and few studies have used these data to investigate broad-scale drivers of population size (Mowat *et al.* 2005, 2013b). To date, these data have not been integrated into a single analytical framework, leveraging the immense amount of monitoring data and ecological gradients between areas, to investigate both fine and broad scale factors limiting bear populations across BC. Here we compile the largest dataset thus far collected for grizzly bear genetic capture-recapture studies—1,913 animals across 27 project areas, many of which were run for multiple years— and leverage recent advances in spatial capture-recapture (SCR) analyses to investigate bottom-up and top-down effects, and the degree of limitation from specific sources on BC's grizzly bear population.

Our objective was to add to our understanding about which factors influence grizzly bear density across space. Specifically, we wanted to examine how top-down factors such as human-caused mortality and disturbance interact with bottom-up factors such as meat availability and vegetation productivity and type limit observed densities across BC.

4.2 Methods

4.2.1 Grizzly bear genetic tagging

We compiled all the genetic capture-recapture studies done across BC, except for those where the principal investigators were not willing to contribute to this analysis (Figure 4-1). Bears were genetically tagged across British Columbia using a standardized methodology (Woods *et al.* 1999; Mowat *et al.* 2005), which included barbed wire to snag hair and well-established genotyping approaches (Paetkau 2003). For this work we only considered bears captured at baited hair snags, not rub trees or trail sites. Descriptions of the three traps can be found in (Kendall & McKelvey 2008; Lamb *et al.* 2016b). We chose to exclude rub trees and trail sets as these sites may have considerable seasonal and sex-specific variation in detection (Lamb *et al.* 2016b; McLellan *et al.* 2019). Further, these sites were not deployed across all study areas and we did not want to introduce model complexity due to differing detection probabilities between rub trees and hair traps that may also correlate with density in complex ways and possibly confound results.

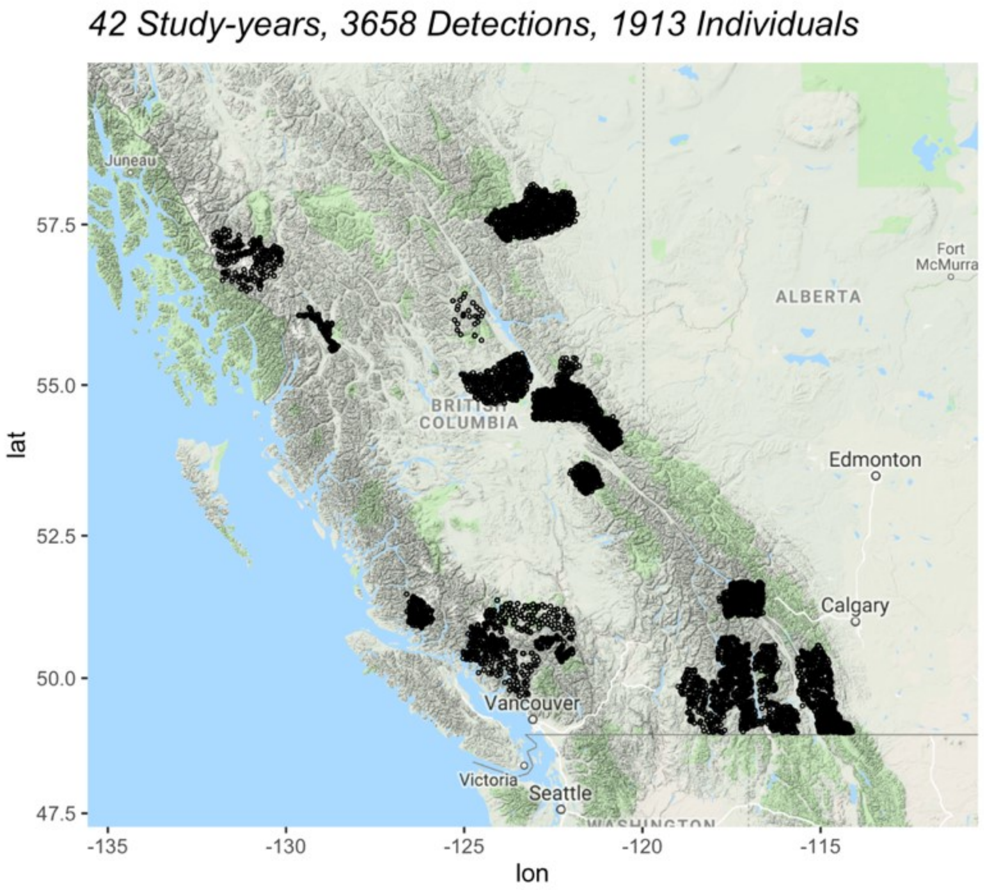


Figure 4-1. Distribution of grizzly bear genetic tagging studies across British Columbia between 1996-2017. Black dots are the locations of each bait site within the study area.

4.2.2 Explanatory variables

All variables used here were resampled to 500 m resolution in BC Albers projection, but their native resolutions and data sources are presented below:

Human population Density- Circa 2000, humans per km^2 from the Gridded Population of the World, Version 3 at 2.5 arc-minute resolution.

https://sedac.ciesin.columbia.edu/data/set/gpw-v3-population-density

Road Density and Secure Habitat- I calculated road density (roads/km^2) at a 500 m resolution using an updated provincial road layer (BC Cumulative Effects Analysis). Secure habitat was calculated as the proportion area that was >500 m from a road (Proctor *et al.* 2018c).

Human Influence Index- global dataset of 1 km grid cells, representing a general index of human influence on the landscape (Sanderson *et al.* 2006). The index is created from nine global data layers covering human population pressure (population density), human land use, and infrastructure (built-up areas, nighttime lights, land use/land cover), and human access (coastlines, roads, railroads, navigable rivers).

Lasting Suppression- Bear populations in south west BC are thought to be below carrying capacity (K) due to intense historic mortality pressure. Further, proximity to BC's largest urban areas: Vancouver and the surrounding Fraser Valley cities has potentially reduced the capacity for population recovery. As a result, we created two sets of binomial variables (under K [1] or not [0]) using BC's grizzly bear population units. The "threatened" variable classified all threatened populations (see (Lamb *et al.* 2018b)) as 1, and the "underK" variable classified three populations in southwest BC (Squamish-Lillooet, Garibaldi-Pitt, Stein-Nahatlatch) as 1. We tested if these variables predicted populations to be below carrying capacity by including these areas as distinct spatial covariate in our models.

Non-Habitat- Large areas composed solely of rock, ice, or water are not productive bear habitat. We calculated a non-habitat layer composed of the % rock, ice, or water to control for the varying amount of usable habitat. Rock, ice and water were taken from landcover data (https://www.esa-landcover-cci.org/?q=node/164) mapped at a 300 resolution.

Salmon- We tested three measures of salmon availability. Two measures of % salmon in bear diets from isotope analysis (13 km res: Mowat and Heard 2006, 2 km res: Adams et al. 2017), and a third predicted average salmon returns by river system (BC Cumulative Effects Analysis). The return was based on empirical estimates of salmon returns at specific locations by Department of Fisheries and Oceans personnel, aggregated to BC Landscape Units.

Terrestrial Meat- Standing estimates of ungulate abundance at the scale of our analysis were unavailable, thus we tested two alternate variables: 1) % meat in bear diets as inferred from stable isotope analysis (13 km res: Mowat and Heard 2006), and 2) an index of the abundance of hunter kills derived from hunter harvest surveys. This index may represent ungulate population size, if hunters harvest more ungulates in areas of higher ungulate density. It is also a direct measure of the hunter-killed ungulate remains (gut pile, and often hide, head, and scraps) available to bears.

Green Vegetation- The degree of canopy closure and rainfall influence the quantity and quality of many herbaceous browse species for bears. We gathered canopy cover information from http://lcluc.umd.edu/metadata/global-30m-landsat-tree-canopy-version-4. This classification was for year 2000 and was mapped at 30 m resolution. Average spring rainfall information was taken from Climate WNA http://cfcg.forestry.ubc.ca/projects/climate-data/climatebcwna/#ClimateWNA/. This tool takes climate normal data collected at weather stations and transforms it to a spatial layer using spatial smoothing techniques.

Fruit Calories- We created predictive models representing caloric landscapes of four important fruiting species for bears: huckleberry (*Vaccinium membranaceum*), buffaloberry (*Sheperdia canadensis)*, oval-leaved blueberry (*Vaccinium ovalifolium*), and saskatoon (*Amalenchier alnifolia)*. We used occurrence and cover (%) plots collected by the Biogeoclimatic Ecosystem Classification (BEC) Program, which is a joint venture between the University of British Columbia and the Provincial Government of British Columbia. We supplemented these data with direct measures of occurrence, cover, and fruit productivity information to predict variation in the fruit on these shrubs across the landscape (Figure 4-2).

Presence, ground cover, and fruit abundance models were produced for each species independently and integrated to create caloric landscapes for each species. Predictor variables hypothesized to influence these species were rasterized to 30 m and included canopy cover, climate (seasonal temperature, precipitation), topography (aspect, elevation, slope, terrain ruggedness), soil, landcover (MODIS [https://landcover.usgs.gov/global_climatology.php] and CRDP [http://maps.elie.ucl.ac.be/CCI/viewer/]), fire, clear cut, and normalized vegetation difference index. Models were created using boosted regression trees (Elith, Leathwick & Hastie 2008).

We estimated calories by multiplying the predicted abundance of each berry species by its dry weight/berry (based on field measurements), and then by the caloric value of each dry berry from (Coogan *et al.* 2014). A single combined measure of fruit calories was created by summing the calories from all four berry species. To reduce the influence of extrapolation issues beyond the range of covariates measured, we trimmed the calorie layer to the upper 95th quantile of values and tested if this trimmed variable better explained bear density.

At each modelling step (occurrence, cover, productivity) model fit was assessed using out of sample data and either R^2 values for linear models or area under the curve (AUC) for binomial models.

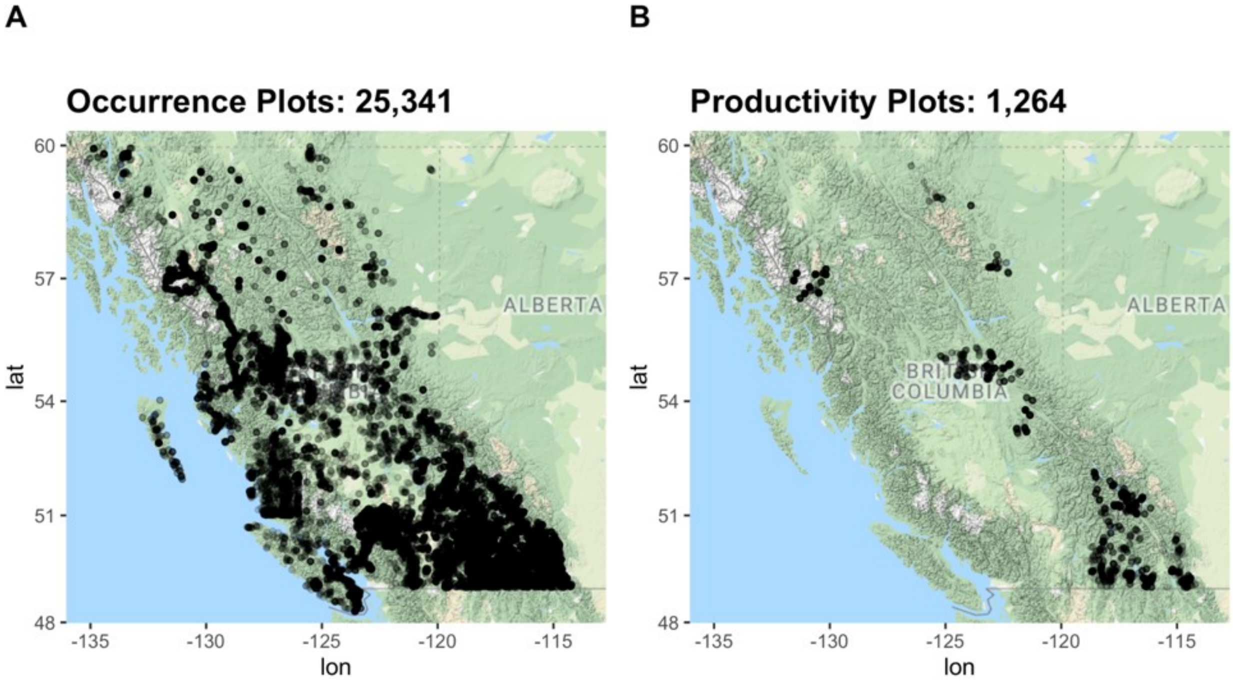


Figure 4-2. Distribution of berry plots to measure: A) species occurrence and cover (%), and B) fruit occurrence and productivity, across British Columbia.

4.2.3 *Spatial Capture-Recapture Analysis*

We used SCR analysis in a meta-analysis framework to estimate population density for each study area sampled. SCR approaches have many advantages over non-spatial methods which have been discussed in detail (Borchers & Efford 2008; Royle *et al.* 2014a; Lamb *et al.*

2018b, 2019) but most importantly these methods estimate unbiased density from spatially open populations. SCR uses detection histories of individuals across a trap array, and a Poisson point process to create a robust density estimate, which can be heterogenous across the landscape if density covariates are included in the analysis. The ability to include spatial covariates allows the direct investigation of factors that are spatially correlated to density. SCR models estimate density, capture probability at the center of an individual's home range, and an index of space use. I used a recently developed R packaged, "oSCR" (Sutherland, Royle & Linden 2019), to conduct the SCR analysis presented here.

Density was integrated over a state space with 5 km resolution, created by buffering each trap by 30 km around each trap and creating a composite outer boundary. Areas outside the documented grizzly bear range, and those pixels with >70% non-habitat (rock, ice, water) were excluded from the state space. All spatial covariates were smoothed (averaged) using a moving window approximately the size of a female home range (8 km radius circle, 201 km^2, (Lamb *et al.* 2018b)). All spatial variables were then scaled between 0-1 to aid model convergence.

Sites were not monitored during all capture sessions for all studies. As a result, we included a "usage" matrix depicting when sites were active. We did not account for sex-specific variation in detection, as heterogeneity in capture probability between the sexes is compensatory and doesn't appear to influence density estimates (Efford & Mowat 2013; Lamb *et al.* 2018b). Thus we opted for the simpler, faster-running models without sex-specific variation in detection.

We tested covariates hypothesized to limit population density by first fitting a set of bottom-up and top-down models independently, then combining these models, followed by the inclusion testing squared terms to examine possible non-linear relationships, the influence of historic harvest, and non-habitat. We choose this ad-hoc approach to model selection because

SCR models are slow to run, especially for large study areas and many spatial covariates and we wanted to minimize the number of model runs.

We then used the top model from this process to create a density surface which we extrapolated across the province. We combined this density layer with the recorded human-caused kill of grizzly bears between 1995-2018 to create an average reported kill rate for each 5 km cell. We summarized kill rate between 1995-2018 because this spanned the period of the genetic tagging. A female only kill rate was also calculated using female kill data and density*0.6, a common sex ratio observed in bear populations across BC (Lamb *et al.* 2017b; McLellan *et al.* 2017; Lamb *et al.* 2018b). Separate variables were created for hunter kills and non-hunting kill. We then smoothed these predictor variables using a moving window at two scales: 35 and 105 km to test if differing spatial scales would overcome the confounding effects of source-sink dynamics on the density~mortality rate relationship (Lamb *et al.* 2017b). Each of these kill rate variables were added into the model to test for a negative influence of harvest on bear population density.

4.2.4 Sensitivity analysis

The response of bear density to changes in individual variables was assessed by increasing the scaled variable in each pixel in the state space by 0.01 and measuring the absolute response in bear density compared to the reference (or unchanged) density values. Bottom-up vs. top-down limitation was assessed by classifying standardized variables as either top-down or bottom-up, and considering the sensitivity analysis in a manner that would mimic a removal experiment (i.e., removing food, or human influence (Peers *et al.* 2018)). When the pixel value was zero, the value would remain unchanged. This approach addresses the concept of bottom-up and top-down factors and asks the question “to what degree are bottom-up or top-down influences currently limiting grizzly bear density in British Columbia?”.

4.3 Results

4.3.1 Grizzly bear genetic tagging

A total of 27 genetic tagging projects, many of which ran for multiple years (42 study-years total between 1996-2017), were combined to yield a final dataset consisting of 4440 hair trap locations which detected 1913 grizzly bears 3658 times (unique site-session detections). Of these 1913 animals, 825 were male, 1004 were female, and 84 were not assigned a sex.

4.3.2 Fruit Calories

We gathered 25,341 occurrence and cover records for the fruiting species of interest. We supplemented these records with 1,264 fruit occurrence and abundance records. Models for each species were predictive and represented good model fit (Table 4-1). Species occurrence models for each species exceeded AUC values of 0.90, and exceeded 0.8 for fruit occurrence. Cover and fruit abundance R^2 values were generally high, but variable. We summed these individual models into a combined final fruit layer for the spatial capture recapture analysis.

Table 4-1. Fruit calories model fits. AUC= area under the curve, R2=coefficient of determination, Occ.=occurrence, Cov.=cover, Abund.=abundance. Fruit was always observed for Oval-leaved blueberry, thus we did not create a fruit occurrence model for this species.

Species	**Occ. AUC**	**Cov. R2**	**Fruit Occ. AUC**	**Fruit Abund. R2**
huckleberry	0.924	0.545	0.802	0.663
buffaloberry	0.916	0.284	0.801	0.250
Oval-leaved blueberry	0.921	0.492	NA	0.492
saskatoon	0.922	0.396	0.808	0.579

4.3.3 Spatial Capture Recapture Analysis

The top SCR density model (Table 4-2) included the following variables: canopy cover, spring precipitation, fruit calories, ungulate harvest, non habitat, secure habitat, human density, lasting suppression, and human-caused mortality rate. A second competing model, dAIC=0.4, included salmon (from (Mowat & Heard 2006)), but this variable was the only non-significant (p>0.05) parameter in the model, and thus we retained the simpler model without salmon as the top model. The direction, shape and influence of each of these covariate responses are summarized in Figure 4-3. Extrapolating this model across the current range of grizzly bears in British Columbia, excluding pixels with >70% non habitat, suggests there are 14,378 (95% CI: 11,684- 17,805) grizzly bears in the Province. Population density and abundances by BC grizzly bear population unit are given in Table 4-3.

Table 4-2. Spatial capture recapture model selection table.

Model	**K**	**AIC**	**dAIC**	**weight**
fruit+cc+cc2+ppt+ppt2+ungulate+secure+hum_dens+underK+nonhab+nonhunt+hunt	16	26184.9	0	0.52
fruit+salm_mowat+cc+cc2+ppt+ppt2+ungulate+secure+hum_dens+underK+nonhab+nonhunt+hunt	17	26185.3	0.4	0.43
fruit+salm_mowat+cc+cc2+ppt+ppt2+ungulate+secure+hum_dens+underK+nonhab+nonhunt_F_big +hunt_F_big	17	26190	5.2	0.04
fruit+salm_mowat+cc+cc2+ppt+ppt2+ungulate+secure+hum_dens+underK+nonhab+hunt	16	26192	7.1	0.01
fruit+salm_mowat+cc+cc2+ppt+ppt2+ungulate+secure+hum_dens+underK+nonhab+hunt_F_big	16	26197.2	12.4	0
fruit+salm_mowat+cc+cc2+ppt+ppt2+ungulate+secure+hum_dens+underK+nonhab+nonhunt	16	26199.6	14.8	0
fruit+salm_mowat+cc+cc2+ppt+ppt2+ungulate+secure+hum_dens+underK+nonhab+nonhunt_F_big	16	26203.3	18.4	0
fruit+salm_mowat+cc+cc2+ppt+ppt2+ungulate+secure+hum_dens+underK+nonhab	15	26208.2	23.4	0
fruit+salm_mowat+cc+cc2+ppt+ppt2+ungulate+secure+secure2+hum_dens+hum_dens2+underK+nonhab	17	26210.1	25.3	0
fruit+salm_mowat+cc+cc2+ppt+ungulate+secure+hum_dens+underK+nonhab	14	26217.3	32.4	0
fruit+salm_mowat+cc+ppt+ungulate+secure+hum_dens+underK+nonhab	13	26219.4	34.5	0
fruit+salm_mowat+cc+ppt+ungulate+secure+secure2+hum_dens+underK+nonhab	14	26219.6	34.8	0
fruit+salm_mowat+cc+ppt+ungulate+secure+hum_dens+hum_dens2+underK+nonhab	14	26221.2	36.4	0
fruit+salm_mowat+cc+ppt+ungulate+secure+secure2+hum_dens+hum_dens2+underK+nonhab	15	26221.5	36.7	0
fruit+salm_mowat+cc+ppt+ungulate+secure+hum_dens+underK	12	26222	37.1	0
fruit+salm_mowat+cc+ppt+ungulate+secure+hum_dens+threatened	12	26258.1	73.3	0
fruit+salm_mowat+cc+ppt+ungulate+secure+hum_dens	11	26258.3	73.4	0
fruit_untrimmed+salm_mowat+cc+ppt+ungulate+secure+hum_dens	11	26274.2	89.3	0
fruit+salm_adams+cc+ppt+ungulate+secure+hum_dens	11	26283	98.1	0
fruit+salm_hamilton+cc+ppt+ungulate+secure+hum_dens	11	26285.6	100.7	0
fruit+salm_mowat+cc+ppt+meat_mowat+secure+hum_dens	11	26321.5	136.6	0
fruit+salm_mowat+cc+ppt+ungulate	9	26375	190.2	0
fruit+salm_mowat+cc+ppt	8	26394.2	209.4	0
fruit+salm_mowat+cc+ppt+meat_mowat	9	26394.4	209.6	0
fruit+cc+ppt+ungulate	8	26403.1	218.3	0
fruit+cc+ppt	7	26444.3	259.4	0
salm_mowat+cc+ppt	7	26461.1	276.2	0
salm_mowat+cc+ppt	7	26461.1	276.2	0
cc+ppt+ungulate	7	26492.8	308	0
cc+ppt	6	26494.8	309.9	0
secure+hum_dens	6	26634	449.1	0
secure	5	26637.5	452.6	0
rd_dens	5	26725.9	541	0
rd_dens+hum_dens	6	26727	542.2	0
fruit+salm_mowat	6	26884.2	699.3	0
hii	5	26929	744.1	0

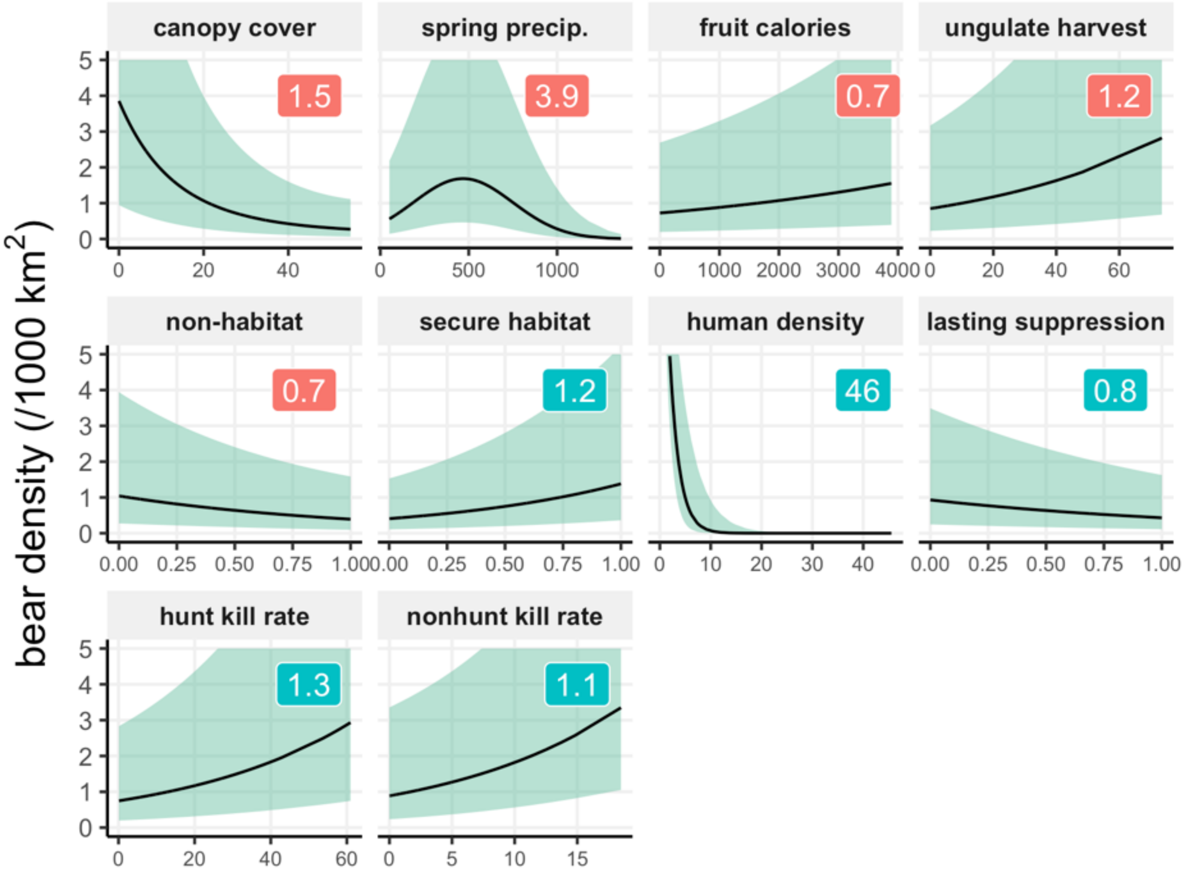


Figure 4-3. A) Direction and response of bear density to changes in predictor variables. Variable influence shown in top right, and represents the % change in bear density calculated by adding 0.01 to each scaled variable in a manner that would increase density and comparing to reference density of each state space pixel. Variable influence colored by bottom-up (red) and top-down (teal). Human density values limited to 50 people/km^2 on x axis, but were as high as 700 in state space pixels.

Table 4-3. Density and abundance estimates by BC grizzly bear population unit.

name	density	d.lwr	d.upr	abundance
Alta	8.2	6.4	10.6	109
Babine	15.5	12.5	19.3	222
Blackwater-West Chilcotin	12	9.3	15.4	237
Bulkley-Lakes	21.9	17.8	27	511
Cassiar	16.9	13.4	21.3	619
Central Monashee	17.3	14.5	20.7	108
Central Rockies	28.2	23.8	33.7	176
Central Selkirk	22.7	18.8	27.8	129
Central-South Purcells	23.7	19.9	28.3	274
Columbia-Shuswap	23.4	19.9	27.7	250
Cranberry	17	13.4	22	198
Edziza-Lower Stikine	37.3	30.5	45.7	520
Finlay-Ospika	19.2	15.9	23.2	584
Flathead	25.9	21.5	31.3	87
Francois	7.6	6	9.8	66
Garibaldi-Pitt	8.6	6.3	11.9	7
Hart	15.6	13.2	18.6	304
Hyland	13.3	10.7	16.5	230
Kettle-Granby	9.1	7.4	11.1	58
Khutzeymateen	21.5	17	27.7	156
Kingcome-Wakeman	20.8	16	27.1	99
Kitlope-Fiordland	24.2	18.7	32	231
Klinaklini-Homathko	33.6	27.3	41.3	391
Knight-Bute	28.9	22.2	38.1	154
Kwatna-Owikeno	23.2	17.2	31.4	219
Moberly	18.5	14.7	24	143
Muskwa	21.4	17.4	26.3	758
Nation	8.7	7	10.8	160
North Cascades	8.2	6.5	10.5	43
North Coast	16.8	11.6	26	103
North Purcells	31.8	27.1	37.3	169
North Selkirk	31.7	27	37.2	190
Nulki	7.1	5.5	9.5	42
Omineca	13.1	10.9	15.9	390
Parsnip	24.5	20.8	29	271
Quesnel Lake North	23.1	19.8	26.9	160
Robson	25.1	21.5	29.4	479
Rockies Park Ranges	29.3	24.4	35.4	171
Rocky	16.2	13.2	19.9	617
South Chilcotin Ranges	24.3	19.7	30.1	372
South Rockies	28.9	23.7	35.5	239
South Selkirk	12.9	9.8	17.1	52
Spatsizi	27	22.3	32.7	579
Spillamacheen	26.6	22.6	31.5	104
Squamish-Lillooet	13.3	9.6	18.5	55
Stein-Nahatlatch	11.5	8.6	15.5	57
Stewart	31.1	25.3	38.3	281
Taiga	7.2	5.5	9.4	361
Taku	26.6	21.4	33.2	720
Tatshenshini	37	29.4	46.8	491
Toba-Bute	28.1	22.6	35.1	171
Tweedsmuir	24.1	19.4	30.1	439
Upper Skeena-Nass	23	19.1	27.8	390
Valhalla	16.1	13.4	19.5	57
Wells Gray	28	23.8	33.1	262
Yahk	13.7	10.2	18.4	37

4.3.4 Sensitivity Analysis

Estimates of individual variable influence (Figure 4-3) suggest human density, canopy cover, and precipitation had the strongest influence on bear density, followed by secure habitat and ungulate harvest, with human density having an order of magnitude greater influence than any other measured variable. Grouping these variables into bottom-up and top-down influences suggests top-down forces have the potential to exert the strongest influence on grizzly bear populations. However, the stronger limitation realized by the current grizzly bear populations in BC is primarily bottom-up limitation (Figure 4-4), largely because human density is concentrated, some secure habitats remain, and the lasting historic suppression is localized in SE BC.

Removing the primary negative human influence on bear density from the landscape (human density, roads, and lingering historic suppression) provides an estimate of 19,102 grizzly bears in BC, or 4,724 more than are currently predicted to reside in the province. The areas where grizzly bears are currently extirpated (Lower Mainland, Okanagan, Peace) could support an additional 2,054 animals without human influence, based on predictions from our best model (Table 4-4). The current carrying capacity of these extirpated areas is <25% of what it would be without human influence (492).

Table 4-4. Density and abundance predictions for extirpated populations in BC.

name	**density**	**abundance**	**density.nohuman**	**abundance.nohuman**
Lower Mainland	2.15	14	20.3	174
Okanagan	5.5	403	20.8	1531
Peace	6.8	75	31.9	349

Between 1995 and 2018 the average annual kill rate from hunting in British Columbia was 2%, and 0.93% for non-hunting (Figure 4-5). However, the estimate of non-hunting kill rates represents a minimum as only 12-50% of non-hunting mortalities are reported (McLellan *et al.* 1999, 2018). Thus the true non-hunting kill rate across the Province is likely between 1.9-7.8%. Average annual kill rates across the province using total provincial kill divided by bear the population size predicted from our model were 1.7% for hunting and 0.4% for non-hunting (0.8-3.3% accounting for under reporting).

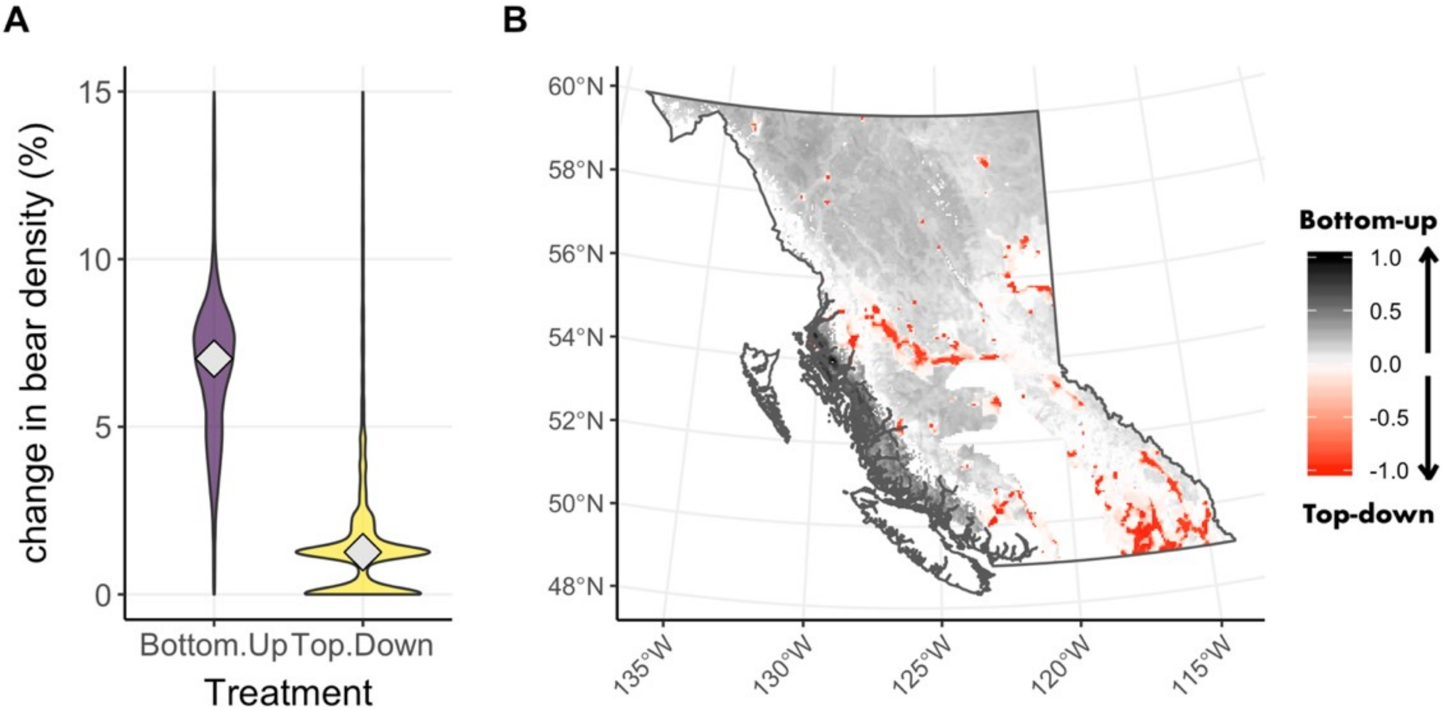


Figure 4-4. A) Realized bottom up or top down forcing from modelled limiting factors that correlated with grizzly bear density in 27 study areas and extrapolated across BC. Forcing was calculated by changing variables in steps of 0.01. The y axis variation was limited to 15% by removing 4% of values which were >15%. Maximum change in the combined bottom up variables was 26%, and 88% for top down variables. B) Spatialized influence of bottom-up and top-down factors, calculated by subtracting bottom up from top down changes, and standardizing between -1 to 1, whereby -1 represents maximal top down influence (88%), 0 represents equal top down and bottom up influence, and 1 represents maximal bottom up influence of 26%.

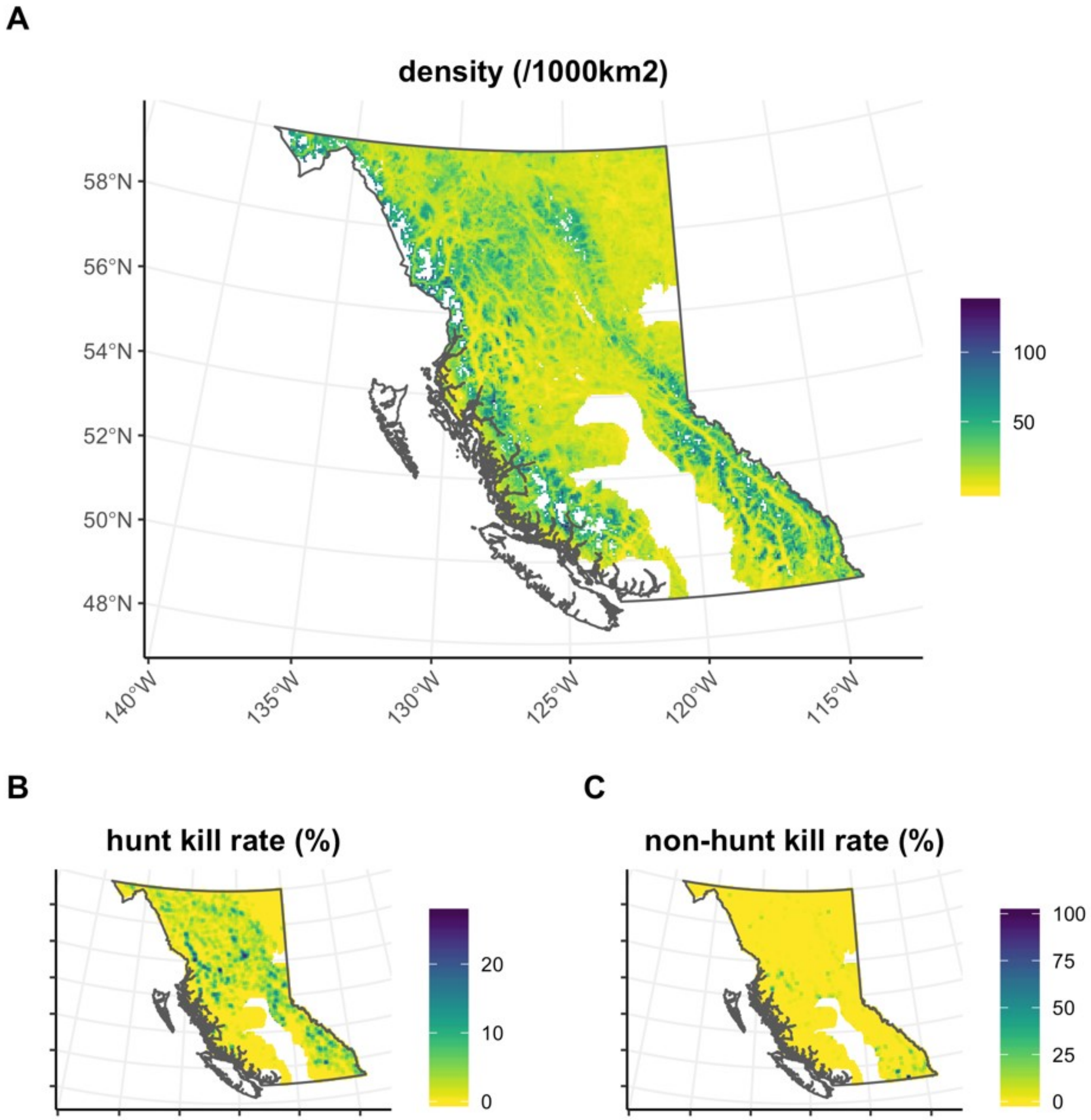


Figure 4-5. A) Estimated grizzly bear population density across BC from top SCR model and estimated annual kill rates between 1995-2018 for hunting (B) and non-hunting (C) sources.

4.4 Discussion

Human influences have the potential to exert major limiting forces on grizzly bear populations. This has been historically documented when humans eradicated grizzly bears from

42% of their North American range (McLellan *et al.* 2019), and the potential for further limitation persists as human density and influence on wilderness areas grows. However, in practice bottom-up forces may be equal or stronger, such as we document in BC. Human density, the strongest limiting factor, occurs in localized areas in BC leaving most of the province unsettled: 98% of the province has <1 human/km^2, and 90% with <0.1 human/km^2. We estimate that bottom-up forces are ~5.5x greater than top-down forces in British Columbia's extant grizzly bear range under current conditions, suggesting that bear populations are primarily bottom-up limited at present levels of human influence. However, bear populations are more strongly top down limited in all areas where humans live in the Province (Figure 4-4), and this effect is especially pronounced when considering the influence of people in the extirpated grizzly bear populations of BC (Table 4-4).

Bottom up influences included the amount of canopy cover, precipitation, energy from fruit, and ungulate harvest or abundance. Of these, canopy cover and spring precipitation had the greatest influence, suggesting that greater abundance of grasses, forbs and shrubs supports higher bear densities (Mowat *et al.* 2013b). Areas with more fruit also supported more bears and this relationship has been regularly proposed although rarely documented (McLellan 2015).

The best predicting salmon layer in our modelling was % salmon in diet from (Mowat & Heard 2006), but this variable had little influence on bear density in the final model. We suspect that the influence of salmon on bear density was weak in our models for the following reasons: 1) the positive influence of salmon on bear density is much weaker when black bears are present, which they were in all of the areas we considered here (Mowat *et al.* 2013b), 2) salmon consumption facilitates larger body size (>50% larger (McLellan 2011)), thus the main influence of salmon in these populations may be more bear biomass, not more individual bears, 3) relatively few of the populations considered here (3 of 27) had high levels of salmon (>25%) in their diet. We note that in British Columbia, grizzly bears are not more abundant in places where bears eat principally salmon than where they eat largely vegetation (Mowat *et al.* 2013b).

Higher ungulate harvest correlated with higher bear densities suggesting a possible effect of terrestrial meat subsidies on bear density which, to our knowledge, has not been previously documented. Bear size increases with the amount of both salmon and terrestrial meat in the diet for grizzly bears in BC (Mowat & Heard 2006). However, terrestrial meat was negatively related to density in Mowat *et al.* (2013b). The relationship between grizzly bear density and meat in the diet appears complex and relationships detected heretofore may simply be related to collinearity with other factors that may or may not have been considered in the models (Mowat et al. 2013).

Top down influences included human density, secure habitat, lasting historic suppression, and human-caused mortality. Of all factors considered in this analysis, human density had the strongest influence on bear density by an order of magnitude but has only localized influence in BC due to spatially constrained human settlement in the Province. Mowat et al. (2013) also found that human density was negatively related to bear density and, they like (Mattson & Merrill 2002) found bear density was zero above ~7 people/km^2, which is supported by our analysis. Road density, as indexed by secure habitat, was also negatively related to bear density and this relationship has been detected at finer scales in several recent studies (Lamb *et al.* 2018b; Proctor *et al.* 2018c). However, these previous studies did not assess the relationship of road density while controlling for human density, and may have over-estimated the actual strength of the relationship between roads and bear density because of the collinearity between road and human density. We conclude that grizzly bear density is reduced across much of the

Province due to high road densities, except in Parks and in the remote northern and coastal regions where habitat is more secure.

We provide evidence here that historic suppression of bear populations in the south coast of British Columbia has persisting influences and bear density is lower in this region than other parts of the Province (McLellan *et al.* 2019). Our estimates of population density and size for the south coast were slightly higher than published studies in a few cases (Apps *et al.* 2014; McLellan *et al.* 2019), suggesting that we provide a conservative effect of lasting historic suppression on these populations. For example, (McLellan *et al.* 2019) estimate the density of bears in a portion of the threatened Stein-Nahatlach population between 6.3 and 7.7 bears between 2005-2017, with 95% confidence intervals between 4.3-9.7. Here, we estimate the density to be 11.5 (95%: 8.6-15.5), which we believe is a overestimate of the current population density, highlighting the degree to which this population is below carrying capacity. Our estimates of other populations on the south coast align closely with published estimates. McLellan *et al.* (2019) estimated a portion of the South Chilcotin population at a density of 21.5 (95%: 17.6-25.4) and (Apps *et al.* 2014) estimates densities of 14.7 (95%: 11.8-18.2) and 37.1 (95%: 30.4-44.3) in other areas of the population. Here we estimate a density of 24.5 (95%: 19.7-30.1) across the population South Chilcotin population.

Excessive human-caused mortality influences bear population dynamics (Schwartz *et al.* 2010; Mace *et al.* 2012; McLellan 2015; Lamb *et al.* 2017b; McLellan *et al.* 2017, 2019). Provincially, the hunting mortality rate was low at 1.74% of the population, and non-hunting mortality was between 0.8-3.3%. After accounting for under-reporting, the provincial human-caused mortality rate was 2.5-5.1%, and lower than the sustainable human-caused mortality rates of 4-10% estimated by (McLellan *et al.* 2017).

We documented a positive relationship between bear density and human-caused mortality. This result suggests that human-caused mortality was unlikely to be limiting grizzly density during the period of study. However, the cause of the positive relationship, as opposed to a null relationship, may be an artifact of the strong spatial selection for bears by hunters and the fact that hunters hunt where they have the best chance of finding their quarry. This choice integrates information on bear behaviour, habitat quality, and local abundance which is acquired in many ways. We suggest this positive relationship is likely due to one of the following 1) underestimates in our density analysis, creating artificially high kill rates, which provide additional information for the model in these areas where density was underestimated and creating a positive relationship, 2) source-sink dynamics, where high mortality rates may be offset by many dispersing individuals, with high turnover (Lamb *et al.* 2017b). Overall, we suggest that this kill rate analysis is a relatively weak test of the direct influence of mortality rates on bear populations for two reasons: 1) Historic suppression (i.e., excessive mortality rates) in areas of high human density clearly produces negative influences on bear density, as shown here via the human density and lasting historic suppression covariates. Thus nested within these covariates is the negative influence of non-hunting kill rates from the past, and 2) Source-sink dynamics have the potential to compensate high kill rates, thus masking effects of mortality. Nevertheless, the provincial mortality rate of bears is generally within sustainable limits, and localized areas of “overmortality” are supported by immigrants.

Human-caused kill rates of grizzly bears in BC are heterogeneous and are high in areas of high human density and wilderness access, likely creating continuous source-sink dynamics across the Province (Figure 4-5). Non-hunting mortality hotspots occur throughout BC’s southeast, the central coast and inland. Localized areas had 100% estimated annual mortality;

suggesting that persisting bear populations in these areas are heavily reliant on dispersers from secure wilderness. It is possible that, after accounting for under-reporting (McLellan *et al.* 1999, 2018), non-hunting mortality rates were as high or higher than hunting mortality for grizzly bears in BC during our study and the spatial impact of non-hunting mortality are more often on small, low density or somewhat isolated populations of bears (Mowat *et al.* 2013b).

Our estimate of 14,378 (95% CI: 11,684- 17,805) grizzly bears in the Province aligns with previous estimates ~14,000 (Mowat *et al.* 2013b), despite the use of different methods, spatial scales, and additional data. Our analysis provides no evidence that the Province had been artificially inflating bear population abundances to justify a hunt as proposed by Darimont *et al.* (2018), or that hunting-induced "overmortality" was a major limiting factor of bear populations as proposed by Artelle *et al.* (2013).

Three main areas of extirpation exist in BC, the Lower Mainland (Vancouver and surrounding areas), the Okanagan Valley north to the Cariboo plateau, and the settled portion of the Peace region. Human occupation of these areas has reduced the potential carrying capacity of bears by >75% compared to potential densities without people. Here we estimate that these areas could currently support ~500 bears if animals were to recolonize. However, the Lower Mainland would likely support too few bears (2.2 bears/1000km^2) for a viable population. The Okanagan and Peace densities (5.5 and 6.8 bears/1000km^2) could be much larger, but may still oscilate between viability and extirpation in at least parts of these areas. Recent observations of grizzly bears dispersing into, and living inside, the Okanagan and Peace extirpation zone suggests that the less human-influenced portions of this area represent viable bear habitat (Lamb *et al.* 2018b). In most of these 3 areas human-density limits grizzly bear population recovery and is not mitigatable. However, in some parts of these zones road density is the main top-down factor which can be mitigated. Mitigation costs will be high because roads densities are high (>1 km/km^2) in much of the extirpated zone. Mitigating conflicts with cattle ranchers is another mitigation that is necessary for grizzly bear recovery in parts of the extirpated zone (Mowat *et al.* 2013b).

This analysis provides the first fine scale, large extent, analysis of factors limiting grizzly bear density and provides a rigorous and spatially explicit estimate of grizzly bear density across BC. The majority of BC's extant bear populations are bottom up limited, but top down pressures are severely limiting bear populations where humans and bears overlap, especially in southeast and central BC. Expanding human populations and road networks in the Province pose the largest threat to bear populations in the future. Efforts to reduce the spatial extent of human population expansion as well as reducing attractants and human-bear conflict will be critical to coexistence. The expanding road network in BC is eroding the amount of secure habitat in BC's globally acclaimed wilderness. Reducing the extent of this road network will yield benefits for bears and many other ecologically and culturally important species.

5 Chapter 5: Forbidden fruit: Human settlement and abundant fruit create an ecological trap for an apex omnivore

5.1 Introduction

Animals tend to use a series of cues established over evolutionary time to select habitats that maximize their fitness (Darwin 1859; Fretwell & Lucas 1970). However, maladaptive habitat selection can occur when novel conditions decouple the link between habitat quality and fitness, resulting in an ecological trap (referred to as ET hereafter; Dwernychuk & Boag 1972). ETs and human activity are often associated because human alteration of the landscape tends to occur more rapidly than cues evolve to guide an animal's response to landscape changes (Robertson, Rehage & Sih 2013; Hale & Swearer 2015).

For an ET to exist, 1) individuals must show equal or greater selection for trap habitat relative to surrounding source habitats, 2) the fitness of individuals using trap habitat must be lower than the fitness of individuals not using the trap, and 3) to have persistent, population-level effects, animals must move from source habitats into the ET (Robertson & Hutto 2006; Runge, Runge & Nichols 2006; Hale & Swearer 2015; Hale, Treml & Swearer 2015). Although ETs have been reported in a number of studies (Hale & Swearer 2015), few cases meet all of the above criteria, and we know of no examples in large mammals. For example, Balme *et al.* (2010) and van der Meer *et al.* (2013) highlight source-sink dynamics for African carnivores across the landscape but do not link this dynamic to truly attractive habitat, the key tenet of an ET. Similarly, Nielsen *et al.* (2006) and Northrup *et al.* (2012) provide evidence of grizzly bear (*Ursus arctos*) selection of habitats associated with high mortality, but do not assess if this results in lower fitness or source-sink dynamics.

Apex consumers are highly vulnerable to ETs because they typically lack natural predators (Ripple *et al.* 2014) and may not perceive or avoid novel sources of risk such as human predation (Robertson *et al.* 2013). Consequently, conflicts with humans for space has resulted in severe range reductions for apex consumers globally (Morrison *et al.* 2007; Ripple *et al.* 2014; see grizzly bear example in Figure 5-1). Conflict with humans is a ubiquitous concern for species in the *Ursidae* family, and the main drivers of conflict are anthropogenic food sources and expansion of human settlement (Can *et al.* 2014). Here we provide evidence for an ET for a wide-ranging, apex omnivore, the grizzly (brown) bear. Grizzly bears have high nutritional demands in preparation for hibernation (McLellan 2011; Lopez-Alfaro *et al.* 2013); therefore, areas with both attractive food resources (natural or anthropogenic) and a high risk of human conflict could produce an ET for grizzly bears. At a fine scale, this mechanism is shown in grizzly bear selection for roads. In areas where road density is high, human-bear conflicts increase and grizzly bear fitness is severely reduced (Boulanger & Stenhouse 2014). However, bears do not consistently avoid roads and often select for spring forage along roadsides (Nielsen *et al.* 2002), which highlights a potential mismatch between perceived habitat quality and realized fitness benefits.

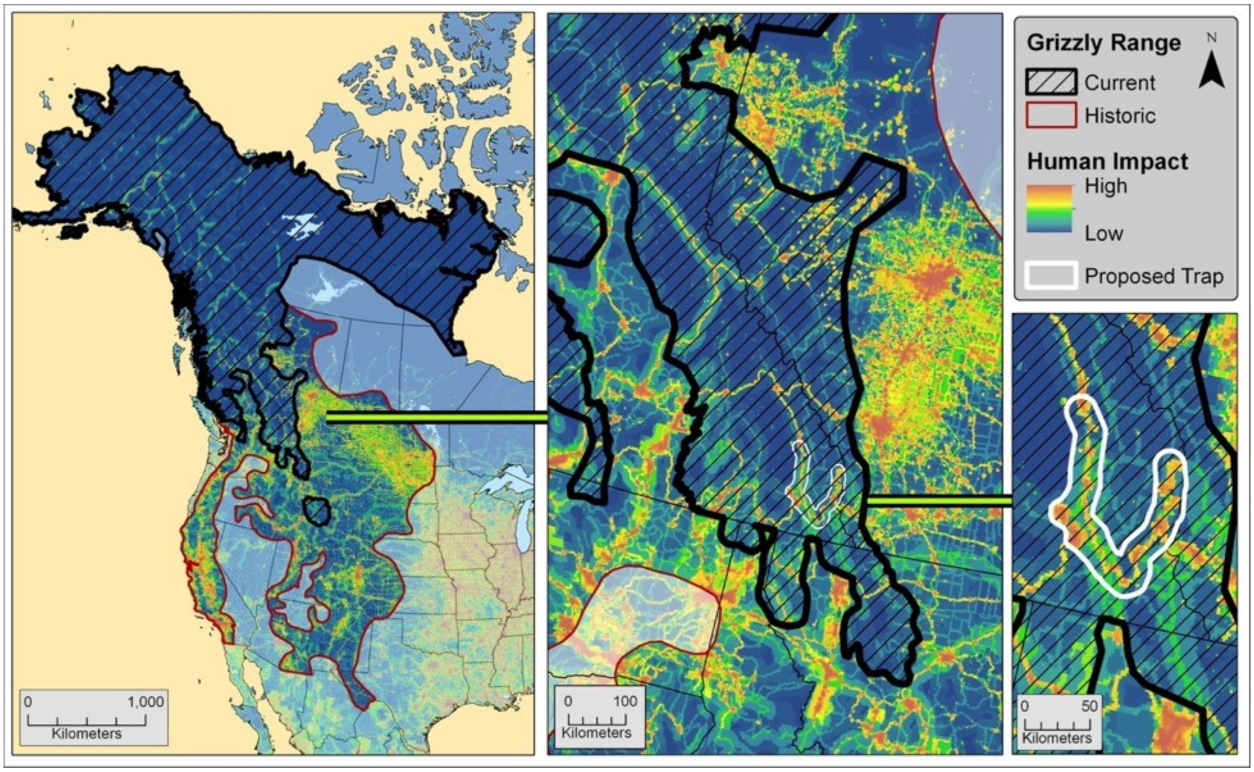


Figure 5-1. Current and historic distribution of grizzly bears across North America (LEFT) with Human Influence Index shown from high to low influence (HII, Wildlife Conservation Society - WCS 2005). MIDDLE: The eastern range margin of grizzly bears, showing the "cookie cutter" grizzly bear range reduction resulting from human influence. RIGHT: Proposed ecological trap area in southeast British Columbia, an area of both concentrated human settlement and rich bear habitat. Current distribution from most up-to-date local distributions from COSEWIC (2012); MFLNRO (2012); Rovang (2013), and historical distribution from Mattson & Merrill (2002); COSEWIC (2012).

Grizzly bears in the Rocky Mountains select habitats with fruit resources (Nielsen *et al.* 2003, 2010), which increase fitness in the absence of human settlement (McLellan 2015). Our study focused on a region with abundant fruit resources for bears and locally concentrated human settlement. Human-caused mortality is the primary cause of death for grizzly bears, particularly in the southern portion of their range (McLellan *et al.* 1999), due to both hunting and non-hunting sources of mortality (e.g. conflicts with humans, road and railway strikes, and poaching).

Consequently, we predicted an ET in our study area where abundant fruit resources and human settlement co-occur.

We tested the hypothesis that an area with intensive human development and rich food resources would produce fitness consequences for a population of grizzly bears because of decreased survival in the trap and net immigration into the trap from adjacent source populations. We determined if: 1) the trap habitat was of equal or greater attractiveness than surrounding habitats; 2) survival and/or reproduction in the trap habitat were reduced and insufficient to meet replacement; and 3) bears from more remote areas moved into the trap habitat. Satisfying all three conditions would provide strong evidence for the presence of an ET.

5.2 Methods

5.2.1 Study Area

The study area covers 10,600 km^2 of the Canadian Rocky Mountains in southeastern British Columbia (BC; Figure 5-2). The region is bounded by the continental divide (BC-Alberta border) to the east, the Canada-United States border to the south, the Kootenay River, Rocky Mountain Trench, and Wigwam River to the west, and the Palliser River to the north.

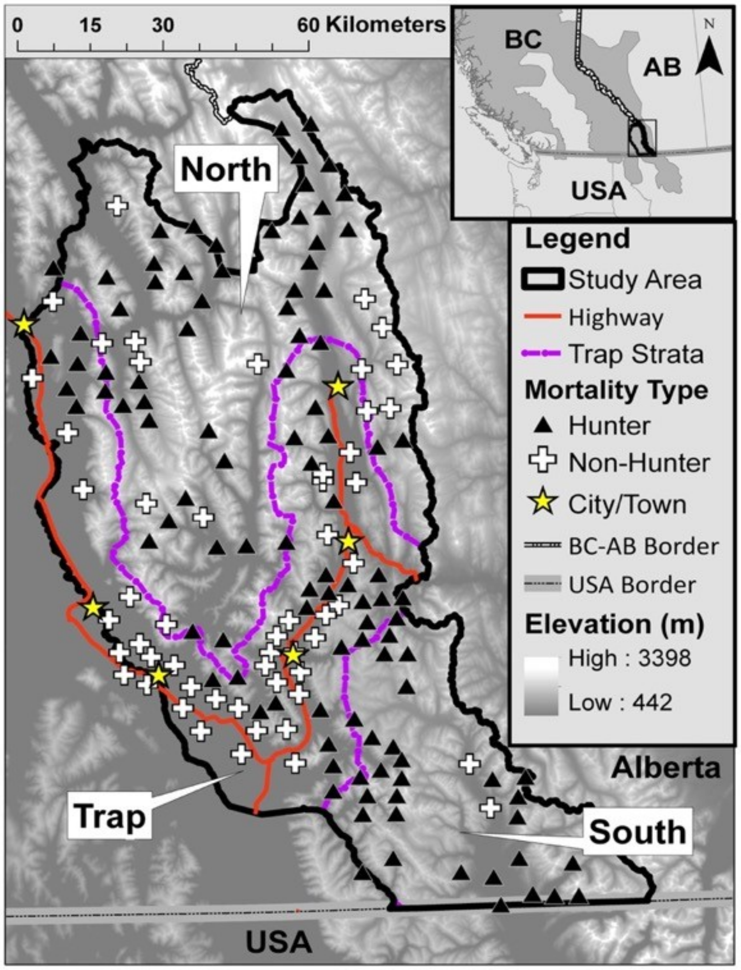


Figure 5-2. Study area for the South Rockies Grizzly Bear Project, and locations of all recorded human-caused grizzly bear mortalities between 2006 and 2014 in southeast British Columbia, Canada. The Trap stratum buffers the highway (red line) and is shown as the polygon enclosed by the thick purple broken line. The recorded human-caused grizzly bear mortalities from 2006 to 2014 are shown by hunter (black triangle) and non-hunter (white cross) symbols. Towns are shown as yellow stars. Grizzly distribution in North America is shown in dark grey on the inset map.

There are approximately 12,000 people (Canadian population census 2006, 2011) residing in the area year-round, with a major influx of tourists during the summer months. The majority of human settlement occurs in the valley bottoms bordering the Elk and Kootenay Rivers. Many highways intersect or border the region (Highway 3, 43, 93, and 95), with high traffic volume during the summer months (>18,000 vehicles per day; BC Ministry of Transport). A railroad (Canadian Pacific Railway) follows the highway from Cranbrook to Elkford and continues to Alberta via Crowsnest Pass. The study area has abundant grizzly food resources, which are responsible for local bear densities exceeding 77 bears/1,000 km^2 in the 1980s (McLellan 1989); the highest recorded interior grizzly densities in North America. Currently, bear density across the region is high and female skewed (F: 28 (±6.8) and M: 15 (±2.7) / 1,000 km^2; Mowat *et al.* 2013).

To assess the potential for an ET, we divided the study area into three strata based on known concentrations of bear mortalities and human habitation in the region (Figure 5-2). An ET stratum (hereafter referred to as the Trap) was created by buffering settled areas and highways by the average radius of a grizzly male home range in the region (11.2 km, Apps *et al.* 2004), amended to local topography (Figure 5-2). Because grizzly female home ranges are smaller than those of males (Apps *et al.* 2004; Graham & Stenhouse 2014), both male and female bears residing outside the Trap buffer should have home ranges that generally do not overlap the highway, or have relatively little interaction with the highway and associated settled areas; the main area of reported grizzly bear mortality in this region (Figure 5-2). We used relocations from collared grizzly bears in the Trap stratum to ensure our buffer encompassed the collared bears residing in the area (Apps *et al.* 2007). The remaining two strata consisted of the regions to the north and south of the Trap stratum, to the bounds of the study area, hereafter referred to as North and South, respectively (Figure 5-2). For each stratum, we summarized the habitat attractiveness, local demography, and movements between neighbouring strata.

5.2.2 Habitat Attractiveness

Black huckleberry (*Vaccinium membranaceum,* generally ripe between Aug. 1 and Sept. 15) and Canada buffaloberry (*Shepherdia canadensis,* generally ripe between July 1 and Aug. 15) are attractive to grizzly bears (McLellan & Hovey 2001b; Nielsen *et al.* 2003, 2010), and consuming these high-energy foods confers fitness benefits in the absence of humans (Welch *et al.* 1997; McLellan 2011, 2015). As a result, we used the occurrence of these two species across the landscape to provide a representative measure of habitat attractiveness for grizzly bears. We built occurrence models for both fruiting shrub species using multivariate logistic regression and occurrence records from 1,779 vegetation plots (20 x 20 m) conducted within the study area. Plots were stratified by biogeoclimatic features to ensure representation of widely differing ecological conditions. Using these data we modeled berry species occurrence as a function of environmental variables hypothesized to predict occurrence, including climate, soil, topographic, and fire variables (see Appendix S1). We built models and occurrence maps and derived stratum-specific predictions of fruit occurrence using program R (R Core Team 2019). Occurrence records for each species were randomly divided into training (85%) and testing (15%) groups for model development and validation, respectively (Nielsen *et al.* 2005). We fit each of the eight models to the data and tested the fit of the data to the model using Akaike's Information Criterion (AIC, Akaike 1974). The model with the lowest AIC score was considered the most parsimonious model, which we retained as our top model. The training data were used to assess the predictability of the top model using Receiver Operating Characteristic (ROC) and the Area Under the Curve (AUC) (Fawcett 2006) statistics.

We quantified a per-capita landscape occurrence of each fruiting species by dividing the total area of predicted fruit occurrence within each stratum by the abundance of bears occupying the stratum. We used this measure as an index to portray the availability and attractiveness of fruit resources in each strata, as the absolute area of fruit occurrence realized by a grizzly bear will depend on the degree of home range overlap and the percent cover of each species within the occupied cells. Nevertheless, we believe this index accurately represents the relative per-capita availability of fruit resources in each stratum.

5.2.3 Demography

We used DNA-based mark-recapture to estimate demographic parameters, and thereby population growth rate, which provides a measure of the mean individual fitness (Fisher 1930) for each stratum. Grizzly bear hair samples were collected over eight years (2006-2013) using two types of genetic sampling: lured bait sites and rub objects. A total of 482 bait site and 406 rub object locations were sampled between 2006 and 2013, for a total of 1,066 bait site sessions and 2,748 rub object sessions. In total, we recorded 1,346 mark and recapture events (unique bear-session detection events) of 489 individuals. Further details on field sampling and individual identification through multi-locus microsatellite genotyping can be found in Appendix S3.

Capture histories were constructed for each stratum from DNA capture-recapture data and analyzed using a Pradel robust design model (PRDM, Pradel 1996; Nichols *et al.* 2000) for open populations implemented in Program MARK (White & Burnham 1999) using the RMark package (Laake 2013) accessed in Program R. We estimated apparent survival (ϕ), apparent recruitment (f), realized population growth (λ), abundance (N), and probability of capture (p) for each of the three strata (North, Trap, and South). The PRDM is a combination of the Pradel estimator (Pradel 1996), which estimates demographic parameters of open populations (Nichols

& Hines 2002), and the Huggins formulation of the closed population design, used to estimate detection probabilities and population size (Huggins 1991). The robust design is based on multiple sampling sessions (years, in our case), and within each sampling session multiple secondary sessions are nested (Gardner *et al.* 2010). The annual capture histories for each stratum are comprised of two bait site and one rub tree session per year, except in 2012, when we only deployed rub trees and had four secondary sessions. We split rub trees and bait sites into separate sessions as these traps are known to have different capture probabilities (Boulanger *et al.* 2007; Lamb *et al.* 2016b).

The PRDM estimates “apparent” survival because actual mortality cannot be distinguished from emigration (i.e. in both cases the bear is never recaptured in the population). Similarly, “apparent” recruitment is estimated because detection of a new individual is indistinguishable from the detection of an individual moving into the stratum (i.e. in both cases a new bear is captured that had not been previously detected). The resulting measure of realized population growth (λ) is simply the sum of the probability of entering the population (apparent recruitment [f]) and the probability of remaining in the population (apparent survival [ϕ]) (Nichols & Hines 2002). We met all assumptions of the PRDM (for information on assumptions and further detail on modeling methods see Appendix S3). Statistical comparisons between parameters were conducted using two-tailed Z tests. We conducted a sensitivity analysis to ensure our demographic inferences were not affected by buffer choice (Appendix S5).

The province of British Columbia has kept records of all known human-caused grizzly bear mortalities since 1978 as part of compulsory inspection. The database includes the date, location, and cause of death, as well as the sex, age, and skull size for each individual. We used these data in conjunction with the abundance estimates generated by our capture-recapture model to calculate annual human-caused mortality rates for all strata. For each stratum, we calculated mortality rates using the average abundance of grizzly bears across all years and averaged annual hunter and non-hunter mortalities using mortality data between 2006 and 2014.

Although reporting of grizzly bear mortalities is mandatory, approximately half of all non-hunting, human-caused grizzly bear mortalities are not reported (McLellan *et al.* 1999). To account for this, we inflated all reported non-hunting mortalities by a factor of two following the estimate from McLellan *et al.* (1999), which we later validated using the estimated survival rates for each stratum (Appendix S4) as these estimates are generated independent of the mortality data. Statistical comparisons of mortality rate between strata were conducted using analysis of variance (ANOVA) and the associated post-hoc Tukey HSD test (further information on methods, equations, and validation can be found in Appendix S3).

5.2.4 Movement

One of the limitations of apparent recruitment estimates is ambiguity between recruitment of cubs and movements from elsewhere. We combined information from our mark-recapture sampling with records of human-killed bears from the compulsory inspection database to identify the effects of movement between strata on apparent survival and recruitment for each stratum. We successfully genotyped samples from 102 of the 163 recorded human-caused grizzly bear mortalities in the study area since 2006, and we matched these to genotypes of bears in our capture-recapture sample using a genetic match test of all 9 microsatellite markers. Our capture-recapture sample included 56 of the 102 bears that were killed and produced a genotype. Using these data, we investigated the movement of bears that were killed and used a two-tailed proportion test in R to test whether there were more bears entering the Trap than leaving it (further information on methods and equations used can be found in Appendix S3). We chose to use the movements of bears that were first detected live and later identified as a mortality in the compulsory inspection database (live-dead), as opposed to bears that were still alive in our population (live-live, i.e. caught live and still alive at last capture). Using the movements of the live-dead bears required us to assume less about the end point of the bear's movement since the location of the mortality is final, and there could be no further dispersal.

Dispersal in grizzly bears is male and sub-adult biased (McLellan & Hovey 2001a; Proctor *et al.* 2004; Graham & Stenhouse 2014). Therefore, if bears move from elsewhere into the Trap, we predicted the age structure in the trap to be skewed towards young male bears. We used the human-killed bear data to measure the age structure, and our population estimates to measure sex ratios of bears in each stratum. Statistical comparisons between strata were conducted using analysis of variance (ANOVA) and the associated post-hoc Tukey HSD test (further information on methods, equations and validation can be found in Appendix S3).

5.3 Results

5.3.1 Habitat Attractiveness

The best huckleberry model included percent of area burned, percent sand, average winter temperature, precipitation as snow, canopy cover, average pH, slope, and solar heat load (Table S3). The best buffaloberry model was similar to that found for huckleberry, but the summer climate better explained occurrence for this species (Table S3). Both models displayed good model accuracy for predicting occurrence using testing data (AUC, huckleberry = 0.855 ± 0.016, buffaloberry = 0.791 ± 0.031). These are the most predictive models published for either species in the Kootenay Region (Hobby & Keefer 2010).

Huckleberry occurrence decreased with latitude, while buffaloberry was more evenly distributed (Fig. S1). Huckleberry and buffaloberry showed very little spatial overlap with less than 6% of berry occurrence cells containing both species.

Fruit-producing shrubs (huckleberry and buffaloberry) covered a greater proportion of the Trap stratum (0.44) than the North (0.29) or South (0.37) strata. Similarly, the per-capita availability of these species was highest in the Trap stratum (24.8 km^2 / bear) than the North (7.0 km^2 / bear) or South (9.3 km^2 / bear) strata (Figure 5-3A).

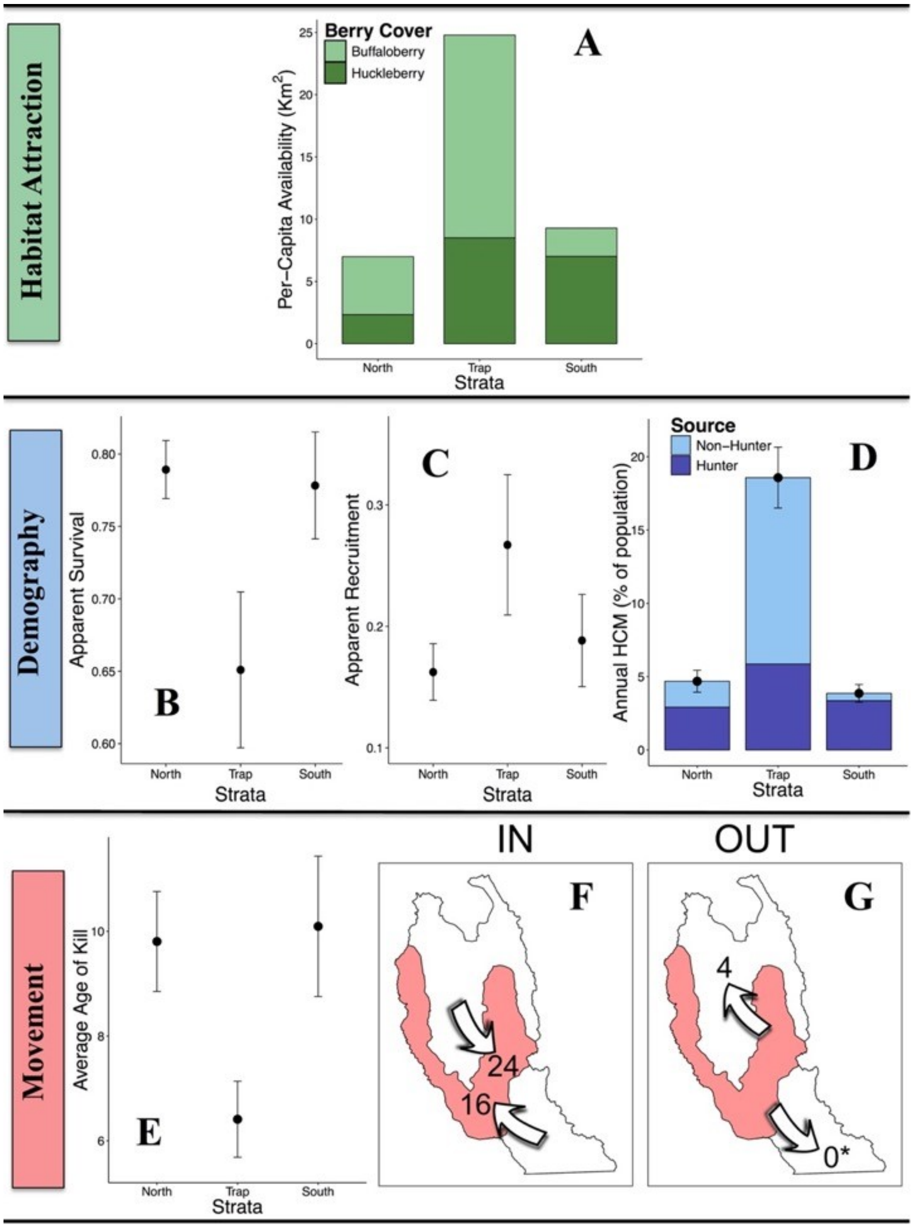


Figure 5-3. Information required to classify the Trap stratum as an ecological trap. Habitat Attraction: (A) Per-capita availability of huckleberry and buffaloberry shrubs within each stratum. High coverage and availability of these key nutritional resources represents attractive habitats for grizzly bears. Demography: (B) Apparent survival (survival + emigration), (C) Apparent recruitment (recruitment + immigration), and (D) Annual human-caused mortality (HCM) of each stratum by mortality source. Movement: (E) Average age of bears killed by humans in each strata, (F & G) Decadal flow of bears between strata that are subsequently killed projected using a combination of genetic capture data and mortality information, (F) IN represents flow of individuals into the Trap stratum that were killed, and (G) OUT represents flow out of the Trap stratum that were killed. Overall the flow ratio of IN:OUT is 10:1.

5.3.2 Demography

Estimates of grizzly bear demography across strata were within the standard target for robust estimates of population size (Pederson *et al.* 2012); a coefficient of variation (CV) < 20% (CV = 7.2 - 16.6%, Table 5-1). Average annual capture probabilities were similar between strata and to previous work on this species (Trap = 0.35 ± SE = 0.04, North = 0.40 ± 0.04, and South = 0.40 ± 0.05; Boulanger *et al.* (2008a)). Covariates that best explained variations in capture probability included sex of the bear, the type of trap used (rub object or bait site), trapping effort, time of year, year of sampling, and a project-specific covariate (full model selection table can be found in Appendix S4, Table S6). Males had higher capture probabilities than females, and bait sites detected more bears than rub objects with effort (trap nights) being positively related to detection (Lamb *et al.* 2016b).

Table 5-1. Estimated population sizes for each stratum from the Huggins estimator, including measures of confidence (SE = standard error, CV = coefficient of variation), the area of each strata, and the resulting grizzly bear density per 1000 km^2. Uncorrected Density is the density of grizzly bears predicted to use the stratum from the Huggins closed estimator divided by the stratum area; this does not account for lack of population closure and is thus biased high (~17% as calculated by Mowat & Lamb 2016). We retain the measure for comparison between strata only.

Stratum	Population Size	SE	CV (%)	Area (km^2)	Uncorrected Density (bears/1000 km^2)
North	166	11.9	7.2	3983	41.7
Trap	66	11	16.6	3584	18.5
South	88	10.5	11.9	2190	40.3

Grizzly bears attained the highest estimated densities in areas of low mortality (Figure 5-3D, Table 5-1). Estimated human-caused mortality rates were approximately 3 times greater in the Trap than in adjacent strata ($p \leq 0.0001$ between all strata except North-South where $p = 0.91$, Figure 5-3D). Estimated apparent survival rates were lower in the Trap ($\phi = 0.65 \pm SE = 0.053$) than in surrounding areas (North $\phi = 0.79 \pm 0.020$, and South $\phi = 0.78 \pm 0.037$), and also differed statistically in Trap-North and Trap-South comparisons ($p \leq 0.05$) but not in North-South comparisons ($p = 0.79$) (Figure 5-3B). Validation of non-reporting rate suggested the non-hunter *2 correction was conservative for the Trap (Appendix S4).

Apparent recruitment rates were highest in the Trap ($f = 0.27 \pm SE = 0.058$), which was marginally higher than in the North ($f = 0.16 \pm 0.023$, $p = 0.09$), but not higher than in the South ($f = 0.19 \pm 0.038$, $p = 0.25$, Figure 5-3C), with no statistical significant difference detected between the North and South ($p > 0.56$). All strata demonstrated annual growth rates below 1: Trap = 0.92 ± SE = 0.040, North = 0.95 ± 0.023, and South = 0.97 ± 0.037, $p > 0.05$ for all comparisons.

5.3.3 Movement

A large proportion of the mortalities that occurred in the Trap stratum were bears previously detected in the North (26%) or South (18%), while few North (5%) and South (0%) strata mortalities were bears first detected in the Trap stratum. Of the movements we documented, the proportion of bears that moved into the Trap and died (0.43) was greater than those leaving the Trap and dying (0.04) ($p = 0.003$, Figure 5-3F & G). This difference is not simply a function of decreased survival rates in the Trap because there were 10 times more detections of bears that moved into and died in the Trap than moved out of the trap and died, but only 1.6 times greater mortality risk in the Trap compared to adjacent strata (Figure 5-3B). The remaining proportion of movements (0.53) were within individual strata.

Average age of bears killed was approximately 3 years younger in the Trap (mean = 6.4 ± 0.7 years old) than in the backcountry regions (North; mean = 9.8 ± 1.0 and South; mean = 10.1 ± 1.3 years old, Figure 5-3E). Bears killed in the Trap were younger ($p < 0.01$) than in surrounding strata, even after accounting for the different sources of mortalities between strata (Figure 5-3D, Appendix S4). No age differences were detected between the North and South strata ($p = 0.99$) or between sexes ($p = 0.56$).

Average annual sex ratio in the Trap was 1.17 (± SE = 0.20) males to every female bear, but only 0.69 (± 0.04) and 0.85 (± 0.07) males per female in the North and South, respectively. Sex ratios were different between the North and Trap ($p = 0.02$), but not between the South and Trap ($p = 0.13$) or the North and South ($p = 0.07$). Over 60% of bears killed in the Trap were sub-adults or cubs (< 6 years of age), while bears of these age classes only composed 38 and 24% of the recorded mortalities in North and South, respectively. The proportion of sub-adult and cubs killed was greater in the Trap than in the other areas ($p < 0.001$).

5.4 Discussion

We show that grizzly bears face an ET produced by human-caused mortality in an area of high human density and rich food resources for bears. This trap produces realized population declines of approximately 8% per year in the Trap and at least 1.5% per year in source populations (North and South). Specifically, we demonstrate that the ET had: 1) greater cover and per-capita availability of fruit-producing shrubs (that are selected by grizzly bears and increase fitness in the absence of humans (McLellan 2015)); 2) greatly reduced survival and insufficient compensation in recruitment to prevent population declines; and 3) compensatory immigration of individuals into the ET from adjacent strata at a ratio of 10 entering the ET and dying to every 1 leaving and dying. Overall, highly attractive habitat in close proximity to lethal human settlement created a ‘severe’ trap (Robertson *et al.* 2013; Hale *et al.* 2015) that exacerbated demographic loss in source populations.

Two small areas within the Trap area were sampled during 2002 and 2003, and average density for these areas was 36.5/1000 km^2 (Mowat *et al.* 2013a); much higher than we found a decade later (18.5/1000 km^2). Projecting the 2002/2003 density through time using the growth rate estimated here for the Trap (λ=0.92) to the median year of this study suggests a density similar to our estimated density (density projected = 18.7/1000 km^2). We speculate the cause of the decline in the Trap is an interactive effect of high human-caused mortality and multiple successive years of fruit crop failure (2004-2007) and poor fruit production (2008, 2010, and 2012, McLellan 2015) producing increased human-bear conflicts (Pease & Mattson 1999; Gunther *et al.* 2004) and reduced reproduction (McLellan 2015).

Between 2006 and 2013, human-caused non-hunting mortalities in the Trap were largely due to collisions with vehicles and trains (54%), with control kills due to human-bear conflicts and illegal kills accounting for 33% and 13%, respectively. The majority of human-caused mortalities in the Trap are attributed to non-hunting sources (75%), an exceptionally pervasive mortality source that cannot be mitigated through simple regulatory changes, as is done with hunting. Since the 1980s, non-hunting bear mortalities have steadily increased in the Trap and surrounding areas (Mowat *et al.* 2013a) and across the species range (Can *et al.* 2014), likely due to increasing human settlement and development in grizzly bear habitat.

High mortality rates can create vacancies that are subsequently occupied by young dispersers. Our results are consistent with the compensatory immigration hypothesis (Cooley *et al.* 2009); bears killed in the Trap were on average 3 years younger than those killed outside the

Trap, and the proportion of males was higher in the Trap than elsewhere. This young and male-skewed composition of individuals in the Trap suggests dispersing juvenile males filled vacancies in this area, and areas with few females and many young males have much lower reproductive potential than areas with more females of reproductive age. Our minimum estimate of 4 bears moving into the Trap stratum per year represents 66% of the difference between apparent recruitment in the Trap and the mean recruitment of the North and South strata. Thus recruitment in the Trap is, at most, only marginally greater than in the other two strata, with the majority of this difference in apparent recruitment (at minimum, two-thirds) due to individuals moving in and occupying vacancies.

Compensatory reproduction may account for a small portion (maximum 33%) of the increased apparent recruitment observed in the Trap, relative to other strata, but is clearly not sufficient to meet replacement nor deter the immigration of individuals from elsewhere. We acknowledge that social structure can alter the spatio-temporal distribution of subordinate individuals, where sub-adults and females with cubs may avoid potentially infanticidal males (Nevin & Gilbert 2005; Elfstrom *et al.* 2014). However, we believe any degree of socially-driven spatial structure will occur within a home range, and we have not found support for sexually selected infanticide in our study area (McLellan 2005). The ecological trap outlined here represents a population-level phenomenon that cannot be explained by social factors alone and must be driven by population dynamics, food availability, habitat selection, and perceived fitness outcomes. Individuals likely spend more time in the Trap because the per-capita food resources are more abundant, and due to increased proximity to humans, mortality is higher. Similar landscape-level redistributions of individuals due to food resources near human settlements have been observed in black bears (*Ursus americanus*, Beckman 2003).

Although the dispersal capability of wide-ranging species is large, it can be impeded by habitat fragmentation (Holderegger & Di Giulio 2010). Proctor *et al.* (2012) identified genetic differentiation and low dispersal across highways and settled areas throughout the southern grizzly distribution—including our study area—and highlighted a correlation between genetic distance and the degree of human settlement and highway traffic. Here we document the causal mechanisms fracturing demographic connectivity in the Trap, a key connectivity corridor for the largest southern peninsular grizzly bear population in North America (Figure 5-1). Specifically, our findings suggest gametes are not shared between the North and South because: 1) attractive fruit resources provide little motivation for dispersers to move through the Trap, and the longer individuals stay in the Trap the more likely they are to be killed by humans as a result of the many sources of mortality in the area (anthropogenic food source conflicts, road/rail strikes, etc.); 2) movements into the Trap are largely by younger bears that are likely not motivated to move into the North or South and compete for mates, food, and space with the older bears occupying these areas; and 3) high female mortality rates in the Trap mean that many females are too young to have a litter, which results in low recruitment in the Trap and contributes to low dispersal out of the Trap. The behavioral and demographic mechanisms identified here explain the genetic differentiation observed by Proctor *et al*. (2012) despite documentation of occasional movements across proposed fracture areas. These mechanisms may also explain population fractures in other wide-ranging species that are similarly susceptible to human-caused mortality and genetic isolation.

In classic source-sink dynamics, source habitats produce dispersers because local recruitment exceeds replacement (Pulliam 1988). The areas we considered as sources supplied dispersers to the Trap, but these sources were declining, although more slowly than the Trap.

Cooley *et al*. (2009) observed a similar pattern, where juvenile cougars (*Puma concolor*) dispersed from source habitat where the population was declining ($\lambda < 1$) to an area with high vacancy rates caused by human-predation. The authors proposed that this dispersal was due to the intrinsic nature of dispersal in cougar populations. Bears likely disperse due to an intrinsic dispersal mechanism as well (McLellan & Hovey 2001a), but may disperse much less if intraspecific competition is low, as is likely in the Trap. Although lower densities may indicate lower intraspecific competition, male-skewed sex ratios may increase sexually selected infanticide (SSI) in the Trap; however, investigations into the effects of SSI in our region of study and elsewhere in North America do not support SSI as a strong limiting factor across a range of male sex ratios (Miller, Sellers & Keay 2003; McLellan 2011).

We note that emigration out of a declining population due to an ecological trap has the potential to create a severe conservation concern if source populations are small and the ecological trap is exceptionally attractive. In the case of the South strata, these bears face multiple threats and sanctuaries as they range beyond BC into Alberta, and Montana in the United States. Bears in the southeast corner of BC provide a population source for potential ecological traps on agricultural land to the west in Alberta (Northrup *et al.* 2012b; Morehouse & Boyce 2016); however, demographic rescue may be compromised if these core populations are demographically overdrawn. The spatial scale at which an ET affects adjacent, secure populations should be related to the dispersal capability of the species affected. Wide-ranging apex consumers are especially vulnerable to anthropogenic ETs due to a lack of natural predators reducing evolutionary vigilance in the face of a human threat. As such, the large dispersal capabilities of these species should produce large-scale demographic consequences in the presence of an ET, as noted by Hale *et al.* (2015). We documented a number of long-distance movements into the Trap, including a 58-kilometer displacement of one individual initially detected in the North that was subsequently killed in the Trap. These dynamics highlight the insidious and far-reaching demographic effects of ecological traps for apex consumers, where declines are further exacerbated due to the presence of ETs.

The idea that the evolutionary cues animals use to select habitats can be poorly matched with novel conditions is the basis for ETs (Robertson *et al.* 2013). ETs are most lethal when they arise rapidly (in evolutionary time) and, as a result, many ETs are associated with anthropogenic disturbance (human-induced rapid ecological change (HIREC); Robertson *et al.* 2013). Our findings demonstrate the deleterious effects of human settlement on grizzly bear demography, which are exacerbated by attractive habitat creating an ET. Due to the large home ranges of grizzly bears and movement of young bears, the effects of localized mortality in our study area resulted in demographic consequences for areas far removed from the Trap. Furthermore, the ability of individuals to identify and respond to the consequences of occupying the Trap is low, due to the Trap causing death (a non-repeating event). This is in contrast to a failed reproduction event, (another potential consequence of occupying an ET, Dwernychuk & Boag (1972)), which could afford an individual a chance to alter their behaviour to habitat cues during a subsequent reproduction attempt (Battin 2004; Hale *et al.* 2015). To date, the drastic range contractions for grizzly bears have been tightly linked to human impact (Figure 5-1), and we see no reason that a similar contraction could not occur in the Trap unless mortality is mitigated. Focusing on mortality sources that can be immediately reduced (e.g. hunting) may help alleviate the broad population consequences of the Trap in the short term, but addressing the larger and more insidious sources of non-hunting mortality (e.g. road, rail, and human-bear conflicts) will be required for long-term viability. However, mitigation of these non-hunting mortality sources, such as fencing towns or rail and road ways, can come at high monetary and ecological costs unless connectivity is maintained through alternate means (Holderegger & Di Giulio 2010; Sawaya *et al.* 2014). More broadly, the population dynamics presented here highlight the imperative need to maintain the integrity of intact landscapes that provide critical habitat for grizzly bears and refuge from human development and associated human-bear conflicts.

An ET where food is the attractant is a specialized case of the more general evolutionary trap, where any resource (mate, food, or habitat) is perceived as attractive despite reduced fitness (Robertson *et al.* 2013). The co-existence of humans and apex consumers is difficult and often incompatible (Can *et al.* 2014), and the occurrence of such species within human-dominated areas highlights the evolutionary mismatch between perceived resource quality and realized fitness. In particular, range reductions have been documented in all species in the order *Carnivora* due to human impacts (Ripple *et al.* 2014), and the expansion of human settlement continually brings the human-carnivore conflict into new arenas. There is an urgent need to mitigate human-carnivore conflict as all successful cases of recovery include mitigation of human activity, not the evolutionary adaption of carnivores to human threats.

5.5 Supporting information and data accessibility

Supporting information available from https://besjournals.onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2F1365-2656.12589&file=jane12589-sup-0001-Suppinfo.docx

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.bg2s4. (Lamb *et al.* 2016a)

6 Chapter 6: Wilderness and adapt-or-die landscapes shape carnivore coexistence

6.1 Introduction

Coexistence with large carnivores poses one of the greatest conservation challenges of our time. From tiger (*Panthera tigris*) and leopard (*Panthera pardus*) attacks in rural Asian villages (Dhanwatey *et al.* 2013), shark-attack hotspots (Chapman & McPhee 2016), to brown bear (*Ursus arctos*) conflicts in urban areas of North America and Europe (Bautista *et al.* 2017; Bombieri *et al.* 2018), carnivores pose real and perceived threats to human life, livelihoods, and property (Bautista *et al.* 2017; Bombieri *et al.* 2018), making human-dominated areas highly lethal for many species (Wolf & Ripple 2017). Carnivores also profoundly influence ecosystem dynamics (Estes *et al.* 2011), provide socioeconomic benefits to society (Gilbert *et al.* 2017), and receive disproportionate attention in conservation and the media (Martín-López *et al.* 2009). This juxtaposition of lethality and fasciation towards carnivores exposes a profound tension in conservation: how can people and carnivores coexist?

Historically, carnivore populations have been suppressed in many areas, with remnant populations persisting in areas of minimal human influence (hereafter wilderness) (Wolf & Ripple 2017). However, carnivore populations are now re-occupying human-influenced landscapes in western Europe (Chapron *et al.* 2014), East Africa (Woodroffe 2011), Midwest USA (LaRue *et al.* 2012), and southeast Asia (Wikramanayake *et al.* 2011). Such occupation has led to the suggestion that carnivore coexistence—enduring populations of wildlife in human-dominated landscapes—is possible, and that wilderness areas are no longer required (Lopez-Bao *et al.* 2015), but this view is not universal (Karanth *et al.* 2013; Gilroy *et al.* 2015).

When coexistence occurs, success is often attributed to the role of people taking action to reduce barriers to connectivity and human-caused mortality (Sawaya *et al.* 2014; Chapron *et al.* 2014; Lopez-Bao *et al.* 2015). However, animals are not passive actors and may be actively shaping coexistence landscapes themselves. For example, carnivores are known to reduce their home range extent in human-dominated areas (Tucker *et al.* 2018), and to increase their activity at night to avoid people (Carter *et al.* 2012; Gaynor *et al.* 2018). In the absence of mechanistic, demographic causality, these responses could be either a signal of coexistence or a portend of extirpation. For example, these depressed vagility could have fitness consequences that are leading to population declines, or it could be an adaptive response that is enabling coexistence.

Carnivore adaptation to people can signal coexistence if at least at least one the four following, non-exclusive mechanisms facilitates enduring populations. First, carnivores can increase their survival through spatial avoidance of risky human-dominated areas. Second, carnivores may overlap in space with people, but increase their survival through temporal avoidance of humans (e.g., nocturnality). Third, high mortality could be compensated by high rates of reproduction for co-occurring animals. Finally, high mortality could be subsidized by immigration from areas with lower human-caused mortality, thus sustaining co-existence through connectivity. Evidence of enduring populations is the primary arbitrator between the co-occurrence and co-existence of carnivores and people (Woodroffe & Ginsberg 1998; Harihar *et al.* 2013). Understanding how these mechanisms combine to influence carnivore demography is a critical knowledge gap that needs to be resolved as coexistence increasingly dominates conservation policy and practice (Chapron *et al.* 2014).

6.2 Methods

To evaluate these mechanisms, we focused on brown bears, one of the world's most widely distributed and conflict-prone carnivore (Bautista *et al.* 2017; Wolf & Ripple 2017; Bombieri *et al.* 2019). Brown bear conflicts with, and attacks on, humans are increasing across their range (Bombieri *et al.* 2019). These dramatic conflicts between people and bears generate more mass media coverage than those with any other terrestrial or aquatic predator (Bombieri *et al.* 2019). Such intense conflicts threaten coexistence for this recolonizing species. We compiled data on the mortality rates, movement, habitat use, and demography of 2,500 brown (grizzly) bears over a 378,191 km^2 human footprint gradient in North America. Our data included 793 bear years of individual demographic monitoring, 451,039 telemetry relocations, and 15,462 genetic detections of marked animals. We integrated individual and population-level responses with satellite-derived measures of landscape productivity and human influence (Figure 6-1A, see Supplemental Methods). These data revealed that, despite excessive lethality in human-influenced areas, coexistence is possible via a combination of individual behavioral shifts and connectivity to wilderness areas that rescue populations from extirpation.

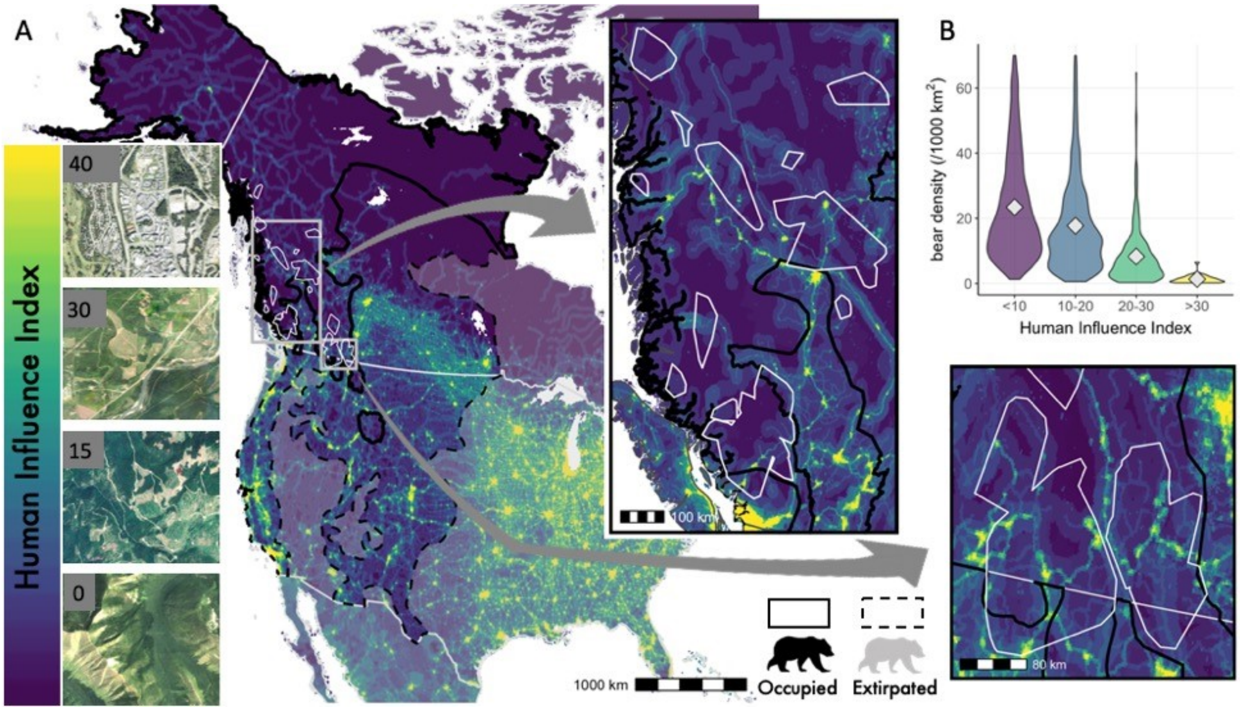


Figure 6-1. A) Study extents (white polygons) for each of 12 telemetry, and 25 genetic tagging studies on brown bear. Human influence index, HII, shown via satellite images from across brown bear range on left. National borders in white. Inset maps show the variation in human influence within and among studies. B) Relationship between brown bear population density and HII.

6.3 Results and Discussion

Bear density was negatively correlated with Human Influence Index (hereafter HII, Figure 6-1B), driven by unsustainable levels of human-caused mortality. Mortality risk from people was higher in human influenced areas (Figure 6-2A), while reproduction did not change across HII (see Supplemental Methods). The cause of bear mortality was primarily people (76%) and human-caused mortality rates increased by 2% for every unit change in HII (Figure 6-2C). Compared to adults, subadults faced a 7.5x higher mortality risk in the highest human-influenced areas where bears occur (Figure 6-2A).

In spite of these high mortality rates, some bears were able to mitigate exposure to people by shifting to a nocturnal activity pattern (Figure 6-2B & D). Bears in human-influenced areas increased their nocturnality by 2-3% per year past the age of 3, which led to a 2-3% increase in survival per year. In wilderness areas, we detected no significant, age-related shift in brown bear nocturnality (Figure 6-2E). The landscape context in which bears change their activity patterns suggests that humans are inducing the shift of bears towards nocturnality, which is not an inherent expression of bears in wild areas. The benefits of nocturnality not only enhance bear survival but reduces conflicts with people. The observed nocturnal shifts in the highest human influenced areas (Figure 6-2D) reduced annual conflict probability by >50% (Supplemental Methods). Bears are actively shifting their daily activity patterns to increase their survival, with benefits to bears and people through reduced conflict.

Despite the lower risk of mortality in wilderness areas, individual bears did not ‘learn’ to avoid spaces used by people - we found little to no spatial avoidance of human-influenced areas as bears age (Figure 6-2E). This suggests that once a bear establishes a home range following dispersal, there is limited behavioural plasticity to avoid areas used by people, or that safer, wilderness areas are at carrying capacity and cannot absorb immigrants. Consequently, there are two outcomes for young animals in landscapes of coexistence: adapt to people by becoming more nocturnal (Figure 6-2D) or die because of people (Figure 6-2A).

Although bears occurred in lower densities near people (Figure 6-1B), and face higher mortality rates (Figure 6-2A), there were areas where bears and people co-occur, and these populations were stable or increasing for decades (i.e., coexistence, (Morehouse & Boyce 2016; Proctor *et al.* 2018a; Lamb *et al.* 2019). Bear populations persist in human-dominated landscapes through immigrant subsidies (Lamb *et al.* 2017b). Beyond an HII of 14, bear populations were no longer self-sustaining without immigrants (Figure 6-2F, hereafter “sink”, where intrinsic population growth <1). The immigrant requirements of sinks increased by 1-2% with each unit increase in HII (Figure 6-3A). Immigrants were supplied via connected landscapes from over 80 km away (average distances 10-40 km, see Supplemental Methods) and provided a male-biased compensatory source of learners to offset the survival deficit caused by human-caused mortality (see Supplemental Methods). This finding exposes a striking paradox of coexistence – the mobility of brown bears through the landscape condemns individual animals to death by people yet rescues populations from extirpation.

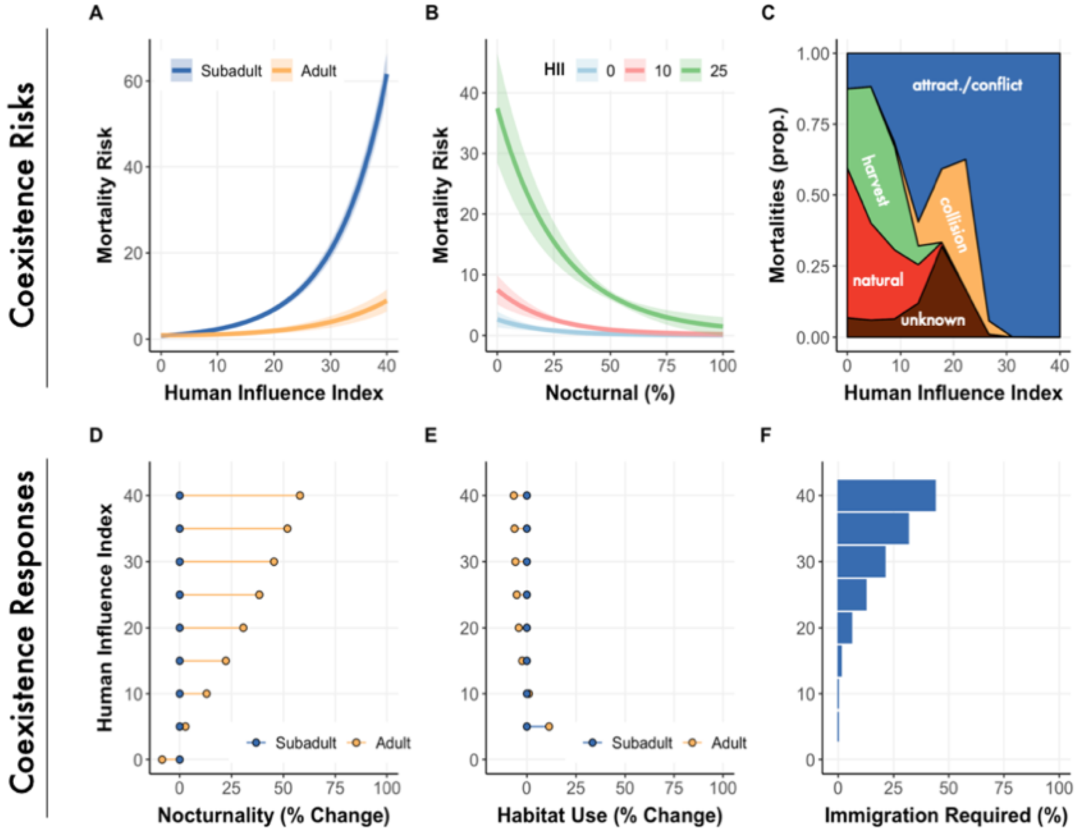


Figure 6-2. Per-capita risk of mortality predicted from cox proportional hazard model for subadult [3-6yo] and adult [>6yo] bears across HII gradients (A) and for HII and nocturnality (B). C) Proportion of mortalities by cause, by HII. Influence of HII on D) change in nocturnality between age classes, and E) change in habitat use between age classes, and F) immigration required to sustain brown bear populations (lambda=1).

While immigration is critical to supporting coexistence in human-dominated areas, only 1.5% of the brown bears' 4.44 million km^2 North American range required immigrants to sustain coexistence; this increases to 3.7% in the more human-dominated 1.1 million km^2 southern range margin (Figure 6-3A). However, due to dispersal, these localized, high-mortality, immigrant-dependent sinks have a disproportionately large, and far-reaching demographic effect on bear populations. Using a conservative dispersal distance of 20 km (Supplemental Methods), we estimated that sink habitats directly impacted 17% of the North American brown bear range, and 42% of the southern range margin (Figure 6-3A). The catchment of coexistence— the extent over which dispersal mediates the supply of animals—for a typical (5,000 person) town was ~ 1,500 km^2 (Figure 6-4). It is these bear immigrants that supply the raw material for coexistence: for every successful 12-year-old coexister, there will be approximately 75 dead conflict bears. These coexisters will generally have to attain nocturnality levels exceeding 80% to survive (Figure 6-3B). Because coexistence is demonstrably an adaptive and subsidized process, the importance of retaining high quality habitat adjacent to human-influenced areas cannot be overstated - these wilderness areas are one of the main factors allowing coexistence to occur.

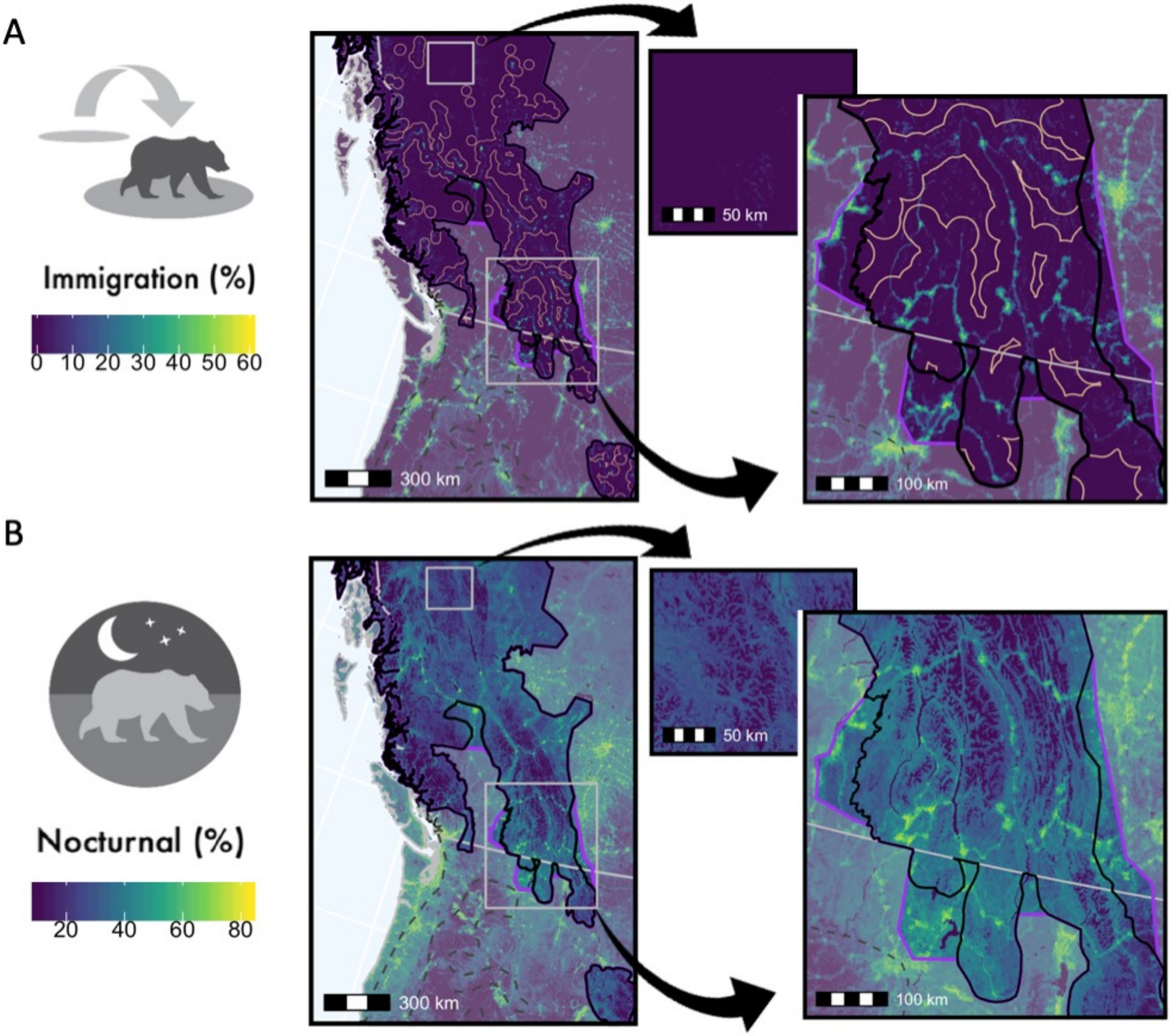


Figure 6-3. Spatial depiction of the landscape of coexistence and what sustains it across the southern range margin of brown bears. Black lines represent the current extent of the brown bear distribution and purple represents the contemporary recolonization frontier. A) percent immigration required to sustain the population. Tan lines represent a conservative extent of influence these localized areas have on the larger population (20 km buffer on sinks). B) Percent nocturnality displayed by adult bears (15 years old) across the landscape. Inset maps depict the coexistence landscape in a wilderness, and in areas of high human-influence and recolonization at the international brown bear range-margin.

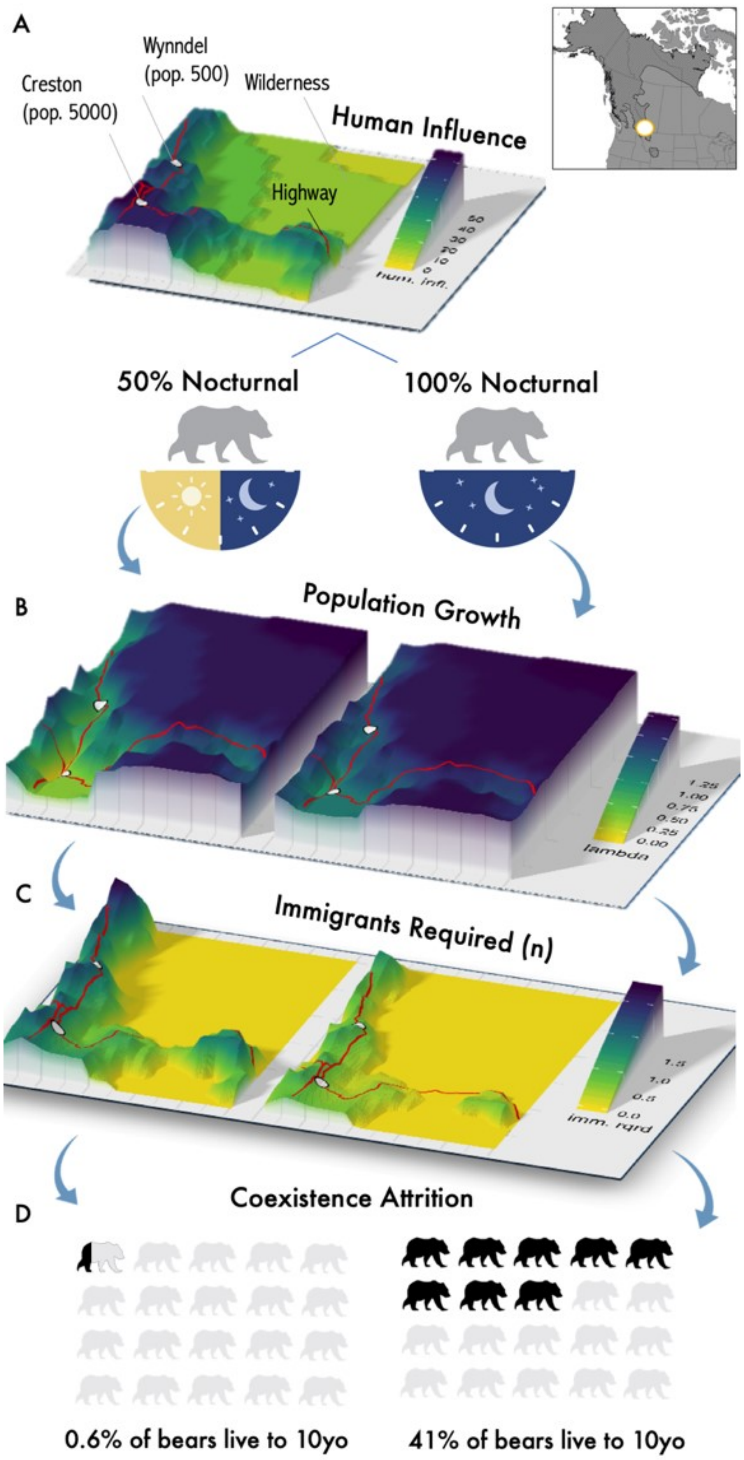


Figure 6-4. An international basin of coexistence near Creston, British Columbia, Canada showing A) human influence, towns, highways, and wilderness, B) population growth, C) number of immigrants (per 25 km^2 per decade) to support coexistence, D) survival for 50% and 100% nocturnality.

Given the intense human-induced pressure on survival rates of brown bears, it is possible that micro-evolutionary process could lead to a greater proportion of coexisting phenotypes (e.g., earlier ontogenetic shifts to nocturnality). In other cases of human-induced "unnatural selection" (*sensu* (Allendorf & Hard 2009)) (e.g. harvesting targeted at size of horn, tusk, or body) microevolution only emerged when populations were sufficiently closed to genetic swamping by immigrants not under such selection (Coltman *et al.* 2003). In contrast, brown bears in coexistence landscapes are sustained by immigrants, weakening the capacity for microevolution to take place. Connectivity is critical for demographic rescue and to supply enough 'learners' to human influenced areas that can adapt to risk of mortality from people. If connectivity were impeded to allow for the accumulation of coexistence genotypes, populations would be extirpated (10-15 years), well before sufficient microevolution could take place (Supplemental Methods). Thus, it is unlikely that bears in human-influenced landscapes will evolve a more positive genotype for coexistence as a direct result of unnatural selection.

The landscape of carnivore co-existence is rapidly evolving - expanding human and carnivore populations continue to compete for remaining space. A central disagreement among researchers and managers is the role of wilderness in promoting carnivore coexistence (Karanth *et al.* 2013; Gilroy *et al.* 2015). Here we provide mechanistic and generalizable insight into the behavioural and population processes facilitating carnivore co-existence across massive spatial extents, indicating that wilderness and connectivity are currently a necessity. Efforts to protect intact wilderness areas for carnivores, maintain and enhance connectivity, and reduce human-caused mortality will allow carnivores to be active participants in co-existence and bolster population persistence. On the human side, social tolerance for carnivores, and creative solutions for coexistence, are increasing. Reducing human influences at night can restore carnivore movement (Whittington, Low & Hunt 2019), and highway crossing structures can increase carnivore survival and connectivity without interfering with human transportation (Gilhooly *et al.* 2019). The behavioural adaptation and demographic processes of large carnivores will support global large carnivore coexistence efforts (Carter *et al.* 2012; Gaynor *et al.* 2018), provided that there is sufficient wilderness connected to these areas for demographic rescue.

6.4 Supplemental Methods

All analyses were conducted in program R (R Core Team 2019). For all models we tested competing models using AICc, and model-averaged results by model weight when models were competing.

6.4.1 Remotely-sensed data:

6.4.1.1 Human Influence Index

Human Influence Index (HII, http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic) Dataset of the Last of the Wild Project, Version 2, 2005 (LWP-2) is a global dataset of 1-kilometer grid cells, created from nine global data layers covering human population pressure (population density), human land use and infrastructure (built-up areas, nighttime lights, land use/land cover), and human access (coastlines, roads, railroads, navigable rivers). The dataset in Clarke 1866 Geographic Coordinate System is produced by the Wildlife Conservation Society (WCS) and the Columbia University Center for International Earth Science Information Network (CIESIN).

6.4.1.2 Normalized Difference Vegetation Index

We included measures of vegetative productivity in our models to account for differences in habitat quality across the landscape. The Normalized Difference Vegetation Index (NDVI) provides a measure of vegetative abundance on the landscape and has been widely used in animal ecology (Pettorelli *et al.* 2011). We calculated NDVI (Pettorelli 2013) for the period between June 30-Aug 1, averaged across 2014-2018, using imagery from the Copernicus Sentinel 2 satellite. Calculations were made in Google Earth Engine (https://code.earthengine.google.com/ceb21ebebd5a9742f520a89a0bf6ac31). We downscaled the 10 m sentinel product to 100 m as our relocation interval for telemetry data (>=1 hour) did not require such fine scale data, and the larger pixels allowed for more efficient processing. We chose to create a temporally static (averaged between 2014-2018) NDVI layer, instead of a temporally dynamic layer (matched with the season and year of relocation) because we were not interested in fine-scale habitat dynamics, but in generalizable and broad trends across large landscapes. Further, grizzly bears may utilize resources that are not indexed by fine-scale NDVI, such as roots or berries that do not give off a strong greenness signal during the late summer and fall when they are used, but their presence is strongly correlated with high summer NDVI values (Figure 6-5).

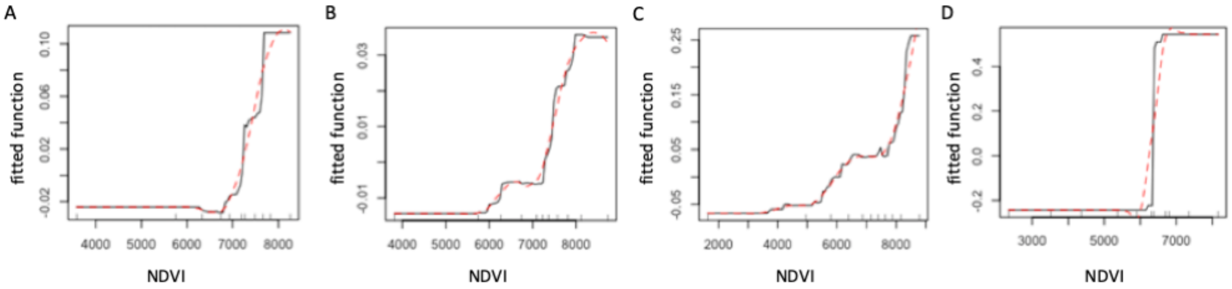


Figure 6-5. Relationship between NDVI (x1000) and A) saskatoon berry abundance, B) buffaloberry berry abundance, C) huckleberry berry abundance, and D) hedysarum root abundance. Relationships from marginal effects plots of boosted regression models fit to vegetation occurrence and productivity data (n=25 458, Lamb unpublished data).

6.4.2 Telemetry Data

We used GPS and VHF telemetry data collected on 456 grizzly bears across BC between 1979-2018 (Table 6-1). These data consist of telemetered animals of known sex and age, monitored for 793 bear years, with 73 mortalities and 451,039 relocations spread across multiple ecosystems and 12 research projects (Table 6-1). Animals were monitored for an average of 1.7 years (range=0.01-21) each, and project length averaged 8.8 years (range: 2-41). We extracted a measure of HII and NDVI for each live and mortality location. Mortality locations required the animal to carry a functioning collar at the time of death. Distribution of HII values by project shown in Figure 6-6.

Table 6-1. Summary stats for telemetered grizzly bears by project. n=number, min=minimum, max=maximum, hii=human influence index, perc=percent, yr=year, GPSindividuals_perc= % individuals with GPS collars, GPSrelocations_perc= % relocations from GPS collars.

StudyArea	animals_n	age_min	age_max	yr_min	yr_max	hii_min	hii_max	morts_n	relocations_n	GPSindividuals_perc	GPSrelocations_perc
BabineKispiox	5	4	21	2001	2002	0	16	0	2445	100	100
Elk Valley1	23	3	18	2003	2011	0	46	3	66686	100	100
Elk Valley2	44	2	22	2015	2018	0	46	11	19478	100	100
Flathead	141	0	32	1979	2018	0	26	33	26395	20	67
Khutzeymateen	19	4	25	1989	1991	0	13	1	793	0	0
Lilloet	10	3	16	2014	2018	0	12	0	26353	100	100
Parsnip	53	1	23	1998	2003	0	38	10	17789	28	32
SelkirkPurcell	49	3	21	2004	2018	0	56	4	110864	100	100
SouthCoast	38	3	21	2008	2016	0	46	2	174741	100	100
Tulsequah	9	3	17	2000	2001	0	13	1	3217	100	100
Tweedsmuir	16	2	33	1992	1994	0	16	3	586	0	0
Westslopes	49	1	26	1994	2000	0	29	7	1692	0	0

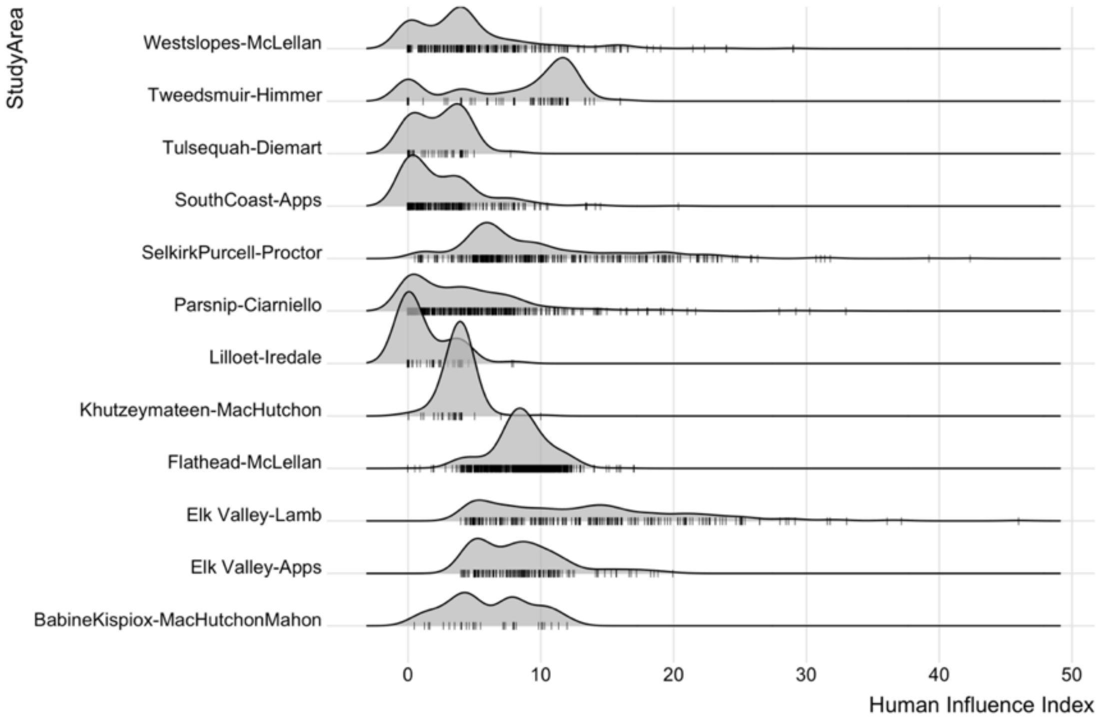


Figure 6-6. Distribution of relocations across HII gradient for each telemetry project.

6.4.3 Genetic Tagging Data

We compiled data from 27 genetic tagging projects (Figure 6-7). Genetic tagging data and approaches are described in (Lamb *et al.* 2019), and project-specific information can be found in the project's reference (

Table 6-2). Generally, these data are collected by snagging grizzly bear hair with barbed wire across large spatial extents using minimally invasive collection methods. The hair is then used to extract DNA from the follicle and molecularly assign individual, sex, and species identities.

Between 1996-2017, 2,226 grizzly bears were genetically tagged across 204 sampling occasions. These 2,200 bears were detected 5,867 times (unique site-occasion-individual combinations).

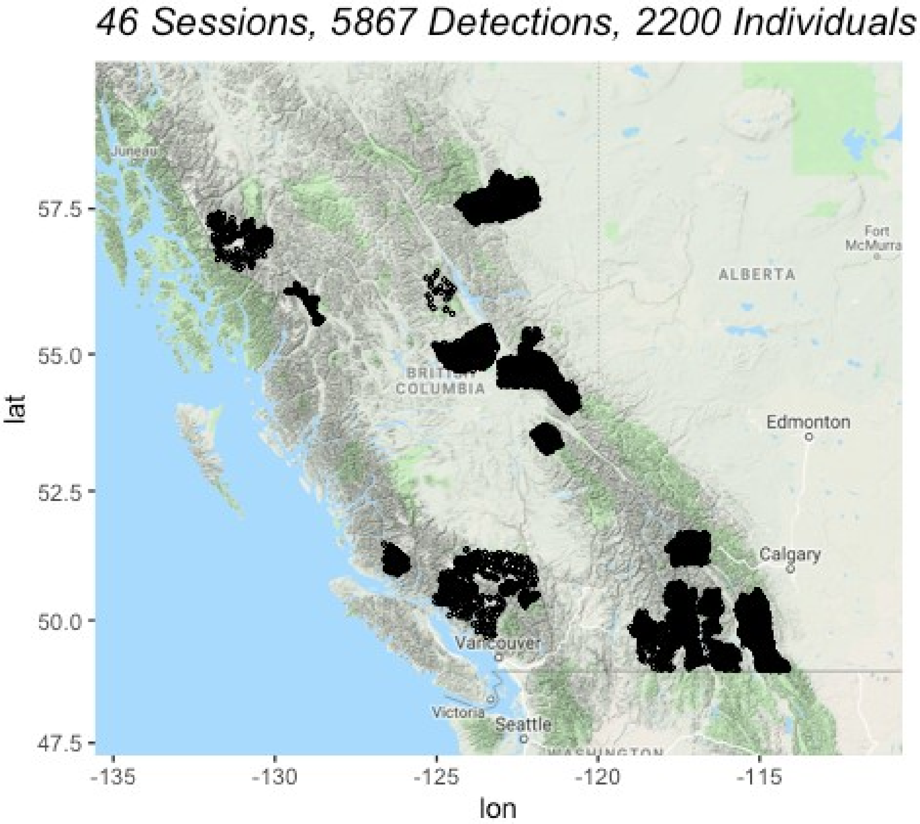


Figure 6-7. Spatial distribution and detection summaries for 29 genetic tagging studies conducted on grizzly bear between 1996-2017.

Table 6-2. Project information and citations for each of 29 grizzly bear genetic tagging projects conducted on grizzly bear between 1996-2017

Session_Year	Project	Reference
BurntRiver_1997	BurntRiver	(Westworth Associates Environmental Ltd 1998)
Central_Selkirk_Mountains_1996	Central_Selkirk	(Mowat *et al.* 2005)
Flathead_2007	Flathead	(Boulanger *et al.* 2007)
Herrick_2000	Herrick	(Mowat *et al.* 2005)
HWY3_2004	HWY3	(Proctor *et al.* 2007)
HWY3_2005	HWY3	(Proctor *et al.* 2007)
Jumbo_1998	Jumbo	(Strom, Proctor & Boulanger 1999)
Kettle-Granby_Grizzly_Bear_Population_Unit_2015	Kettle-Granby	(Lamb *et al.* 2017c)
Kingcome_1997_1997	Kingcome	(Boulanger & Himmer 2001)

Lower_Bowron_River_2001	Lower Bowron	(Mowat *et al.* 2005)
Lower_Stikine_River_2004-2005	Lower_Stikine	(Rescan Environmental Services Ltd. 2006)
Mid_Nass_Valley_1997-1999	Mid_Nass	(Demarchi 2002)
Nation_River_2003	Nation	(Mowat & Fear 2004)
Osilinka_River_2005	Osilinka	NA
Parsnip_2000	Parsnip	(Mowat *et al.* 2005)
Prophet_River_1998	Prophet	(Mowat *et al.* 2005)
PWC_2002	PWC	(Proctor *et al.* 2007)
Region_2004	Region_2004	(Apps *et al.* 2014)
Region_2005	Region_2005	(Apps *et al.* 2014)
Region_2006	Region_2006	(Apps *et al.* 2014)
Region_2007	Region_2007	(Apps *et al.* 2014)
S_Purcell_1998	S_Purcell	(Proctor *et al.* 2007)
S_Purcell_2001	S_Purcell	(Proctor *et al.* 2007)
S_Selk_2005	S_Selk	(Proctor *et al.* 2007)
Southern_Rockies_2006-2017	Southern_Rockies	(Lamb *et al.* 2017b, 2019)
Southgate_2010	Southgate	(Apps *et al.* 2014)
Stein_SC_2010-2014	Stein_SC	(McLellan *et al.* 2019)
Toba_2008	Toba	(Apps *et al.* 2014)
WestSlopes_1996-1998	WestSlopes	(Woods *et al.* 1999)

6.4.4 Spatial capture recapture

We conduct a spatially-explicit capture recapture (SCR) analysis with the genetic tagging data to parameterize a density~HII relationship. We controlled for habitat productivity with NDVI, and included canopy cover (cc, https://landcover.usgs.gov/glc/TreeCoverDescriptionAndDownloads.php) to refine the density estimates. We controlled for variation in detection by including the type of detector (Trap_Type) used in sampling (bait site or rub tree, see (Lamb *et al.* 2016b) for more information on each trap type). Details on SCR can be found in (Efford & Fewster 2013; Royle *et al.* 2014a). We followed the SCR analysis methods of (Lamb *et al.* 2017c) and fit models with the 'oSCR' package (Sutherland *et al.* 2019). Model selection is shown in Table 6-3.

Table 6-3. SCR model selection table. AIC= Akiake Information Criteria. K=number paramatrs, dAIC= delta AIC.

model	K	AIC	dAIC
D(~hii_log + ndvi_scale + cc_scale) p(~Trap_Type) sig(~1) asu(~1)	8	53519.92	0
D(~hii_scale + ndvi_scale + cc_scale) p(~Trap_Type) sig(~1) asu(~1)	8	53522.16	2.24
D(~ndvi_scale + cc_scale) p(~Trap_Type) sig(~1) asu(~1)	7	53805.03	285.11
D(~hii_scale) p(~Trap_Type) sig(~1) asu(~1)	6	54712.42	1192.5
D(~hii_log) p(~Trap_Type) sig(~1) asu(~1)	6	54720.28	1200.36
D(~1) p(~Trap_Type) sig(~1) asu(~1)	5	54905.53	1385.61

6.4.5 Mortality hazard analysis

We parameterized a spatially-explicit mortality risk model using the telemetry relocations as the live location and contrasted these against the HII at mortality locations. We only considered dependent animals (>=3 years old) and the active (non-denning) season between April and November. Fix rates ranged between projects (1 hour-1month [for some VHF collared bears]). We conducted our survival analysis at the coarsest temporal scale of the data: monthly. We considered relocation intervals >1 month a new monitoring interval. For each individual, we averaged covariates within each month, and produced a monthly monitoring dataset of known fate, age, sex, HII, and NDVI, spanning 4, 853 bear-months.

We used Cox-proportional hazard models with Bear ID as a clustered effect to account for clusters of correlated observations (i.e., monthly sampling of the same individual) to estimate differences in hazard rates between sexes, age classes, HII gradients. The models assume proportional hazards over time, which we tested for, and found no evidence that our data violated this assumption (p=0.2). We include sex in all of our models, but average the results for each sex in plots to simplify interpretation. Model selection is shown in Table 6-4, and standardized model coefficients from the top model (dAICc=0) are shown in Figure 6-8.

Table 6-4. Model selection for per-capita mortality risk using cox proportional hazard models. Df= degrees of freedom, AICc= Akiake Information Criteria corrected for small sample size, dAICc= delta AICc, weightt= AICc Weight.

Model	df	AICc	dAICc	weight
Sex + ageclass + hii + ndvi + ageclass:hii	5	1,082.73	0	0.32
Sex + ageclass + hii + ndvi + Sex:ageclass + Sex:hii + ageclass:hii + Sex:ageclass:hii	8	1,082.78	0.05	0.31
Sex + ageclass + hii + ndvi	4	1,083.59	0.86	0.21
Sex + ageclass + hii + Sex:ageclass + Sex:hii + ageclass:hii + Sex:ageclass:hii	7	1,085.82	3.09	0.07
Sex + ageclass + hii + ageclass:hii	4	1,086.36	3.63	0.05
Sex + ageclass + hii	3	1,087.73	5	0.03
Sex + hii + ageclass + Sex:hii	4	1,089.6	6.87	0.01
Sex + ageclass + Sex:ageclass	3	1,106.16	23.4	0
Sex + ageclass	2	1,106.91	24.2	0
ageclass	1	1,110.1	27.4	0
Sex	1	1,112.84	30.1	0

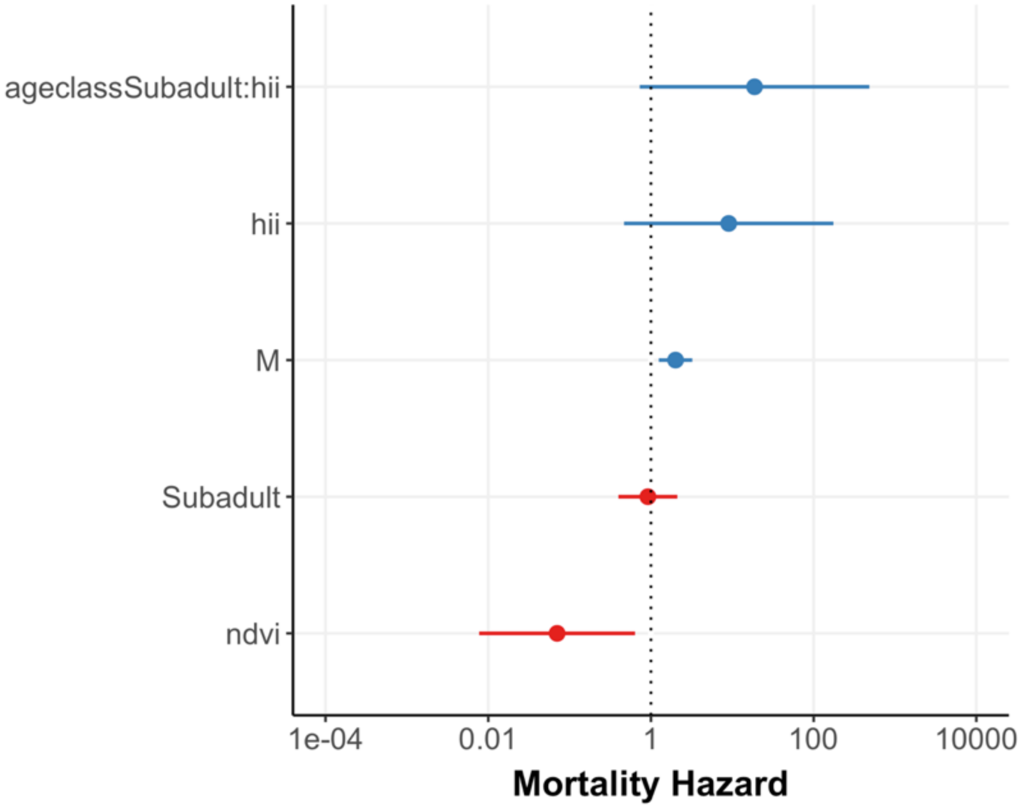


Figure 6-8. Standardized model coefficients for mortality hazard from top cox model (dAICc=0) predicting the influence of ageclass, hii, sex, and ndvi on bear mortality risk.

We tested the sensitivity of results to variations in mortality risk between study areas by including a random effect of study area in our models (Figure 6-9). The inference from these results did not differ from the non-mixed effects model, thus we retain the simpler non-mixed model. We tested the sensitivity of results to our index (HII). We used a measure of road density (including backcountry resource extraction roads) weighted by use, where highways get 5x the weighting due to more traffic and risk (Figure 6-10). The inference remained unchanged, thus we suggest the inference appears to be robust regardless of index used, and we retained HII as the index for future analyses. We also explored the sensitivity of our results using a weekly time scale, instead of monthly. We found comparable results with either timeframe, but the weekly timeframe violated model assumptions (p<0.0009) likely influenced by this timescale being finer than the scale some of the data was collected, thus we retained the monthly scale as the results were robust and did not violate model assumptions.

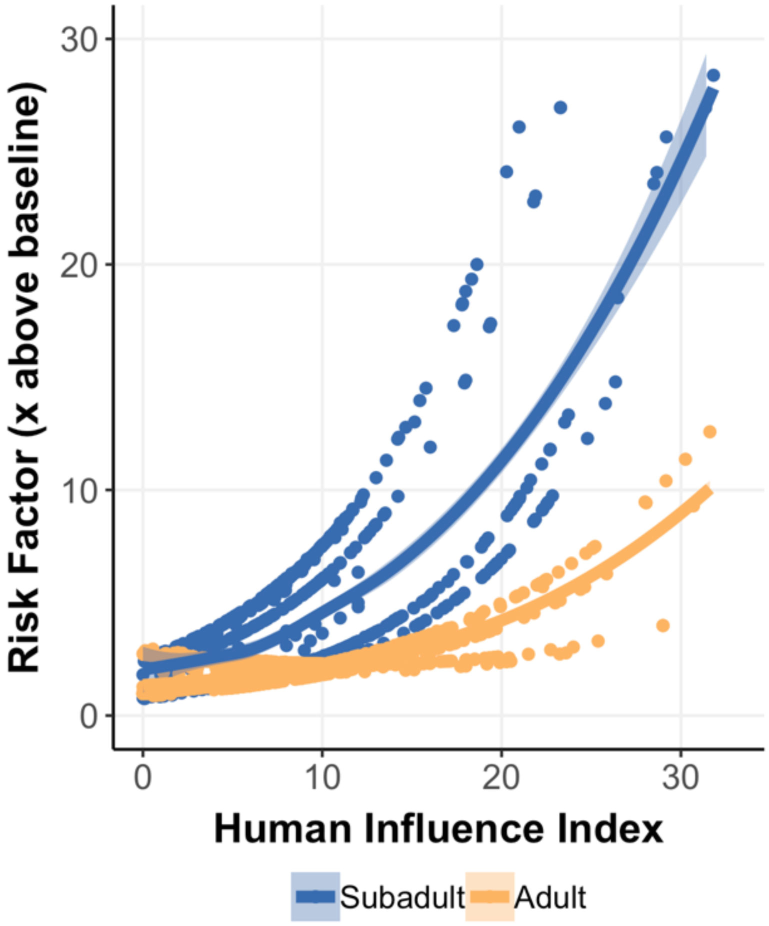


Figure 6-9. Per-capita risk of mortality by human influence and age class (bottom) predicted from mixed-effect Cox proportional hazard model accounting for variation in mortality risk within each study area (random effect) for 4,853 monitoring months.

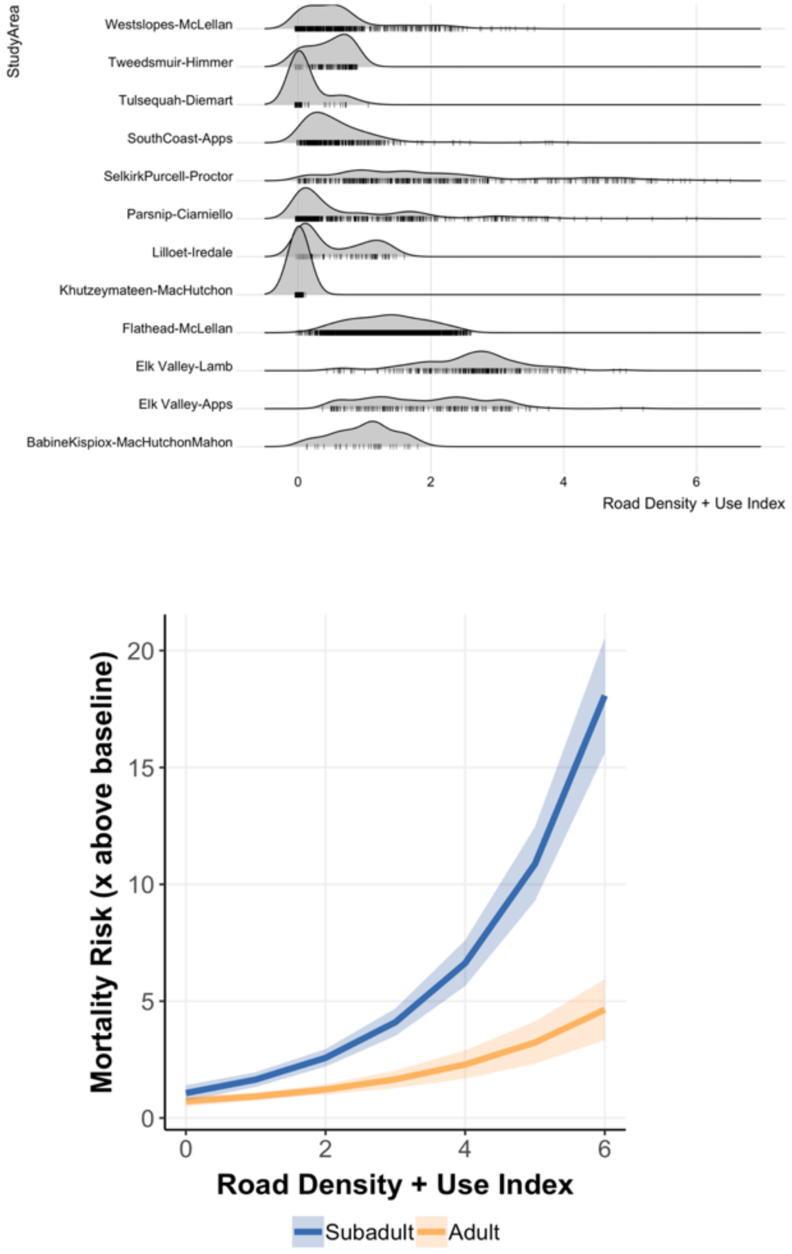


Figure 6-10. Top) Distribution of relocations based on road density and use, for each project. Black ticks denote marginal distribution of data across road density and use gradient. bottom) Per-capita risk of mortality by road density + use index predicted from Cox model.

We assessed the influence of nocturnality on mortality hazard across a gradient of human influence. We calculated daily and nightly step lengths for 325,350 successive relocations that were <7 hours apart and fell completely within the day or night. We defined night as 22:00-06:00 and day as 06:00-22:00 based on change in human activity and luminescence cover between these two periods (Benítez-López 2018). We exclude erroneous and long-distance relocations (>15 km apart, 45 records) and duplicated fixes (219 records), which reduced the 325,614 records by 264 records, or 0.08%. We calculated % nocturnal as (nightly movement/daily movement *100). We fit a GLM to predict % nocturnal for each individual bear-month, based on HII, age class, and month, while controlling for fix rates (more details on nocturnal modelling below). We found no evidence that our data violated proportional hazard assumption (p=0.9). Model selection is shown inTable 6-5, and standardized model coefficients from the top model (dAICc=0) are shown in Figure 6-11.

Table 6-5. Model selection for per-capita mortality risk in relation to nocturnal behaviour using cox proportional hazard models. Noc=% nocturnal , Df= degrees of freedom, AICc= Akiake Information Criteria corrected for small sample size, dAICc= delta AICc, weightt= AICc Weight.

Model	df	AICc	dAICc	weight
noc + hii + Sex	3	1,087.73	0	0.6
noc + hii + Sex + noc:hii	4	1,089.67	1.94	0.23
hii + Sex	2	1,090.45	2.72	0.16
hii	1	1,095.66	7.93	0.01
Sex	1	1,112.84	25.1	0
noc	1	1,117.01	29.3	0

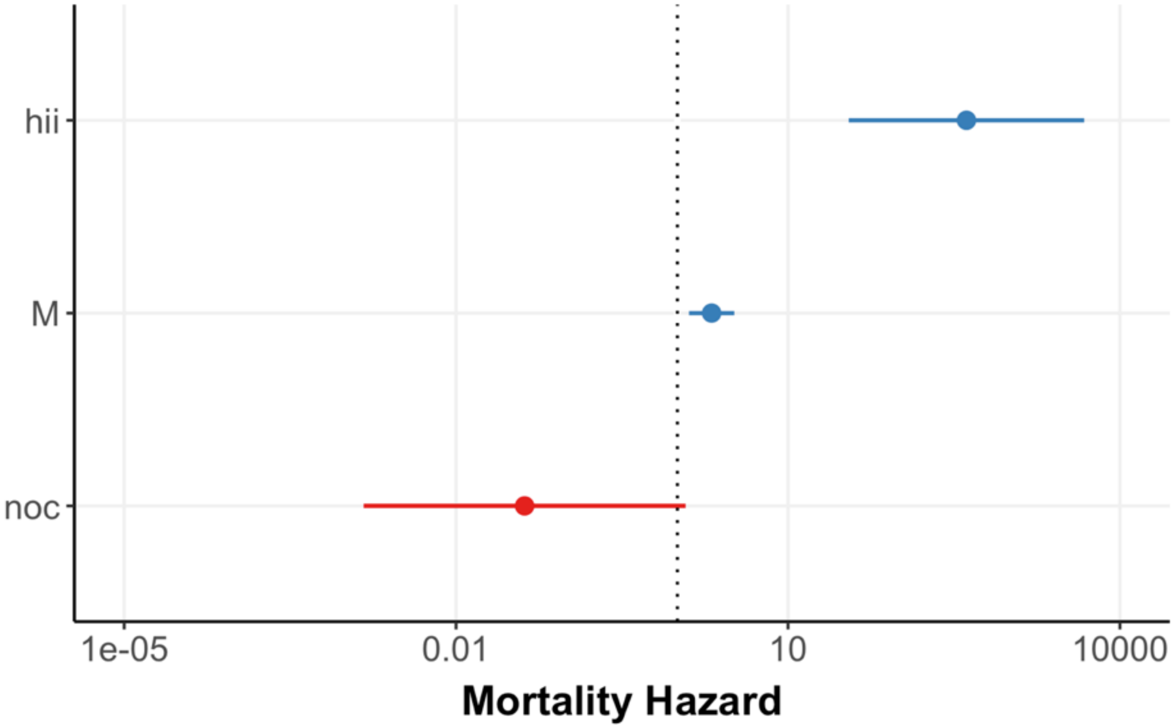


Figure 6-11. Standardized model coefficients for mortality hazard from top cox model (dAICc=0) predicting the influence of hii, sex, and nocturnality on mortality risk. Noc=% nocturnal, M= Male (female is the baseline here).

6.4.6 Risk mitigation strategies: spatial and temporal risk avoidance

We explored spatial and temporal risk avoidance by bears in response to the mortality risk of human influenced areas. We used generalized linear mixed effects models with a random effect for individual, and month. We assessed changes in the values of HII as an indicator of spatial avoidance of human influence, and changes in daily timing of use of HII as an indicator of temporal avoidance of human influence. The random effects model allows individuals to have different baseline values (intercept) for a parameter, but the model tests if variable coefficients (slopes) are different than 0 within each individuals time monitored. Thus, we could test if individuals were behaviourally adapting to risk as they aged. We provide a description of each analysis below.

6.4.6.1 Spatial avoidance

We tested if individuals were changing their habitat use patterns as they aged. We measured the individual change as deviation from their habitat use as subadults, and assessed if this change differed depending on the values of HII the animals occupied as subadults. Model selection is shown inTable 6-6, and standardized model coefficients from the top model (dAICc=0) are shown in Figure 6-12.

Table 6-6. Model selection for spatial HII avoidance random effect analysis, Age2= monthly age (e.g. 1st month at age 4= 4.1), m=month, med.hii2=median HII as a subadult. , Df= degrees of freedom, AICc= Akiake Information Criteria corrected for small sample size, dAICc= delta AICc, weightt= AICc Weight.

Model	df	AICc	dAICc	weight
Age2 * med.hii2 + ndvi + (1 | BearID) + (1 | m)	8	9,902	0	0.88
Age2 + med.hii2 + (1 | BearID) + (1 | m)	6	9,907.33	5.33	0.06
Age2 * med.hii2 + (1 | BearID) + (1 | m)	7	9,908.59	6.58	0.03
Age2 + (1 | BearID) + (1 | m)	5	9,910.8	8.8	0.01
1 + (1 | BearID) + (1 | m)	4	9,911.01	9.01	0.01
1 + (1 | BearID)	3	9,916.04	14	0

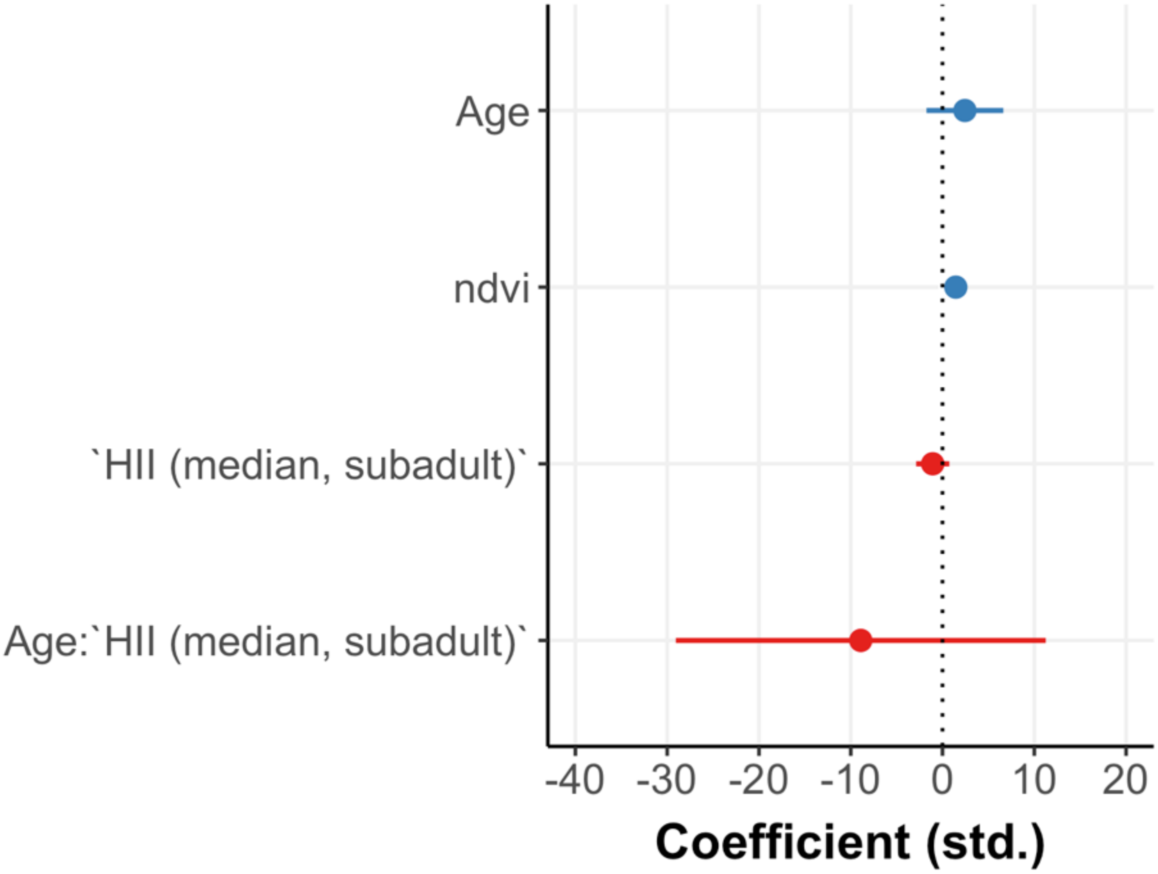


Figure 6-12. Standardized model coefficients from generalized linear mixed model predicting the influence of age, ndvi, and median HII as a subadult, on changes in HII as animals aged. Age= monthly age (e.g. 1st month at age 4= 4.1), HII (median, subadult)=median HII as a subadult.

6.4.6.2 Temporal avoidance

We tested for changes in % nocturnality as predicted by animal age, HII, and fix rate. Model selection is shown in Table 6-7, and standardized model coefficients from the top model (dAICc=0) are shown in Figure 6-13.

Table 6-7. Model selection for temporal HII avoidance random effect analysis. Age2= monthly age (e.g. 1st month at age 4= 4.1), m=month, timedif=relocation interval. Df= degrees of freedom, AICc= Akiake Information Criteria corrected for small sample size, dAICc= delta AICc, weightt= AICc Weight.

Model	df	AICc	dAICc	weight
Age2 * hii + timedif + ndvi + (1 | BearID) + (1 | m)	9	36,653.91	0	0.93
Age2 * hii + timedif + (1 | BearID) + (1 | m)	8	36,659.2	5.3	0.07
Age2 + hii + timedif + ndvi + I(ndvi^2) + (1 | BearID) + (1 | m)	9	36,667.14	13.2	0
Age2 + hii + timedif + ndvi + (1 | BearID) + (1 | m)	8	36,675.16	21.2	0
hii + timedif + (1 | BearID) + (1 | m)	6	36,679.65	25.7	0
Age2 + hii + timedif + (1 | BearID) + (1 | m)	7	36,680.83	26.9	0
timedif + (1 | BearID) + (1 | m)	5	36,753.83	99.9	0
Age2 + timedif + (1 | BearID) + (1 | m)	6	36,755.84	102	0
(1 | BearID) + (1 | m)	4	36,761.94	108	0

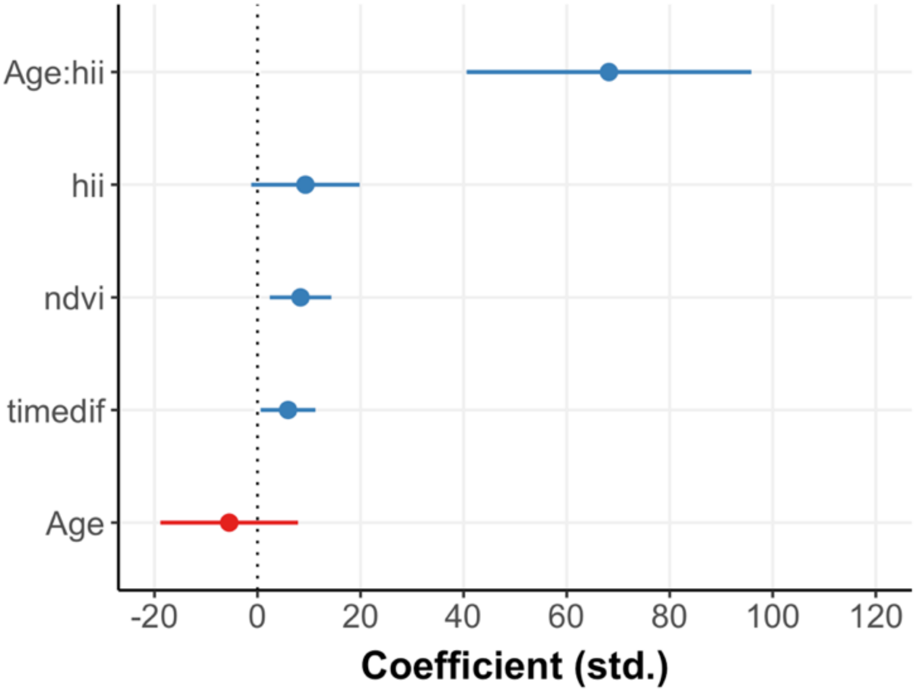
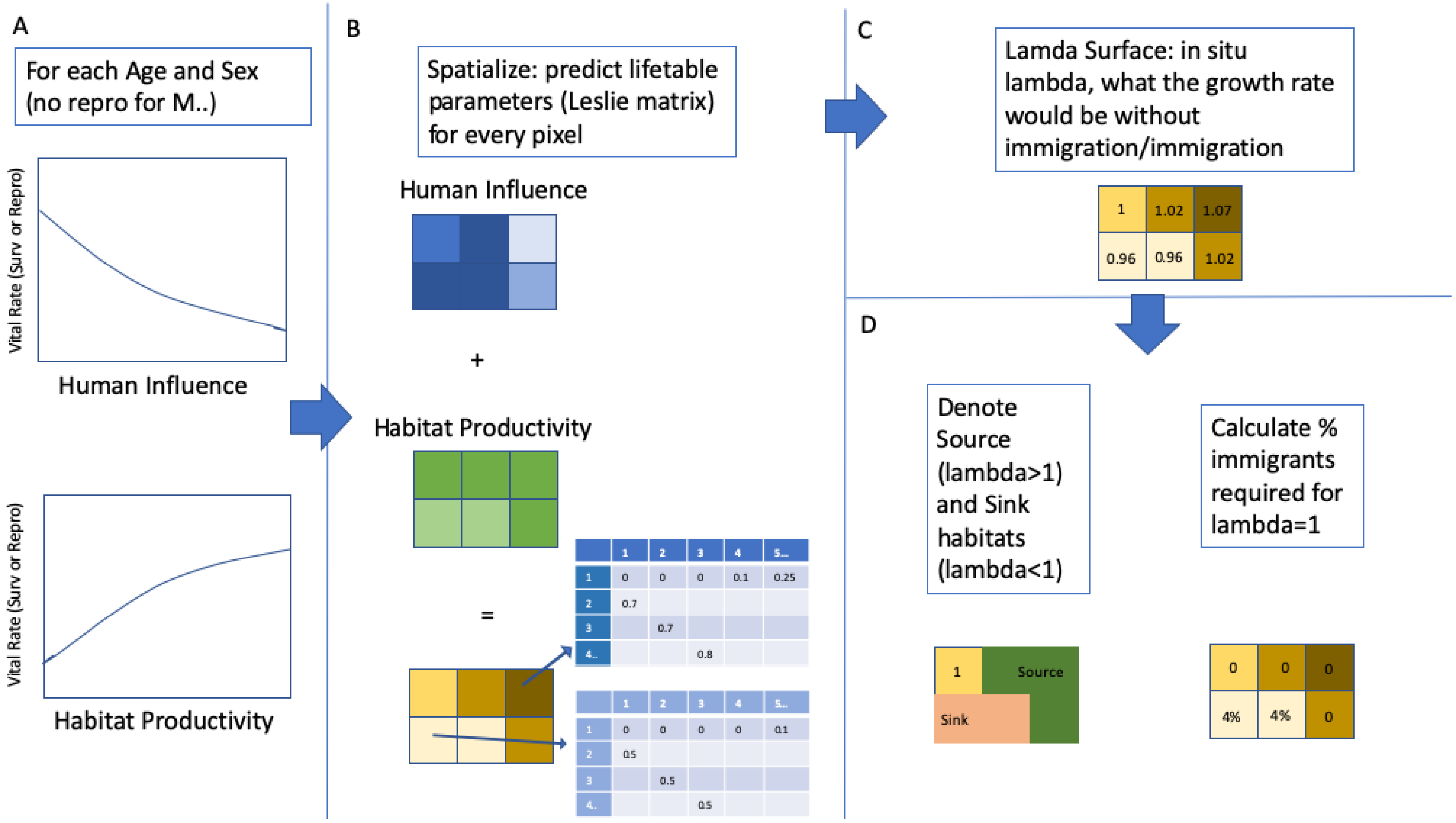


Figure 6-13. Standardized model coefficients from generalized linear mixed model predicting the influence of age, ndvi,HII, and fix rate (timedif).

6.4.7 *Immigration required*



	1	2	3	4	5…
1	0	0	0	0.1	0.25
2	0.7				
3		0.7			
4..			0.8		

	1	2	3	4	5..
1	0	0	0	0	0.1
2	0.5				
3		0.5			
4..			0.5		

Figure 6-14. Schematic outlining estimation and spatialization of population growth and percent immigration required.

We calculated intrinsic population growth–population trajectory without immigration and emigration—across human influence and productivity gradients (Figure 6-14). To do this we first required survival and reproduction values for each female age class (0-30) ((Figure 6-14A). For all models we assessed the influence of bear age, human influence (HII) and habitat productivity (NDVI) on the respective vital rate. For each model we created 500 bootstrapped predictions to quantify and visualize uncertainty in our estimates. We calculated survival rates for bears aged 2-30 using Cox proportional hazard models and the same analysis approaches as explained in the mortality risk analysis above (

Table 6-8). We transformed the predictions of mortality hazard to monthly survival by negative exponentiation. We calculated annual survival by multiplying monthly survival rates over the 6 month active period for female bears (May-Oct), and used a static monthly denning survival rate of 0.997 (McLellan 2015) for each of the remaining 6 months in the den (Nov-April). Cub (<1 year old animals) and yearling (1 year old) survival was estimated using annual areal cub counts conducted each spring (Table 6-9). We did not collar cubs and yearlings, as these animals grow too fast and collaring would pose a risk to them. Therefore, our cub counts are done on collared adult females, for whom we track their annual reproduction (# cubs), and if these cubs are present (survive) in following years. We assumed cubs not seen the following year as yearlings were killed. We also assumed yearlings not seen as 2 year olds were killed, but this could be influenced by early dispersal of these animals. Thus we compare our estimates of yearling survival to other published studies and scale our estimates to reflect these other studies where possible, based on study-specific human influence and habitat productivity. We estimated reproduction (cubs per female) using a generalized linear mixed model (Table 6-10). We divided the predictions from the reproduction model by two, to represent female cubs/female (assuming a 50:50 sex ratio at birth, which is common (Schwartz *et al.* 2006; McLellan 2015). Vital rates by age and HII are shown in Figure 6-15.

Table 6-8. Model selection for per-capita mortality risk using cox proportional hazard models for bears aged 2-30. Df= degrees of freedom, AICc= Akiake Information Criteria corrected for small sample size, dAICc= delta AICc, weightt= AICc Weight.

Model	df	AICc	dAICc	weight
Sex + Age + hii + I(Age^2) + ndvi + Age:hii	6	1,117.65	0	0.5
Sex + Age + hii + I(Age^2) + I(Age^3) + ndvi + Age:hii	7	1,119.25	1.59	0.22
Sex + Age + hii + I(Age^2) + I(Age^3) + I(Age^4) + ndvi + Age:hii	8	1,119.55	1.9	0.19
Sex + Age + hii + I(Age^2) + ndvi + Sex:Age + Sex:hii + Age:hii + Sex:Age:hii	9	1,122.15	4.5	0.05
Sex + Age + hii + I(Age^2) + I(Age^3) + ndvi + Sex:Age + Sex:hii + Age:hii + Sex:Age:hii	10	1,122.97	5.31	0.03
Sex + Age + hii + ndvi + Age:hii	5	1,130.48	12.8	0
Sex + ageclass + hii + ndvi + Sex:ageclass	7	1,132.37	14.7	0
Sex + Age + hii + Age:hii	4	1,133.45	15.8	0
Sex + Age + hii	3	1,134.59	16.9	0
Sex + hii + Age + Sex:hii	4	1,136.72	19.1	0
Sex + ageclass + hii + ndvi + Sex:ageclass + Sex:hii + ageclass:hii + Sex:ageclass:hii	12	1,138.51	20.9	0
Sex + ageclass + hii + ndvi + Sex:ageclass + Sex:hii + ageclass:hii + Sex:ageclass:hii	12	1,138.51	20.9	0
Sex + Age	2	1,155.74	38.1	0
Age	1	1,160.32	42.7	0

Table 6-9. Model selection for per-capita mortality risk using cox proportional hazard models for bears aged 0-1. Df= degrees of freedom, AICc= Akiake Information Criteria corrected for small sample size, dAICc= delta AICc, weightt= AICc Weight.

Model	df	AICc	dAICc	weight
ndvi + AgeClass	2	1,073.89	0	0.35
hii + AgeClass	2	1,074.34	0.45	0.28
hii + ndvi + AgeClass	3	1,075.86	1.96	0.13
ndvi	1	1,076.49	2.6	0.1
hii	1	1,077.38	3.49	0.06
hii + ndvi + AgeClass + ndvi:AgeClass	4	1,078.03	4.13	0.04

hii + ndvi	2	1,078.47	4.58	0.04

Table 6-10. Model selection for per-capita reproduction using generalized linear mixed models for female bears. Df= degrees of freedom, AICc= Akiake Information Criteria corrected for small sample size, dAICc= delta AICc, weightt= AICc Weight.

Model	df	AICc	dAICc	weight
Age + I(Age^2) + (1 | Year)	5	1,037.08	0	0.53
Age + I(Age^2) + ndvi + (1 | Year)	6	1,038.22	1.15	0.3
1 + (1 | Year)	3	1,040.84	3.76	0.08
Age + I(Age^2) + hii + (1 | Year)	6	1,042	4.92	0.05
Age + I(Age^2) + ndvi + hii + (1 | Year)	7	1,042.83	5.75	0.03
Age + (1 | Year)	4	1,043.96	6.88	0.02

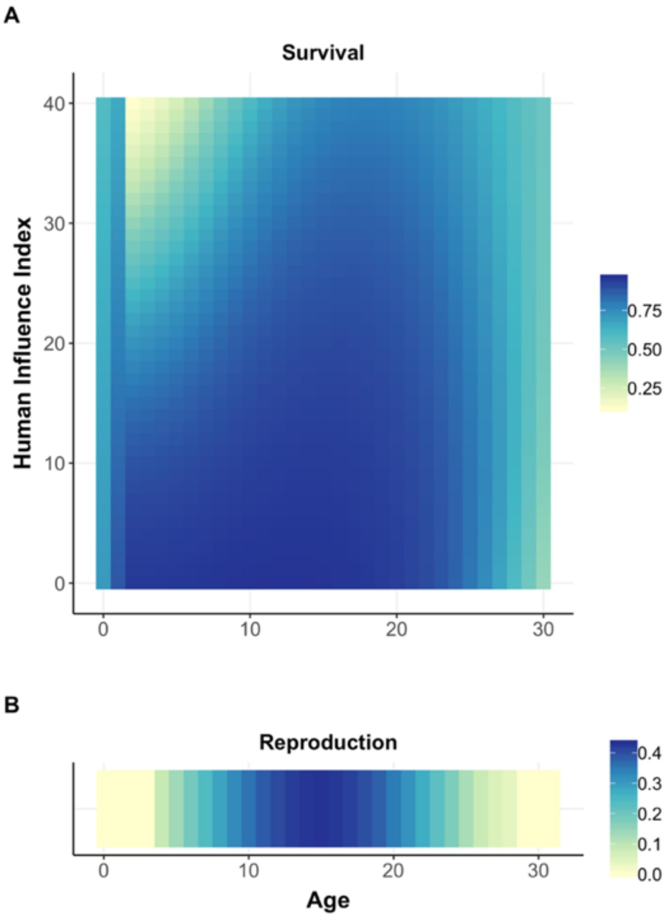


Figure 6-15. Predicted vital rates for female bears, based on mean ndvi (0.6). A) Annual survival rates for female bears aged 0-30 across HII gradient. B) Reproductive rate (female cubs/ female/ yr) for female bears aged 0-30, there was no evidence for influence of HII on this vital rate.

We created Leslie population projection matrices (ages 0-30 years) for each unique combination of human influence (0-40) and habitat productivity (0.5-0.7, the range of mean NDVI values used by bears across the 12 studies considered here) (Figure 6-14B). We estimated the intrinsic population growth rate (Figure 6-16A) for each of these matrices using the dominant eigenvalue of the matrix (Figure 6-14C). If the intrinsic growth rate is <1, i.e., the population can not intrinsically sustain itself, and the % immigrants required to sustain the population can be calculated via (1-lambda)*100 (Figure 6-14D, Figure 6-16B).

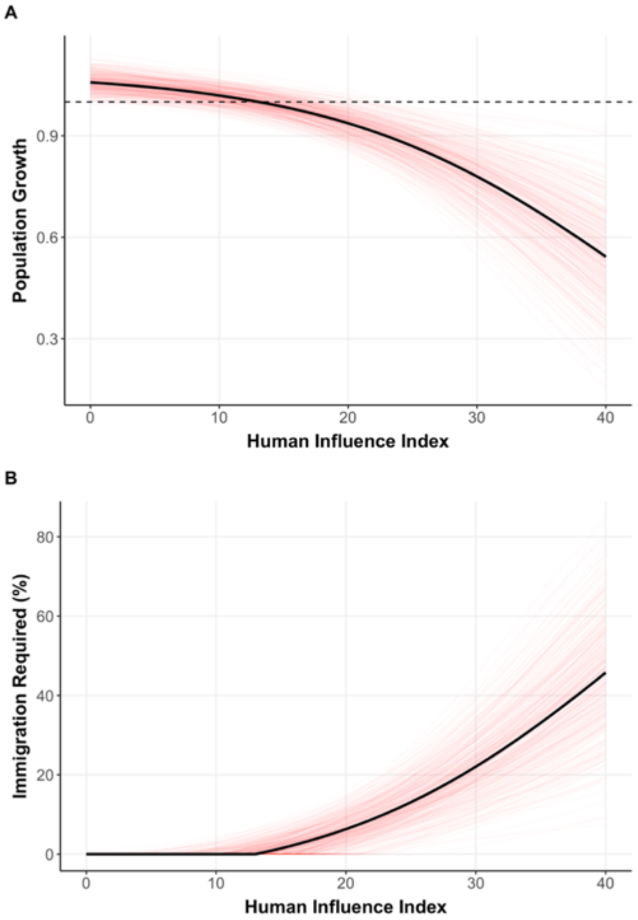


Figure 6-16. A) Predicted population growth rate for mean ndvi (0.6) across human influence index.). B) Immigration required to sustain population (1- lambda[where<1))*100. Black line represents the mean value for 500 bootstrapped replicates (red thin line).

6.4.7.1 Time to create a coexister

Adult survival is relatively similar across HII gradients, but subdadult survival varies greatly (Figure 6-15). As a result, we wanted to predict the age at which bears became successful coexisors across the HII gradient. Adult females in sustainable populations (lambda >=1) had annual survival rates > 0.9 (Figure 6-15, Figure 6-16), thus we used this as the benchmark of what defines an adult bear successfully surviving (Figure 6-17). We show that adult female bears (age >6) in HII<15 attain or exceed survival rates of 0.9 as adults. However, for bears in HII of 25, a typical HII value for multi-use co-existence landscapes, it takes 15 years to attain survival rates of 0.9. For every co-exister that survives to 15 years of age in these landscapes there are ~ 90 conflict bears that will die of human causes before reaching that point. Bears in the most human influenced areas (HII=40) never attain annual survival rates of 0.9.

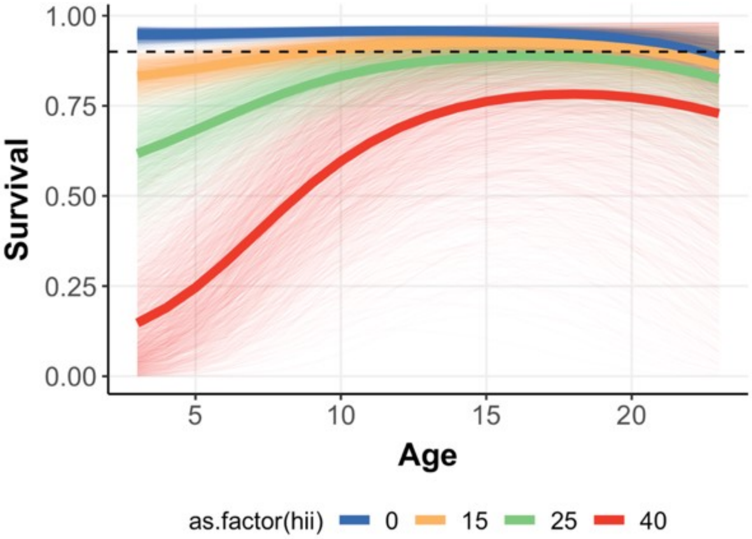


Figure 6-17. Time to create a coexistor, based on 500 bootstrapped estimates of continuous age-based survival across HII gradients. Dashed line represents survival of 0.9, which is generally required by adult females to sustain a population. 500 boostrapped samples for each of four HII classes (0,15,25,40) shown in thin lines, heavy line represents mean of samples for each HII class.

6.4.7.2 Immigration distance

We provide evidence above that bear populations in human influenced areas occur at low densities, are stable or increasing (Morehouse & Boyce 2016; Lamb *et al.* 2017c, 2019; Proctor *et al.* 2018a), and dependent on immigrants. We leveraged data from multi-year genetic tagging projects, and known dispersal of collared bears, to investigate the potential distance that bears will immigrate to occupy sink habitat (lambda<1).

Of the 29 genetic tagging projects, 5 were conducted over >1 year, and provided an opportunity to monitor annual changes in home range centers across large extents. We detected 430 grizzly bears in >1 year, and for each of these animals we calculated HII values for their first, and last year of monitoring, and the distance between their mean capture locations in each of those years (Figure 6-18). Many of these bears would have established home ranges, and we expect home range displacements of <10km for these animals. Results suggested that the distance between annual home range was much less for animals who settled in low human influenced areas. Bears were detected moving over 80 km into sink habitats, but 20-40 km likely represents an average dispersal distance into these habitats. Two telemetered bears, caught as cubs, confirmed that bears can disperse >80 km into sink habitats (Figure 6-19). In this case, these two bears were born in a Provincial Park, independently dispersed into another Province, and began living near the town of Elkford, British Columbia, Canada. Both of these bears were killed within 2 years of living in their new home, one by a car and the other due to conflict in town.

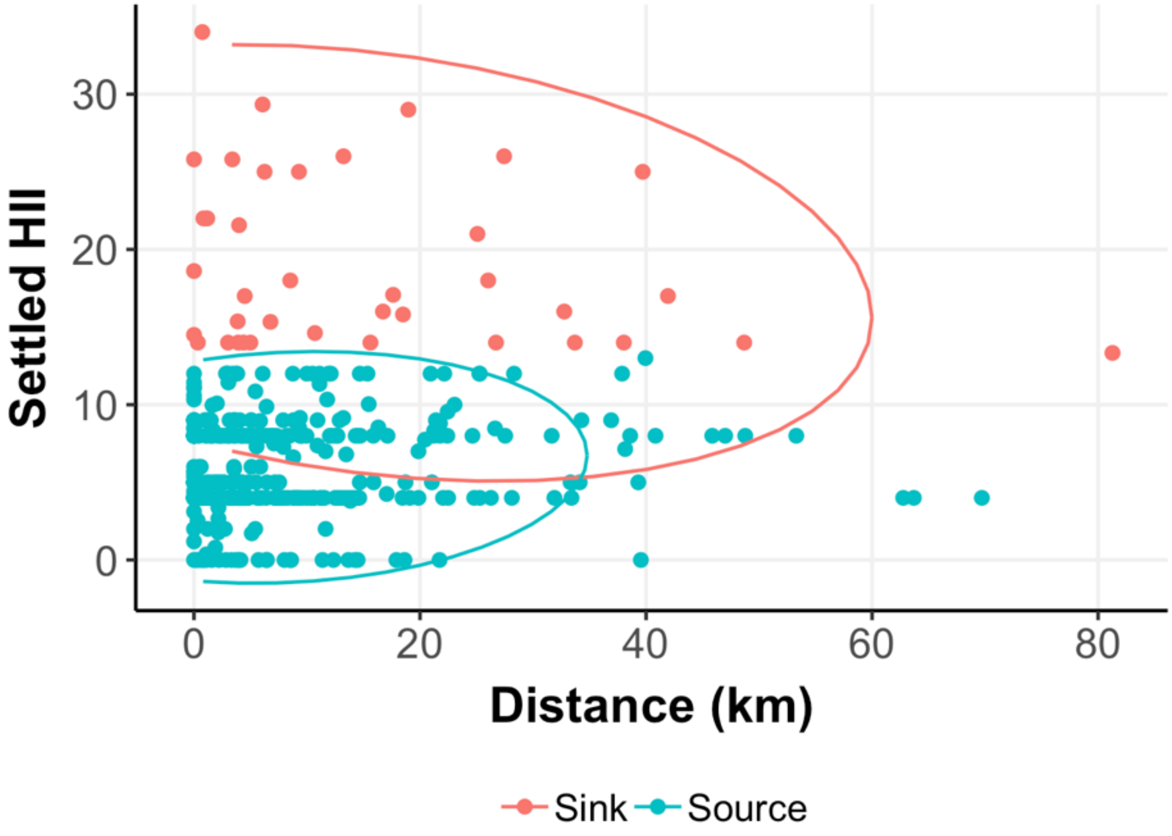


Figure 6-18. Distance between annual home range centers of genetically tagged grizzly bears across British Columbia. Settled HII represents the Human Influence Index of the last known home range center for each individual.

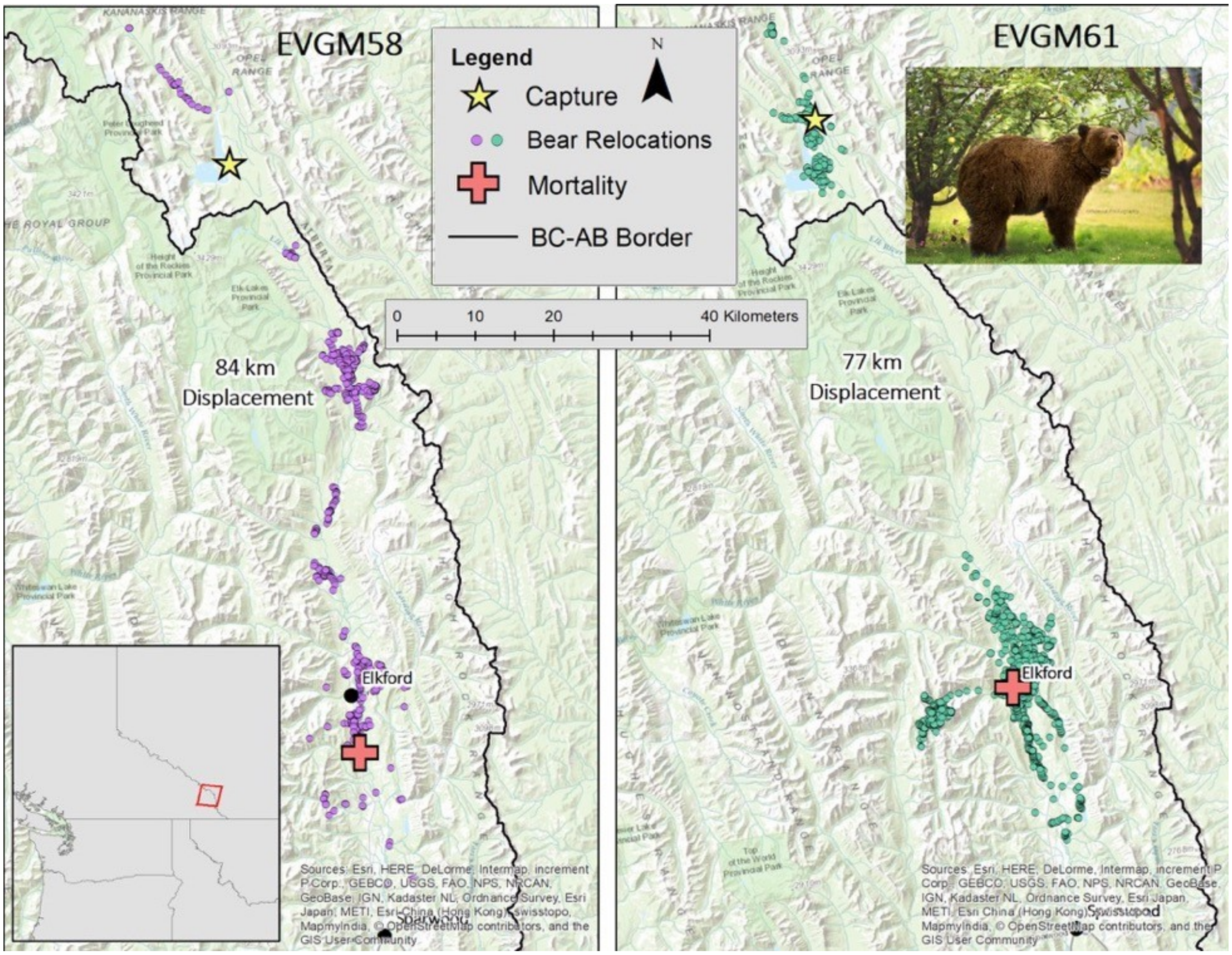


Figure 6-19. Example of source-sink dynamics, dispersal distances, and fates two grizzly bear tracked since birth in Alberta and British Columbia. These two bears independently dispersed from the wilds of Kananaskis Provincial Park, Alberta, to the town of Elkford, British Columbia, where they were both eventually killed (one by a car, and one in town conflicts).

6.4.8 *Conflict*

We used 1,848 grizzly bear conflict records collected across British Columbia between 2014-2019 to estimate the conflict density across HII gradients (https://warp.wildsafebc.com/warp). We modelled conflict density (calls/90 km^2) by HII and NDVI using a generalized linear model (Table 6-11). Conflict density increased by 1 call with every 3.5 unit increase in HII (Figure 6-20), with a maximum estimated call density of 11 calls/90km2 in highest influence category recorded (HII=50).

Table 6-11. Conflict call density model selection table. Df= degrees of freedom, AICc= Akiake Information Criteria corrected for small sample size, dAICc= delta AICc, weightt= AICc Weight.

Model	df	AICc	dAICc	weight
hii + I(hii^2)	4	19,374.2	0	0.72
hii + I(hii^2) + ndvi	5	19,376.12	1.92	0.28
hii + ndvi	4	20,416.71	1,042.51	0
hii	3	20,435.05	1,060.85	0
1	2	21,237.75	1,863.55	0

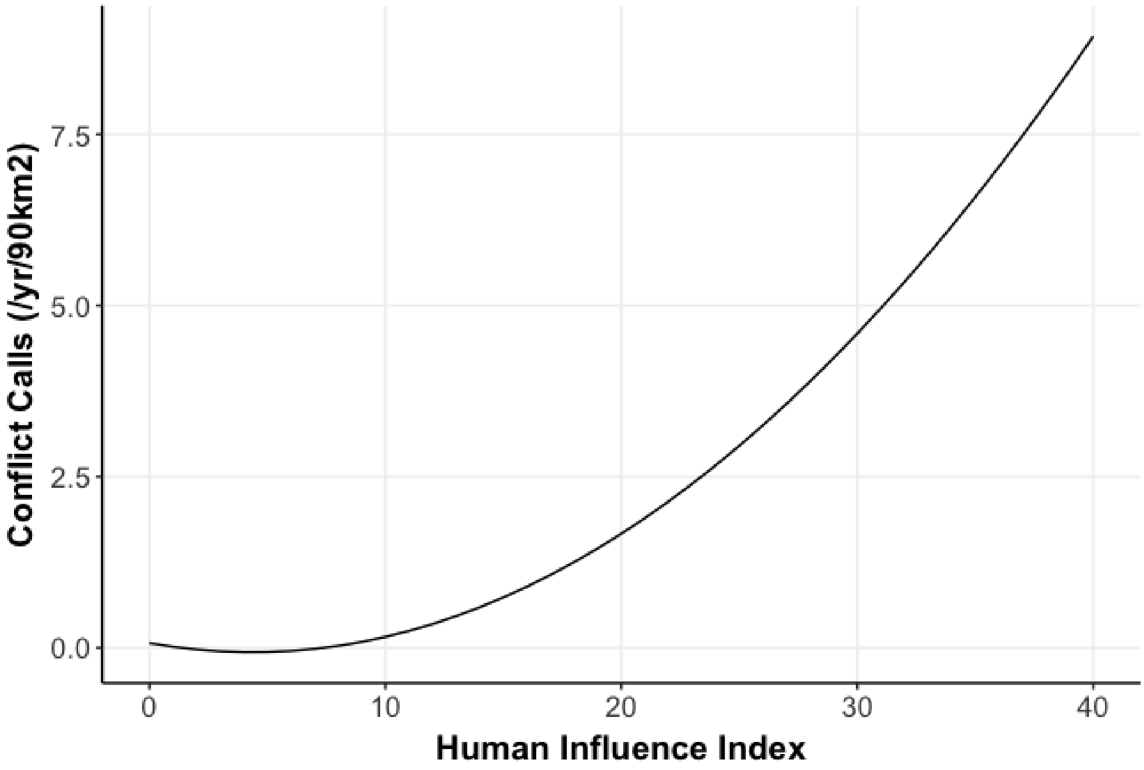


Figure 6-20. Conflict call density predictions across human influence index.

We investigated the relationship between a bears' nocturnal behaviour and its' probability of being in conflict with people using a subset of 40 GPS-collared bears for which we have maintained records of conflict incidents (35 animals with no conflict, 5 with conflict, as reported by the BC government). We modelled the probability of animals having a conflict, at least once in a year, as a function of HII, NDVI, and % nocturnality using logistic regression (Table 6-12). We show, in the highest human influenced areas, adults' increases in nocturnality reduces their chance of conflict by 50% compared to subadults (Figure 6-21).

Table 6-12. Model selection table for bear annual conflict analysis. Df= degrees of freedom, AICc= Akiake Information Criteria corrected for small sample size, dAICc= delta AICc, weightt= AICc Weight.

Model	df	AICc	dAICc	weight
hii + noc + hii * noc + ndvi	5	601.92	0	0.83
hii + noc + ndvi	4	606.06	4.14	0.11
hii + noc + hii * noc	4	607.68	5.76	0.05
hii + noc	3	610.16	8.24	0.01
hii	2	619.34	17.4	0
1	1	647.98	46.1	0
noc	2	648.22	46.3	0

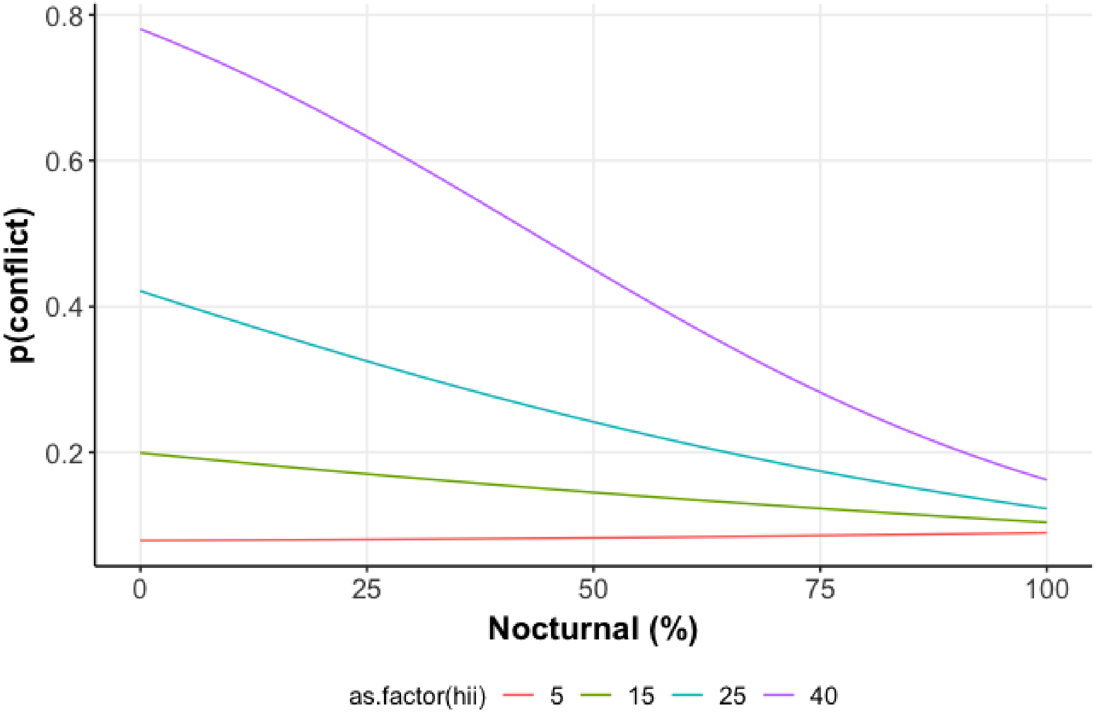


Figure 6-21. Predicted annual conflict probability for bears based on % nocturnality and human influence index.

7 Chapter 7- Conclusion and Synthesis

7.1 Dissertation Synthesis

Grizzly bears (*Ursus arctos*) are wide-ranging, slow-reproducing, and live at low densities. These animals can be conflict-prone and pose real or perceived threats to human life and property. Although grizzly bears are a symbol of wildness to society, the management of this species can divide communities, derail collaborative conservation initiatives, and is the focus of high-profile media coverage and lawsuits. At the center of this controversy is scientific uncertainty around population dynamics of the species, primarily relating to population size, limiting factors, and the ecology of conflict. The goal of this Dissertation was to test the factors limiting grizzly bear population dynamics across ecosystems, update local population estimates, and identify the mechanisms promoting carnivore coexistence and exacerbating conflict.

Recent advances in wildlife tracking technologies, immobilization techniques, and analytical approaches have revolutionized ecologists' ability to investigate large carnivore ecology across massive spatial extents and long timeframes. Such approaches have made tracking of wildlife safer for animals and researchers, while simultaneously allowing for the collection of large amounts of data. For example, consider the Craighead brothers putting VHF collars on grizzly bears in Yellowstone National Park between 1959-1971. These were the first tracking collars put on large mammals, a major step for wildlife tracking, but were not without their foibles. Wildlife immobilization drugs were not nearly as reliable as they are now (see video of a research bear chasing the Craighead brothers (Schloss 1987)), VHF collars generated few data points because they required researchers to physically relocate animals, and were prone to being lost if animals ranged wider than researchers could follow the animals. Today, immobilization drugs are much safer, while GPS collars can collect hundreds of relocations a day and are remotely relocated via satellite anywhere in the world. These advances have been paired with the advent of non-invasive technologies such as genetic tagging, and remote cameras, which offer significant insight when paired with spatial capture-recapture and population genetic techniques. Collectively, these advances have allowed ecologists to overcome logistic and methodological limitations to studying large carnivore population dynamics.

I was able to leverage 40 years of research on grizzly bear ecology across British Columbia to provide mechanistic insight into grizzly bear population dynamics across ecosystems. This approach was only possible due to a collaborative research framework and advances in telemetry and genetic tagging. The chapters in this Dissertation collectively suggest that grizzly bear populations are limited by both bottom-up and top-down processes, and these forces can act in a dynamic manner to create source-sink dynamics that influence populations far removed from localized mortality hotspots.

Regions of low canopy cover, high precipitation, and abundant fruit crops create ideal caloric landscapes for grizzly bears, and roadless areas with no human settlement (i.e., wilderness) provide habitat security these animals. Taken together, areas of high caloric and habitat security value harboured the greatest density of bears in British Columbia. The negative effects of top-down pressures from humans, such as those exerted through human access into bear habitat via roads, can be mitigated. Road closures, either complete, or to the public only, provide an evidence-based approach to increase habitat security for bears and many other species. Similarly, fencing and crossing structures can separate bears and people, providing safer highways and cities for people, and safer habitats for bears.

Grizzly bear survival was too low in most heavily human-influenced landscapes to allow for sustainable population growth (lambda >1). However, heavily human-influenced landscapes in British Columbia's grizzly bear range are generally small-extent and nestled within a matrix of wilderness. Such a spatial configuration allows dispersing bears from wilderness areas to provide demographic rescue to these heavily human-influenced landscapes, creating potentially sustainable landscapes of coexistence so long as the spatial integrity of the wilderness mosaic is maintained. I provide replicated and mechanistic insight into the role of source-sink dynamics—and the special case of this phenomena where attractive habitat creates an ecological trap—and suggest that demographic rescue from wilderness plays a critical role in creating coexistence landscapes. Individuals were detected dispersing into sink habitat from over 80 kilometers. A single town drawing bears from up to an 80 km radius, or ~20,000km^2 area, suggests the landscape of coexistence acts across a much larger extent than the focus of most current grizzly bear science and management. Further, I show that grizzly bears actively contribute to coexistence via nocturnal behaviour, which increases their survival while reducing human-wildlife conflict. Maintaining and promoting landscapes of coexistence in the future will require preserving or increasing current wilderness areas, connectivity of the wilderness-coexistence matrix, and mitigation of sources of caloric attractants near people.

7.2 Evidence to Action

Conservation actions generally stem from multiple lines of evidence and an inclusive, diverse group of invested partners. To date, the conservation actions supported by evidence from this dissertation have been no different and included a wealth of previous and ongoing research, as well as many invested partners. Below I highlight conservation actions that relied on evidence generated from this dissertation. I discriminate when evidence from this dissertation was the primary, or secondary (i.e., one of many sources of evidence) evidence used. Where appropriate I point to an example news article highlighting the issues and actions.

7.2.1 Commercial huckleberry picking- secondary support

The importance of productive wilderness areas for grizzly bear populations can not be overstated, and these areas provide demographic rescue to coexistence landscapes through dispersal of young. Fruiting shrubs form a critical component of grizzly bear habitat selection (Nielsen *et al.* 2003) and demography (Ch4-6)(McLellan 2015), but commercial harvest of huckleberry (*Vaccinium* membranaceum) in southeast British Columbia posed a threat to the security of this culturally and ecologically important fruit. In 2018, and expanded in 2019, the commercial picking of huckleberries was banned in sensitive areas (media: “Huckleberry win for bears: B.C. restricts harvesting to protect grizzlies’ food” (CBC 2018), Figure 7-1). This important effort was supported by maps of huckleberry patches (Proctor, Lamb & MacHutchon 2016), paired with inference of the demographic importance of this species for grizzly bears (Ch4-6)(McLellan 2015).

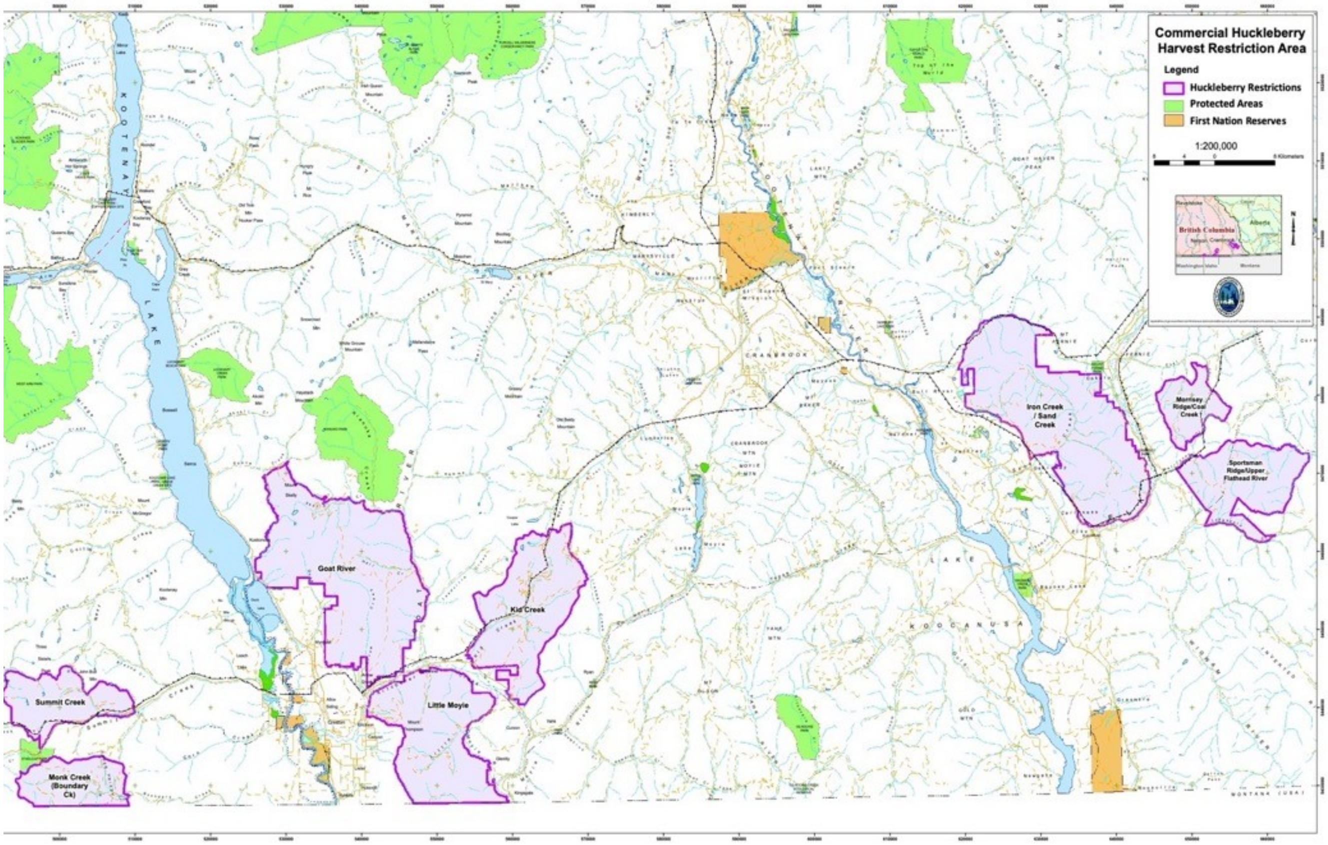


Figure 7-1. Commercial huckleberry picking closure areas in southeast British Columbia in 2019.

7.2.2 Reducing human-caused mortality- primary support

The Province of BC managed for ~6% annual allowable human-caused bear mortality, and when this threshold was exceeded in hunted populations the harvest was reduced. In the Southern Rockies Grizzly Bear Population Unit, the non-hunting mortality from conflicts and road/rail collisions would often consume the 6% human-caused mortality target. As a result of my work investigating ecological trap dynamics, mortality rates, and population growth in the region it was determined that hunting mortality was additively contributing to mortality and hunting opportunity was ended in 2015-2018.

7.2.3 Roadkill pits- primary support

Attractants are a major threat to carnivore coexistence, and bear populations across the globe (Can *et al.* 2014). Attractants contribute to the source-sink dynamics and intense conflicts with people explored in Chapters 5 and 6. Roadkill disposal sites are an overlooked carnivore attractant in British Columbia, which I discovered while capturing and tracking grizzly bears in southeast British Columbia's Elk Valley. Roadkill was being dumped in open, uncontrolled gravel pits near the highway, which were used intensely by grizzly bears (Figure 7-2), but also wolves (*Canis Lupus*) and coyotes (*Canis latrans*). These roadkill pits created a barrier coexistence, as they were brining fed bears closer to communities, which posed risks for bears and people. Two collared bears were killed within 1km of the main roadkill pit in the Elk Valley.

The evidence presented in this dissertation elevated the urgency and profile of the mitigating the roadkill pit issue. Starting in 2018, numerous news articles (media: "Carcass pits, rural attractants contribute to Jaffray bear conflict": (McLachlan 2019a), and "RDEK takes steps towards reducing carcass pit use" (McLachlan 2019b)) highlighted the role of these pits in elevating human-carnivore conflict and the risks these pits posed to human safety through their attraction of carnivores. In early 2019, a collaborative group consisting of myself, the Mayor of Fernie, BC Ministry of Transportation, Wildsight, and BC Ministry of Forests, Lands and Natural Resources Operations, began designing evidence-based strategies for disposing of roadkill in a proper fashion.

As of August 2019 one exclusion pit has been built (Figure 7-3), which is electric fenced and electric gated. Carcasses will be deposited in this carnivore proof area and later buried. Future plans include static carcass composting methods which have been used successfully in many places including Alberta, Montana, and Virginia. The rapid approach of chronic wasting disease to British Columbia may necessitate composting or incineration methods of all roadkill in the near future. Nevertheless, I am encouraged to see that evidence from this dissertation has led to changes in practices at the Ministry level, with direct benefits to people and carnivores as a result of reducing dangerous attractants.

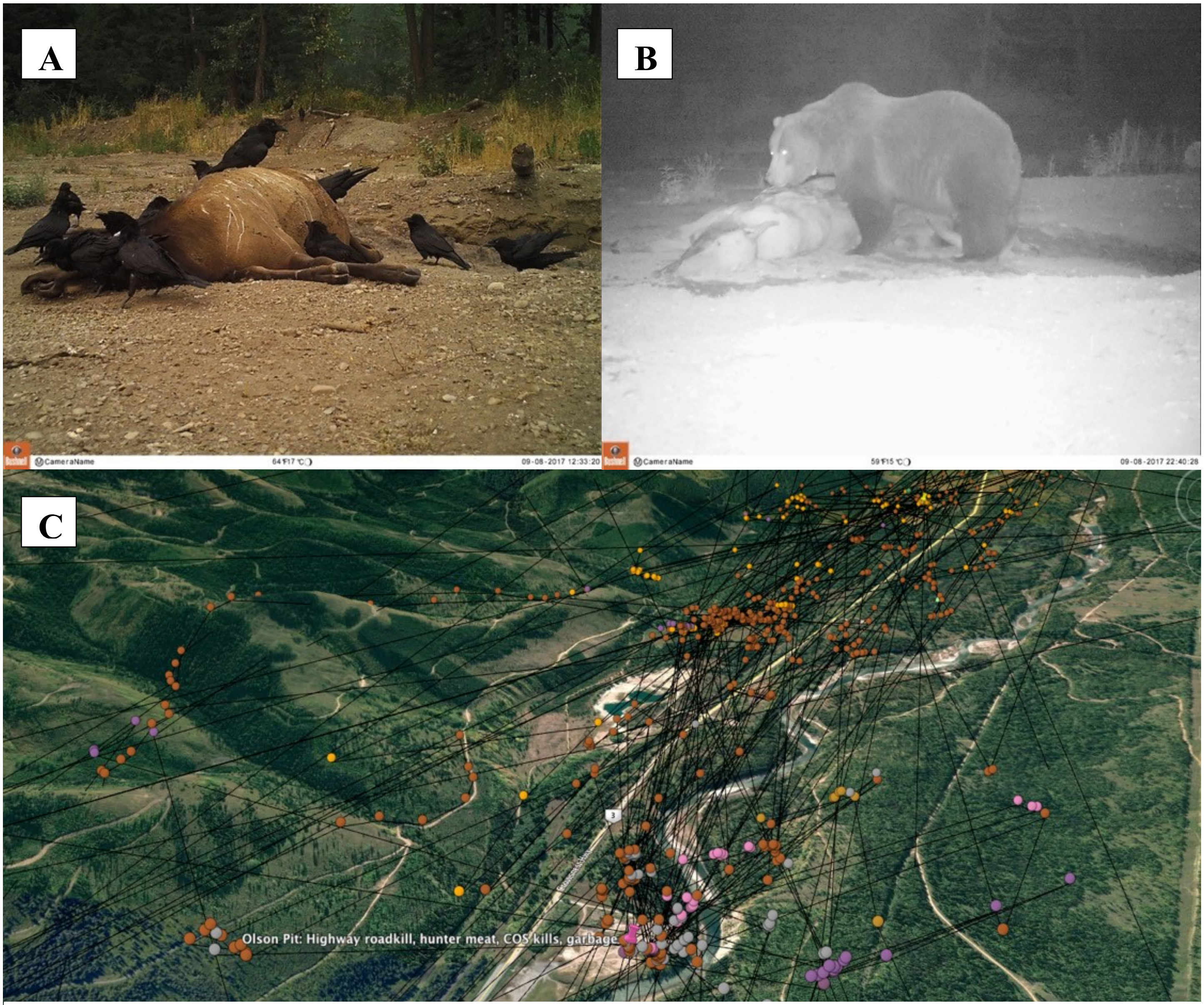


Figure 7-2. A) an elk carcass deposited in an uncontrolled roadkill carcass pit (Olson Pit) near Hosmer, BC. B) A collared grizzly bear (EVGF56) consuming the elk from A the same day. C) GPS telemetry for grizzly bears (each color is an individual) attracted to Olson Pit (bottom, pink pin). Bears would come to the pit to consume carcasses almost exclusively at night, then cross the highway and rest during the day in the forest.

Figure 7-3. Enclosure built by BC's Ministry of Transport to aid in responsible disposal of roadkill carcasses. The enclosure is ~1600m^2 and is fully electric fenced and electric gated to ensure no entry of large carnivores.

7.2.4 Missing Toes- primary support

A value-added conservation product of invasive methods such as radio collaring animals, is an opportunity to directly assess the health and condition of live animals across human influence and productivity gradients. My research team and I noted that 4 of the 45 bears (8.9%) that we live-captured in the Elk Valley were missing toes (Figure 7-4). Sometimes all their toes on one foot. Further investigation revealed that this issue had been seen in other parts of British Columbia, but primarily in the Kootenays. The primary reason for these missing toes was suspected to be from killing traps designed to capture marten (*Martes americana*). These baited traps (120 Conibears) are often set late in the fall during the legal trapping season which unfortunately overlaps with the period when some bears are still active. I ended up being one of the main contacts for folks to share their observations of this phenomena, which lead to 4 confirmed cases in the Kootenays (Canal Flats, Passmore, and Flathead) where photo evidence confirmed bears were losing toes with these traps still affixed to their feet.

This evidence has lead the Ministry of Forests, Lands, and Natural Resource Operations, during spring 2019, to propose a change in the start of marten trapping season, from Nov 1, to Dec 1. I was able to use the bear telemetry data to determine when most bears had denned, and Dec 1 was an appropriate, and evidence-based time when trapping would not overlap with active grizzly bears in the Kootenays.

Figure 7-4. A) Missing toes (3) on right front leg of EVGM55. B) EVGM55 was killed in a conflict on a farm. We had his foot x-rayed. C) remote camera footage of a 120 Conibear on the foot of a grizzly bear in Canal Flats, BC.

7.2.5 Road Density- secondary support

I suggested at the beginning of this dissertation that the failure to reduce global road densities to benefit large carnivore populations represented an example of a conservation program with sufficient evidence but insufficient action. Although sufficient scientific evidence does exist, I learned through my work with road density that evidence linking road densities to carnivore densities was lacking and that specific, localized evidence has strong influence on policy and collaborators. The Province of British Columbia is now actively working to reduce road densities across the southern Kootenay region. This increase in evidence-based policy follows a number of important efforts, including 1) my work linking road densities to reductions in bear densities, and the potential for access management to mitigate these negative effects, 2) cross-discipline scientific consensus on the topic (Proctor *et al.* 2018c), and importantly, 3) collaborative cumulative effects analyses started in 2014 by the Province. Efforts are underway to reduce road densities in southeast BC, through road revegetation and other strategies (Figure 7-5), and these efforts are expected to expand across the southern Kootenay Region in the near future.

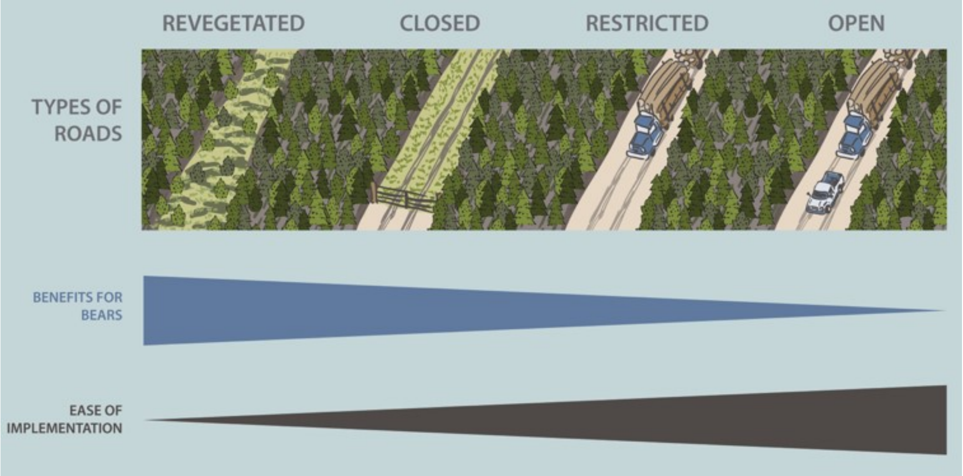


Figure 7-5. Options for road mitigation reproduced from (Proctor *et al.* 2018c).

7.2.6 Highway collision mitigation- secondary support

Collisions between vehicles and wildlife pose serious threats to the safety of humans and wildlife (Gilbert *et al.* 2017; Gilhooly *et al.* 2019). Further, highways can severely impact wildlife connectivity (Proctor *et al.* 2012; Lamb *et al.* 2017b) and abundance (Fahrig & Rytwinski 2009). However, the negative impacts of highways can be mitigated by providing safe passages for wildlife under, or over, highways paired with fencing (Ford *et al.* 2017). Indeed, following highway mitigation, wildlife mortality can be reduced by 80-100%, and re-establishing connectivity of large carnivores can even be detected genetically within 2 decades after mitigation (Sawaya *et al.* 2014). Reconnecting wildlife populations along Highway 3 has been a goal for conservationists (Proctor *et al.* 2005), and detailed plans were drafted over a decade ago (Clevenger *et al.* 2008). We recently updated these detailed plans (Lee, Clevenger & Lamb 2019) and through collaborative initiatives with the Ministry of Transport, environmental groups, and Teck Coal, we have formed a Highway 3 Connectivity Working Group and are breaking ground on highway mitigation projects. To start, the Ministry of Transport has invested $6.3M for the first wildlife crossing—a bridge replacement and engineered wildlife underpass—with 5 more structures to be transformed into wildlife underpasses and fenced starting in 2020.

Figure 7-6. A $6.3M Highway 3 bridge replacement over Lizard Creek, near Fernie, BC, taken summer 2019. This bridge replacement includes an engineered wildlife underpass.

7.3 Outlook

The insights presented here are poised to aid in evidence-based conservation of grizzly bears and fill a knowledge gap surrounding grizzly bear population dynamics across productivity and human influence gradients. Beyond grizzly bears, there is insight to be gleaned for large carnivore ecology and conservation as a whole. Undoubtedly there are differences between many of the large carnivores, such as diet, degree of conflict with humans, and influence on ecosystem processes. However, the similarities within this group of animals dwarfs the differences. Large carnivores as a whole have seen large range reductions across the globe, are feared by humans, conflict with people over life and property, range widely, and are generally slow reproducing. As such, key insights into the ecology of grizzly bears can be used to better understand the role of human conflicts, productive habitat, attractants, and wilderness in structuring large carnivore population dynamics.

Substantial uncertainty surrounds the degree to which large carnivore populations will be limited by increasing human occupation in their habitat. Here I show that human occupied landscapes exert strong, limiting forces through decreased survival and population densities. Human settlement and transportation corridors tend to be located in productive, lowland habitat. These areas represent important habitat and connectivity corridors for large carnivores and their prey, suggesting human-carnivore overlap and conflict is not surprising. Further, human influenced landscapes offer attractive caloric benefits to large carnivores through fertilized crops, livestock, roadkill, fruit trees, and garbage. Human settlement in productive carnivore habitat paired with anthropogenic food subsidies create a difficult situation for carnivore coexistence.

The mechanisms promoting large carnivore coexistence in human influenced landscapes is a source of considerable scientific debate, especially surrounding the demographic rescue from wilderness areas. On one side, there is an idea that wilderness is not required (Lopez-Bao *et al.* 2015) and behavioural adaptation can buoy populations in human influenced landscapes (Carter *et al.* 2012). This view is not universally held and is contested by the idea that wilderness areas demographically rescue coexistence landscapes (Karanth *et al.* 2013; Gilroy *et al.* 2015). Evidence from this dissertation supports the idea that secure wilderness areas are critical for carnivore coexistence, as carnivore populations in human influenced areas face excessive mortality and are not self-sustaining without immigration. However, I also show that behavioural adaptation through nocturnality reduces, but does eliminate, reliance on immigration and provides evidence that carnivores are active contributors to coexistence. The conservation of large carnivores will likely remain reliant on traditional approaches of protecting wilderness areas, or at a minimum the ecological processes associated with wildness (Perino *et al.* 2019).

Recent advances in evidence-based technology to coexist with large carnivores creates hope for large carnivore conservation. The primary goal of these technologies is to reduce the limiting effects of human influence on carnivore populations. When human influence is concentrated, opportunity exists to fence cities and highways, and bridge these excluded areas with wildlife crossing structures (either under or overpasses). This approach promotes human and carnivore safety by excluding carnivores from the riskiest sink habitats, while not limiting their vagility.

The mechanistic and large extent insights provided here were facilitated by a collaborative framework resulting in the sharing of massive amounts of data and creating a conduit for evidence to drive change. Collaboration between individual research projects and personnel advances carnivore ecology and conservation more rapidly than summed individual efforts. I mirror the sentiment of (Redpath *et al.* 2017; Hartel *et al.* 2019) that collaboration outside of academia, with Indigenous peoples, stakeholders, industry, technology sectors, and local/Provincial governments stands to mainstream evidence-based conservation and facilitate more efficient, effective, and robust conservation efforts that ultimately provide more benefits to wildlife.

Advances in wildlife monitoring technology has created immense opportunity for ecologists to investigate large carnivore population dynamics across massive spatial extents. This dissertation highlights the value of exploiting gradients of productivity, human influence, and management actions, as sources of manipulation (i.e., a natural experiment) which can create strong, mechanistic inference. Further, the line between applied, conservation-focused work and traditional hypothesis-driven theoretical work is not as definitive as once thought, and I suggest there is considerable overlap between the two. In fact, ecologists should aim to create evidence that has applied outcomes but also is supported by, and can test, a body of theory. Such an approach adds rigour and generality to the applied outcomes while contributing to important advances in our understanding of ecology.

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