Spatial and dietary niche variation associated with diverse resource availability, competitive environment, and landscape heterogeneity; ecology and conservation of bear-salmon systems in coastal British Columbia

by

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B.Sc (Hons), University of Victoria, 2011

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Supervisory Committee

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Abstract

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The niche concept provides a tractable measure of the ecological roles and requirements of organisms, which can inform our understanding of the patterns of biodiversity, and subsequently, direct conservation policy. Although niche is most commonly considered for species, variation nested within lower hierarchies of biological organization (*i.e.*, phenotypes, genotypes) also contributes to maintaining biodiversity. Herein I examine spatial and dietary niche variation among and within species in a consumer–resource system where resources and competition are structured by a heterogeneous environment. An underlying theme of this dissertation was developing research through a community-engaged approach that not only contributed to conceptual advancements in niche theory but also to applied conservation priorities.

The marine archipelago of the central coast of British Columbia, Canada structures salmon (*Oncorhynchus* spp.) resources and the inter- and intraspecific competitive context for coastal grizzly (*Ursus arctos*) and black bears (*Ursus americanus*). This assembly of ursids represents nested levels of biological organization (*i.e.*, species, phenotypes (white vs black-coated morphs of black bears) and genotypes (dominant homozygote black-coated black bears, heterozygote black-coated black bears, recessive homozygote white-coated ‘Spirit’ black bears)), which allows for investigation into niche variation across and within species.

I investigated niche variation using a suite of non-invasive methods. Local and Traditional Ecological Knowledge (LEK/TEK) provided complementary information to genetic and stable isotope (δ^{13}C and δ^{15}N) data from hair samples. First, I investigated changes in the spatial niche of coastal grizzly bears. By combining western scientific approaches with TEK/LEK interviews I found the range of coastal grizzly bears has expanded westward onto several coastal islands. The economic, cultural, and ecological impacts of this shift in spatial niche are not yet understood. Second, I tested hypotheses related to variation in the foraging niche of black bears in response to the competitive environment and salmon resource availability. I found that grizzly bear presence reduced the proportion of salmon in black bear diets by ~40%. I also found that salmon species diversity, and not biomass abundance, was positively correlated to salmon in black bear diets. This highlights the importance of resource diversity to consumers beyond the consideration of abundance. Third, I explored spatial niche patterns of Spirt bears in relation to protected areas. I found that landscape-level Spirit bear allele frequency and population estimates were lower than previously reported. Approximately ~50% of Spirit bear allele hotspots corresponded to protected areas. This finding suggests Spirit bears are rarer and less protected than previously assumed. Finally, I tested hypotheses related to niche variation between phenotype and genotypes of Spirit bear populations. I found both phenotypes and genotypes diverged in foraging niche, with Spirit bears and black-coated heterozygotes having elevated stable isotope signatures compared to black-coated homozygotes. This result supports the role of ‘multi-niche’ mechanisms in maintaining this rare polymorphism.

Results from all chapters contributed to land- and marine-use stewardship efforts of collaborating First Nations. Collectively, this dissertation offers novel contributions towards understanding how niche variation at multiple levels of biological organization can contribute to conservation planning.

Table of Contents

List of Tables

List of Figures

Acknowledgments

In recognition of the contributions of co-authors, ‘we’ is used as the subject throughout all data chapters (2-5). In line with academic requirements, ‘I’ is used as a subject throughout the Introduction and Conclusion of this document. In reality, this ‘I’ represents an entire team of people who have supported both the “Bear Project” and myself directly. As such, the completion of this dissertation is largely a testament to the communities, landscapes, and relationships that supported this work from its inception.

I am grateful for the leadership of the Resource Stewardship Departments of the Gitga’at. Kitasoo/Xai’xais, Haíłzaqv, Nuxalk, and Wuikinuxv Nations, whose foresight and concern for bears was the impetus for this work.

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Co-authorship Statements

Chapter 2-5 of this dissertation were co-authored. Below I outline my contributions and that of each author.

Chapter 2

Service, C. N., M. S. Adams, K. A. Artelle, P. Paquet, L. V. Grant, and C. T. Darimont. 2014. Indigenous knowledge and science unite to reveal spatial and temporal dimensions of distributional shift in wildlife of conservation concern. PLoS ONE 9:e101595.

Conceived and designed the work: CNS CTD PP. Collected the remote camera and genetic data: CTD CNS LVG MSA KAA. Analyzed the data: CNS MSA KAA LVG. Wrote the paper: CNS CTD PP KAA MSA LVG. GIS analysis support: KAA. Interview data collection: CNS LVG MSA. All authors contributed to every draft and approved the final version for publication.

Chapter 3

Service, C. N., A. W. Bateman, M. S. Adams, K. A. Artelle, T. E. Reimchen, P. C. Paquet, and C. T. Darimont. 2018. Salmonid species diversity predicts salmon consumption by terrestrial wildlife. Journal of Animal Ecology 00:1–14.

Conceived and designed the work: CNS CTD PP TER. Collected the data: CNS MSA KAA. Analyzed the data: CNS AWB. Led writing: CNS CTD. All authors contributed to every draft and approved the final version for publication.

Chapter 4

Service, C. N., K. A. Artelle, M. Bourbonnais, M. S. Adams, T. E. Reimchen, P. Paquet, L. Henson, C. Picard, and C. T. Darimont. In preparation. Indigenous-led research reveals rarity of the white-phased ‘Spirit bear’ and gaps in habitat protection.

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Chapter 5

Service, C. N., T. Ingram, T. E. Reimchen, L. Henson, P. Paquet, C. Picard, and C. T. Darimont. In preparation. Intrapopulation foraging niche variation among genotypes and between phenotypes; Stable isotopes reveal dietary niche divergence in Spirit bear populations of coastal British Columbia.

Conceived and designed the work: CNS TER PP TI CTD. Collected the data: CNS LH CP. Analyzed the data: CNS TI. Led writing: CNS CTD. All authors contributed to every contributed to the concept and provided edits and advice.

Chapter 1 Introduction

The concept of the niche – a tractable measure of the requirements and specific ecological roles of all organisms - underpins much of the ecological and evolutionary theory that aims to explain patterns of biodiversity. The understanding of factors that could structure biodiversity (*e.g.*, species life histories and interactions) has been advanced considerably by Hutchinson's commonly accepted definition of niche as an *n*-dimensional hyper-volume. Within this framework, Hutchinson describes the *n*-resource dimensions as every possible (*n*) biotic and abiotic limiting factor of organisms (Hutchinson 1957). Accordingly, the space defined by the hypervolume quantifies the range of conditions that organisms can exist (Hutchinson 1957, Chase and Leibold 2003).

The niche concept provides a useful framework to examine the role of competition and resource availability in structuring biodiversity in ecological communities. Theoretically, in the absence of interspecific and intraspecific interactions (*i.e.*, competition and predation), an organism can exist across a wide range of resource gradients - a space referred to as its *fundamental niche*. However, in real ecological communities that are subject to inter- and intraspecific interactions, organisms are restricted to a much smaller niche - a region termed their *realized niche* (Hutchinson 1957, Chase and Leibold 2003). Accordingly, contemporary niche studies often define key constraints of the fundamental niche (temperature constraints, habitat needs etc.), while also defining the competitive environment (inter- and intraspecific interactions) as one critical component that restricts organisms to their realized niche (Case and Gilpin 1974, Chase and Leibold 2003, Valeix et al. 2007, Costa-pereira et al. 2018). Additionally, resource availability may fluctuate in space and time (Takimoto et al. 2009, Armstrong et al. 2016), which in turn can drive patterns of niche variation (Deacy et al. 2018). Despite the rapid recent advancement in theory (Takimoto et al. 2009, Armstrong et al. 2016) and empirical studies (Sawyer and Kauffman 2011, Lok et al. 2012) related to variation in resource availability in space and time, gaps still exist in the ecological understanding of how this variation might interact with differing inter- and intraspecific competitive environments. Although there are near infinite numbers of realized niche dimensions that organisms may differ in due to competition and resource availability, spatial and foraging (*i.e.*, food-type) dimensions comprise two primary niche axes that are frequently quantified (Schoener 1974).

Spatial and foraging niche axes are fundamental in shaping organisms' life histories. One aspect of an organism's spatial niche is represented by their distribution (or "range"), which can be driven by abiotic factors (*e.g.*, CO_2 enrichment, nitrogen deposition, climate; reviewed in Tylianakis et al. 2008), biotic processes (*e.g.*, competition and facilitation; Boulangeat et al. 2012), and dispersal capability (MacArthur and Wilson 1967, Pulliam 2000). By contrast, an organism's foraging niche is characterized by its diet and is determined by complex relationships between that organism's ecological environment (*i.e.*, resource availability (Chase and Leibold 2003), predation risks (Lima and Dill 1990) etc.) as well as individual traits (*i.e.*, phenotype

(Miner et al. 2005) and social context (Slagsvold and Wiebe 2011)). More broadly, shifts in spatial and foraging niche can occur rapidly and may impose cascading ecological (Estes and Palmisano 1974), economic (Pimentel et al. 2005), and cultural (Zahn et al. 2018) consequences, highlighting niche variation's importance as an area of academic inquiry that merges theory and application.

A core assumption of most conceptual and empirical research into niche variation is that niches are defined at the species level. This premise assumes that conspecific individuals are ecological equivalents. By contrast, there has been increasing recognition of the prevalence of niche differentiation at the intraspecific level among populations (*e.g.*, Armstrong et al. 2016), genotypes (*e.g.*, Cook and Saccheri 2013), phenotypes (*e.g.*, Reimchen 1980, Hoekstra et al. 2004), and individuals (Bolnick et al. 2003). The diversity of intraspecific niches can provide opportunities for the maintenance of many forms of diversity, including polymorphisms (Levene 1953, Reimchen 1979, Hedrick 1986, Reimchen and Klinka 2017). Specifically, it has been proposed that the diversity of discrete phenotypes (via genotypes) can be maintained in perpetuity by occupying distinct niches (Levene 1953, Van Valen 1965). Opportunities for additional empirical case studies of niche-phenotype associations may offer insight into the generalizability of this proposed mechanism across taxa and ecosystems.

The understanding of spatial and foraging niche can offer fundamental and important dimensions to the conservation of biodiversity. Many policy-relevant processes, such as protected areas design, mapping of critical habitat, and land-use planning require the distributional information provided by data on spatial niche (Araújo and Williams 2000, Laliberte and Ripple 2004). Holistic approaches to conservation planning that consider ecosystem connections can employ data on foraging niche to consider how to allocate sufficient resources to organisms of conservation concern (*e.g.*, Levi et al. 2013). Current information on niche can also inform proactive conservation intervention in the face of climate change and other stressors that may alter habitat or food availability (*e.g.*, Guisan and Thuiller 2005, Bennie et al. 2013). Shifts in spatial and foraging niches can signal underlying ecological changes within an ecosystem, providing early insight to managers that changes might be occurring in other species and communities. Accordingly, understanding the dimensions of spatial and foraging niche at multiple scales of biological organization can offer not only contributions to our conceptual understanding of ecological systems, but also valuable information to aid in conservation decision making.

Translating theory-based niche analyses into applied conservation measures requires high resolution, place-based data. Although niche variation is most commonly explored through western scientific methods, traditional and local ecological knowledge (TEK/LEK) can offer novel information that can add resolution to niche characterization. Traditional Ecological Knowledge is ecological knowledge that is transmitted through generations and is developed through a reciprocal relationship between people and place (Berkes 2000). LEK differs from TEK in that it does not require intergenerational transmission, but rather can be accumulated over a single lifetime (*e.g.*, a first-generation fisher; Gilchrist et al. 2005). Western scientific approaches for wildlife research use a variety of empirical techniques that span different temporal and spatial resolutions and provide detailed, quantitative information on populations and individuals (Gilchrist et al. 2005). However, scientific data are often expensive to acquire, are most feasible to acquire for common species, and are typically limited temporally and spatially (Anadón et al. 2009). In contrast, TEK/LEK information can be summarized and analyzed to yield information on elusive species across large spaces and time periods that are otherwise too expensive or difficult to monitor with western scientific tools (*e.g.,* Anadón et al. 2009, Carter and Nielsen 2011). Species of cultural significance that draw the attention of local human populations may be especially suitable for niche characterization via TEK/LEK (*e.g.*, Garibaldi and Turner 2004). Despite the benefits of increased data resolution at a reduced cost, multiple knowledge systems are rarely leveraged in ecology (Sagarin and Pauchard 2012). As such, the concordance between western scientific and TEK/LEK approaches presents the opportunity to yield more comprehensive and detailed information about niche, and its potential changes over time and space, than either method alone (Huntington 2000, Moller et al. 2004).

Scope

My research took place in the territories of the Wuikinuxv, Haíłzaqv (Heiltsuk), Nuxalk, Kitasoo/Xai'xais and Gitga'at First Nations, who collaborated in this work and provided direction on developing research questions towards conceptual ecological contributions while also offering applied relevance for conservation management. This collaborative research effort among Nations and academic partners broadly centers on the ecology and stewardship of coastal bear (*Ursid* spp.) populations (2010 to present), of which my research is one component (see Bryan et al. 2013, 2014, Adams et al. 2017, Artelle et al. in review, and the work presented below). My research was built upon principles of community engagement and was designed to meet the diverse needs of all collaborators (Adams et al. 2014). For example, in additional to meeting academic requirements, this research was crafted to be inclusive of community members, including youth and Elders, for both field work and knowledge sharing. 'Process values' - including community members' access to land and sharing place-based information - were explicitly valued in this collaborative effort. The applied contributions of this dissertation presented below were designed to address the specific research needs of the collaborating Indigenous governments in addition to contributing towards conceptual and applied dimensions of niche ecology.

The conceptual contributions of my dissertation are centered around testing hypotheses related to the spatial and dietary niche divergence among sympatric ursids in coastal British Columbia (BC), Canada. Specifically, I focus on niche variation among coastal grizzly (*Ursus arctos*), black (*Ursus americanus*), and 'Spirit' (a rare white-coated colour morph of *Ursus americanus*) bears at the landscape scale of BC's central coast, an area popularly referred to as the "Great Bear Rainforest" (study area ~25,000 km^2). This assembly of ursids represents nested levels of biological organization, including different species (grizzly vs black bears), phenotypes (white vs black-coated morphs of black bears) and genotypes (dominant homozygote black-coated black bears, heterozygote black-coated black bears, recessive homozygote white-coated black bears), which allows for investigation into niche variation across and within species.

The ecological relationships in the study area of my dissertation are structured by a heterogeneous landscape composed of ocean fjords, mainland valleys, and a vast archipelago separated by tidal waters (Bryan et al. 2013, 2014, Service et al. 2014, Adams et al. 2017). Accordingly, this region provides an excellent model system for examining spatial and foraging niche across different scales of biological organization (*e.g.*, species, population, genotypes, phenotypes) in response to environmental variability that in turn defines resource availability and competitive environment. I capitalize on this natural experimental context where coastal bears use the same broad geographic region but occur in different combinations throughout space at a finer resolution. Primarily, mainland areas host grizzly bears and black morph black bears, whereas islands support black and white ‘Spirit’ morphs of black bears (Chapter 4). Black bears on islands were, up until recently, released from competition with the physically dominant grizzly bear, however a recent range shift of grizzly bears suggests the competitive landscape may have shifted (Chapter 2).

Salmon consumption is a relevant dimension of dietary niche to characterize for coastal bears. Across this landscape, a focus of the competitive environment among coastal bear species is the consumption of spawning Pacific salmon (*Oncorhynchus* spp.) (Fortin et al. 2007, Chapter 3, 5), which is a crucial food resource that affects the health of individual bears and their populations (Hilderbrand et al. 1999). Salmon consumption is positively related to body condition and size, mating success, litter size (Hilderbrand et al. 2000, Kovach and Powell 2003, Costello et al. 2009), and population densities (Hilderbrand et al. 1999). Black bears generally are smaller than sympatric grizzly bears and occupy smaller home ranges, often consuming less salmon than the more dominant grizzly bears (Adams et al. 2017, Chapter 3). The five main species of Pacific salmon (pink (*Oncorhynchus gorbuscha)*, chum (*O. keta)*, Chinook (*O. tshawytscha)*, coho (*O. kisutch)*, and sockeye (*O. nerka)*) are well distributed throughout the landscape, but vary in abundance spatially and temporally (Quinn 2005; Chapter 3) Although coastal bears prey on all salmon, each species offers varied foraging opportunities in terms of biomass, nutrient and lipid content, spawn timing, and spawning habitat (Koch and Phillips 2002, Quinn et al. 2003, Gende and Quinn 2004, Robbins et al. 2004).

Characterizing the spatial and dietary niches of sympatric grizzly, black, and Spirit bears in the region is important for determining the ecological mechanisms supporting biodiversity and the conservation of important habitat and dietary resources. The occurrence and persistence of an enigmatic and conspicuous colour morph, the white coated Spirit bear, presents an opportunity to study evolutionary mechanisms that may support the existence of rare morphs (Klinka and Reimchen 2009, Reimchen and Klinka 2017). Coastal bears, grizzly, black, and Spirit alike, are also a conservation priority regionally. They are important participants in the fertilization of coastal ecosystems via the marine nutrients transported from salmon carcasses (Reimchen 2000, Quinn et al. 2009), which in turn structures other aspects of the ecosystem including plant

(Mathewson et al. 2003), songbird (Christie et al. 2008, Wagner and Reynolds 2019), and insect communities (Reimchen et al. 2002). In addition, bears are increasingly important for economic ventures in the region, as conservation-based economies based on bear viewing provides revenue and employment to Indigenous communities in the region (Lemelin et al. 2015). Finally, bears are an important biocultural indicator (Sterling et al. 2017) as they are considered kin by many First Nations in the region and carry tremendous cultural importance as indicated by their tribute in song, dance, and stories (Housty et al. 2014, Artelle et al. 2018). Local communities prioritized supporting this research from a technical standpoint (*i.e.,* co-developing research questions and participating in field work), but also by contributing longstanding LEK/TEK to complement scientific approaches (Chapter 2, 5). Given this context of close collaboration, information on the dietary and spatial niche of coastal bears presented here contributes to the conceptual understanding of niche variation while also simultaneously offering direct applications for conservation and local land-use planning by Indigenous governments.

Methods

This dissertation relies exclusively on non-invasive monitoring methods that align with and respect the Indigenous laws of the Wuikinuxv, Haíłzaqv (Heiltsuk), Nuxalk, Kitasoo/Xai’xais and Gitga’at First Nations. Specifically, all chapters rely on data gathered from the aforementioned collaborative study of bear ecology on the central coast of BC. I used hair samples that provide insight into individual identity, species, sex, mc1r genotype (coat colour morph for black bears), and the bio-tracers δ^{13}C and δ^{15}N, which provide information on diet. Remote cameras paired with hair sampling sites provide images that offered insight into bear age class (Chapter 2). Traditional and Local Ecological Knowledge from members of the Haíłzaqv (Heiltsuk) and Gitga'at communities offered a deeper understanding of grizzly (Chapter 2) and Spirit bears' (Chapter 5) spatial niche. Additionally, I use stable isotope analysis (SIA) of δ^{13}C and δ^{15}N to characterize foraging niche through both Bayesian mixing models (Stock and Semmens 2013) that allow the estimation of annual salmon consumption (Chapter 3) as well as multivariate approaches of niche characterization (Ingram et al. 2018; Chapter 5). Finally, I apply spatial capture-recapture models to black bear data to estimate the spatial niche of Spirit bears (Royle et al. 2014; Chapter 4).

Purpose

The aim of this dissertation is to test hypotheses related to spatial and foraging niche variation of coastal bear populations to illustrate the mechanisms that maintain biodiversity while also informing land-use planning and conservation decision-making. Specifically, I investigate four interrelated themes:

i) the spatial niche of coastal grizzly bears (Chapter 2)

ii) foraging niche variation in black bears in response to varying levels of resource availability and intra- and interspecific competition (Chapter 3)

iii) the spatial patterns in niche of Spirit bears in relation to protected areas (Chapter 4)

iv) the intrapopulation foraging niche variation between phenotypes and genotypes of Spirit bear populations (Chapter 5).

Chapter 2 The spatial niche of coastal grizzly bears

Below follows a brief summary of:

Service, C. N., M. S. Adams, K. A. Artelle, P. Paquet, L. V. Grant, and C. T. Darimont. 2014. Indigenous knowledge and science unite to reveal spatial and temporal dimensions of distributional shift in wildlife of conservation concern. PLoS ONE 9:e101595.

A reprint PDF of this publication appears as Appendix A.

Chapter Summary

Range shifts among wildlife can occur rapidly and impose cascading ecological, economic, and cultural consequences. However, occurrence data used to define distributional limits derived from scientific approaches are often outdated for wide ranging and elusive species, especially in remote environments. Accordingly, our aim was to amalgamate Indigenous and western scientific evidence of grizzly bear (*Ursus arctos horribilis*) records and detail a potential range shift on the central coast of British Columbia, Canada. In addition, I test the hypothesis that data from each method yield similar results, as well as illustrate the complementary nature of this coupled approach. Combining information from traditional and local ecological knowledge (TEK/LEK) interviews with remote camera, genetic, and hunting data revealed that grizzly bears are now present on 10 islands outside their current management boundary. LEK interview

data suggested this expansion has accelerated over the last 10 years. Both approaches provided complementary details and primarily affirmed one another: all islands with scientific evidence for occupation had consistent TEK/LEK evidence. Moreover, our complementary methods approach enabled a more spatially and temporally detailed account than either method would have afforded alone. In many cases, knowledge already held by local Indigenous people could provide timely and inexpensive data about changing ecological processes. However, verifying the accuracy of scientific and experiential knowledge by pairing sources at the same spatial scale allows for increased confidence and detail. A similarly coupled approach may be useful across taxa in many regions.

Chapter 3 Foraging niche variation in black bears in response to varying levels of resource availability and inter- and intraspecific competition

Below follows a brief summary of:

Service, C. N., A. W. Bateman, M. S. Adams, K. A. Artelle, T. E. Reimchen, P. C. Paquet, and C. T. Darimont. 2018. Salmonid species diversity predicts salmon consumption by terrestrial wildlife. Journal of Animal Ecology 00:1–14.

A reprint PDF of this publication appears as Appendix B.

Chapter Summary

Resource waves—spatial variation in resource phenology that extends feeding opportunities for mobile consumers—can affect the behaviour and productivity of recipient populations. Interspecific diversity among Pacific salmon species (*Oncorhynchus* spp.) creates staggered spawning events across space and time, thereby prolonging availability to terrestrial wildlife. We sought to understand how such variation might influence consumption by terrestrial predators compared with resource abundance and intra- and interspecific competition. Using stable isotope analysis, we investigated how the proportion of salmon in the annual diet of male black bears (*Ursus americanus*; n = 405) varies with species diversity and density of spawning salmon biomass, while also accounting for competition with sympatric black and grizzly bears

(*U. arctos horribilis*), in coastal British Columbia, Canada. We found that the proportion of salmon in the annual diet of black bears was ≈40% higher in the absence of grizzly bears, but detected little effect of relative black bear density and salmon biomass density. Rather, salmon diversity had the largest positive effect on consumption. On average, increasing diversity from one salmon species to ~four (with equal biomass contributions) approximately triples the proportion of salmon in diet. Given the importance of salmon to bear life histories, this work provides early empirical support for how resource waves may increase the productivity of consumers at population and landscape scales. Accordingly, terrestrial wildlife management might consider maintaining not only salmon abundance but also diversity.

Chapter 4 Indigenous-led research reveals rarity of the white-phased ‘Spirit Bear’ and gaps in habitat protection

Chapter Summary

Preserving genetic and phenotypic diversity can help safeguard not only biodiversity but also cultural and economic values. Here, we present data that emerged from community-engaged work at the intersection of applied evolutionary ecology and Indigenous Local Ecological Knowledge (LEK) to support conservation planning of a culturally salient and rare phenotypic variant. We addressed a range of conservation objectives for the white-phased “Spirit bear” polymorphism, a rare white-coated phenotype of black bear (*Ursus americanus*) in coastal British Columbia. First, we used non-invasively collected hair samples to assess the spatial variation in the frequency of the allele that controls the white morph (mc1r). Second, we present preliminary estimates of the population size of white phenotypes using the product of allele frequencies and population estimates from spatial capture-recapture methods and LEK. Finally, we examined how well current protected areas in the region aligned with spatial hotspots of Spirit bear alleles. In contrast to previous research, we found that landscape level allele frequency was lower than previously estimated and failed to detect a statistically significant departure from Hardy Weinberg Equilibrium at mc1r. Our preliminary estimate of total population of white-phased Spirit bears (95% CI from 8 to 57) is much lower than previously reported (100 to 500). We found a discrepancy between the placement of protected areas and hotspots (upper 10%) of Spirit bear alleles, with ~50% of hotspots falling outside of protected areas. These results provide new insight into hypotheses related to the maintenance of this rare polymorphism, potential gaps in conservation planning, and the power of locally-led applied conservation science.

Introduction

Although protected areas and conservation strategies are often designed to protect populations, species, and community diversity, preserving genetic and phenotypic diversity is increasingly considered. Whereas most conservation genetics programs aim to preserve diversity by ensuring gene flow, considering the opposite – safeguarding spatially restricted phenotypic variants – is rare (Funk et al. 2012). Such variants, which may have unique morphology, life-history traits, or habitat use, often signal local adaptation to ecological conditions (Crandall et al. 2000). Indeed, rare variants can represent a unique evolutionary lineage, and may warrant special protection as part of an Evolutionary Significant Unit (ESU; Moritz 1994). Unique phenotypes may also have differing ecological relationships than the dominant form. For example, flower colour morphs in monkeyflowers determine whether their primary pollinators are bumblebees or hummingbirds (Bradshaw and Schemske 2003). In the context of rapidly changing ecological conditions under climate change (Barnosky 2008), habitat degradation (Newbold et al. 2016), and invasive species (Mack et al. 2000), populations with unique phenotypic variants may have additional potential to adapt (Forsman et al. 2008).

Accordingly, there is increased urgency to plan for resilience by identifying and managing for the spatial distribution of rare variants.

Rare or otherwise striking organisms can also carry cultural significance, thus additionally increasing interest in protection. Culturally salient organisms may be recognized in part by their unique naming and associated terminology, role in narratives, symbolism, and ceremonies, use in food or social practices, and persistence of use relative to cultural change (Garibaldi and Turner 2004). Although biocultural significance is often considered for species (Garibaldi and Turner 2004), or more recently, places (Cuerrier et al. 2015) - unique forms of variation within species may also confer saliency, and therefore be of conservation importance. For example, the panther (*Panthera onca*), a rare dark-coated morph of the more common spotted-coated jaguar, plays an integral part of culture and mythology in Indigenous communities in the Americas (Saunders 1994). More broadly, the need to safeguard organisms of cultural significance in relation to Indigenous people’s rights has been reaffirmed at international (United Nations General Assembly 2007) and national (Indigenous Circle of Experts (of Canada) 2018) governance forums. Important to both cultures and ecosystems, conservation is often more effective when targeted towards cultural valuable species or forms (Gavin et al. 2015, Artelle et al. in review).

A portion of coastal British Columbia, Canada, hosts an endemic and rare form of a mammal about which little is known to Western ecologists, yet has been of cultural significance to local Indigenous Nations since time immemorial. There, the white-coated black bear (*Ursus americanus kermodei*) referred to as a “Kermode” or “Spirit bear”, is one of the most conspicuous coat colour polymorphisms among all mammals (Caro 2005). Previous genetic research identified a recessive mutation at the melancortin 1 receptor (*mc1r*) gene underlying the white coat colour (Ritland et al. 2001). Heterozygotes are indistinguishable to black coated homozygotes and were estimated as deficient in a previous study (*i.e.*, departing from Hardy-Weinberg Equilibrium; Ritland et al. 2001). Population genetic models suggested the role of genetic drift in the establishment of the Spirit bear allele, and the potential for selection and positive assortative mating in its maintenance (Ritland et al. 2001, Hedrick and Ritland 2011). Additional work has also empirically examined how this polymorphism could be maintained by a multi-niche mechanism, whereby different morphs occupy unique niches and the fitness of each morph is paired to the appropriate niche (Klinka and Reimchen 2009, Hedrick and Ritland 2011). The Spirit bear has a limited distribution, primarily on a handful of islands and nearby mainland (~ 6500 km^2). Reported white coat phenotypic frequencies are as high as 43% in the core range, away from which its frequency drops to near zero (Ritland et al. 2001, Marshall and Ritland 2002). Although capture-recapture sampling has never been applied to this population, existing population estimates based on expert opinion or presumed black bear densities combined with available allele frequency estimates vary from 100 to 500 white-phased individuals (Blood 1997, McCrory et al. 2001, Sachs 2010). Despite this limited information and uncertainty, Spirit bears were used as a flagship element to design a recently legislated protected area network and garner worldwide attention to the area, commonly referred to as the “Great Bear Rainforest” (Ministry of Forests, Lands, and Natural Resource Operations 2016).

Addressing some of this uncertainty and with the intention of supporting Indigenous-led landscape planning, the First Nations whose territories are shared with Spirit bears embarked on work to determine the spatial distribution and population estimates of the rare white bear and the allele underlying it. These efforts emerged from relationships with, respect for, and reciprocity between people and wildlife of the region (Adams et al. 2014, Artelle et al. 2018). In the Tsimshian language group, Spirit bears are referred to as *Moksgm’ol* and relationships with and respect towards these unique bears is expressed through traditional stories, dance, and songs. Oral history belonging to the Kitasoo Nation tells of *Wee’get* (Raven, the Trickster) changing the coat colour of every tenth black bear on Princess Royal Island white as a reminder of the harsh conditions endured during the ice-age (Wisconsin glaciation: ~11,000 before present; Carter 1966). In addition to cultural relationships, both Nations operate successful bear-based ecotourism businesses. Against this cultural, ecological and economic backdrop, and reciprocating these benefits, local First Nations have invested in monitoring and conservation of these rare variants throughout their territories.

Here we describe community-engaged work at the intersection of applied evolutionary ecology and Indigenous Local Ecological Knowledge (LEK) to support conservation planning of a culturally salient and rare phenotype variant. We address three objectives related to the conservation of the Spirit bear polymorphism: 1) assess the spatial variation in the frequency of the allele that controls the Spirit bear morph, 2) provide preliminary estimates of the population size of Sprit bear phenotypes, and 3) examine how well current protected areas in the Great Bear Rainforest align with spatial hotspots of Spirit bear alleles.

Methods and Materials

Study area

To survey for mcr1 beyond its previously documented range (Blood 1997, Ritland et al. 2001), we included in our study area additional portions of the territories of the Kitasoo/Xai’xais, Gitga’at, Haíłzaqv (Heiltsuk), and Wuikinuxv First Nations on the central coast of British Columbia that were not previously sampled (Figure 4.1). This area consists of a large archipelago and nearby mainland valleys of temperate rainforest (Service et al. 2014). Whereas black bears are present across the entire landscape, grizzly bears occur in mainland watersheds but are largely absent in most island watersheds (Service et al. 2014). The Spirit bear phenotype was previously reported to occur at the highest frequencies on Gribbell Island (~43%), followed by Princess Royal Island (~17%), with the frequency decaying to near zero on neighboring islands and mainland watersheds (Marshall and Ritland 2002; Figure 4.1, Table 4.2).

Spatial scale

We used two different spatial scales of analysis. To allow for direct comparisons, we matched our primary study area to previous research on Spirit bears in the region

(~6,660 km^2, Ritland et al. 2001, Marshall and Ritland 2002, Hedrick and Ritland 2011; Figure 4.1). We used this study area extent to bound our population estimates and allele frequency estimates (see analysis approaches i) and ii) below). Accordingly, in line with Ritland et al.'s approach (2001), we compared allele frequencies and population estimates at the island scale for all detections on islands. For mainland detections, we used combinations of the ecologically informed management '"Landscape Units" (LUs) that best matched the spatial extent described in Ritland et al. 2001 (Ministry of Forests, Lands, and Natural Resource Operations 2016). We refer to each island or mainland LU as a "landmass" throughout our analysis (Figure 4.1). The landmass "East of Gribbell" was excluded from the analysis of allele frequency and Spirit bear population size due to its low sample size (n = 2 individual black bears detected over the study).

We used a larger spatial area and dataset for our analysis of how hotspots of G allele frequency (*i.e.*, the top 10% of values across the landscape) might align with protected areas (~19,000km^2; analysis approaches iii) and iv) below). This secondary spatial scale extends from the previously described extent of the G allele, particularly to the south to ensure we captured the full distribution of the G allele (Figure 4.1).

Field sampling

During May and June each year (2012 to 2017) we assembled non-invasive hair snagging sites (n = 175 average among years) baited with a non-reward bait (Woods et al. 1999, Bryan et al. 2013, 2014, Adams et al. 2017) to collect hair samples. The spatial design for sampling was originally for estimating population and spatial dynamics of grizzly bears (Artelle et al. in review), which are more mobile animals than black bears. Sites were approximately evenly spaced (~1 per 50km^2), and spanned ecological and elevation gradients (Figure 4.1). Hair samples were collected every ten to fourteen days over two or three sampling sessions each year. Our protocol was approved by the Stewardship Departments of the Kitasoo/Xai'xais, Gitga'at, Haíłzaqv (Heilstuk), and Wuikinuxv First Nations. Sampling in Parks occurred under BC Parks Use Permit 108648. Research was approved by the University of Victoria's Animal Care protocol 2016-020 and followed the Canadian Council for Animal Care's requirements concerning animal care and wildlife (Sikes and Gannon 2011).

Laboratory analysis

We determined individual identity and species using seven microsatellites, plus a sex marker, at a commercial laboratory (Wildlife Genetics International Ltd, Nelson, BC). The laboratory also assigned mc1r genotypes (AA (black coat homozygote), AG (black coat heterozygote), GG (white coat homozygote)) following a protocol they developed (see full details in Appendix C S1) based on the general process previously described by Ritland et al. (2001). All hair samples of known individuals within the primary study area were typed for their mc1r genotype. A random subsample of all known individuals (n = 120 of 444) within the secondary study area (detected as part of a larger unrelated ecological project in partnership with the aforementioned Nations; Bryan et al. 2013, 2014, Service et al. 2014, Adams et al. 2017, Service et al. 2018, Artelle et al. in review) was screened for the mc1r genotype. These assignments allowed us to estimate the spatial variation of the G allele frequency across the study area.

Data analysis

We compared patterns of Spirit bear allele frequencies with those expected under Hardy- Weinberg Equilibrium, estimated total Spirit bear population size, and compared Spirit bear allele hotspots with protected areas. All analyses were carried out in R (version 3.1.05; R Core Team 2018).

i) Testing whether the mc1r gene is in Hardy-Weinberg equilibrium

We tested whether our observed mc1r genotype frequencies conformed to expected Hardy Weinberg proportions (Hardy 1908) at the landmass scale. To match the approach previously applied to an independent dataset (Ritland et al. 2001), we used a Monte Carlo Exact Test derivation of a chi-squared goodness of fit test to compare expected versus observed genotypes. Additionally, we specifically tested for a deficit of heterozygotes as previously reported (Ritland et al. 2001) using a Monte Carlo Exact Test U-score statistic, where positive values indicate an excess of homozygotes, and negative values signal a surplus of heterozygotes. All calculations were conducted in the *HWxtest* package (Engels 2009). We calculated a 95% confidence interval around all allele frequency estimates using a Jeffery’s interval distribution in the R package *binom*, an approach suitable when values approach 0 or 1 (Brown et al. 2001). Finally, we tested for differences between our allele frequency estimates by landmass with those calculated during previous sampling efforts (Ritland et al. 2001) using Fisher’s Exact tests.

ii) Estimating Spirit bear population size

To estimate the density of black bears in our study area, we applied spatially explicit capture-recapture (SECR) models (Efford 2004, Royle et al. 2014; Appendix C S2). SECR models build off traditional capture-recapture approaches by estimating an animal's "activity center" (analogous to center of home range) while accounting for spatial heterogeneity in capture probability (Efford 2004). Using site-specific detection histories, SECR models estimate how individual capture probability declines with the increased distance between an individual’s activity center and sampling site. These detection models estimate capture probability (g_0) for an individual whose activity center occurs at a distance of 0 from a sampling site, and a spatial scale parameter, sigma (σ), which describes rate at which the capture probability declines with increasing distance between the sampling site and activity center (Efford 2004, Royle et al. 2014). *D*, the parameter for density, describes the number of estimated activity centers per unit area in a null SECR model. The full spatial scale across which SECR models are performed is called the "state-space". This region contains the sampling site array plus a buffer large enough to contain the home range of all individuals that could have been encountered the sampling site array (Borchers and Efford 2008).

We fit separate SECR models to calculate mean density for males in for each landmass for data from 2016 to 2017. As there were very few female recapture events (Appendix C S2 Figure S2), we constructed total density instead by extrapolating from the male estimate. Because bear male:female sex ratios are often assumed to be near 50:50 in unhunted populations (Beecham 1980), for our main analysis we calculated estimates for each year by doubling the male component because hunting pressure is limited in our study area. As this ratio estimate is plausible, but arbitrary, and following a recent SECR modeling for bear population estimates in the area (Artelle et al. in revision), we also constructed estimates from other reasonable alternative ratios (60:40; 40:60; Noyce and Garshelis 1997, Loosen et al. 2018), and report results in Appendix C S2.

We used the package *secr* (version 3.1, Efford 2018) to fit likelihood based SECR models in R. As *secr* models are computationally intensive, we employed a two-step modeling process. We used AIC model selection to assess whether or not to include a term for heterogeneity in detection across projects (*i.e.*, across the efforts of the Nations leading sub-components of the research (Figure 4.1)). Based on these AIC values we used the term for project-specific g_0 in subsequent analyses (Appendix C S2 Table S1). Given our relatively low levels of redetection (Appendix C S2 Figure S2), we lacked the power to address trap or individual-specific detection covariates. We also considered models that allowed density to vary by landmass. However, our low power estimates from these models offered low levels of precision (*e.g.*, estimates of 105 to 1,014 bears per 1000 km^2). Accordingly, given our objective to estimate the total number of white phenotypes at a broad spatial scale, we only drew inference from null density models (D~1). Finally, given the archipelago nature of our study area, we incorporated ecological distance into models (Sutherland et al. 2015), which assumed restricted bear movement across ocean >100 m as supported by multi-year movement and detection data in this study area (Darimont et al. unpublished data). As such, the model we used for inference included parameters that allowed variation in detection by project node (*i.e.*, study area maintained by each Indigenous Nation), incorporated ecological distance to account for ocean barriers to movement, and calculated density (D) at a global spatial scale.

We estimated total population size at the landmass scale by multiplying our average (across 2016 and 2017) global density (*D*) by the total area of each landmass (Appendix C S2 Table S2). We estimated total mean population size of white Spirit bears for each landmass by multiplying its mean population estimate with the mean G allele frequency estimate for that landmass. To incorporate the uncertainty inherent in modelling parameters of small populations, we also calculated all combinations of 95% confidence intervals of Spirit bear population estimates by multiplying all mean estimates and lower/upper confidence intervals for both G allele frequency and total population estimates, respectively. This approach resulted in nine combinations of possible point estimates of Spirit bear population size, ranging from the multiplicative product of lower 95% estimates to the multiplicative product of the upper 95% estimates.

We assessed if our Spirit bear population estimates aligned with estimates of abundance derived from an existing Indigenous Local Ecological Knowledge (LEK) dataset curated by the Kitasoo/Xai’xias First Nation (Kitasoo/Xai’xais Resource

Stewardship Authority, unpublished data with permission). This dataset covers three of the eleven landmasses, and includes records of unique sightings of Spirit bears and interview data related to Spirit bears. Data were collected annually from the Kitasoo/Xai’xais’ Indigenous ecotourism operation (Spirit Bear Lodge) whose guides each spend 60 to 80 days across the southern extent of the smaller, primary study area (spatial scale i), prioritizing efforts to observe Spirit bears. Head guides of this operation maintain photo records of individual bears and can distinguish individuals via size, body shape, sex, behaviour, and scar patterns. As bear appearance can change across years, we only considered counts of unique Spirit bears in a single year (2017). Given that all ecotourism in the nearly roadless study area is boat-based, interior areas of landmasses were not censused in this manner. Accordingly, LEK estimates provided can be interpreted as a minimum Spirit bear population estimate to guide interpretation of the variation across our SCR-derived Spirit bear population estimates.

iii) Estimating spatial patterns of G allele frequency

We estimated the spatial pattern of G allele frequency at a landscape scale (18,861 km^2) with a weighted-kriging approach that considers cost-based distance. This approach generates estimates of a response variable across a sampled landscape, while considering landscape connectivity (López-Quílez and Muñoz 2009). Our input datapoints were the G allele frequency values (number of G alleles/total allele count) at each sampling site (n = 175 sites), pooled across years. When individual bears (n = 385) were detected in multiple locations, we allowed their alleles to contribute to all sites of detection (n = 988 alleles included in analysis). We defined the boundaries of our spatial extent as 20 km away from outermost sampling sites to match our *secr* approach and we excluded islands that did not have any sampling sites. Given that our multi-year (2009 to 2018) detection data suggest black bears in our study area rarely cross ocean channels (Darimont, unpublished data), we weighted the resistance of the ocean as 100 times greater than land, using the *gdistance* package (van Etten 2017). As the number of alleles detected varied across sampling sites (range = 2 to 28), we also weighted the contributions of each sampling site to the model by the number of total alleles. We fit a Matern variogram model (Cressie 1990) using maximum likelihood to account for spatial structure in G allele frequency values. The selected variogram model was used to fit a cost-based-weighted kriging model using the *krig.conv* function in the *geoRcb* package (López-Quílez and Muñoz 2009) to create the interpolated raster surface. This raster surface was then used to identify hotspots of G allele frequencies that were compared with protected areas (analysis iv below).

iv) Assessing alignment of protected areas with G allele hotspots

We assessed the alignment between our krigged G allele frequency surface and protected areas through two complementary approaches. First, we identified hotspots of allele frequency, defined as pixels with values in the 90th percentile (*i.e.*, top 10% of the entire interpolated raster surface from analysis iii) and assessed the percentage of the hotspot that corresponded with protected areas. To assess sensitivity of this arbitrary, but logical cutoff value, we additionally report values for the 95th (top 5%) and 85th percentile (top 15%). Secondly, we calculated the percentage of protected area in each landmass and tested whether this value was predicted by G allele frequency through a linear regression model and a Pearson's correlation.

Results

Broadly, our estimates of Spirit bear allele frequencies and population densities differed from previous work. Mean estimates for G allele frequencies varied by landmass (from 0.0 to 0.26), were mostly lower than previously reported estimates, and were significantly lower on Roderick (Odds ratio= 0.091; p = 0.018) and Gribbell (Odds ratio= 0.261; p = 0.007) Islands (Table 4.2). In contrast with previous sampling efforts, we did not detect a heterozygote deficiency in any landmasses; we failed to detect a statistically significant departure from Hardy Weinberg Equilibrium across all populations (Table 4.1; Table 4.2).

The mean estimate derived from spatial capture-recapture for global black bear density in our defined state-space was 120 bears/1000km^2 (95% CI: 88 to 165; Table 4.3). Accordingly, within the bounds of the primary study area landmasses (spatial scale i); Figure 4.1) our mean estimate for the total black bear population was 817 (95% CI: 598 to 1,116).

Broadly, our 95% CI estimates of preliminary Spirit bear population size (8 to 57) aligned with LEK at a landmass scale (*i.e.*, the minimum count for certain landmasses via LEK was contained within the 95% CI, Table 4.4). However, only one of nine potential Spirit bear population point estimates aligned with Indigenous Local Ecological Knowledge, where point estimates were determined from combinations of G allele frequency estimates (mean, upper and lower 95% confidence limit) and black bear population estimates (mean, upper and lower 95% confidence limit) per landmass (Table 4.4). The model that best aligned with the minimum count LEK was derived from the upper confidence limits of both G allele frequency and black bear population size (Table 4.4), the product of which estimated ~57 Spirit bears in our study area (*i.e.*, the only population estimate combination that exceeded the LEK minimum count in each landmass).

We found that ~50% of the 90th percentile of the hotspot area of G allele frequency corresponded with protected areas (Figure 4.2; Table 4.2). Similar results emerged for the 95th and 85th percentiles, at 50% and 45% protected area coverage, respectively. Across landmasses, protected area coverage was not related to the G allele frequency ($R = -0.012$; $F = 0.001$; $p = 0.971$). The two landmasses with the highest G allele frequency differed strongly in protected area coverage, with Princes Royal having high coverage (52%) and Gribbell having low protection (0.05%) (Table 4.2).

Discussion

Our results suggest that landscape-level frequency of the G allele is lower than previously estimated, and that populations previously reported to demonstrate a heterozygote deficiency are in fact in Hardy Weinberg Equilibrium. These data, combined with our population abundance estimates of black bears in the region, suggest that the highest range of total population of the white form or Spirit bear (57; 8 to 57) is also substantially lower than previous estimates (100 to 500; Blood 1997, Sachs 2010, McCrory 2012). Finally, despite the role of Spirit bears as a flagship organism for conservation planning, we found a discrepancy between the placement of protected areas and hotspots of G alleles, with ~50% of ‘90% hotspots’ falling outside of protected areas.

Although several limitations related to our restricted sampling in space and time exist, our approach produced estimates that aligned with those derived via independent lines of evidence. First, although we did not sample one nearby but non-adjacent mainland region with known Spirit bear phenotypes (near the town of Terrace, B.C; Figure 4.1), the previously estimated G allele frequency for this area is low (0.05; Ritland et al. 2001). We suspect that observations are common there because the area has orders of magnitude greater human population density, an extensive road network, and bear attractants (*e.g.*, landfills) compared with the areas we sampled. Accordingly, we estimate that the total number of additional bears in this region to be minimal, nowhere near the number necessary to resolve the large discrepancy between our estimates and previous estimates of total Spirit bear population size (Blood 1997, McCrory 2012). Additionally, we know of several sightings across our broader study area (spatial scale used for analysis iii and iv) where local Indigenous knowledge has documented the rare occurrence of Sprit bears previously (pers comm. Jennifer Walkus; Wuikinuxv Nation).

Although our sampling over five years failing to detect a G allele in these regions, G allele detections were focused in the core of the primary study area and our G frequency estimates decayed to zero at the far boundaries of our sampling extent (Figure 4.2). Accordingly, we are confident that our sampling efforts were suitable to capture regions with high frequencies of G alleles (and phenotypes) that currently exist. Notably, we were able to compare the ranges of our estimates with Local Ecological Knowledge (Kitasoo/ Xai'xais Resource Stewardship Authority, unpublished data). The combination of these independent knowledge sources, not available in previous efforts, aligned to a specific subset of the range, thus allowing us greater inference than any one method alone. We additionally note that our estimate of G allele frequency (on Gribbell Island) generally aligned with observational studies in the mid-2000s (Klinka and Reimchen 2009), which estimated G frequency to be approximately one quarter the estimated frequency reported in Ritland et al. 2001.

Our results show that Spirit bear populations are in Hardy Weinberg Equilibrium for mc1r, providing new insight into hypotheses related to the maintenance of this rare white variant. Specifically, the earlier reported patterns of a heterozygote deficiency for mc1r (Ritland et al. 2001), but not for microsatellite loci (Marshall and Ritland 2002), led to subsequent research to assume those conditions when attempting to understand the maintenance of this polymorphism (Hedrick and Ritland 2011). Specifically, Ritland et al. (2001) suggested several hypotheses: assortative mating, recent immigration of black-coated homozygotes, a heterozygote fitness disadvantage, or some combination of these processes. Recent classical population genetic modeling, however, has identified that positive assertive mating would need to be as high as 50% (50% white-white or black-black; and 50% random) to create the previously observed patterns of heterozygote deficiency (Hedrick and Ritland 2011). Additionally, the proposed presence of a heterozygote fitness disadvantage would not maintain a balanced polymorphism (Futuyma 1997). This is counter to the understanding of this polymorphism being stable, at least on Princess Royal Island, where First Nation oral history (which identifies a 1:10 frequency for the white phenotype, Carter 1966), previous sampling efforts (Ritland et al. 2001), and our recent sampling all suggest similar phenotype frequencies (Table 4.2). Finally, recent studies on gene flow using F_{ST} confronted the role of gene swamping of white form-containing island populations by homozygotes from the mainland, concluding that migration levels were not high enough to contribute substantially to the previously estimated pattern of a heterozygotic deficiency (Harestad 2007). Collectively, these findings and our results do not support the hypothesis of a heterozygote deficiency, and associated mechanisms, in the maintenance of this polymorphism.

Our results suggest that Spirit bears are considerably rarer than previously estimated in the peer-reviewed, technical, and popular literature**.** This result is driven in part from lower estimates of G frequency at a landscape scale (Table 4.2). Specifically, sampling on Gribbell Island revealed lower estimates of G allele frequency (mean: 0.25, 95% CI 0.13 to 0.41) compared with previous mean estimate of 0.57 (Ritland et al. 2001). This discrepancy could in part be driven from the earlier work’s spatially-limited sampling, which occurred only at or near the mouths of salmon (*Oncorhynchus* spp.) spawning streams in fall and targeted known areas of Spirit bears (Ritland et al. 2001, Marshall and Ritland 2002).

Our sampling program allowed for increased knowledge on spatial patterns of allele frequencies. We sampled a variety of elevational and ecological gradients via boat and helicopter (~1 sampling site per 50 km^2), which supported a more representative coverage of available habitat (including that far from shore in this nearly roadless environment) than was previously studied. Notably, sampling further from the shore provided novel insight. For example, in the Mainland East of Princess Royal Island, the one landmass where our G allele frequency estimate was higher than previous estimates (Table 4.2), we failed to detect G alleles at the shore (as per Ritland et al. 2001), but detected the allele in heterozygotes consistently far into the interior at the headwaters of watersheds. Additionally, recent observational and isotopic research has identified the potential selective advantage of white phenotype during predation of salmon (Klinka and Reimchen 2009, Reimchen and Klinka 2017). As such, Reimchen and Klinka (2017) proposed that targeted sampling during previous research near the mouths of salmon streams (where much of the spawning occurs) during the fall could have over-estimated G allele frequency as the white morph might be more likely to be detected in those streams to capitalize on this foraging advantage. This potential over-representation of G allele frequency in previous estimates, likely driven by non-random sampling, could also explain the perceived heterozygotic excess. Specifically, the observed patterns could be driven by a Wahlund effect, which is caused by non-random sampling of a population with sub-structure (Reimchen and Klinka 2017).

A second discrepancy between our estimate of Spirit bears and previously published estimates is the divergence in our estimates of total population of black bears across the study area. Whereas expert opinion (derived from applying density estimates from other areas to coastal BC) suggested up to 250 bears/1000 km^2 across the whole distribution of white phenotypes (Blood 1997, McCrory 2012), our spatial capture-recapture estimates suggested a mean estimate of 120 bears/1000 km^2 (95% CI: 88 to 165; Table 4.3). At smaller spatial scales (*i.e.*, landmasses), however, we were unable to estimate density with reasonable precision. Moreover, the large spacing among traps relative to moderately constrained mobility of black bears, a result of this monitoring program being designed for grizzly bears (*e.g.,* Artelle et al in review), might have resulted in inaccurate population estimates (Sollmann et al. 2012, Royle et al. 2014). Specifically, given our estimate of sigma (σ) was approximately 50% of the distance of our trap spacing, previous simulation modelling suggests that there is potential that our density estimates may be biased low by as much as half (Sollmann et al. 2012). However, we note that even our doubled point estimate of Spirit bears (114; based on upper confidence intervals of both allele frequency values and population size) is still substantially lower than previously reported. Although these data are the best currently available for coastal black bears in the region, decreased trap spacing would benefit future inquiry that aims to increase the precision and accuracy of estimates of black bear density. The limitations of the current work make LEK data particularly valuable. For example, LEK data suggest that application of global density estimates at landmass scales might have underestimated the number of white bears for Gribbell and overestimated them for Princess Royal Island (Table 4.4). More broadly, these patterns suggest that employing independent lines of empirical evidence (in our case, population modeling and Local Ecological Knowledge) can provide complementary and thus more robust inference.

We found a potential limitation in land-use plans to conserve Sprit bears as assessed by the spatial patterns in the mc1r G allele frequency. Specifically, hotspots of G allele exist outside of protected areas on Gribbell and Princess Royal Islands, as well as watersheds on the Mainland East landmass of Princess Royal (Figure 4.2). Areas outside of formal protection are potentially subject to large-scale clearcut logging and the creation of new road networks in watersheds never before subject to industrial activity. These disturbances could modify resources available to bears over the long term (Neilson et al. 2004) and expose them to increased human-caused mortality (Boulanger and Stenhouse 2014). We note, however, that we were only able to assess formally gazetted protected areas. Complementing this existing protection are opportunities for negotiations via the Landscape Reserve Design (LRD) process among First Nations, the provincial government, and industrial forestry operators (Ministry of Forests, Lands, and Natural Resource Operations 2016). If additional protection for Spirit bears is desired by Indigenous governments, Indigenous Protected and Conserved Areas (IPCAs) may provide an appropriate mechanism to protect these culturally salient and economically important animals for communities of the area (Zurba et al. 2019).

Although this research necessarily focused on the small spatial-scale of this geographically restricted rare animal, several more broadly applicable lessons emerge. First, this research provides an example of local Indigenous communities identifying and investing in a unit of biodiversity of high local cultural, economic, and conservation value. Although the Spirit bear phenotype diverges from the more common species-based taxonomy that serves as the usual biological unit of conservation planning, this work builds upon examples in other taxa and geographies where Indigenous knowledge has helped shape the priority units of biological diversity for conservation. For example, both the Indigenous knowledge of the Sahtú Dene and Métis communities and genetic approaches guided the novel identification of caribou (*Rangifer tarandus*) population structure in Canada's north (Polfus 2016). Collectively, approaches like these add to an emerging global trend of reconciling Indigenous values and scientific approaches to improve conservation and management outcomes (Ban et al. 2018).

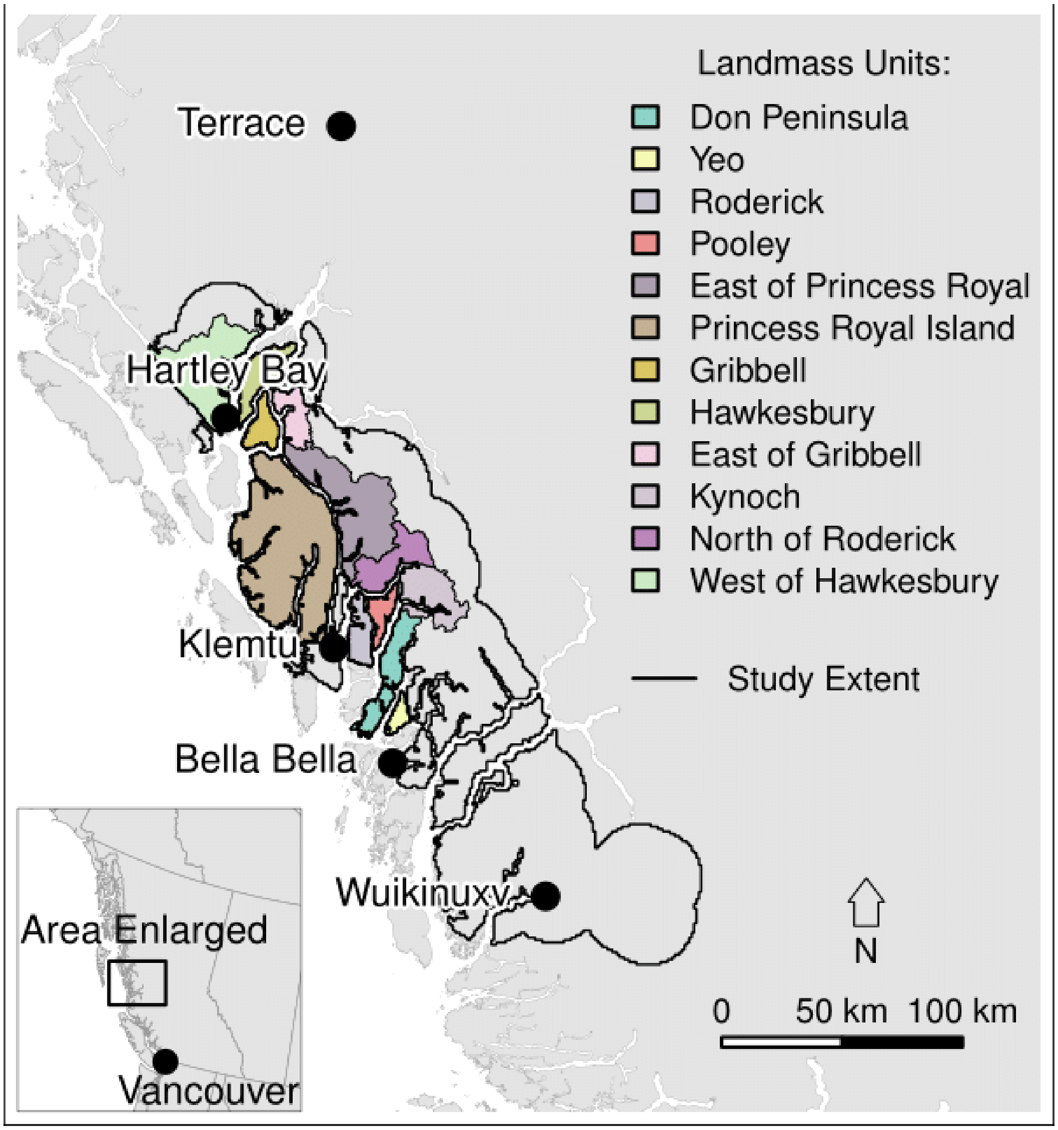

Figure 4.1. Study area and corresponding communities in coastal British Columbia, Canada. Coloured polygons indicate each unique landmass for spatial scale i) and the dashed line indicates the extent of spatial scale ii).

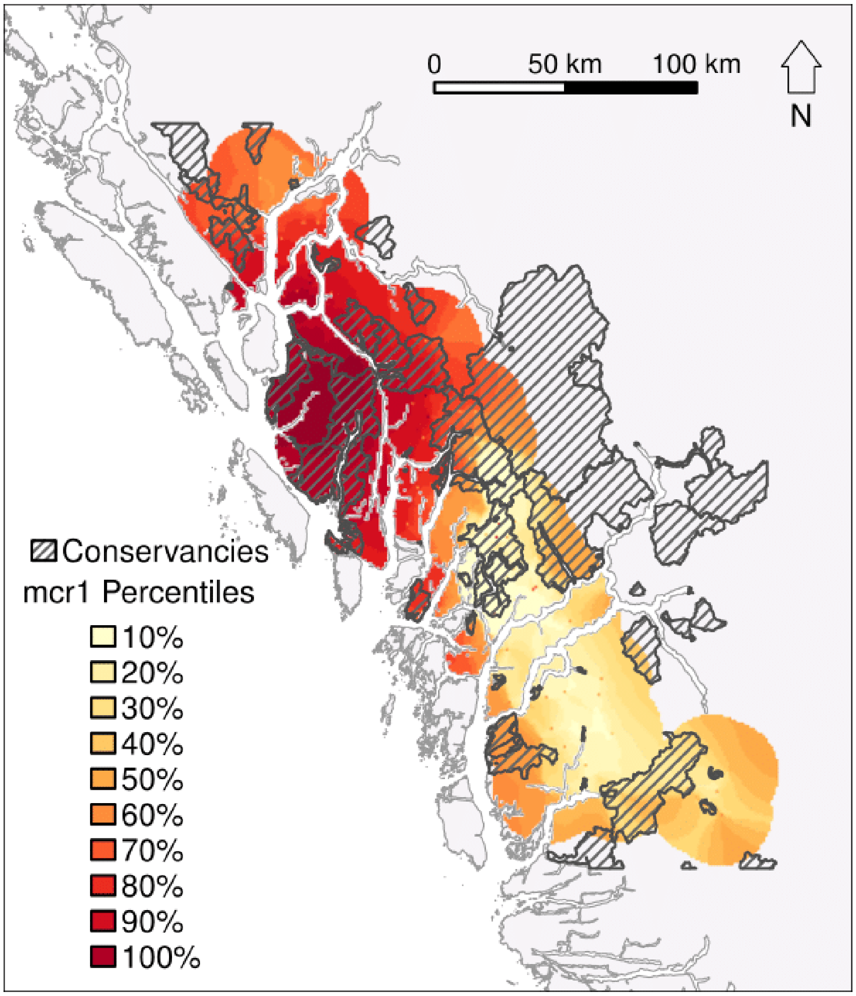

Figure 4.2. Comparison between protected areas (‘Conservancies’), and percentiles (10 to 100%) of G allele frequency of black bears (*Ursus americanus*) as estimated by cost-weighted kriging of allele ratio (n = 988 alleles) across 175 sampling sites in coastal British Columbia, Canada.

Table 4.1. Observed versus expected mc1r genotypes of black bears (*Ursus americanus*) by landmass in coastal British Columbia, Canada (2012 to 2017). Monte Carlo Exact Chi square P values reflect results from tests for departures from genotype frequencies expected under Hardy Weinberg Equilibrium. U-Score P values reflect tests for an excess or deficiency of heterozygosity at mc1r.

	GG (white)		**AG (black)**		**AA (black)**			
Landmass	**O**	**E**	**O**	**E**	**O**	**E**	**Chi^2 P**	**U-score P**
Island							-	-
Hawkesbury	0	0.00	0	0.00	24	24.00	-	-
Gribbell	1	1.13	7	6.75	10	10.12	1.00	0.74
Princess Royal	8	5.32	25	30.36	46	43.32	0.14	0.09
Roderick	0	0.01	1	0.98	21	21.01	1.00	1.00
Pooley	0	0.00	0	0.00	6	6.00	-	-
Yeo	0	0.00	0	0.00	5	5.00	-	-
Mainland								
West of Hawkesbury	0	0.03	2	1.94	34	34.03	1.00	0.99
East of Princess Royal	0	0.15	4	3.70	23	23.15	1.00	0.89
North of Roderick	0	0.02	1	0.96	11	11.02	1.00	1.00
Kynoch	0	0.00	0	0.00	15	15.00	-	-
Don Peninsula	0	0.01	1	0.98	21	21.01	1.00	1.00

Table 4.2. Estimated mean, 95% lower (LCL) and upper (UCL) confidence limits of G allele frequency (q(G)) in coastal black bears (*Ursus americanus*) by landmass estimated in this this study and previous work by Ritland et al. 2001. 'PA coverage' denotes the percentage of each landmass in protected areas. Bolded q values differed significantly between our sampling effort and previous estimates by Ritland et al. (Fisher Exact Test; both P < 0.05)

					Ritland et al. 2001		
Landmass	***q*(G)**	***q*(G) *LCL***	***q*(G) *UCL***	**n**	***q(G)*(2001)**	**n (2001)**	**PA coverage**
Island							
Hawkesbury	0.00	0.00	0.36	24	0.02	25	0
Gribbell	***0.25***	0.13	0.41	18	***0.57***	23	0
Princess Royal	0.26	0.20	0.33	79	0.34	52	52
Roderick	***0.02***	0.00	0.10	22	***0.21***	12	1
Pooley	0.00	0.00	0.15	6	0.10	10	29
Yeo	0.00	0.00	0.17	5	0.05	10	0
Mainland							
West of Hawkesbury	0.03	0.01	0.09	36	0.08	6	26
East of Princess Royal	0.07	0.03	0.17	27	0.00	25	61
North of Roderick	0.04	0.00	0.18	12	0.13	12	59
Kynoch	0.00	0.00	0.06	15	-	-	100
Don Peninsula	0.02	0.00	0.10	22	0.04	24	21

Table 4.3. Estimates of black bear (*Ursus americanus*) population density (‘D bears/1000km^2’, g_0 (capture probability), and sigma (spatial scale parameter) for 2016, 2017 and the grand mean of those years. LCL and UCL represent the lower and upper 95% confidence interval. g_0 values are reported as an average across all projects. Raw values were estimated based on spatial capture recapture modelling (*secr*) from a male only dataset. Accordingly, estimates displayed in the table have been doubled to reflect a presumed 50:50 sex ratio.

	2016			***2017***			***grand mean***		
secr estimates	*mean*	*LCL*	*UCL*	*mean*	*LCL*	*UCL*	*mean*	*LCL*	*UCL*
Density (bears/1000 km^2)	109	81	146	132	95	183	120	88	165
g_0	0.26	0.16	0.41	0.54	0.33	0.73	0.40	0.24	0.57
sigma	2535	2188	2936	2104	1776	2491	2319	1982	2714

Table 4.4. Estimates of Spirit bear population size by landmass based on differing combinations of mean, lower ('LCL') and upper ('UCL') 95% confidence intervals of black bear (*Ursus americanus*) population size ('bb'), and G allele frequency ('q') based on field data collected between 2012 to 2017 in coastal British Columbia, Canada. 'Local Ecological Knowledge (LEK) count' represents minimum counts of unique Spirit bears for 2017. Columns with grey text represent estimates that are below minimum Spirit bear count data per LEK at the landmass scale. The total denoted by a * indicates the count value we use for inference, based on alignment with LEK estimates.

Landmass	***bb mean*q mean***	***bb LCL*q LCL***	***bb UCL*q UCL***	***bb LCL*q mean***	***bb UCL*q mean***	***bb mean*q LCL***	***bb mean*q UCL***	***bb LCL*q UCL***	***bb UCL*q UCL***	***LEK count***
Don Peninsula	0	0	1	0	0	0	1	0	0	-
East of Princess Royal	1	0	5	1	1	0	4	3	0	-
Gribbell	2	0	6	1	2	0	4	3	1	-
Hawkesbury	0	0	0	0	0	0	0	0	0	-
Kynoch	0	0	0	0	0	0	0	0	0	-
North of Roderick	0	0	2	0	0	0	2	1	0	1
Pooley	0	0	1	0	0	0	0	0	0	1
Princess Royal Island	18	8	41	14	25	11	30	22	14	10
Roderick	0	0	0	0	0	0	0	0	0	-
West of Hawkesbury	0	0	1	0	0	0	1	1	0	-
Yeo	0	0	0	0	0	0	0	0	0	-
Total count	21	8	57*	16	28	11	42	30	15	12

Chapter 5 The intrapopulation foraging niche variation between phenotypes and genotypes of Spirit bear populations

Chapter Summary

Foraging niche variation within a species can contribute to the maintenance of diversity. The multi-niche model, for example, posits that phenotypes occupying different niches can contribute to the maintenance of balanced polymorphisms. Using coastal populations of black bears (*Ursus americanus kermodei)* from British Columbia, Canada, we examined potential foraging niche divergence between phenotypes (black & white coated ‘Spirit’ colour) and between black-coated homozygote and heterozygous genotypes. We applied Bayesian multivariate models, with bio-tracers of diet (δ^{13}C and δ^{15}N) together comprising the response variable, to draw inference about foraging niche variation. Variance-covariance matrices from multivariate linear mixed effect models were visualized as Bayesian standard ellipses in δ^{13}C and δ^{15}N isotopic space to assess potential niche variation, annually and seasonally. We did not detect a difference in isotopic foraging niche area in annual comparisons between genotypes or phenotypes. Similar to previous univariate analyses and observational studies, we found that white phenotype Spirit bears were modestly more enriched in δ^{15}N during the fall foraging season. Variation in isotopic niches between genotypes revealed that heterozygotes were moderately more enriched in δ^{13}C, also in hair grown during fall foraging. To the extent to which elevated δ^{15}N and δ^{13}C signal the consumption of salmon

(*Oncorhynchus* spp.) as well as the influence of salmon consumption on reproductive fitness, these results suggest that black-coated heterozygotes could have a selective advantage in the fall compared with black-coated homozygotes. However, we anticipate that white phenotypes maintain the largest advantage in the fall in the context of foraging on marine foods compared to both black-coated genotypes. More broadly, our multivariate approach, coupled with knowledge of genetic variation underlying a polymorphic trait, provides new insight into the potential role of a multi-niche mechanism in maintaining this rare morph of conservation priority in Canada’s Great Bear Rainforest, and could offer new understanding into polymorphisms in other systems.

Introduction

Niche partitioning among and within species comprises a central process underlying biodiversity. A historical assumption underlying most research on niche variation is that niches are properties of populations or species (Hutchinson 1957, Chase and Leibold 2003). However, diversity has increasingly been shown to also be driven by niche partitioning among age classes (Polis 1984), sexes (Shine 1989), and individuals (Newsome et al. 2009, Araújo et al. 2011). Additionally, early theoretical and empirical work revealed the potential for niche differentiation between genotypes and/or phenotypes (‘multi-niche polymorphisms’) to maintain intraspecific diversity (Ford 1975, Reimchen 1979).

Intraspecific body colour variation is common in vertebrates and increasing evidence has shown niche divergence among colour morphs. Colour polymorphisms occur across taxa including mammals (Majerus and Mundy 2003), birds (Galeotti et al. 2003), and reptiles (Rosenblum et al. 2004). Across most terrestrial mammals, coat colour is often associated with habitat, suggestive of the prominent role of camouflage (Caro 2005, Suzuki 2013). This role is relevant for prey and predator alike; prey generally match substrate background to avoid detection by predators, and predators colour match to avoid detection by desired prey (Caro 2005). For example, rock pocket mice (*Chaetodipus intermedius)* have dark and light coat colour morphs, with lighter morphs selecting for habitat with light substrates, and dark morphs selecting for dark substrates (Nachman et al. 2003, Hoekstra et al. 2004). Given their conspicuous nature, colour polymorphisms provide an exceptional opportunity to study the maintenance of intraspecific diversity.

Coastal British Columbia (BC) hosts one of the most striking coat colour polymorphisms known in mammals: a rare white coated morph of the American black bear (*Ursus americanus kermodei;* Ritland et al. 2001). Referred to commonly as a “Spirit bear”, genetic research has identified their unique coat colour to be controlled by a recessive mutation at the melancortin 1 reception (*mc1r*) gene (Ritland et al. 2001). Heterozygotes and dominant homozygotes have black coats and are visually indistinguishable (Ritland et al. 2001). Spirit bears have a limited distribution, primarily on several islands and the nearby mainland on the central coast of BC (Ritland et al. 2001, Marshall and Ritland 2002). In this region, frequencies have been estimated as high as 43% (Gribbell Island), but their probability of presence drops to near zero within ~3 km from this concentrated area (Ritland et al. 2001, Marshall and Ritland 2002). Population estimates throughout their distribution vary from ~50-500 individuals (Chapter 4; Blood 1997, McCrory et al. 2001, Sachs 2010).

The evolutionary and ecological context that supports this unusual polymorphism, and specifically the interplay between neutral and selective forces, is yet to be resolved. The Kitasoo/Xai'xais First Nation's oral history from the area documents the presence of white bears at similar frequencies to present day since the Wisconsin glaciation (Carter 1966), suggesting that the polymorphism is stable. Balanced polymorphisms, such as this, can be maintained through multiple mechanisms including inverse frequency dependence, heterozygote advantage, gene flow, disassortative mating, and niche differentiation between morphs (Ford 1975). Hedrick and Ritland (2011) assessed the theoretical impact of selection, genetic drift, gene flow, and positive assortative mating on coastal black bear populations in the region to determine the conditions that could support the maintenance and restricted distribution of the white coat polymorphism. From these models they concluded that genetic drift was important in the establishment of the white allele, but suggested that selective advantage was critical for counteracting gene flow from homozygous populations without the white allele (Hedrick and Ritland 2011). Further, previous empirical and experimental studies on bear foraging behaviour and a dual-isotope ($\delta^{13}C$ and $\delta^{15}N$) analysis on a sub-set of the population have indicated that the white morph has a more marine-associated diet. Specifically, the white coated morph was found to be enriched in ^{15}N in the fall foraging season compared to the black coated morph (Reimchen and Klinka 2017). Additionally, the isotopic enrichment in foraging niche between white and black morphs was greatest in environments where the mc1r Spirit bear allele was the highest (*i.e.*, white morphs demonstrated the greatest enrichment in ^{15}N across seasons on the island with the highest mc1r allele frequency (Reimchen and Klinka 2017)). Given these results, the authors have suggested that ecological segregation has promoted the persistence of this polymorphism through a multi-niche mechanism (Klinka and Reimchen 2009, Reimchen and Klinka 2017). However, how selection might act on black-coated heterozygotes in the maintenance of this polymorphism has not been confronted with data. Early research reported a deficiency of a heterozygotes at a landscape scale, suggesting potential selection against heterozygotes (Ritland et al. 2001). A recent, more spatially comprehensive, and independent sampling effort and genetic analysis did not identify a deficiency (Chapter 4). Differential selection among genotypes that share the same phenotype of coat colour has been demonstrated in other mammals (Coulson et al. 2011), but the potential role of fitness differences among genotypes with the same coat colour is uncertain in this system.

Stable isotope analysis provides a useful tool to account for and characterize the multi-variate nature of foraging niche space in this coastal bear system. Specifically, $\delta^{13}C$ and $\delta^{15}N$ can differentiate foraging niche by terrestrial vs. marine diet (elevated $\delta^{13}C$ and $\delta^{15}N$ in marine foods) and trophic level (elevated $\delta^{15}N$ with increasing trophic step (Ben-David and Flaherty 2012)). For coastal bears, the landscape of their foraging niche is thought to be constrained among terrestrial plant matter (low $\delta^{13}C$ and $\delta^{15}N$), intertidal resources (high δ^{13}C and lower δ^{15}N), and spawning Pacific salmon (*Oncorhynchus* spp., as indicated by elevated δ^{13}C and δ^{15}N; Hilderbrand et al. 1999, Adams et al. 2017, Service et al. 2018). Although the description of the classical niche concept describes a multivariate construct (*i.e.*, n-dimensional hyper volume; Hutchinson 1957), earlier ecological investigations into intraspecific niche variation, including those of coastal bear populations (Reimchen and Klinka 2017, but see Lafferty et al. 2015), have occurred along only one axis at a time (*e.g.*, prey size, δ^{13}C, δ^{15}N). Such a univariate approach has recently been shown to affect estimates of niche overlap (Friedemann et al. 2016, Pulla et al. 2017, Ingram et al. 2018). In response, a new analytical framework addresses the discrepancy between the commonly estimated univariate niche axis and the multivariate nature of conceptualized niche space by employing multivariate mixed effects models (Ingram et al. 2018). Using this multivariate stable isotope approach to characterize and compare the foraging niche between phenotypes (white vs black coat) and genotypes (black coated heterozygote vs. black coated homozygote dominant) of coastal black bears, we draw inference at both an annual and seasonal temporal scale to confront the hypothesis that a multi-niche model underlies this polymorphism.

Methods and Materials

Study area

Our remote study area consists of coastal islands and adjacent mainland regions of temperate rainforest previously reported to host Spirit bear alleles on the central coast of British Columbia, Canada (Marshall and Ritland 2002; Figure 5.1), an area popularly referred to as the ‘Great Bear Rainforest’. Throughout the study area, black bears have access to spawning salmon in the fall, and plant-based foods (*e.g.*, berries, roots, emergent vegetation, sedges), and intertidal resources (*e.g.*, mussels, crabs, and other shoreline invertebrates) throughout the year. Terrestrial meat contributions to diet are negligible (Adams et al. 2017). Bears in the region are particularly motivated to prey on salmon when they return to spawn in fall months because of their high lipid and protein content, offering a lucrative food source prior to their winter sleep (Hilderbrand et al. 1999, Ben-David et al. 2004). The nutritional benefits from salmon contribute to body condition and litter sizes in coastal bear populations (Hilderbrand et al. 1999, Bryan et al. 2014), though the presence of sympatric, dominant grizzly bears (*U. arctos horribilis*) reduces black bears’ salmon foraging behaviour (Jacoby et al. 1999, Belant et al. 2006, Chapter 3).

Datasets

Owing to sampling limitations related to this very rare polymorphism, we used two spatially complementary, but temporally exclusive, datasets to address our objectives. We refer to them as the *phenotype* and *genotype* datasets. The phenotype dataset compares potential niche divergence between white- and black-coated colour morphs (*i.e.*, GG and pooled AG and AA genotypes, respectively). This dataset consists of individuals collected during sampling by the Province of British Columbia during the fall (September, October) between 1997 to 2000. We used our multivariate approach to examine the ^{13}C and ^{15}N data from these samples, which were first reported in Klinka (2004) and then in Reimchen and Klinka (2017).

The genotype dataset distinguishes between the black-coated heterozygote and black-coated homozygote individuals (*i.e.*, AG and AA genotypes). We collected hair samples via research partnerships with the Gitga'at and Kitasoo Xai'xais First Nations during May and early June, 2012 to 2017, which we genotyped at the mc1r locus (below). Despite six seasons of sampling over ~22,000 km^2, which identified 148 genotyped individuals with sufficient material for segmented isotopic analysis, only five were white-coated homozygotic genotypes. Consequently, they could not be considered in this analysis.

Given that the annual moult of black bears occurs in late spring (~June), the isotopic data (below) correspond to different periods of foraging. Specifically, the spring-collected hair in the genotype dataset reflects foraging over the entire previous year of hair growth. In contrast, the fall hair in the phenotype dataset records only the period of growth up to the point during fall growth when the hair was sampled. As such, the base, mid, and tip segments of these datasets do not correspond with each other. Owing to this fundamental difference, we separately explore hypotheses related to niche divergence between phenotypes and subsequently between genotypes, using near-identical methods applied to these parallel datasets.

Field sampling

Phenotype dataset

The phenotype dataset consists of data that were originally collected from field sampling efforts led by the Province of British Columbia, and were subsequently provided to D. Klinka and T. Reimchen by K. Ritland (Klinka 2004, Reimchen and Klinka 2017). This dataset contains hair samples from 35 individual black bears (17 black coat; 18 white coat). Samples were obtained from passive, non-reward baited hair snags located on bear trails near salmon-bearing rivers (n = 11 hair snags with samples that contribute to this analysis; full details of the Province's approach in Ritland et al. 2001, Marshall and Ritland 2002).

Genotype dataset

The genotype dataset contains hair samples from 143 individuals (30 AG heterozygote, and 113 AA homozygote). Using approximately evenly spaced non-invasive hair snagging sites (mean n = 103; range n = 77-128 per annum) baited with a non-reward bait (Woods et al. 1999, details in Bryan et al 2013, 2014, Adams et al 2017, Service et al. 2018), we annually collected bear hair samples every ten to fourteen days during May and June. We collected hair in the southern half of the study area from 2012 through 2017 (n = 77 sites), and the northern half from 2015-2017 (n = 51 sites). The number of sampling days (n ≈ 30-40 per site per year) was consistent across years. Through boat and helicopter access, we sampled across a range of elevations (0 to 574 m), and in salmon bearing and non-salmon bearing watersheds.

Genetic analyses

For the phenotype dataset that was provided to us, coat colour phenotype was confirmed by identifying the recessive mutation (GG) at the mc1r locus for the white-coated individuals (Ritland et al. 2001). Individual identity was resolved using 8 microsatellites (see full details in Ritland et al. 2001). Sex data were not available in the dataset we acquired.

For the samples contributing to the genotype dataset, we contracted a commercial laboratory, Wildlife Genetic International, to conduct genetic analyses. Information from seven microsatellite loci plus a sex marker revealed species, sex, and individual identity (Wildlife Genetics International, Nelson, BC, Canada). Owing to incomplete descriptions of laboratory protocol in earlier publications, Wildlife Genetic International developed a new approach to discriminate reliably among mc1r genotypes at GG (recessive homozygote, white coat phenotype); AG (heterozygote, black coat phenotype); or AA (dominant homozygote, black coat phenotype) (Wildlife Genetics International, Nelson, BC, Canada; Chapter 4).

Stable isotope laboratory analysis

Phenotype dataset

We obtained the stable isotope values for the phenotype dataset from T. Reimchen (Klinka 2004, Reimchen and Klinka 2017). Reimchen and Klinka used the following approach for stable isotope preparation: for samples for which polarity could be identified (*i.e.*, presence of a follicle) hair was cut into three approximately equal length segments that were processed and analyzed separately (Klinka 2004). Segmented samples were washed and rinsed with a 2:1 mixture of chloroform: methanol to remove oils and surficial debris. After the samples were dried at 60 C for at least 48 hours, the hair was ground and subsampled ~1mg into tin capsules for continuous flow isotope ratio mass spectrometry analysis (University of Saskatchewan, Canada; Darimont and Paquet 2002, Reimchen and Klinka 2017)

Genotype dataset

The genotype dataset's stable isotope laboratory analysis and preparation was near identical to the phenotype dataset with a few exceptions. These include the hair being washed before being segmented, using chloroform: methanol for cleaning instead of chloroform: ethanol, and packaging the hair for the mass spectrometer after cutting it into small segments rather than grinding.

All isotope ratios are expressed as δ values, which report parts per mil (‰), according to the equation:

$$\delta X = ((R_{sample}/R_{standard}) - 1)$$

where X represents ^{13}C or ^{15}N, and R represents the ratio of heavy to light isotopes. Vienna-Pee Dee Belemnite limestone (V-PDB) and atmospheric N_2 are the standard for carbon and nitrogen, respectively.

Isotopic values across individuals and between seasons were variable in both the phenotype and genotype dataset: *i)* phenotype dataset: N‰ mean = 4.36‰, range 0.27 to 14.36 and C‰ mean = -22.84, range -25.52 to -17.41, and *ii)* genotype dataset: N‰, mean = 5.23, range -0.93 to 14.24 and C‰ mean = -22.88, range -26.21 to -17.66).

Statistical analysis of isotopic data

We applied Bayesian multivariate linear mixed effects models (MLMM), with δ^{13}C and δ^{15}N together comprising the response variable, to draw inference from data on potential foraging niche divergence between black bear phenotypes (black & white) and between homozygote black and heterozygous genotypes. Variance-covariance matrices from multivariate linear mixed effects models were visualized as standard ellipses in δ^{13}C and δ^{15}N isotopic space to assess potential niche variation as described by metrics of area and overlap (Jackson et al. 2011, Ingram et al. 2018). In line with previous bivariate isotopic foraging studies, we compared phenotypes and genotypes using “core” foraging niche, which are expected to contain approximately 40% of bivariate isotope data regardless of sample size (Jackson et al. 2011, Lafferty et al. 2015). Additionally, we compared model parameters directly to assess whether the 95% credible intervals for parameters overlapped zero. We analyzed variation in isotopic data using annual and seasonal measures of resource use (*e.g.*, δ^{13}C and δ^{15}N).

We tested our hypotheses related to isotopic niche divergence between genotypes and between phenotypes with Bayesian multivariate linear mixed effect models (MLMM), from which we visualized ellipses. Employing Markov Chain Monte Carlo (MCMC) estimation in the package *MCMCglmm*, we ran 250,000 iterations for each model with a thinning interval of 50 and discarded the first 10,000 iterations as a burn-in (Hadfield 2010). Individual ID was included as a random effect in all models to account for repeated measures. We confirmed suitable mixing and convergence of all models by applying Gelman-Rubic diagnostic tests after running multiple chains with staggered starting points (Brooks and Gelman 1998). All analyses were conducted in R Studio version 3.4.3 (R Core Team 2017).

Annual dietary niche variation

We analyzed annual niche variation with a multivariate Bayesian MLMM model, with individual ID included as a random effect. As all hair was segmented, each individual was represented by three samples corresponding to three time periods. The variances and covariances among individual mean isotope values based on the random effect of ID were interpreted as the multivariate Between Individual Component (BIC) of the population niche. The residual variances and covariances were taken to represent the Within Individual Component (WIC) of the population niche, and the BIC and WIC matrices were added together to estimate the population multivariate Total Niche Width (TNW). The TNW matrix for a population was represented graphically using standard ellipses, and the size of the TNW matrix was calculated as the sum of its eigenvalues (Ingram et al. 2018). Area of the standard ellipse and overlap between phenotypes and genotypes was calculated in the R package *spatstat:utils*. Ninety five percent credible intervals of overlap and area estimates were determined by subsampling every 100th iteration of the Markov Chain Monte Carlo model. As TNW ellipse shape and size could vary within phenotypes and genotypes, overlap percentages could differ when calculated for Ellipse A (*i.e.,* white phenotype or homozygote genotype) in Ellipse B (*i.e.,* black phenotype or heterozygote genotype) versus Ellipse B in Ellipse A. Accordingly, we report two asymmetric overlap metrics for each phenotype/genotype comparison at the annual temporal scale. Additionally, we examined model parameters of phenotype and genotype to assess the magnitude and direction of the effects of predictors on isotope values.

Seasonal dietary niche variation

Seasonal dietary niche variation between phenotypes and genotypes was assessed by building more complex MLMMs that included random effects of landmass (location of detection summarized by island name or ‘coastal mainland’), in addition to individual ID. Landmass was included to account for features of the environment that vary across space and are known to influence foraging niche, but were not directly related to our simplified hypotheses (*e.g.*, competitive environment (Service et al. 2014), mc1r allele frequency (Reimchen and Klinka 2017), salmon availability (Service et al. 2018)). To account for known sexual dimorphism in black bear foraging (Adams et al. 2017), sex was also included as a fixed effect in the genotype models. As above, the Bayesian ellipse estimation by season was used to calculate area and overlap of core isotopic niches between genotypes and between phenotypes. As sex was not a parameter of interest, we fixed the sex parameter’s contributions to the ellipse model at its mean value. To avoid overparameterization, we allowed the TNW area to vary between seasons, but not within phenotypes and genotypes. As such, we report only one overlap value for each season. Finally, we assessed mean model parameter estimates and credible intervals to determine the magnitude and direction of the phenotype or genotype predictors.

Results

Annual dietary niche variation between phenotypes and among genotypes

Ellipses representing annual core Total Niche Width (TNW) did not vary substantially in area between phenotypes (black coat: mean 9.89, 95% CI 7.46-13.90; white coat: mean 10.99, 95% CI 8.41-15.48). Overlap in TNW ellipses between phenotypes, as measured as a percentage of a total area, was 86% (95% CI 47-99%) between black and white coated individuals and 76% (95% CI 41-94%) between white and black-coated individuals (Figure 5.2a). Parameter values from the core MLMM model revealed that phenotype had no influence on isotopic variation (Table 5.1).

We did not detect a difference in isotopic foraging niche area in annual comparisons between genotypes, with an estimated mean TNW area for homozygotes of 10.99 (95% CI 7.87-10.07) compared with an estimated mean TNW area for heterozygotes of 10.70 (95% CI 8.63-13.65) (Figure 5.2b). Similar to phenotypic comparisons, niche overlap was high between genotypes. Homozygote/heterozygote overlap was 87% (95% CI 66-

100%), whereas heterozygote/homozygote overlap was 71% (95% CI 54-90%). Additionally, the core MLMM model did not detect an influence of genotype on isotopic niche at the annual temporal scale (Table 5.1).

Seasonal comparisons

In both the phenotype and genotype datasets, the base (fall) hair segment was the most enriched in ^{15}N and ^{13}C. The tip (spring) segment was consistently the most depleted in both isotopes, and the mid (summer) segment was indistinguishable from the tip (Table 5.1).

We did not detect a difference in the core Total Niche Width (TNW) area across seasons in the phenotype dataset (fall mean: 6.42 (95% CI 2.43-17.68); summer mean 3.41 (95% CI 1.95-5.52); spring mean 3.49 (95% CI 1.93-5.65)). In contrast, seasonal niche TNW area diverged in the genotype dataset; the core niche area was the largest in the fall (genotype mean: 15.01 (95% CI 6.91-27.10)), with a smaller and similarly sized TNW area for both summer (phenotype mean 2.62 (95% CI 1.31-4.55)) and spring segments (genotype mean 3.31 (95% CI 1.49-5.59)).

The white phenotype was moderately more enriched in ^{15}N during the fall season (Table 5.1; Figure 5.3). However, there was no directional pattern in ^{13}C differences between phenotypes across all seasons. Additionally, niche overlap varied across seasons (spring 55% (95% CI 9-87%); summer 75% (95% CI 25-92%); fall (63%; 95% CI 0-77%)).

Our analysis of the genotype dataset revealed that heterozygotes were moderately more enriched in ^{13}C in the base segment of hair that represents fall foraging (Table 5.1). Additionally, though confidence intervals slightly overlapped zero, tip hair segments of homozygotes were modestly enriched in both ^{13}C and ^{15}N compared to heterozygotes (Table 5.1). No directional pattern was observed in the remaining seasons across both isotopes and mean overlap varied across seasons (spring 58% (95% CI 4-94%); summer 32% (95% CI 0-83%); fall 64% (95% CI 26-93%)).

Discussion

Our results suggest that both phenotypes and genotypes diverge modestly in foraging niche at a seasonal temporal scale (Figure 5.3, Figure 5.4). Although no MLMM parameters related to genotype and phenotype were statistically significant at an alpha value of 0.05, the directional trend was consistent towards enrichment for heterozygote genotypes and white phenotypes (Table 5.1). Differentiation was most pronounced in the base hair segment, which represents fall foraging, suggesting the potential role of the arrival spawning salmon underlying this divergence. Across phenotypes and genotypes TNW area was largest in the fall, and smaller in the spring and summer (Figure 5.3, Figure 5.4). This pattern suggests that black bears widen their niche breadth in response to the additional resource availability afforded by salmon, rather than exclusively prey switching to this lucrative resource (Hilderbrand et al. 1999). This result is consistent with recent studies across taxa, which demonstrate that populations of generalist consumers with access to variety of prey types may be comprised of individuals whose dietary niches are smaller subsets of the population’s total niche width (Bearhop et al. 2004, Bolnick et al. 2007).

The small sample sizes inherent with studying rare organisms pose several limitations to our work. Specifically, we are unable to make direct comparisons of the magnitude of niche differentiation across the phenotype and genotype datasets, given the difference in their temporal scope (fall only vs. spring to fall) and period of hair collection (1990s vs. 2010s). Additionally, we acknowledge that our strength of inference and potential model complexity is limited by relatively small sample sizes. These limitations highlight the importance of continued research and monitoring investment of this polymorphism of conservation concern.

Our observed pattern of fall foraging divergence between phenotypes aligns with previous studies on Spirit bear foraging and provides context for the patterns we observe between genotypes. Reimchen and Klinka (2017) provided univariate stable isotope evidence of white morphs on Gribbell Island (where previous genetic work suggested mc1r G allele frequency was highest), demonstrating elevated δ^{15}N across all seasons but with a pronounced departure during fall foraging. This result suggested the role of a multi-niche mechanism in supporting this polymorphism. Additionally, their previous observational and experimental work suggested that the observed niche divergence might be attributed to the reduced evasiveness of salmon when approached by experimentally produced white-bodied models of predators compared with black-bodied models (Klinka and Reimchen 2009). Given the evidence that salmon consumption enhances the fitness of coastal bears (Hilderbrand et al. 1999, Bryan et al. 2014), these combined results support the hypothesis that the white morph could have a greater selective advantage than black coated black bears during the fall. The convergence of our multivariate analysis results with previous univariate, observational, and experimental research (Klinka and Reimchen 2009, Reimchen and Klinka 2017) provides additional support for the role of a multi-niche mechanism in maintaining this rare morph.

The modest foraging niche divergence between genotypes requires broader consideration than camouflage (Table 5.1; Figure 5.4). Specifically, the mechanism of reduced salmon evasiveness proposed to underlie niche divergence between phenotypes does not apply between visually-indistinguishable black-coated heterozygotes and homozygotes (Klinka and Reimchen 2009). Our data do not address mechanisms that may explain the pattern of divergence, but we offer several hypotheses. Owing to the prolonged period of sow-cub association, cubs likely learn about predators, foraging strategies, and feeding sites from their mothers (Gilbert 1999, Mazur and Seher 2008). Accordingly, the modestly elevated marine isotopic signal we observe in heterozygotes might result from a learned behaviour from those black heterozygotes raised by white-coated mothers that specialized on marine diets

(Reimchen and Klinka 2017). Additionally, the proposed ecological and geographic segregation of colour morphs, with black morphs closer to forests and white morphs suggested to occur on average closer to marine habitat and its resources (Reimchen and Klinka 2017), could also contribute to this observed pattern. Specifically, given black bear cubs overlap their mother’s home range (Rogers 1987, but see Schenk et al. 1998), generations of heterozygote cubs from white mothers could be occupying home ranges at the marine interface. This explanation aligns with the recently reported discrepancy between a shoreline-only sampling program that reported higher G allele frequencies (Ritland et al. 2001) compared with a more systematic sampling approach across all elevations (Chapter 4). Finally, divergence between black-coated genotypes could be could also be driven by a process previously not identified in the genetic architecture of the polymorphism. For example, genotypes at mc1r could be related to traits associated with foraging behaviour through pleiotropy or genetic linkage (Allendorf et al. 2016). Accordingly, future research would benefit from the use of modern genomic tools to provide a more comprehensive understanding of the potential ecological associations.

Our results provide novel insight into the mechanisms that may contribute to the maintenance of this rare polymorphism. Broadly, they reaffirm the potential role of a multi-niche polymorphism in maintaining this rare morph. Our analysis provides new detail into the role heterozygotes may play in this maintenance. Although black morphs (pooled heterozygote and homozygote genotypes) were previously assumed to have reduced fitness compared with the white morph (Klinka and Reimchen 2009, Reimchen and Klinka 2017), the potential niche divergence between heterozygotes and black homozygotes genotypes was unexplored. If the elevated marine signatures of heterozygotes relate to fitness in the same way it is considered for white morphs, selective advantage may be highest for white morphs, followed by black heterozygotes, and finally black homozygotes (Table 5.1; Figure 5.4). This structure of selection pressure over certain times and in specific environments (Svardal et al. 2015) would further support the continued maintenance of the G allele.

Despite their potential selective advantage under certain conditions, the persistence of individuals carrying the G allele (white-coated homozygotes and black-coated heterozygotes) has been challenged by numerous historical and contemporary factors. For example, salmon populations in the region, which individuals carrying G alleles appear to have an advantage in accessing, have been substantially reduced from historic levels (Gresh et al. 2000). Additionally, numerous Spirit bears were targeted by hunters before they were protected through regulation, which could have reduced the prevalence of G alleles in this landscape (McCrory 2012). Moreover, the inter-specific competitive environment has recently shifted with the range expansion of grizzly bears onto several islands with the highest G allele frequencies (*e.g.*, over the past 20 years, Service et al. 2014). This change to the ecological community could impact G-carrying individuals through direct predation by larger carnivores (Palomares and Caro 1999) – as well as humans – and reduced salmon consumption (Service et al. 2018).

The insular environment these bears primarily inhabit presents additional challenges to the persistence of the G allele. First, the isolation and restricted area of these island environments can only support small population sizes, a demographic factor that should not in theory support the long-term persistence of this polymorphism in the absence of selection (Traill et al. 2007). Additionally, the reported low values of G allele frequencies should result in a disproportionately high number of G alleles being carried by heterozygotes rather than homozygotes if the population is in Hardy-Weinberg Equilibrium (Allendorf et al. 2016). These two factors combined may be problematic for persistence, as heterozygosity is predicted to be reduced in small populations (Allendorf et al. 2016).

Deeper understanding of intraspecific niche variation can inform conservation strategies that protect phenotypic diversity. Relevant to coastal Spirit bear populations, individuals carrying the G allele (white dominant homozygotes and black coated homozygote) appear to diverge in foraging niche by occupying a more marine-based diet. Accordingly, conservation action may maximize benefit to these bears by targeting initiatives that protect marine resources. Such management decisions are particularly timely against a backdrop of reduced Pacific salmon returns (Price et al. 2017), industrial logging operations in the region’s salmon-bearing watersheds (McCrory 2012), and realized and potential marine contamination risks associated with industrial marine shipping accidents in the area (Heiltsuk Tribal Council 2018). Against this backdrop of cumulative environmental stressors, targeted conservation action that benefits niche diversity can play a significant role in maintaining biodiversity.

Figures and Tables

Table 5.1 Parameter estimates and associated 95% credible intervals for Bayesian multivariate linear mixed models that relate δ^{13}C and δ^{15}N values of coastal black bear hair samples to their phenotype and genotype. Seasonal models include interactions with hair segment as a proxy for foraging season, with tip, mid, and base representing spring, summer, and fall, respectively. All models include individual ID as a random effect to account for the repeated measures structure that results from each bear contributing three hair segments. Both seasonal models include landmass (island name or 'coastal mainland') as a random effect and the genotype model additionally includes sex as a fixed effect. We used δ^{13}C values, black phenotypes, the female sex, AA genotypes, and base hair segments as reference conditions for all models for which those terms apply. Parameters with estimates that did not overlap zero are **bolded**.

Model	*Effect*	*mean estimate*	*U - 95%*	*L - 95%*	*effective n*	*pMCMC*
annual phenotype	**intercept**	-22.98	-23.58	-22.37	4800	**~0.00**
	δ^{15}N	26.76	26.02	27.53	4800	**~0.00**
	phenotype (white coat)	0.20	-0.72	1.03	4575	0.65
	δ^{15}N *phenotype (white coat)	0.68	-0.40	1.77	4800	0.22
annual genotype	**intercept**	-23.07	-23.62	-22.55	4800	**~0.00**
	δ^{15}N	28.04	27.50	28.61	4800	**~0.00**
	genotype (AG)	0.66	-0.40	1.67	4439	0.21
	δ^{15}N *genotype (AG)	0.24	-0.89	1.33	4800	0.67
seasonal phenotype	**intercept**	-21.70	-23.07	-20.36	4800	**~0.00**
	δ^{15}N	28.07	26.06	30.15	4800	**~0.00**
	phenotype (white coat)	0.21	-1.21	1.51	4929	0.77
	seg (mid)	-1.81	-2.85	-0.75	4586	**~0.00**
	seg (tip)	-2.63	-3.65	-1.50	4800	**~0.00**
	δ^{15}N *phenotype(white coat)	1.24	-0.22	2.75	4800	0.09
	δ^{15}N *seg (mid)	-1.68	-2.89	-0.40	4800	0.09
	δ^{15}N *seg (tip)	-1.96	-3.21	-0.70	4800	**0.01**
	phenotype(white coat)*seg (mid)	-0.20	-1.67	1.27	4920	0.78
	phenotype(white coat)*seg (tip)	0.26	-1.22	1.74	4981	0.72
	δ^{15}N *phenotype(white coat)*seg (mid)	-0.80	-2.61	0.93	5022	0.38
	δ^{15}N *phenotype(white coat)*seg (tip)	-0.81	-2.58	1.01	4800	0.37
seasonal genotype	**intercept**	-22.58	-23.56	-21.06	4572	**~0.00**
	δ^{15}N	27.84	26.90	28.87	4800	**~0.00**
	sex (male)	0.54	0.18	0.92	4800	**0.01**

genotype (AG)	1.10	-0.17	2.39	4800	0.09
seg (mid)	-1.49	-2.12	-0.87	4812	**~0.00**
seg (tip)	-2.30	-2.93	-1.68	4800	**~0.00**
δ^{15}N *sex (male)	0.69	0.24	1.10	4800	**~0.00**
δ^{15}N *genotype (AG)	0.77	-0.41	1.98	4800	0.19
δ^{15}N *seg (mid)	-1.12	-1.07	-0.52	4587	**~0.00**
δ^{15}N *seg (tip)	-1.60	-2.15	-1.01	4800	**~0.00**
genotype (AG)*seg (mid)	-0.31	-1.42	0.93	4800	0.62
genotype (AG)*seg (tip)	-0.92	-2.10	0.15	4800	0.11
δ^{15}N *genotype (AG)*seg (mid)	-0.43	-1.45	0.64	4800	0.41
δ^{15}N *genotype (AG)*seg (tip)	-0.86	-1.92	0.17	4800	0.10

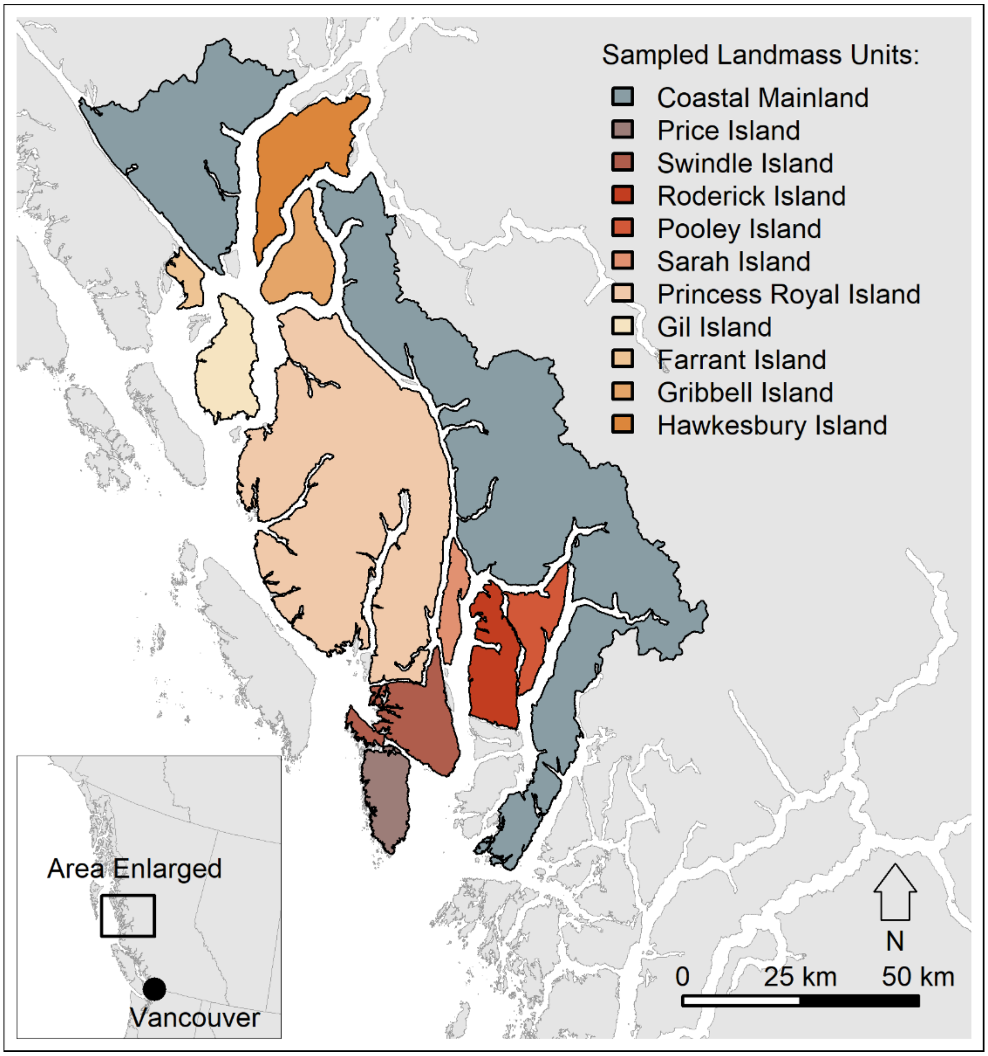

Figure 5.1 Study area as defined by the extent of sampled “landmass units” in coastal British Columbia, Canada

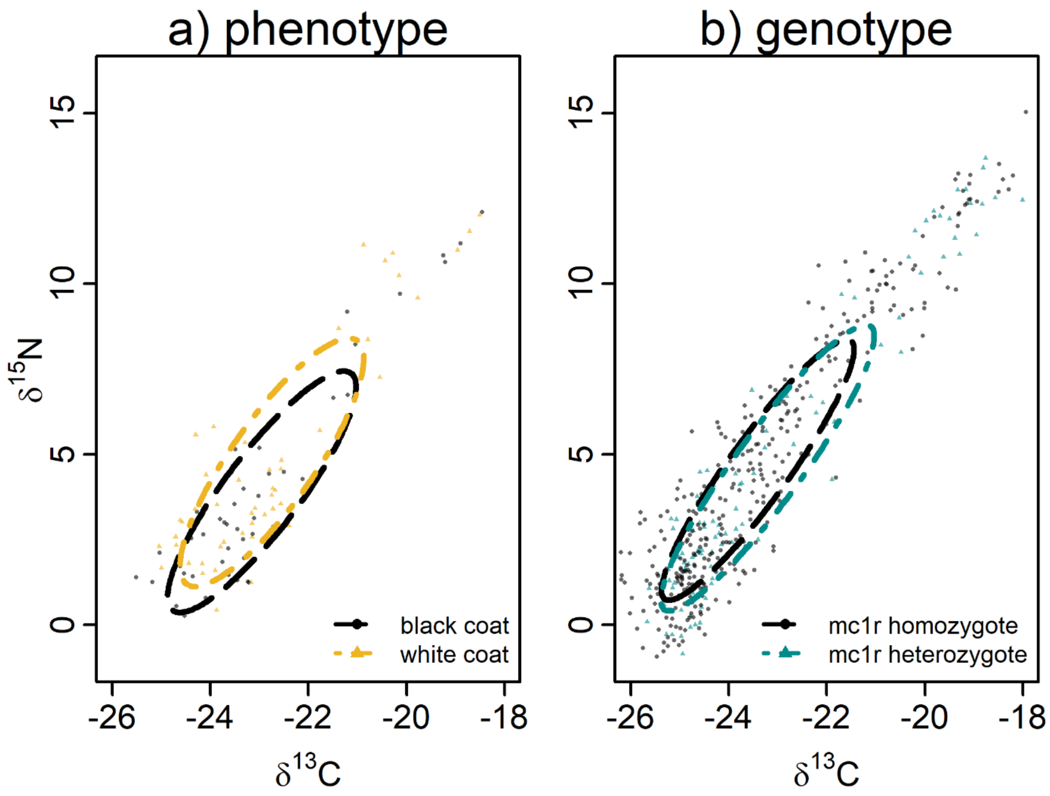

Figure 5.2 Annual δ^{13}C and δ^{15}N isotopic foraging niche variation in coastal black bears (*Ursus americanus kermodei*) between a) coat colour phenotype (n = 35) and b) mc1r dominant homozygote and heterozygote genotypes (n = 143). Ellipses represent core Total Niche Width (TNW) as inferred by a multivariate repeated measures Bayesian linear mixed effect models. Points are raw data observations of tip, mid, and base hair segments of each detected individual.

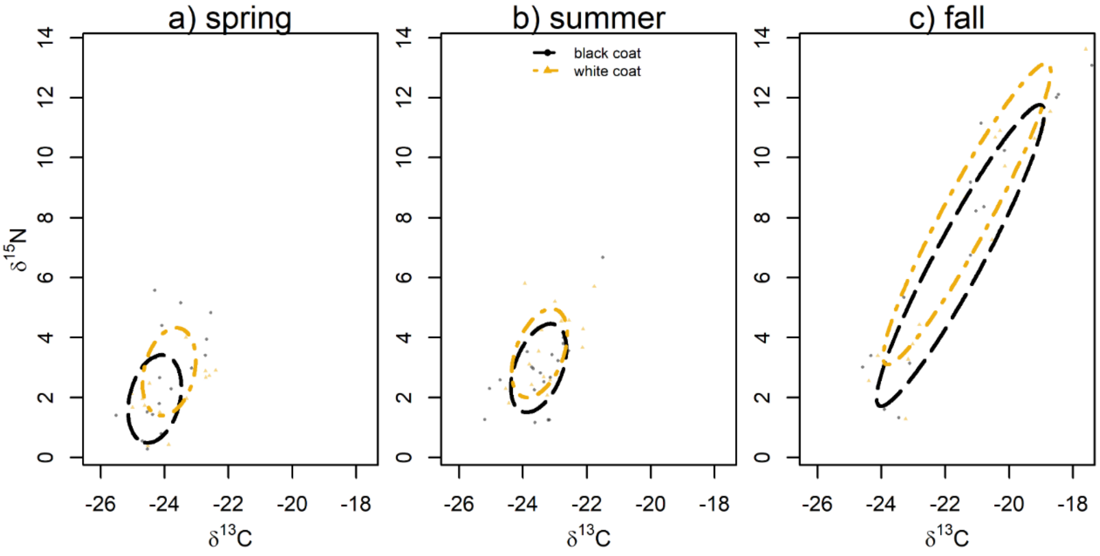

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Figure 5.3 Seasonal isotopic foraging niche variation ($\delta^{13}C$ and $\delta^{15}N$) in coastal black bears (*Ursus americanus kermodei*) between coat colour phenotypes (n = 35) during a) spring (tip hair segment) b) summer (mid segment) and c) fall (base segment). Ellipses represent core niche area as inferred by a multivariate repeated measures Bayesian linear mixed effect models. Semi-transparent black and yellow points are raw data observations of tip, mid, and base hair segments of each detected individual.

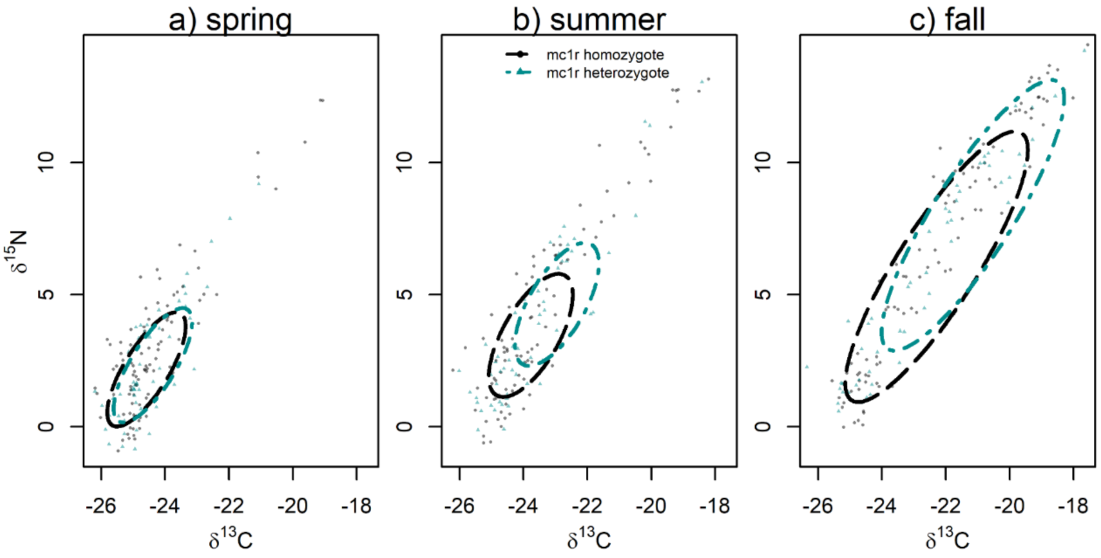

Figure 5.4 Seasonal isotopic foraging niche variation (δ^{13}C and δ^{15}N) in coastal black bears (*Ursus americanus kermodei*) between dominant homozygote and heterozygote mc1r genotypes (n = 143) during a) spring (tip hair segment), b) summer (mid segment) and c) fall (base segment). Ellipses represent core niche area as inferred by multivariate repeated measures Bayesian linear mixed effect models. Semi-transparent black and teal points are raw data observations of tip, mid, and base hair segments of each detected individual

Chapter 6 Conclusion

Key Findings and Opportunities for Future Research

The research in this dissertation identified several key findings from testing hypotheses related to spatial and/or dietary niche variation at multiple levels of biological diversity. As I demonstrate below, the results from each chapter have conceptual contributions to ecological and evolutionary theory and implications for applied policy. In addition, I identify useful avenues of future research for each chapter.

Chapter 2

Summary

My second chapter applied a combined approach of western scientific methods (*i.e*, using remote camera data, genetic data) and traditional and local ecological knowledge (TEK/LEK) to document a westward range expansion of grizzly bears (*Ursus arctos*) onto several coastal islands. I found that TEK/LEK and western scientific methods provided complementary spatial and temporal resolution and primarily affirmed one another.

Conceptual contributions

These results highlight the rapid pace by which spatial niche can shift, emphasizing the importance of consistent monitoring to detect change. My findings align with global patterns of range shifts across taxa in response to environmental change, that have resulted in latitude-, elevation-, and longitude-based distributional shifts (Chen et al. 2011, Bellard et al. 2012, Lenoir and Svenning 2015). This analysis suggests that in this system, coastal grizzly bear range expansion has occurred relatively recently - within the past two decades. Comparable rapid range expansion, with similarly uncertain ecological consequences, has occurred in the northern extent of grizzly bears' range in the Arctic region of Canada, where grizzly bears, black bears, and polar bears (*Ursus maritimus*) are now newly sympatric due to northward grizzly bear range expansion (Clark et al. 2018).

Given range constraints are driven by biotic, abiotic, or dispersal factors (Soberon 2009), the novel range shift of coastal grizzly bears suggests a change in one of these dimensions. It seems unlikely that dispersal capabilities of grizzly bears have changed over this time period, therefore these results suggest that a recent change in biotic or abiotic conditions in the region may be contributing factors. Regardless of the motivating drivers of the range shift, these results demonstrate that grizzly bears are in fact able to reproduce in landscapes that were previously assumed to be outside of their spatial niche.

This work adds to the growing body of literature that advocates for and highlights the value of triangulating between western science and traditional and local ecological knowledge. Increasingly, interdisciplinary approaches that combine various knowledge sources (*e.g.*, scientific, LEK/TEK) are being applied beyond distribution studies

(Chapter 2, Carter and Nielsen 2011) to offer novel insight into abundance (Brittain et al. 2018), diversity (Polfus 2016) and behavioural (Bonta et al. 2017) research in ecology. Such combined approaches can offer higher resolution data than either method could afford alone, while simultaneously aiding the potential success of conservation outcomes by increasing the perceived validity of research from community members and conservation practitioners alike (Bennett et al. 2017).

Applied contributions

The policy implications of this research relate to the recently agreed upon Great Bear Rainforest Land Use Order. This legal agreement mandates protection of "Class 1 and 2" habitat in land-use planning (*i.e.*, highest habitat value and second highest habitat value for bears, respectively; (MacHutchon 2007)) for all regions within grizzly bear distribution in the Great Bear Rainforest as defined by Grizzly Bear Population Units (GBPUs; Austin et al. 2004). The protection of habitat for grizzly bears on islands was identified as a conservation priority by the Kitasoo/Xai'xais Nation because Class 1 and 2 habitat, and associated protection during forestry and land-use management, was unaccounted for on islands in the region because they appeared outside of the official grizzly bear range. Previous efforts by the Kitasoo/Xai'xais to address the range expansion were not successful; the convergence of LEK/TEK and scientific methods allowed Nation-driven conservation priorities to come to negotiation with provincial managers (pers comm. D Neasloss). As such, this research led to Kitasoo/Xai'xais leadership in negotiations (2014 to 2018), for which I lead the technical contributions, on the westward range expansion of the Kitlope-Fjordland GBPU. We subsequently mapped Class 1 and 2 habitat on Swindle, Princess Royal, and Sarah Islands, and the Don Peninsula, which will inform land-use planning and forestry by both the Kitasoo/Xai'xais and the provincial government.

Future directions

Although this work did not address drivers of the observed range expansion, future work could empirically confront factors that might be contributing to this distributional change. I speculate that some combination of changes in salmon availability via both abundance and diversity (Chapter 3, Price et al. 2017), bear density (Artelle et al. in revision, Mattson et al. 2005), and alternative food resource availability in response to climate (Deacy et al. 2017) may be responsible for this trend. As grizzly bears are known to avoid human activity (Shackelford et al. 2017, Lodberg-holm et al. 2019), a contributing factor to this range shift could be the sequential depopulation of people from islands through the closure of canneries, mills, mines, and the abandonment of traditional village sites in response to the small-pox epidemic over the past two centuries. This depopulation may have provided a novel opportunity for bears to colonize islands without risks previously associated with human settlement. With increased and continued investment in the monitoring of this range expansion and hypothesized drivers, these hypotheses could be tested at a landscape scale.

Additionally, future research could identify the potential niche variation of individuals on the range edge. Across taxa, individuals at the leading edge of a range expansion have demonstrated distinct morphological, physiological, and behavioural traits that enhance fitness in the challenging environments encountered at range margins (Krause et al. 2016). Several observations of local knowledge holders since 2016 suggest grizzly bears that now occupy islands use intertidal food resources extensively, as opposed to their mainland counterparts. Specifically, island grizzly bears have been observed fishing for sea urchins (assumed *Strongylocentrotus franciscanus*; Figure 6.1; pers comm. Ernest Mason III and Sandie Hankewich), a behaviour that has not previously been observed in this species. Future work could use stable isotope analysis to test this hypothesis with data on foraging niche. To partially address the potential ecological consequences of this expansion, I explore the impact of grizzly bears on the annual salmon consumption of black bears in Chapter 3.

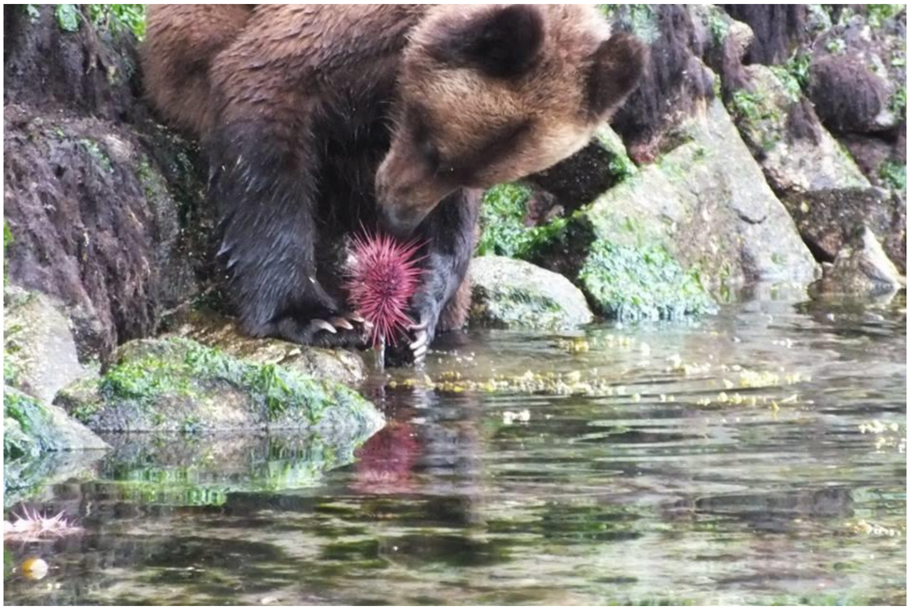

Figure 6.1. Grizzly bear foraging on red sea urchin (*Strongylocentrotus franciscanus*) on Swindle Island, British Columbia. Photo credit with permission: Ernest Mason III.

Chapter 3

Summary

Chapter 3 addresses the relative importance of resource availability and competition on foraging niche in black bears. I found that the presence of grizzly bears reduces annual black bear salmon consumption by approximately 40%. Salmon diversity also had a large and positive effect on black bear foraging. For example, the same amount of salmon biomass across four species (instead of one big run of single species) allows black bears to approximately triple their salmon consumption each year.

Conceptual contributions

This chapter makes novel conceptual contributions towards understanding dietary niche in response to resource waves (via species diversity), competitive environment, and their interaction. Previous research has documented benefits to dominant competitors who have access to resource waves (Deacy et al. 2018). To complement this work, my research presents new contributions on the benefits of a resource diversity to food consumption, and presumably fitness (Hilderbrand et al. 1999, Costello et al. 2009), of a subdominant consumer. The interaction I detected between the presence of a dominant competitor (grizzly bears) and resource waves (salmon diversity) was expected, as low diversity systems result in resources being clustered in space and time, conditions under which smaller bodied competitors presumably do poorly. By contrast, increased salmon species diversity distributes resources over space and time, a foraging context that could reduce interference competition. However, this research failed to find support for this hypothesis. Rather, the dietary consequences of black bears sharing watersheds with grizzly bears was consistent with previous research demonstrating that across taxa, larger-bodied species tend to dominate interference competition (Peters 1985, Palomares and Caro 1999). Notably, salmon diversity did not lessen the effect of grizzly bears on black bear salmon consumption, suggesting that access to resources waves did not diminish this pattern. More broadly, this research offers additional support to the expanding literature highlighting the relevance of resource waves to the diet and movement of consumers (Ruff et al. 2011, Schindler et al. 2013, Deacy et al. 2016, 2018).

Applied contributions

If managers want to maintain opportunities for optimal salmon consumption by bears, then maintaining the diversity of salmon species present in watersheds is important. In Canada, the Department of Fisheries and Oceans' "Wild Salmon Policy" explicitly highlights the need to allocate salmon to consumers other than humans (Price et al. 2017), and this research suggests that to do so, salmon species diversity, and not only abundance, should be considered in fisheries allocations. Retaining healthy populations of diverse salmon species requires safeguarding smaller, less commercially important salmon species, which are currently often neglected in federal salmon management (Price et al. 2008, 2017). Future management towards sustained salmon diversity will require substantial re-investment of salmon monitoring, which has been dramatically reduced (Price et al. 2017). Such an investment would allow the identification of river systems may be contributing disproportionally to temporal and spatial foraging opportunities for terrestrial consumers of salmon.

Future directions

Future research would benefit from addressing how intraspecific diversity in salmon phenology may be interacting with these results. The benefits of population-level phenological diversity have been demonstrated in multiple consumers, wildlife (Ruff et al. 2011, Bentley et al. 2012, Deacy et al. 2018), and humans alike (Nesbitt and Moore 2016). However, the study area currently lacks reliable run timing data for salmon populations (pers comm. Doug Stewart; Jason Moody). Given the importance of salmon population-level diversity in other geographies, future investment and subsequent empirical investigation would provide useful insight into the ways by which salmon management might benefit terrestrial consumers. This may be especially relevant as climate could affect alternative food resources (*i.e.*, berries, forbs), salmon run timing, and subsequently the strength of consumer relationships with salmon (Deacy et al. 2017).

Chapter 4

Summary

In Chapter 4, I explore landscape level mc1r allele frequency in relation to previous research (Ritland et al. 2001) and current protected area configuration. Additionally, I apply spatial capture recapture methods to assess preliminary estimates of black bear density in combination with allele frequency to emerge with estimates of total Spirit bear population size. Broadly, landscape level allele frequency is lower than previously reported, and approximately 50% of allele frequency hotspots fall outside protected areas. In contrast with previous assessments, this research failed to detect a heterozygote deficiency and instead observe that all populations are in Hardy Weinberg Equilibrium.

Conceptual contributions

This work provides conceptual insight into the maintenance of the rare white coat polymorphism in black bears. Previous research (Ritland et al. 2001) suggested a heterozygotic deficiency, which lead to additional population genetic modelling work to consider complex situations by which this pattern could hold true, assuming a balanced polymorphism (Hedrick and Ritland 2011). If these populations are in fact in Hardy Weinberg Equilibrium, the improbable constraints on the previous models (*i.e.*, 50% positive assortative mating) can be relaxed. I note that although this dissertation tests the hypothesis of potential heterozygotic deficiency with data, the hypothesis emerged from the work of Reimchen and Klinka (2017), who predicted that the observed pattern of a heterozygotic deficiency in Ritland et al. (2001) was a vestige effect of a shore-based sampling approach, rather than a true characteristic of the population.

Applied contributions

Several potential policy implications emerge from this work. First, these results highlight gaps in the spatial protection of the Spirit bear allele in the Great Bear Rainforest, a management region inspired in part by the conservation of this rare colour morph. Additionally, the estimated black bear population sizes and allele frequencies produced Spirit bear population estimates that were lower than previously presented in the literature (Ritland et al. 2001). Although the formal process of gazetting protected areas as part of the Great Bear Rainforest Land Use Order has been completed, alternative options of protection exist that could fill these conservation gaps. Specifically, regions of higher allele frequency could be considered in planning industrial logging through zoning as part of the Landscape Reserve Design (LRD) process. Alternatively, these regions could be conserved through (re)emerging forms of protection that includes Indigenous governance such as Indigenous Protected Areas (Garnett et al. 2018, Porten et al. 2019).

Future directions

Future work can build upon ongoing monitoring efforts to characterize population density and allele frequency in coastal black bear populations. Precision of populations estimates could be substantially improved by increasing the number of sampling rounds, and decreasing trap spacing (Sollmann et al. 2012). Additionally, the continued monitoring of allele frequency would be useful in detecting potential changes over time and could test whether this is a balanced polymorphism as presumed. This inquiry could be timely given the small population size of Spirit bears, whereby the removal of individuals via fur trading and museum collections (1800's to the 1960's; n=~30-; (McCrory 2012)) could have reduced the resilience of this polymorphism.

Chapter 5

Summary

I explore the dietary niche variation between phenotypes (black coated vs white coated) and genotypes (black coated heterozygotes vs black coated homozygotes) in the fifth chapter of my dissertation. As previously demonstrated by Reimchen and Klinka (2017) in a complementary analysis framework, I observe a moderate enrichment in N^{15} signatures of the white phenotype in the base hair segment that represents fall foraging. Although the results are modest, this multivariate approach also suggests a slight enrichment in C^{13} in the fall season for black-coated heterozygotes compared to black-coated heterozygotes.

Conceptual contributions

These results provide insight into the potential mechanisms that may be supporting the continued existence of the rare white-coat polymorphism in coastal black bear populations. The divergence of the stable isotope signatures between phenotypes supports previous research suggesting the role of the multi-niche polymorphism in maintaining the white phenotype (Klinka and Reimchen 2009b, Reimchen and Klinka 2017). If the elevated marine signatures of heterozygotes relate to fitness in the same way that is presumed for white morphs, selective advantage may be highest for white morphs, followed by black heterozygotes, and finally black homozygotes. This structure of selection pressure would further support the continued prevalence of the G allele. Similarly, research suggests that wolves (*Canis lupus*) have differential fitness between black-coated genotypes that are visually indistinguishable (Coulson et al. 2011). As such, this work contributes to the very limited literature of empirical examples of the role heterozygotes may be playing in the maintenance of polymorphisms.

Applied contributions

These results carry several applied implications. First, the elevated N^{15} and C^{13} isotopic signatures suggest marine resources are disproportionately used by individuals carrying the G allele. Management that seeks to preserve this morph may want to consider ensuring access to marine resources (*i.e.*, healthy salmon stocks, uncontaminated intertidal resources). Second, although white-coated black bears are protected from hunting, black-coated heterozygotes and homozygotes are not (McCrory 2012). Given the apparent tendencies to forage at the marine interface demonstrated by black-coated heterozygotes, they may be more susceptible to hunting due to hunters' increased access and visibility along the shoreline compared with forested landscapes. Such inadvertently targeted exploitation could negatively impact the frequency of the mcr1 allele.

Future directions

Future work would benefit from investments into genomic approaches and continued monitoring. Employing a genomic approach could allow inference to go beyond phenotype/genotype-niche associations with the exploration of potential signatures of selection at mc1r (Hedrick 2006). Additionally, genome-based analyses could address the possibility that genotypes at mc1r could be related to additional traits associated with foraging behaviours through pleiotropy or genetic linkage (Hedrick 2006). Even in the absence of genomic investigation, continued investment in monitoring could explore additional ecological relationships between genotypes, food resources, and competitive environments. For example, with more data it would be possible to address whether the recent movement of grizzly bears onto islands (Chapter 2) with high frequencies of Spirit bears (especially on Princess Royal Island, which supports elevated mcr1 allele frequencies and numbers of grizzly bears) has impacted the observed niche divergence of white morphs. Additionally, the impact of variable salmon resource availability (via abundance and diversity) on phenotypic/genotypic niche divergence could also be explored.

Concluding Remarks

My dissertation highlights the value afforded to ecological inquiry and conservation by transcending conventional boundaries in the consideration of marine-terrestrial ecosystems and the inclusion of multiple knowledge systems in the research process. As an applied scientist, I found that the lens of niche variation provides a useful perspective and suite of tools for uniting these themes that are often siloed into independent inquiries.

Marine-terrestrial ecosystems in research and in management

Considering the linkages between marine and terrestrial ecosystems at the coastal margin is important to guide conservation action for organisms that rely on the resources offered by both environments. Although grizzly and black bears occur elsewhere in the world, including many places without access to marine resources (Hatler et al. 2008), the niche variation revealed in this dissertation is shaped by interactions with the marine environment (Chapter 3, 5). Similar patterns of marine subsidies influencing the population niche of terrestrial species' have been shown across taxa. Indeed, previous research has shown that coastal humans (Mckechnie et al. 2013, Jackley et al. 2016), wildlife (Christie and Reimchen 2008, Fox et al. 2018), and plants (Hocking and Reynolds 2011) alike are heavily subsidized by nutrients from the marine environment. Accordingly, the dietary niche variation observed across multiple levels of biological organization in this dissertation (Chapter 3 and 5) suggests that research and policies that consider terrestrial-marine linkages may best benefit intraspecific diversity.

Current administrational separation of land and marine resource management departments into separate agencies (*e.g.*, in Canada, lands and marine, via Provincial FLNRO and Federal DFO, respectively) may not best provide for the many species that exist in coastal environments. In British Columbia, fisheries management was formally separated from the land when BC joined the Dominion of Canada in 1871 (Harris 2001). The arbitrary severing of these connected ecosystems for legal jurisdiction (Harris 2001) was in direct contrast with longstanding Indigenous legal systems that holistically managed regions encompassing marine- terrestrial connections (Harris 2001, Porten et al. 2019). The current disconnect in governance of marine and terrestrial environments has been suggested to reduce efficacy of gazetted terrestrial protected areas (Darimont et al. 2010), unravel predator-prey relationships inland that rely on marine nutrient inputs (Darimont et al. 2010), and has had detrimental impacts on human Indigenous populations who have been separated from the legal jurisdiction of their local fisheries (Harris 2001). A beneficial solution for both local people and wildlife may exist in resource management strategies that can consider coupled marine and terrestrial environments. Precedent for this solution already exists in the place-based, decentralized forms of Indigenous governance that inherently reflect the linkages among ecosystems (Harris 2001). This holistic policy approach may benefit the many “terrestrial” organisms whose life and evolutionary histories are defined by marine subsidies (Ben-David et al. 1997a, 1997b, Darimont et al. 2009, Station et al. 2013).

Bringing together multiple knowledge systems and research approaches

Conservation research can benefit from recognizing and valuing humans as a part of ecological systems. Throughout my dissertation, this integration took several forms. First, my work benefited from multiple ways of knowing, including the coming together of traditional and local ecological knowledge (TEK/LEK) and western scientific approaches. Such an integrated approach is increasingly being applied in ecological research and management because it can prioritize conservation assessments and strategies across taxa and ecosystems, with greater spatial and temporal resolution than either method could offer alone (*e.g.*, Brittain et al. 2018). For example, TEK has been applied in combination with genetic methods to identify caribou (*Rangier tarandus*) diversity that reflect units of conservation distinction in Canada’s north (Polfus 2016). Whereas the majority of ecological research is still conducted through a scientific methodology, the acknowledgement of local peoples as both knowledge holders of and participants in local ecosystems enriches research that takes a multi-method approach.

Second, using a collaborative and community-engaged approach to develop research questions can ensure that research makes both conceptual and place-based contributions to ecology and conservation (Adams et al. 2014, Berkes 2004). By centering around this ethic, I was able to more directly translate research outcomes from my dissertation into policy through direct engagement with Indigenous governments from the beginning of the research process (Adams et al. 2014). The community-engaged ethos of this work also allowed for bi-directional process values (*i.e.*, emergent properties of learning and relationships developed through the research process that were not part of the original goals of the project) that emerged from conducting field work on the land together, and subsequently, resulted in shared capacity for both scientists and community. For example, the youth research internships this research provided exposed community members to more diverse career options and provided opportunity to gain more familiarity of their territories, while academic colleagues and I benefited from informally shared knowledge on culture, place, and ecology.

More broadly, including Indigenous people in environmental research and decision making is critical to effective policy development and is a necessity for just engagement in conservation processes (Houde 2007, Ban et al. 2018). As conservation fundamentally includes social dimensions (Bennett et al. 2017), inclusive conservation approaches can yield effective protected areas and wildlife policies (*i.e.*, community-led monitoring/enforcement programs in remote geographies, community investment in providing knowledge (Polfus 2016, Bennett et al. 2017, Ban et al. 2018)). Further, United Nations Declaration on the Rights of Indigenous Peoples (UNDRIP) highlights the requirement of “free and informed consent prior to the approval of any project affecting their lands or territories and other resources”, a statement which encompassed both research and conservation activities (Ban et al. 2018). As such, the alignment of social justice and conservation research requires the consent, and ideally, involvement and collaboration between Indigenous communities and scientists. My approach in this dissertation provides a modest example of how research can be done through the principles of respect, inclusion, and collaboration.

Scientists often struggle to connect with policy makers to translate their results into evidence-based policy (Likens 2010). The community-engaged research approach applied in my dissertation is timely; applied research and evidence-based decision making are emerging priorities in Canada and beyond (Bailey et al. 2016). As

Indigenous governments in Canada continue to (re)assert their authority over the stewardship of their territories, and as scientists and decisions makers are called upon more to collaborate, my research and that of my colleagues is uniquely situated to inform place-based resource management in the territories of the Indigenous governments with whom we collaborate. The opportunity to actively contribute to place-based resource management stems from direct and productive relationships with policy makers, an immense privilege that many scientists are not afforded.

Niche and conservation

As global biodiversity continues to erode in response to human-induced environmental change, supporting resilient, diverse populations is of critical importance. Increasingly, anthropogenic disturbance affects the availability of food and space on the landscape, disrupting interactions in and among species (Mcgill et al. 2015, Tucker et al. 2018). In addition, humans are often active competitors for the same resources as consumers (Darimont et al. 2015, Ponchon et al. 2018). Conserving biodiversity that is resilient to compounding environmental stressors will require diverse approaches of ecological inquiry (Berkes 2004). Niche, by definition, provides insight into the conditions an organism requires to thrive (Chase and Leibold 2003). Employing the conceptual niche framework can offer novel insight into the patterns of variation across multiple scales of biological diversity, and subsequently, the biotic or abiotic requirements that support this diversity. The niche concept provides deeper understanding of the ecological and evolutionary mechanisms that support diversity, and if leveraged for applied purposes, offers a road map of how to best conserve organisms and the resources they require in era of increasing environmental change.

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Appendix A: Supporting Information for Chapter 2

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Indigenous Knowledge and Science Unite to Reveal Spatial and Temporal Dimensions of Distributional Shift in Wildlife of Conservation Concern

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Abstract

Range shifts among wildlife can occur rapidly and impose cascading ecological, economic, and cultural consequences. However, occurrence data used to define distributional limits derived from scientific approaches are often outdated for wide ranging and elusive species, especially in remote environments. Accordingly, our aim was to amalgamate indigenous and western scientific evidence of grizzly bear (*Ursus arctos horribilis*) records and detail a potential range shift on the central coast of British Columbia, Canada. In addition, we test the hypothesis that data from each method yield similar results, as well as illustrate the complementary nature of this coupled approach. Combining information from traditional and local ecological knowledge (TEK/LEK) interviews with remote camera, genetic, and hunting data revealed that grizzly bears are now present on 10 islands outside their current management boundary. LEK interview data suggested this expansion has accelerated over the last 10 years. Both approaches provided complementary details and primarily affirmed one another: all islands with scientific evidence for occupation had consistent TEK/LEK evidence. Moreover, our complementary methods approach enabled a more spatially and temporally detailed account than either method would have afforded alone. In many cases, knowledge already held by local indigenous people could provide timely and inexpensive data about changing ecological processes. However, verifying the accuracy of scientific and experiential knowledge by pairing sources at the same spatial scale allows for increased confidence and detail. A similarly coupled approach may be useful across taxa in many regions.

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Introduction

Distributions of organisms are shaped and re-shaped over geological and ecological timescales. Broadly structured by a suite of natural processes and their interactions, changes to species distributions (hereafter 'range shifts'), can be driven by abiotic factors (*e.g.*, CO_2 enrichment, nitrogen deposition, climate; [1]), biotic processes (*e.g.*, competition and facilitation [2]), and dispersal capability [3,4]. In recent history, distributional shifts have often been rapid and associated with human-caused drivers. Causes include climate change, habitat modification, over-exploitation, persecution, introduction of exotic species, and re-introduction of native species (*e.g.*, [5–10]). The increased pace of range shifts caused by humans can impose ecological effects on other species, communities, and ecosystems by exposing recipients to novel predation pressure, competition, and diseases [11]. For example, the rapid, human-aided range expansion of the brown tree snake (*Boiga irregularis*) to Guam decimated native bird populations, which in turn reduced the reproductive success of vertebrate-pollinated native plant species [12].

Given such potential impacts, current and accurate knowledge of species distributions comprises a fundamental and important dimension in conservation management. For example, many policy-relevant processes, such as protected areas design, mapping of critical habitat, and land-use planning require distributional data [13,14]. Moreover, current distribution information can also inform proactive conservation intervention in the face of climate change and other stressors (*e.g.*, [10,15]). More generally, detecting shifts in species' distributions can signal underlying ecological changes within an ecosystem, providing managers with early insight that changes might be occurring in other species and communities.

Identifying contemporary ecological change requires knowledge of the past. A complementary methods approach that combines traditional and local ecological knowledge with conventional scientific methods can provide data that not only offer detailed occurrence data across large areas but also over long time periods [16]. Traditional ecological knowledge (TEK) of indigenous people is transmitted through generations and revolves around a cumulative body of knowledge, practice, and belief surrounding the relationships of living and nonliving beings with their environment and one another [17]. Local ecological knowledge (LEK), often but not exclusively associated with indigenous people, also provides information about ecosystem change, but is gained from observations over lifetimes and not via inter-generational transmission [18]. However, in practice the distinction between TEK and LEK is often imprecise as they may share many similarities [18,19]. In contrast, wildlife science uses a variety of empirical techniques that span differing temporal and spatial resolutions and can provide detailed and quantitative information on populations and individuals [18]. Such data, however, are often very expensive to acquire and temporally and spatially limited. Accordingly TEK/LEK data – potentially spanning decades or longer – can be summarized and analyzed to yield information on elusive species across large areas that are otherwise too expensive or difficult to monitor with conventional scientific tools (*e.g.*, [20,21]). Employing TEK/LEK and wildlife science approaches together might yield more comprehensive and detailed information about changes over time and space than either method alone [22,23]. Importantly, incorporating TEK/LEK into ecological research also can facilitate the engagement of communities [24,25]. Social research components of LEK and TEK necessarily include local people and affirms the importance of their contributions [[24]]; in turn, a collaborative methods approach can be a critical first step in establishing more collaborative management [17,19,25].

Grizzly bear (*Ursus arctos horribilis*) distribution on the remote and now sparsely populated central coast of British Columbia (BC), Canada, provides an ideal system to examine the temporal and spatial components of potential range shifts using a complementary methods approach. The provincial government's current management boundary, delineated as the western (*i.e.*, seaward) extent of the so-called Grizzly Bear Population Units (GBPUs), is the spatial scale at which grizzly bears are managed for hunting, habitat protection, and human-wildlife conflict [26]. Whereas formalized species accounts do not include details of coastal grizzly distribution at an appropriate spatial scale for this study [27], the current management boundary suggests grizzlies are functionally absent from all but five of the dozens of islands in the vast archipelago ([26,28–32]; T. Hamilton, BC Ministry of Environment, pers. comm; Figure 1). In contrast, local people in the area, including several First Nations communities that still rely heavily on subsistence activities and travel across their expansive Territories, now commonly observe grizzlies on islands. If present, subsistence hunters and fishers are likely to sight and remember large-bodied, diurnal and iconic wildlife, like grizzly bears.

Our overarching aim was to combine TEK, LEK, and western scientific methods (human-caused mortality records, non-invasive genetic sampling, and remote camera data) to record grizzlies on islands and detail a potential range shift. Understanding the potential colonization and occupancy of grizzly bears onto islands in the region has significant conservation implications because these animals possess tremendous ecological, cultural, and economic importance in this area and indeed, where they still exist throughout their global range (*e.g.*, [33–36]). More broadly applicable to other areas and taxa, we also test the hypothesis that data from each method yield similar spatial and temporal patterns. Finally, we explore how these approaches reveal complementary spatial and temporal dimensions of data and emerge with broadly applicable conclusions relevant to many systems.

Methods

Study area

The islands and nearby mainland of the central coast of BC (8800 km^2) occur within a nearly road-less and now sparsely populated region extending from its southern boundary of Calvert Island (51.58° N, 127.81° W) north to Princess Royal Island (53.21° N, 128.05° W) (Figures 1a & 1b). A complex matrix of landmasses, the central coast as a whole is composed of mainland valleys divided by extensive fjords and various sized islands ($<$ 1 km^2 to $>$2200 km^2) separated by tidal waters [37]. Eighteen major islands (*i.e.*, greater than 45 km^2) were included in the study area. The closest major island to the mainland (Yeo) is separated by 230 m of tidal water. The Coastal Western Hemlock biogeoclimatic zone dominates low elevations of the region [38]. Potential foods for bears are well distributed across the coastal mainland and islands and include spring (sedges and forbs), summer (berries), and fall (spawning salmonids) resources [39,40]. Since colonization by Europeans, most people in the area now live in the communities of Bella Bella (Heiltsuk Nation, population ~2200) and Klemtu (Kitasoo/Xai'xais Nation, population ~400). Our study area comprised four islands (of five) now recognized by the current management limit and 14 islands beyond this management range (Figures 1 & 2; Table 1).

Data types

Interview data. Ethics Statement: The interview component of this study was approved by the Human Research Ethics Board at the University of Victoria (Victoria, BC, Canada - Protocol # 12-385), Heiltsuk Integrated Resource Management Department, and Kitasoo/Xai'xais Integrated Resource Authority. All participants provided written informed consent. Field sampling was approved by the Heiltsuk Integrated Resource Management Department, Kitasoo/Xai'xais Integrated Resource Authority, and BC Parks.

We conducted 22 LEK and seven TEK interviews using a "snowball sampling" method [41]. For TEK interviewees, the Kitasoo/Xai'xais Stewardship Department and the Heiltsuk Integrated Resource Management Department recommended initial participants, who hold traditional oral and observational history knowledge, and who in turn suggested additional experts to interview (University of Victoria Human Research Ethics Approval # 12-385) [22,42]. The LEK participant pool included mostly indigenous (19 of 22) candidates, including subsistence and commercial fishers, hunters, eco-tour operators, salmon counters, bear viewing guides, and biologists.

Using adapted general guidelines of TEK/LEK data collection, we guided participants through target questions while also recording additional comments [22]. To assess historical grizzly distributions, comprising occupancy over the past century and beyond, we asked TEK participants about their experience and cultural transmission of knowledge about bears. We asked them to depict on their Traditional Territory map where, based on their Nation's oral histories, they would historically expect to see grizzly bears (hereafter 'Pre 1992'). Given inter-generational transmission of knowledge, we estimate that this TEK 'temporal window' provides information about island occupancy that spans centuries or more.

We used a mapping approach to complement interview data. Specifically, LEK participants indicated on a map the islands on which they had observed a grizzly bear. For each observation,

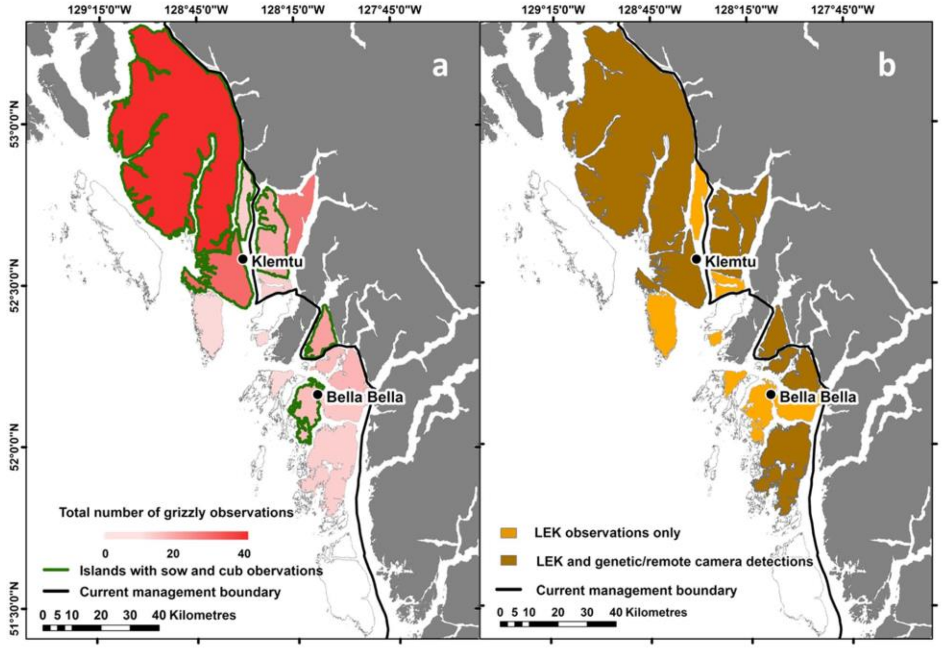

Figure 1. Spatial pattern of evidence of island occupancy and detection type. a) Weight of evidence of grizzly bear (*Ursus arctos horribilis*) occupancy at the island scale within Heiltsuk and Kitasoo/Xai'xais Territories in coastal British Columbia, Canada. Each data type (local ecological knowledge observation, mortality record, genetic ID and remote camera observation) was weighted equally to provide an indication of occupancy rather than bear density. Dark grey areas were not included in our study. The 'current management boundary' is the westward (i.e., seaward extent) of the Province of British Columbia's Grizzly Bear Population Units, the spatial scale at which grizzly bears are managed in the province. Spatial pattern in data types used to detect grizzly bears (*Ursus arctos horribilis*) in sampled areas within Heiltsuk and Kitasoo/Xai'xais Territories. Eighteen islands were included in the study.
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participants provided supporting information including the island name, year, and season. We also asked LEK participants to draw on a map the areas they would define as coastal grizzly bear distribution during two timespans (1992–2002, 2003–2012). In addition, an estimate of survey effort for each LEK participant was quantified spatially – by indicating the extent of their area of expertise on a map – and temporally – as the estimated number of years and days per year the participant was in the field and potentially able to observe bears. All TEK/LEK data were verified with interview participants through follow up workshops. Once verified, interview data in transcript form were returned to both the participants and the Nations' Resource Stewardship offices in digital and print versions.

Genetic, remote camera, and mortality data. We used genetic data, remote camera images, and mortality records to identify location, date, and – in some cases sex, individual identity, and age class – of grizzly bears detected in the same area from 2009–2012. We sampled genetic data from non-invasive hair-snagging stations baited with a non-reward bait [43,44]. These stations (n = 33) were part of longitudinal carnivore monitoring programs across 10 islands in Kitasoo/Xai'xais (2012) and Heiltsuk (2009–2012) Territories (Table 1 & 2). In addition, 18 remote trail cameras (n = 1268 trap nights) were deployed on four islands in 2012 (Table 1 & 2). Finally, we queried island locations within the BC Ministry of Environment's kill records from their Compulsory Inspection Database [39,40], yielding dates, locations, and sexes of known human-killed grizzly bears. All island mortality records (n = 3) were hunted individuals rather than animal control (i.e., human-wildlife conflict) kills (Table 1 & 2).

Analyses

Occupancy. We summed the number of grizzly bear observations from all data sources on each island to assess the weight of evidence for contemporary occupancy. We accounted for observations of (genetically) undocumented bears from sightings and camera images equally with known, specific individuals from mortality and genetic data. Accordingly, it is possible that multiple observations were from the same individual bear. However, we did not expect bias across candidate islands in the spatial pattern where such multiple counting might have occurred. We calculated detection-per-unit-effort (DPUE) for all data types except mortality data (Table 1 and Table 2). For remote camera and genetic data, we quantified DPUE for each island by dividing the number of observations by the cumulative number of

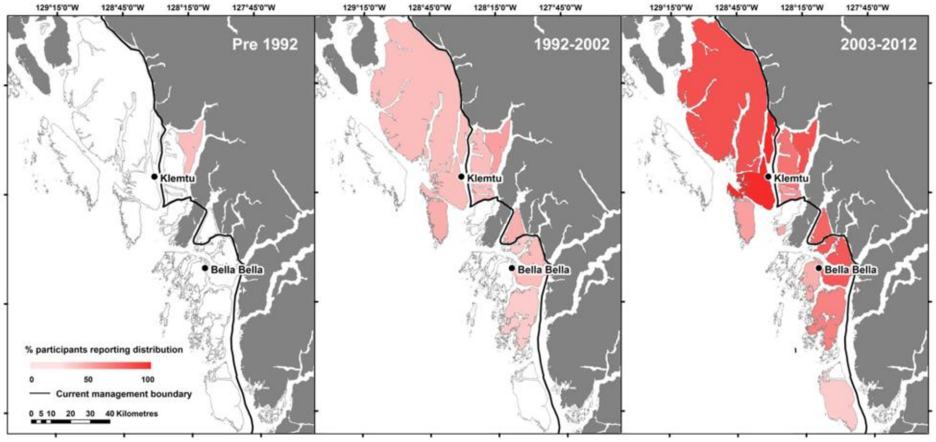

Figure 2. Time series of island grizzly bear occupation over three time periods. Local residents' perception of grizzly bear (*Ursus arctos horribilis*) distribution throughout Heiltsuk and Kitasoo/Xai'xais Territories in coastal British Columbia, Canada during the Pre 1992 (traditional ecological knowledge data), 1992–2002 (local ecological knowledge data) and 2003–2012 (local ecological knowledge data) time periods. Data are reported at the island scale (n = 18 islands) as the percentage of participants who indicated the island was within their area of observation and supported grizzly bears. Dark grey areas were not included in our study and the 'current management boundary' is the westward (i.e., seaward extent) of the Province of British Columbia's Grizzly Bear Population Units, the spatial scale at which grizzly bears are managed in the province.
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days each camera (n = 18) or hair snag (n = 33) was employed (Table 2). We standardized LEK observations by dividing the total number of observations for each island by the total number of survey days each interviewee estimated s/he spent within their identified geographic area of expertise. Both survey effort and total number of observations were summed for all participants at the island scale. As level of experience could not be reliably estimated, we assumed the same observational abilities of all participants. To assess which islands contain reproducing females, we used both remote camera and LEK observations to identify all detections of sows with cubs.

Temporal Trends in Occupancy. We assessed temporal occupancy across three intervals: Pre 1992 (n = 7 interviewees), 1992–2002 (n = 27 interviewees), and 2003–2012 (n = 27 interviewees). We estimated 'Pre 1992' occupancy from TEK data, and 1992–2002 and 2003–2012 periods from LEK data. Because LEK observations are likely increasingly comprehensive with increasing proximity to communities of residence [18], for each island we only used interview data from the closest community. We indexed the total number of observations across all islands by dividing them by the total number of survey days in each year. Survey effort was calculated annually using Equation 1:

$$\text{Survey Effort} = \frac{\sum(\text{Survey days per participant})}{\#\text{ of participants} \times 365} \quad (1)$$

where # of participants is the number of LEK interviewees, 365 denotes the total possible number of survey days a year, and survey days per person indicates the total number of survey days for each participant. The number of island LEK observations per year was then divided by annual survey effort across all islands. This metric allows survey effort to be calculated per annum across all participants for all islands.

Results

We identified 149 grizzly bear observations across 15 major islands, including 10 islands outside the current grizzly bear management boundary (Figure 1a, Table 1). LEK yielded the largest number of data points relative to other sources, with 110 observations across 15 major islands (Table 1 & 2). Twelve islands hosted more than one observation (mean = 9.93, range = 1 to 39) (Table 1; Figure 1a). Across all LEK participants, 86% (19 of 22) reported at least one observation of an island grizzly (Table 1). Data on known individuals (genetic data and mortality records) indicated the presence of at least nine unique individuals (three female, five male and one of unknown gender) across 10 locations on seven islands. Remote cameras yielded a total of 28 observations of grizzlies on four islands (Table 1), two of which are outside of the current management boundary. Sow and cubs were detected in 23 LEK observations and seven remote camera observations across six islands (Table 1).

TEK/LEK data sources revealed a similar pattern of island occupation as did evidence from genetics, cameras, and hunting records; all newly occupied islands identified by scientific evidence were affirmed by complementary TEK/LEK observations (Figure 1b; Table 1). Of the seven islands solely associated with TEK/LEK evidence, all but one (Denny Island) lacked scientific evidence (Figure 1b).

Indigenous knowledge additionally yielded historical information suggesting that bear colonization of islands occurred recently, and that the process has increased in pace. Only one of seven TEK interviewees identified grizzly bears on an island before 1992. Accounts of island occurrence, within and outside the currently recognized distribution, were increasingly common and spatially widespread in 1992–2002 and 2003–2012 periods (encompassing 12 and 15 islands, respectively; Figure 2). The total island

Table 1. Detections of island grizzly bears (*Ursus arctos horribilis*) by data type (presented as raw observations and as detection-per-unit-effort (DPUE) values) within Heiltsuk and Kitasoo/Xai'xais Territories in coastal British Columbia, Canada (n = 18 islands).

Island	Total Remote Camera Observations	Remote Camera Detections Per Trap Night[a]	Total Hair Snag Observations	Hair Snag Year	Hair Snag Detections Per Trap Night[b,d]	LEK Observations	Total Sow/Cub Observations	Mortality Observation
Aristazabal	-	-	-	-	-	0	0	0
Calvert	-	-	-	-	-	0	0	0
Campbell	-	-	0	-	-	6	0	0
Chatfield	-	-	2	2009–2012	0.03	6	0	0
Cunningham	-	-	1	2009–2012	0.01	7	3	0
Denny	-	-	0	2009–2012	0	5	0	0
Dufferin	-	-	-	-	-	1	0	0
Hecate	-	-	-	-	-	0	0	0
Hunter	-	-	-	-	-	1	0	1
Yeo**	-	-	1	2009–2012	0.04	12	4	0
Lady Douglas	-	-	-	-	-	1	0	0
Pooley**	7	0.02	0	2012	0.01	15	0	0
Price	0	0	0	2012	0	1	0	0
Princess Royal	19	0.03	3	2012	0.02	16	17	1
Roderick**	1	0.01	0	2012	0.01	12	3	1
Sarah	-	-	-	-	-	9	3	0
Susan**	-	-	-	-	-	2	0	0
Swindle	1	0.03	1	2012	0.03	22	15	0

[a] For islands with remote cameras.
[b] For islands with hair snags.
[c] Indicates number of observations, not number of individual grizzly bears, across study period.
[d] Summed across seasons and years.
** Indicates islands within the current management boundary'.
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Table 2. Sampling effort of island grizzly bears (*Ursus arctos horribilis*) by data type within Heiltsuk and Kitasoo/Xai'xais Territories in coastal British Columbia, Canada (n = 18 islands).

Island	Number of Remote Cameras	Total Remote Camera Nights[s]	Number of Hair Snag Sites	Hair Snag Year	Total Hair Snag Nights	Number of LEK Interviewees Who Reported on Island[b]	Average Number of Report Days Per Year[c]
Aristazabal	0	-	0	-	-	13	120
Calvert	0	-	0	-	-	9	120
Campbell	0	-	0	-	-	14	142
Chatfield	0	-	2	2009–2012	159	14	142
Cunningham	0	-	4	2009–2012	304	14	142
Denny	0	-	2	2009–2012	178	13	148
Dufferin	0	-	0	-	-	13	148
Hecate	0	-	0	-	-	9	120
Hunter	0	-	0	-	-	12	146
Yeo**	0	-	3	2009–2012	221	15	145
Lady Douglas	0	-	0	-	-	14	137
Pooley**	3	357	3	2012	416	10	136
Price	1	23	1	2012	23	13	140
Princess Royal	9	661	9	2012	1217	8	140
Roderick**	4	192	3	2012	398	11	139
Sarah	0	-	0	-	-	8	128
Susan**	0	-	0	-	-	14	145
Swindle	1	135	1	2012	121	11	140

[a] For islands with remote cameras.

[b] Across entire study period.

[c] Average number of 'report days' (i.e., days interviewees reported on for each island) per year from 1992–2012. Data derived from all participants who included.
the island in their area of expertise.

** Indicates islands within the "current management boundary".

doi:10.1371/journal.pone.0101595.t002

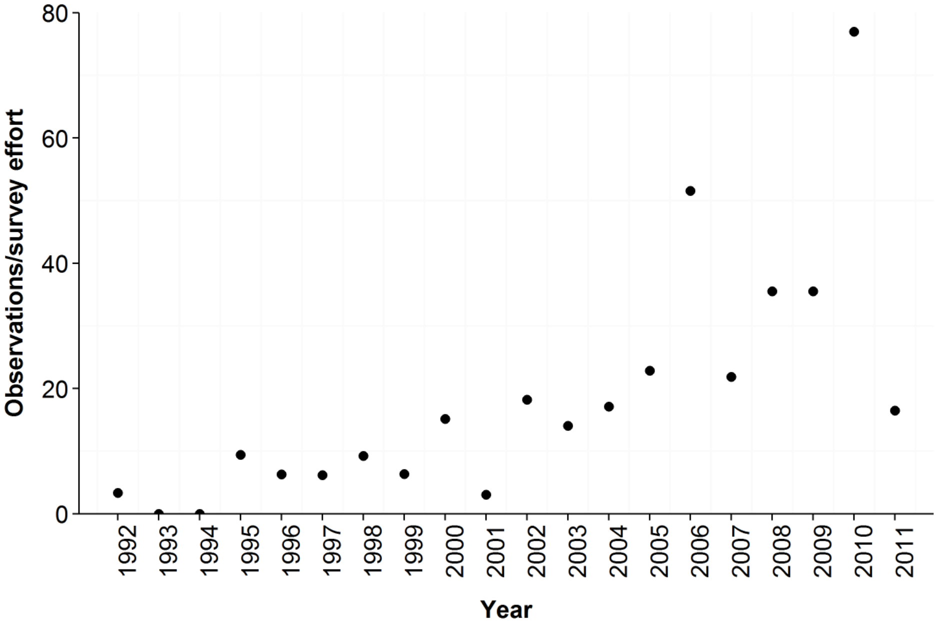

Figure 3. Trend of island grizzly occupation over time as derived from LEK data. Yearly number of island grizzly bear (*Ursus arctos horribilis*) observations per unit survey effort (a summation of all participants' observations across all islands; local ecological knowledge data only) between 1992–2011 in the Traditional Territories of the Heiltsuk and Kitasoo/Xai'xais First Nations in British Columbia, Canada. These observations encompass islands within and outside the current management boundary (n = 18 islands).
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observations per year, indexed by survey effort, increased between 1992–2011 (Figure 3).

Discussion

Our approach coupling indigenous knowledge and western science offered multiple lines of evidence that grizzly bears of both sexes have recently colonized 10 islands outside of the currently accepted distribution. Moreover, camera and interview data provided strong evidence for reproductive individuals and their offspring on four islands. Collectively, this suggests a distributional process beyond any exploratory extra-range movements of mobile males. Such an abrupt distributional shift of an apex predator may invoke cascading ecological consequences (*e.g.*, [45]). More broadly, the drivers of such change may also act on other less iconic and recognizable species and processes at differing spatial and temporal scales [46,47].

Though trends in these data are apparent, our approach also presents some inherent limitations. Specifically, although highly useful, TEK/LEK data are not systematic in coverage [23]. Accordingly, use of islands by interviewees likely varies in their mode of use (hunting, fishing, ecotourism, etc.) and as a result the habitat types people frequent may differ. As such, some interviewees may be more likely to encounter grizzly bears than others. Additionally, it is possible that black bears may have been mistaken for grizzly bears by some interviewees. Furthermore, TEK/LEK may not always be appropriately responsive to detect re-colonization and abandonment events that could accompany dynamic distributional processes. Snowball sampling methods may have also excluded some knowledgeable participants who were outside of the social networks of interviewees [48]. Finally, we note that recent observations might be more likely to be remembered and reported. More likely, however, we postulate that older observations of grizzlies outside their known range would have been interpreted as surprising and, accordingly, equally or even more memorable. Despite these limitations, the inclusion of TEK/LEK data provides important process values through the engagement of local people and as a result this approach may facilitate collaborative rather than antagonistic conservation efforts (*e.g.*, [49–51]).

Conventional scientific tools, such as remote cameras and genetic identification through hair snagging, also present limitations. Although more systematic in their deployment, the temporal resolution of these data types are limited, both on an annual basis (*i.e.*, spring sampling) and over longer timeframes (most ecological monitoring programs span years rather than decades or centuries) [20]. Additionally, these tools are spatially static and can be impacted by poor placement. Indeed, in the nearly road-less landscape we study, most snag station are set up close to shorelines where they can be accessed by boat. Importantly, though all data sources have potential weaknesses, uniting these independent sources provides increased temporal and spatial detail of the range shift we describe.

Interviewee comments and relevant literature allow us to offer working hypotheses about potential drivers of this shift. Specifically, modifications to the abundance and distribution of food resources as well as changes to intra- and inter- specific competition might be relevant. Many interviewees cited the reduction of salmon (*Oncorhynchus* spp.), which has declined throughout coastal BC, especially since 2000 [52]. As a critical resource that influences ursid body condition, reproductive output, and population dynamics [36,53], salmon abundance could influence bear distribution; individuals within other carnivore species have expanded or abandoned their range following declines in prey and subsequent increased intraspecific competition (*e.g.*, [54–56]). Increasing berry abundance and accessibility, the result of recent logging on islands, might cause individuals on exploratory forays to islands to remain. Grizzly bears in other areas select recently logged habitat to exploit diverse food resources offered in early regeneration stages of disturbed habitat [57]. Alternatively, black bears (*Ursus americanus*) are thought to limit grizzlies via exploitative competition on coastal islands where food resources are more dispersed and more difficult to defend. Acting alone or synergistically with human-caused mortality from trophy hunting of grizzlies, such competition between species has been proposed as a mechanism for excluding grizzly bears from islands [31] or reducing their densities elsewhere [58]. Recent reductions of grizzly bear trophy hunting on the mainland (BC Ministry of Environment, unpublished data), and/or changes in competition from black bears, might have reduced the demographic constraints on grizzly bears, thereby allowing dispersal to nearby islands. Whatever the cause(s) in our system, range shifts observed in closely monitored species may signal changes to underlying ecological conditions and provide resource managers the opportunity to consider and plan for wider implications.

The ecological, cultural, and economic consequences of this distribution shift in coastal grizzly populations might be considerable. As a larger species, grizzly bears outcompete co-occurring black bears (*U. americanus*) for salmon through interference competition [59] and also kill juvenile and adult black bears [60]. In addition, 'spirit bears' (*Ursus americanus kermodei*), a rare and geographically restricted white morph of black bears that occur with relatively high frequency on several islands in the area [61,62], are not only revered culturally but are also economically prized as the foundation of wildlife eco-tourism. Consequently, any mortality or increased avoidance behaviour due to new grizzly bear presence might impact cultural and economic values. Finally, forest management plans for grizzlies – a 'species of conservation concern' in BC [63] – carries legally-binding measures to protect high quality habitat wherever grizzly bears occur [30]. Such multifaceted implications would also be likely for range shifts in other high-profile fauna. Indeed, reintroductions of wolves (*Canis lupus*) to the Yellowstone Ecosystem provide a flagship example of the tremendous ecological, cultural, and economic ramifications associated with a change in distribution [64,65]. Similarly, expansions to sea otter (*Enhydra lutris*) ranges, a system well-suited to TEK/LEK study, carry comparably broad implications for people and ecosystems [66].

Beyond its regional relevance, this study illustrates the synergistic benefits of combining science with TEK/LEK over concurrent and complementary spatial and temporal scales. In our study, both data types predominately affirmed one another; islands without scientific evidence for occupation also lacked concurrent TEK/LEK observations. The co-affirmation of data sources in locations where they overlapped added confidence in patterns observed by LEK where they did not overlap [16]. Genetic and camera data provided precise information on individuals captured, including individual identities, gender, age class, location, and time of visit. These data were captured in all weather and at all hours each day. Costs of these scientific methods, however, necessarily limit their spatial and temporal coverage. Moreover, they can only be employed to capture data in real time. In contrast, although yielding less detailed information on individual bears, TEK/LEK data afforded broader information across a larger area and longer timespan. Finally, despite the inherent value of TEK/LEK, it remains largely ignored as a source of ecological data [19].This case study provides one of the few examples we detected in the literature that illustrates the value in uniting TEK/LEK with scientific methods to provide meaningful input into wildlife management [18,24,25,67].

With careful consideration a TEK/LEK method alone could perform well in other wildlife systems. Such an approach, however, requires careful assessment. Specifically, LEK information might be most useful for questions of distribution but may lack the detail required for other population parameters, such as absolute abundance, without calibration from scientific sources [18,68]. The case for a TEK/LEK approach alone might be particularly compelling with conspicuous and culturally important focal species in data-deficient regions for which species distributions impose serious management implications and funds for science are scarce. Moreover, as many indigenous governments and societies across the globe play increasingly prominent roles in resource management again [69–71], methods that emphasize an integration of, or focus on, existing local knowledge might emerge as default approaches. Such a transition might help overcome the dual common barriers of lack of conservation action due to inadequate data and data deficiency resulting from scarcity of funds. In this way existing indigenous knowledge can be proactively incorporated into management. Such consideration may support a transition to implement management action more rapidly, the timescale in which conservation action is often required.

Supporting Information

Document S1 Interview instruments used in Local and Traditional Ecological Knowledge surveys of island grizzly bears (*Ursus arctos horribilis*) within Heiltsuk and Kitasoo/Xai'xais Territories in coastal British Columbia, Canada.
(DOCX)

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Author Contributions

Conceived and designed the experiments: CNS CTD PP. Performed the experiments: CNS MSA LVG. Analyzed the data: CNS MSA KAA LVG. Wrote the paper: CNS CTD PP KAA MSA LVG. GIS analysis support: KAA. Interview data collection: CNS LVG MSA. Field collection of remote camera and genetic data: CTD CNS LVG MSA KAA.

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Appendix B: Supporting Information for Chapter 3

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RESEARCH ARTICLE

Journal of Animal Ecology BRITISH ECOLOGICAL SOCIETY

Salmonid species diversity predicts salmon consumption by terrestrial wildlife

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Abstract

1. Resource waves—spatial variation in resource phenology that extends feeding opportunities for mobile consumers—can affect the behaviour and productivity of recipient populations. Interspecific diversity among Pacific salmon species (*Oncorhynchus* spp.) creates staggered spawning events across space and time, thereby prolonging availability to terrestrial wildlife.
2. We sought to understand how such variation might influence consumption by terrestrial predators compared with resource abundance and intra- and interspecific competition.
3. Using stable isotope analysis, we investigated how the proportion of salmon in the annual diet of male black bears (*Ursus americanus*; $n = 405$) varies with species diversity and density of spawning salmon biomass, while also accounting for competition with sympatric black and grizzly bears (*U. arctos horribilis*), in coastal British Columbia, Canada.
4. We found that the proportion of salmon in the annual diet of black bears was ≈40% higher in the absence of grizzly bears, but detected little effect of relative black bear density and salmon biomass density. Rather, salmon diversity had the largest positive effect on consumption. On average, increasing diversity from one salmon species to ~four (with equal biomass contributions) approximately triples the proportion of salmon in diet.
5. Given the importance of salmon to bear life histories, this work provides early empirical support for how resource waves may increase the productivity of consumers at population and landscape scales. Accordingly, terrestrial wildlife management might consider maintaining not only salmon abundance but also diversity.

KEYWORDS
black bear, competition, foraging, grizzly bear, resource waves, salmon, stable isotope analysis, *Ursus*

1 | INTRODUCTION

Intra- and interspecific diversity across prey populations can create spatial variation in the timing (phenology) of resource availability for predators (Nesbitt & Moore, 2016; Schindler et al., 2010, 2013). Such variation can comprise *resource waves*—aggregates of food resources that offer ephemeral foraging opportunities at fine spatial scales but exhibit spatial variation in resource timing that prolongs foraging opportunities at larger spatial scales (Armstrong, Takimoto, Schindler, Hayes, & Kauffman, 2016). Mobile consumers can track the shifting mosaic of foraging opportunities offered by these phenologically diverse resource aggregates to maximize overall intake over time (Lok et al., 2012; Sawyer & Kauffman, 2011).

Data from across taxa and ecosystems show that intra- and interspecific prey diversity can expand foraging opportunities across time and space. Examples of consumers responding to the expanded temporal foraging opportunities afforded by resource waves include mule deer (*Odocoileus hemionus*) that track "green-up" timing of plant forage across elevation in Wyoming (Sawyer & Kauffman, 2011), as well as surf scoters *(Melanitta perspicillata)* that follow waves of migrating Pacific herring (*Clupea pallasii)* along the Pacific coast of North America (Lok et al., 2012). In Alaska, different spawn timing across runs of sockeye salmon (*Oncorhynchus nerka*) is reflected in the movement of foraging grizzly bears (*Ursus arctos;* Deacy, Leacock, Armstrong, & Stanford, 2016) and glaucous-winged gulls (*Larus glaucescens*; Schindler et al., 2013). In addition to such temporal expansion of foraging opportunities, and despite the energetic costs of moving between patches of food (Wirsing et al., 2018), consumers may also benefit from increased spatial variation in food availability, which could reduce intra- and/or interspecific interference competition compared with resources concentrated in space. In this way, mobile consumers may benefit from a diverse interspecific prey portfolio via both the added temporal and spatial foraging opportunities. The magnitude of population-level benefits to consumers of these expanded foraging opportunities may depend on their life-history characteristics (e.g., rate of reproduction), which in turn can also influence indirect ecosystem level impacts such as increased or decreased consumption of in situ resources (Takimoto, Iwata, & Murakami, 2009).

Variation in resource availability is clearly important, but its influence on consumption patterns relative to resource abundance is not well understood. Whereas a consumer's ability to capitalize on prey availability in a given period of time is generally constrained by a saturating rate of food intake (most simply represented by a Type-II functional response; Holling, 1965), a spatiotemporally diverse portfolio offered by resource waves may extend available foraging time, so that the consumer may realize the saturated components of their functional response curve for longer periods (Armstrong et al., 2016). A simulated consumer–resource model (Armstrong et al., 2016) found that spatial variation in resource phenology could affect consumer energy gain more than total resource abundance. Furthermore, the model suggested that narrower phenological diversity can reduce foraging opportunities—an effect not alleviated by increased resource abundance. These model results provide a set of predictions related to the relative importance of resource abundance and phenology that could be confronted with empirical, landscape-level data.

The effects of prey diversity and abundance may also depend on the inter- and intraspecific competitive environment of the consumer. Theory predicts that the effects of competition will intensify when resource abundance is low (Chesson, 2000), but we hypothesize that diversity in resource phenology might alter this pattern. Dietary resource competition can occur via interference competition (when individuals directly prevent the foraging of others) or exploitative competition (when individuals remove resources from a common pool; Amarasekare, 2003). Typically, larger-bodied animals dominate in interference competition, whereas smaller species can exert exploitative competition, given their reduced resource demands of smaller body sizes (Palomares & Caro, 1999; Peters, 1986). Additionally, given that competing species can coexist via temporal and spatial resource partitioning (Amarasekare, 2003; Chesson, 2000), diverse prey phenologies may provide smaller-bodied species relief from interference competition by distributing resources across the landscape to places and times—and in smaller quantities—that make it difficult or unprofitable for the larger-bodied competitors to exploit. Accordingly, smaller species may be able to benefit from exploitative competition in systems that have high levels of phenological diversity.

Here, we empirically test how spatial and temporal variation in the availability of resources mediates consumption relative to resource abundance and competitive environment. We use the bear–salmon consumer–resource system, consisting of spawning Pacific salmon (*Oncorhynchus* spp.) and highly mobile black bears (*Ursus americanus*) and grizzly bears that compete for these resources (Hilderbrand et al., 1999). Black bears generally are smaller in body size and occupy smaller home ranges, often consuming less salmon than the more dominant, sympatric grizzly bears (Adams et al., 2017). The study region in coastal British Columbia, Canada, hosts five main species of Pacific salmon, each with different spawn timing and habitat-selection characteristics (Fisheries and Oceans Canada 2014; Groot & Margolis, 1991). For bears, such temporal and spatial variation in spawning, as well as differential foraging access (e.g., mediated by spawning depth), contributes to differences in salmon availability over space and time (Table 1). Higher salmon consumption by coastal bears enhances components of fitness (e.g., body condition, mating success, and litter size; Hilderbrand, Schwartz, Robbins, & Thomas, 2000; Kovach & Powell, 2003; Costello, Creel, Kalinowski, Vu, & Quigley, 2009), and supports higher population densities, compared with populations without access to salmon (Hilderbrand et al.,1999). Combined, these characteristics of salmon and their relationship with bears suggest that the diversity of salmon species could extend a resource wave that bears can exploit over space and time with potential benefits to population productivity (Hilderbrand et al., 1999).

TABLE 1 General life-history characteristics of Pacific salmon species (*Oncorhynchus* spp.) in the study area. Mean biomass values were calculated as grand means across populations within the Pacific North West of North America (Bryan et al., 2014; Groot & Margolis, 1991). Spawning channel descriptions are generalized for each species (Groot & Margolis, 1991). Stream length calculations and run timing estimates were calculated from spawning waterways with available data within the study area (Fisheries and Oceans Canada 2014). The data that contribute to these table are coarse and are only suitable for broad illustrative purposes

Species	Mean biomass (kg)	Mean stream length (n = 971)	Spawning habitat	Maximum time in freshwater (n = 572)
Pink	2.5 kg (odd year); 1.7 kg (even year)	2.7 km	Lower channels below major barriers.	Early July–early November
Chum	5.2 kg	3.2 km	Lower channels below major barriers.	Early July–late October
Coho	3.2 kg	3.5 km	Adaptable to wide variety of spawning habitats from small coastal tributary streams to large main stem rivers.	Mid June–early Feb
Sockeye	2.7 kg	5.2 km	Adjacent to lake rearing areas including lake beaches, tributary creeks, and rivers between lakes.	Late May–late November
Chinook	13.6 kg	7.6 km	Adaptable to wide variety of spawning habitats from small coastal tributary streams to large main stem rivers.	Late April–late December

Building upon previous work that has focused on the movement of consumers, including bears, among patches of prey over time (e.g., Lok et al., 2012; Schindler et al., 2013), we offer an approach that examines the potential ecological importance of a diverse prey portfolio available to mobile predators over greater temporal and spatial scales. Specifically, we use stable isotope analysis to estimate the proportion of salmon in the annual diet of black bears. Although resource waves are sometimes investigated on moderate spatial scales to document phenological tracking by consumers (e.g., along a single waterway or among several; Ruff et al., 2011; Bentley et al., 2012), we use a complementary landscape-scale approach (across ~22,000 km^2) to test for an effect on consumption patterns across many bear home ranges and salmon resource waves. Finally, although the relationship between bear competition and salmon consumption has been examined previously (e.g., Fortin, Farley, Rode, & Robbins, 2007), we aim to better understand the interplay between competition and resource diversity and density.

Using data from a long-term study, we assessed empirical support for several hypotheses of how competition and resource availability might affect consumption of a critical resource. Specifically, we predicted that the proportion of salmon in the annual diet of black bears would be: (a) positively related to densities of spawning salmon biomass, (b) positively related to species diversity of spawning salmon biomass, (c) negatively related to grizzly bear presence and (d) negatively related to relative black bear density.

2 | MATERIALS AND METHODS

2.1 | Overview

We modelled the association between relative black bear density, grizzly bear presence, and salmon biomass density and diversity on the proportion of salmon in the annual diet of black bears. Taking an information-theoretic approach, we compared candidate Generalized Linear Mixed Models (GLMMs) and used model averaging to reveal the best-supported relationship between the predictor variables and dietary proportion of salmon. From an initial dataset of 405 unique bear-year combinations, we performed our main analysis on the 157 bear-year observations for which associated salmon data existed. We used the remaining observations (n = 248) to select the most appropriate spatial scale at which to consider intra- and interspecific competition in our main analysis (Appendix S3).

2.2 | Study system

Our remote study area on the central coast of British Columbia is composed of mainland valleys, ocean fjords, and an assemblage of islands (<1 km^2 to >2,220 km^2) separated by tidal waters (Figure 1; Service et al., 2014). Here, black bears are present across the entire landscape. By contrast, grizzly bears are prevalent in mainland watersheds, but are absent from many island watersheds (Service et al., 2014). Grizzly and black bears prey on all five main species of Pacific salmon, which offer varied foraging opportunities in terms of biomass, spawn timing and spawning habitat (Table 1; Quinn, Gende, Ruggerone, & Rogers, 2003; Gende, Quinn, Hilborn, Hendry, & Quinn, 2004). As the spawning habitat for each species is not uniformly distributed across the landscape, different bear home ranges yield access to different portfolios of salmon species, for example, home ranges with only pink (*O. gorbuscha)* and chum (*O. keta*) spawning streams versus home ranges with access to pink, chum, Chinook (*O. tshawytscha*), sockeye and coho (*O. kisutch*) spawning streams. Home range location thus partially determines salmon foraging opportunities in terms of the total number of spawning days and spawning stream length.

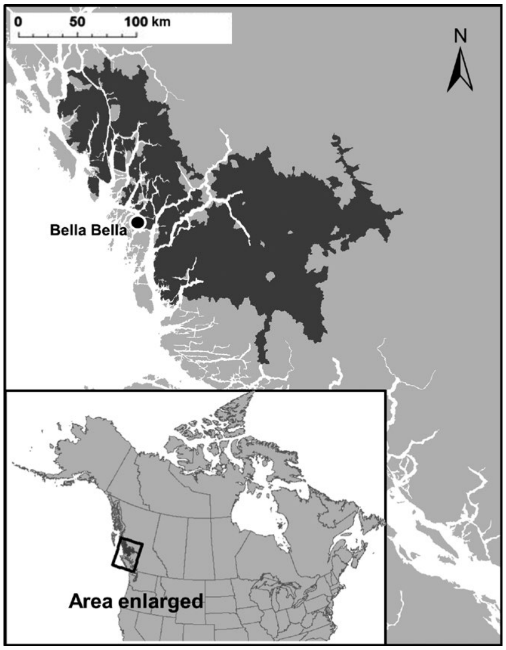

FIGURE 1 Study area in coastal British Columbia, Canada (2009–2014; 22,000 km^2)

2.3 | Field sampling and genetic identification

Using approximately evenly spaced (~1 per 80 km^2) non-invasive hair snagging sites (*n* = 274 per annum) baited with a non-reward bait (Woods et al., 1999, details in Bryan, Darimont, Paquet, Wynne-Edwards, & Smits, 2013, 2014; Adams et al., 2017), we collected bear hair samples across approximately 22,000 km^2, containing 158 watersheds (Figure 1) every ten to fourteen days during May and June from 2009 through 2014. The number of sampling days (n ≈ 30–40 per site per year) was fairly consistent across years.

Information from seven microsatellite loci plus a sex marker revealed species, sex and individual identity from hair samples (Wildlife Genetics International, Nelson, BC, Canada). Our overall dataset included 379 unique male black bears and 122 unique male grizzly bears. The sample size for females, which we captured far less often than males (≈15% of detections), was too small to include in analyses.

2.4 | Proportion of salmon in annual black bear diet

To assess annual diet of black bears, we used hair sampled during the shedding phase of the annual moult. This ensured that the isotopic measures represented the annual assimilated diet during the entire previous year's hair growth (approximately June through October; see experimental work by Hilderbrand et al., 1996 and use by Bryan et al., 2013). Specifically, we measured the stable carbon (13C/12C or δ13C) and nitrogen (15N/14N or δ15N) isotope values from hair collected from black bears via gas chromatography–mass spectrometry (University of Saskatchewan, Saskatoon, SK, Canada). Using these data, we modelled each black bear's annual assimilated diet using Bayesian stable isotope mixing models. Following similar studies of coastal bears in our study area, we used MixSIAR (Stock & Semmens, 2013) to estimate annual dietary contributions from plants, salmon, and intertidal foods by incorporating the δ13C and δ15N values from each of these potential dietary categories with those from the bears. As no reliable trophic discrimination factors (TDFs) exist for bear hair (Hopkins & Kurle, 2016), we followed recent bear hair stable-isotope studies (Hopkins, Ferguson, Tyers, & Kurle, 2017; Hopkins & Kurle, 2016) and used TDF values from laboratory rats fed known diets of plants or animals (Appendix S1, Kurle, Koch, Tershy, & Croll, 2014). Given potential biases possible when not accounting for differences in digestible elemental concentrations in food sources, we evaluated models with and without concentration dependence (Koch & Phillips, 2002). Two separate model-selection approaches suggested that concentration independence provided a better fit to our data (Appendix S1). Accordingly, we proceeded with results from our concentration-independent model. In our subsequent analyses (below), we used the median values from the estimated posterior distributions of proportion of salmon in each individual's diet in each year observed (*n* = 405 individual-years; discussion of limitation of this approach in Appendix S1). A complete description of our stable isotope mixing model approach can be found in Appendix S1.

2.5 | Estimating resource availability

We used geo-referenced annual abundance estimates of the five main Pacific salmon species from the New Salmon Escapement Database (NuSEDS; Fisheries and Oceans Canada 2014) to estimate biomass density and species diversity. To account for data deficiencies, we imputed year-specific missing salmon enumeration data using the estimated total species-specific count for each fisheries management area in combination with long-term relative contribution of each specific watershed. This method was developed specifically for this dataset (*see* Bryan et al., 2014). Even after imputation, owing to incomplete coverage of salmon monitoring, we could only calculate salmon-related predictor variables for a subset of watersheds (*n* = 47 of 158). In these watersheds, we associated salmon data to all bears detected within the watershed in a given year. If bears were detected in multiple watersheds within a season, we used the first watershed of detection. We considered salmon biomass density and diversity from the year before each hair sample was collected, because, given the annual moult of bears, isotopic information in hair collected in the spring relates to the preceding year's growth and associated consumption (Bryan et al., 2014; Felicetti et al., 2004; Hilderbrand et al., 1996).

2.5.1 | Salmon biomass density

We estimated total salmon biomass in each watershed using NuSEDS data and average-mass estimates for each salmon species, assuming a 1:1 sex ratio (Bryan et al., 2014; Groot & Margolis, 1991). Salmon biomass density was calculated as the collective biomass divided by the "functional" area of each watershed, defined as the total land area of watershed minus that of habitat considered unsuitable for bear foraging (i.e., barren rock, snow and ice, and lakes; Carroll, Noss, & Paquet, 2001; Artelle et al., 2016; calculated in ESRI Arcmap 10.2).

2.5.2 | Salmon biomass diversity

We used the Shannon–Weaver (SW) diversity index to estimate salmon diversity:

$$H = -\sum_{i=1}^{S} p_i \ln(p_i) \qquad (1)$$

where S is the number of salmon species in the watershed, and p_i is the proportion of the total estimated salmon biomass comprising the i^{th} species. We used biomass estimates instead of counts because we reasoned that total biomass would be more relevant to bears. Accounting for both species richness and evenness in species abundance, the SW diversity index provides a proxy for salmon resource availability over space and time (Appendix S3). Although this metric does not encompass river-specific details, such as correlation between certain species' run timing (e.g., chum and pink) and differences in the ability of bears to fish certain species depending on spawning habitats (e.g., Chinook spawning in large rivers), it is useful for analysing broader scale patterns related to our hypotheses.

2.6 | Estimating the competitive environment

2.6.1 | Black bear relative density

We estimated the relative density of black bears in each watershed in each year as the average number of bears detected per hair-snag sampling station across the watershed. Here, we made the assumption that each hair-snag station attracts bears from a surrounding area that is consistent across watersheds and years. This allowed us to describe density in units of bears per detection area without knowing the specific area involved. As we were only interested in *relative* density across watersheds and years, this measure is well suited to our purposes. It has been applied previously to this dataset to serve as a proxy for bears' intraspecific competitive environment (Bryan et al., 2014).

2.6.2 | Grizzly bear presence

We characterized grizzly bear presence/absence at the same watershed/year scale as above. Likely because grizzly bears kill black bears (Mattson, Knight, & Blanchard, 1992), the presence of a grizzly bear on a salmon stream has been observed to mostly eliminate use of salmon by black bears (Fortin et al., 2007). Given this natural history, and that many watersheds lack grizzly bears, we categorized grizzly bear abundance as present or absent.

2.6.3 | Spatial scale

We considered three possible spatial scales (Figure 1, Appendix S3; British Columbia Ministry of Environment 1996): (a) focal watershed—the watershed containing a given sample location (n = 158 watersheds; mean area = 72 km^2; SD = 94 km^2); (b) the spatial scale in (a) *plus* all adjacent watersheds (average area = 458 km^2; SD area = 606 km^2; n = 554 contributing watersheds); and (c) the spatial scale in (b) *plus* all adjacent watersheds (average area = 1,363 km^2; SD area = 1,825 km^2; n = 765 contributing watersheds). At each scale, we estimated measures of intra- and interspecific competition as the relative density of black bears and categorized grizzly bear presence, as described above.

Because estimates of coastal bear home range sizes vary (Hatler, Nagorsen, & Beal, 2008), we separately analysed a subset of our data (n = 248 bear-year combinations—those without salmon data) to inform the average spatial scale over which we considered the competitive environment could operate. In this supplementary analysis, we fit GLMMs (see below) relating black bear salmon consumption to competitive-environment (but not salmon-related) variables at different spatial scales and compared model performance (Appendix S3). This analysis identified relative black bear density at the scale of focal watershed as the best intraspecific predictor of salmon consumption (Appendix S3). Accordingly, for our main analysis, we used relative black bear density estimates for each bear's focal watershed of detection. This spatial scale also aligns with estimated home range sizes of black bears in similar temperate rainforest habitat (Hatler et al., 2008; Appendix S3). We categorized grizzly bear presence for each black bear's focal watershed of detection plus all adjacent watersheds (i.e., spatial scale b))—a spatial scale that also aligns with grizzly bear home range sizes (Barnes, 1990; Glenn & Miller, 1980; MacHutchon, Himmer, & Bryden, 1993; Schoen, Lentfer, & Beier, 1986).

2.7 | Data analysis

In our primary analysis, we included the subset of bears with associated salmon abundance estimates (n = 157 individual bear–year combinations). We employed an extended version of a Generalized Linear Mixed Model (GLMM) and information-theoretic model selection to examine the effects of salmon biomass density and diversity, as well as measures of intra- and interspecific competition on the proportion of salmon in annual diets of male black bears (n = 157 individual bear–year combinations). To account for the proportional—but continuous—nature of salmon-consumption rates, we assumed that this response variable was beta-distributed (Moore & Semmens, 2008). While a beta error distribution is outside the original definition of GLMMs, this model falls within the broad GLMM family and the format and interpretation are the same (Fox, 2015). For model fitting, we centred and scaled our continuous predictor variables (first subtracting the sample mean from each observation and then dividing by two standard deviations; Gelman, 2008). We fit GLMMs using the *glmmADMB* package (Skaug, Fournier, Nielsen, Magnusson, & Bolker, 2013) in R (R Core Team 2017), employing a logit link function with intercept-only random effects for year (to account for temporal variation—e.g., in precipitation) and watershed (to account for spatial variation—e.g., in topography). We developed a candidate model set from combinations of parameters that estimate resource abundance, resource diversity, and competitive environment (Table 2). Additionally, we modelled interactions between competition parameters and diversity and abundance, reasoning that salmon availability would be more important in the presence of inter- and intraspecific competitors (Table 2). After fitting all models, we ranked models based on differences in Akaike's Information Criterion (AIC), corrected for small sample sizes ($\Delta\mathrm{AIC}_c$; Burnham & Anderson, 2002).

To assess the strength of evidence for top models and parameters, we calculated Akaike weights of each model and Relative Variable Importance (RVI) values for each parameter by summing

TABLE 2 Candidate model set with corresponding $\Delta\mathrm{AIC}_c$ values and rounded model weights used to assess the effect of ecological variables on annual proportion of salmon (*Oncorhynchus* spp.) in diets of male black bears (*Ursus americanus*) in coastal British Columbia, Canada, 2009–2014. Models with "grizzly bear" account for the presence or absence of grizzly bears (*U. arctos horribilis*), and "black bear" represents the relative density estimate of black bears. "Salmon diversity" measure derived from a Shannon–Weaver diversity index, and "salmon biomass density" indicates annual across-species biomass density. All models included year and watershed as random effects. Models that include "salmon biomass density," "salmon diversity," "black bear," and "grizzly bear" as predictors relate to hypotheses i), ii), iii) and iv), respectively (see main text)

Model	Fixed effects	$-2\log \mathcal{L}$	$\Delta\mathrm{AIC}_c$	K	Weight	R^2
12	Salmon diversity + grizzly bear	−232.25	0.00	6	0.52	0.206
13	Salmon diversity + grizzly bear + salmon diversity × grizzly bear	−232.49	1.96	7	0.19	0.207
19	Salmon biomass density + salmon diversity + grizzly bear	−232.27	2.17	7	0.17	0.202
20	Salmon biomass density + salmon diversity + black bear + grizzly bear	−232.28	4.39	8	0.06	0.205
3	Grizzly bear	−222.97	7.12	5	0.02	0.090
17	Salmon biomass density + grizzly bear + salmon biomass density × grizzly bear	−226.72	7.73	7	0.01	0.149
4	Black bear + grizzly bear	−223.49	8.76	6	0.01	0.096
16	Salmon biomass density + grizzly bear	−223.40	8.85	6	0.01	0.107
6	Salmon diversity	−220.42	9.67	5	0.00	0.046
11	Salmon diversity + black bear + salmon diversity × black bear	−224.28	10.17	7	0.00	0.116
5	Black bear + grizzly bear + black bear × grizzly bear	−223.52	10.93	7	0.00	0.096
9	Salmon diversity + salmon biomass + salmon diversity × salmon biomass density	−223.42	11.03	7	0.00	0.112
10	Salmon diversity + black bear	−221.03	11.23	6	0.00	0.072
8	Salmon diversity + salmon biomass density	−220.91	11.34	6	0.00	0.057
1	Intercept only	−215.91	12.04	4	0.00	0.000
7	Salmon biomass density	−217.11	12.99	5	0.00	0.026
18	Salmon biomass density + salmon diversity + black bear	−221.35	13.10	7	0.00	0.079
15	Salmon biomass density + black bear + salmon biomass density × black bear	−220.88	13.57	7	0.00	0.096
2	Black bear	−215.97	14.12	5	0.00	0.001
14	Salmon biomass density + black bear	−217.11	15.14	6	0.00	0.028

the weights for individual parameters across all models (Burnham & Anderson, 2002). We considered our top model set to include the top ranked candidate models that together accounted for ≥95% of the total model weight. To combine inference across models, we computed model-averaged predictions from this top model set (Burnham & Anderson, 2002; Grueber, Nakagawa, Laws, & Jamieson, 2011) using the *MuMIn* package (Bartoń, 2015) in R (R Core Team 2017). Simple model-averaged parameter and associated error estimates (i.e., effect sizes and confidence intervals) do not exist for nonlinear models, such as generalized linear models (Cade, 2015). Accordingly, we graphically present model-averaged predictions and associated confidence intervals from our averaged model (Cade, 2015). We also present numerical effect sizes and associated confidence intervals for each individual model that contributes to the averaged model from which we draw inference (Table 3). For all models, we report marginal R^2, calculated as:

$$(SS_{\mathrm{total}} - SS_{\mathrm{residual}})/SS_{\mathrm{total}} \tag{2}$$

where SS_{total} is the sum of squared deviations from the mean and SS_{residual} is the sum of squared deviations from model-averaged predictions (both calculated for the response variable; Merlo, Chaix, Yang, Lynch, & Ra, 2005; Nakagawa & Schielzeth, 2013). We note, however, that there are problems associated with using R^2 in the context of nonlinear and non-normal models (e.g., Cox & Wermuth, 1992), and that marginal R^2 does not account for improved fit due to random effects (e.g., Nakagawa & Schielzeth, 2013). Accordingly, to complement this approach, we provide a graphical indication of model fit (Figure 2, Appendix S4: Figure S1).

TABLE 3 Parameter estimates (with confidence intervals given as ±−2 *SE*) for all top (≥0.95 cumulative model weight) GLMMs (Generalized Linear Mixed Models) that contributed to the final averaged model to predict annual proportion of salmon (*Oncorhynchus* spp.) in diets of male black bears (*Ursus americanus*) in coastal British Columbia (2009–2014). Variables represent (a) spawning salmon biomass density ("salmon biomass"), (b) salmon-species diversity according to the Shannon–Weaver index ("salmon diversity"), (c) relative black bear density ("black bear"), and (d) the presence and absence of grizzly bears ("grizzly bear"; *U. arctos horribilis*). Continuous predictors were centred (mean subtracted) and scaled (divided by 2 *SD*). Bold values indicate estimates with confidence intervals that do not overlap zero

Model	Intercept	Salmon diversity	Grizzly bear	Salmon biomass density	Black bear	Salmon diversity × grizzly bear
12	**−0.698** (−1.170, −0.226)	**0.837** (0.305, 1.369)	**−1.006** (−1.554, −0.458)	–	–	–
13	**−0.649** (−1.159, −0.139)	**1.058** (0.002, 2.114)	**−1.053** (−1.629, −0.477)	–	–	−0.277 (−1.417, 0.863)
19	**−0.690** (−1.176, −0.204)	**0.847** (0.553, 1.402)	**−1.016** (−1.584, −0.448)	−0.027 (−0.386, 0.140)	–	–
20	−**0.689**(−1.178, −0.200)	**0.842** (0.276, 1.409)	−**1.021** (−1.600, −0.438)	−0.025 (−0.444, 0.409)	−0.012 (−0.554, 0.516)	–

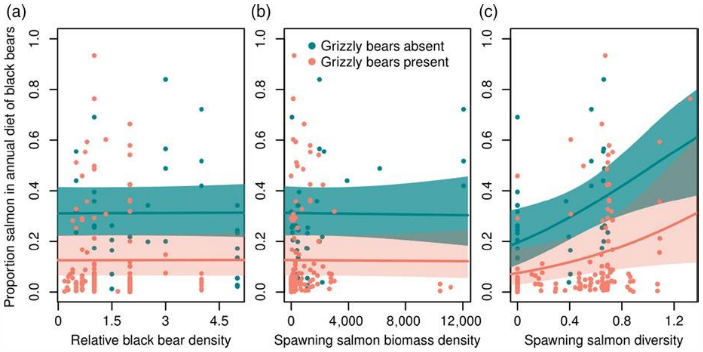

FIGURE 2 Annual proportion of salmon (*Oncorhynchus* spp.) in diets of male black bears (*Ursus americanus*) in coastal British Columbia, Canada as a function of (a) relative black bear density, (b) spawning salmon biomass density, and (c) salmon-species diversity (Shannon–Weaver index) in the presence and absence of grizzly bears (*U. arctos horribilis*). Points show median dietary estimates for unique bear-year combinations (2009–2014; *n* = 157). Curves represent model-averaged predictions from top candidate Generalized Linear Mixed Models (GLMMs) (≥0.95 cumulative model weight), incorporating the effects of competition and salmon, with beta error structure (marginal R^2 = 0.21). Shaded regions represent model-averaged 95% prediction confidence; pink shading representing the model predictions for grizzly bear presence, and blue representing the model prediction for grizzly bear absence. Grey shaded regions represent model prediction overlap between the grizzly presence and absence

To illustrate further the relationship between salmon-species diversity and temporal and spatial foraging opportunities, we computationally reduced species diversity from four to two species in a case-study watershed by removing the two least abundant species, coho and Chinook. From the new data, we recalculated salmon biomass, salmon diversity, and the corresponding change in the number of foraging days and spawning stream length (Figure 3). Using model-averaged parameter coefficients, we compared predicted estimates of the annual proportion of salmon in bear diet across these two scenarios.

3 | RESULTS

The median proportion of salmon in the annual diets of black bears ranged from 0.01 to 0.93 (mean = 0.17; *SD* = 0.20) across individuals and years. Our primary analysis considered the potential influence of salmon biomass density, salmon diversity, grizzly bear presence and relative black bear density on diet, using a dataset with reliable salmon information (*n* = 157 bear-years). Salmon diversity and grizzly bear presence occurred in all top models, the former consistently positively related and the latter negatively related to salmon consumption (Figure 2, Tables 2 and 3). Relative black bear density, salmon biomass density, and the interaction between salmon diversity and grizzly bear presence also occurred in the top model set, but had modest influence and parameter estimates, which overlapped zero (Figure 2, Tables 2 and 3). Relative Variable Importance (RVI) across our candidate model set suggests that both salmon diversity (0.98) and grizzly bear presence (0.99) are approximately four times as important as salmon biomass density (0.26) and approximately ten times as important as relative black bear density (0.07) in predicting annual proportion of salmon in black bear diets.

Our averaged top model (marginal R^2 = 0.21) suggests that black bears occupying areas with grizzlies consumed about 40% less salmon than those in areas without the larger species (Figure 2). With salmon biomass density held constant, salmon consumption by black bears doubled between the first and third quartiles of observed diversity values, corresponding to the approximate difference between access to one salmon species (Shannon–Weaver = 0.00) and two salmon species with equal biomass (Shannon–Weaver = 0.69; Figure 2c). Additionally, salmon consumption approximately tripled across the range of our observed diversity values (Shannon–Weaver = 0.00–1.32), reflecting the approximate difference between a one-species watershed and a watershed with four species of equal biomass contributions.

When we computationally reduced the number of species from four to two in a case-study watershed by removing the two least abundant species, coho and Chinook, we observed that total biomass dropped by only about 3%. By contrast, the associated reduction in diversity (~48%) lowered the total number of days when salmon were available in the watershed by 28% and the spawning stream length by 62% (Figure 3). This change in diversity corresponded to a ~40% reduction in predicted salmon consumption by black bears.

4 | DISCUSSION

Our work finds a positive association between spawning salmon diversity and dietary contribution of salmon in black bear diets, offering empirical support for a dietary response by a consumer to phenological diversity. Moreover, our data represent the integration of foraging behaviour over a relatively long period (a salmon-spawning season) and on a landscape scale. Earlier research has

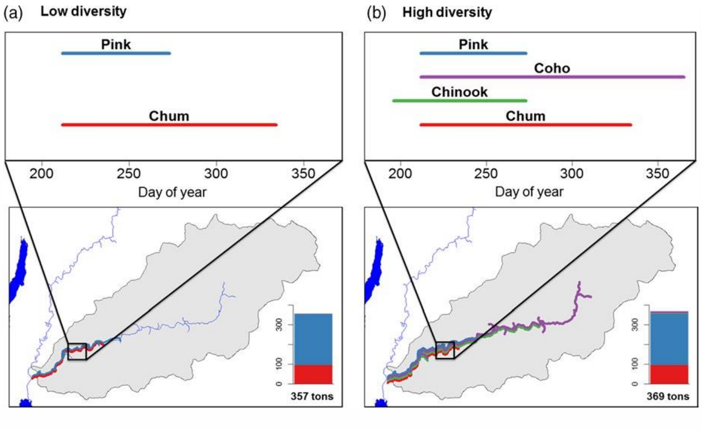

FIGURE 3 Temporal and spatial foraging opportunities afforded by (a) low (Shannon–Weaver diversity = 0.58; two species) vs. (b) high (1.20; four species) species diversity of spawning salmon (*Oncorhynchus* spp.). Actual diversity values from a watershed on the central coast of British Columbia, Canada shown in (b) are predicted to lead to 40% more salmon consumption by black bears (*Ursus americanus*) compared to the artificially reduced diversity shown in (a). Whereas this illustration of increased diversity increased salmon availability by 28% more days and 62% more stream length, total salmon biomass density increased by only 3%

shown consumers tracking prey phenology or increasing their exposure to the resource over smaller spatial and temporal scales (Deacy et al., 2016; Lok et al., 2012; Sawyer & Kauffman, 2011; Schindler et al., 2013). Building off previous research on bear–salmon systems (e.g., Deacy et al., 2016; Schindler et al., 2013), we additionally considered diversity across salmon species, among which we expect substantial spatial and phenological variation, rather than among populations of a single salmon species. Furthermore, we examined resource waves in conjunction with inter- and intraspecific competition, a combination that has not yet been explored theoretically or empirically (Armstrong et al., 2016). We focus on a smaller-bodied, presumably subordinate salmon consumer, offering evidence that the benefits of resource waves might extend beyond the larger-bodied competitor. Our analysis of an integrated dietary measure suggests that a spatially and temporally diverse prey portfolio may provide long-term, measurable benefits to mobile consumers that exploit these resource waves. Finally, these findings complement previously documented observations that salmon diversity can influence salmon consumption by humans (i.e., the maintenance of yields over time; Nesbitt & Moore, 2016).

Past simulation modelling in a generalized resource–consumer system has demonstrated the possibility that resource timing may be more important than abundance under certain conditions (Armstrong et al., 2016), and our study provides empirical support. Although species diversity was important for predicting salmon consumption by bears, total salmon biomass density had only one-fifth as much empirical model-weight support as diversity. Non-informative variables may enter a top model set as a result of the AIC bias correction term being only two; these can be identified by parameter estimates (and corresponding CIs) that overlap zero and unchanged deviance values upon their inclusion in a model set (see discussion from Anderson, 2008). Because the salmon biomass density predictor adds almost no explanatory ability and model likelihoods were nearly identical after its inclusion (Tables 2 and 3), we suspect it to be non-informative (Anderson, 2008). We note, however, that our observations of salmon biomass density occurred in areas with relatively strong salmon runs compared to many areas black bears still inhabit. Indeed, theoretical models predict that foragers might benefit the most from increased phenological diversity when abundance is already high, whereas an increase in abundance might matter more than phenological diversity when abundance is low (Armstrong et al., 2016). Specifically, the apparent lack of evidence for a salmon biomass density effect may be explained by the fact that black bears in our system may be saturated phase of their functional response for the examined salmon runs (Holling, 1965; Quinn et al., 2003).

Given the large spatial scale of our analysis, there were several potential covariates we were unable to explore. Specifically, the conditions that may drive higher interspecific salmon diversity, such as watershed size and habitat complexity (Rogers & Schindler, 2008; Waples et al., 2001), could also contribute to greater intraspecific phenological diversity (Moore, Mcclure, Rogers, & Schindler, 2010). Although we do not have accurate population-level phenological data for salmon that would be required to disentangle these relationships, we address this lack of information by accounting for inherent variability by including a watershed-level random effect in all models. However, it would be informative to explore the relative strength of influence between inter- and intraspecific salmon diversity on black bear salmon consumption in future studies. For example, larger salmon runs often last longer than smaller runs (Davis, 2015; Reimchen, 1994), thereby extending the resource wave—a relationship we did not explore here.

Given that salmon species do not contribute equally to biomass, diversity and biomass need not be tightly correlated (Figure 3a,b). Our model-averaged model suggests that such changes in salmon diversity played a strong role in annual proportion of salmon in diets of black bears, whereas changes in salmon biomass density had little effect. To illustrate, and while holding biomass density constant at its mean, parameter estimates from our top model predicted dietary proportion of salmon in black bears doubled when observed diversity values increased from one salmon species (Shannon–Weaver = 0.00) to two salmon species with equal biomass (Shannon–Weaver = 0.69; Figure 2) and tripled across the range of our observed diversity values (Shannon–Weaver 0.00–1.32), reflecting the approximate difference between a single-species watershed and a watershed with four species each with equal biomass contributions.

Despite the value of salmon diversity to foraging black bears, we suggest that interference competition with larger grizzly bears reduced annual salmon consumption (*see also* Mattson, Herrero, & Merrill, 2005; Fortin et al., 2007; Figure 2). We predicted that the availability of diverse opportunities to forage for salmon across space and time could moderate interference competition (by limiting interaction between competing species at clumped resources). Our results, however, suggest that salmon diversity is no more important for black bears in the absence of grizzly bears than when grizzly bears are present (Figure 2c). Additionally, intraspecific competition, as measured by relative black bear density, had an ambiguous effect on salmon consumption, occurring in several of the top models with a negative association and high uncertainty (Tables 2 and 3). Similar to salmon biomass density, likelihood values and parameter confidence intervals suggest that relative black bear density may be a non-informative variable (Tables 2 and 3; Anderson, 2008). Finally, we were not able to account for the presence or density of wolves (*Canis lupus*) as potential competitors and known salmon consumers (Darimont, Paquet, & Reimchen, 2008), an additional relationship that could be explored in further work.

Together, salmon diversity and the presence of grizzly bears explained more than a fifth of the total variation in estimated proportion of dietary salmon. The overall moderate fit of our final model-averaged model (R^2 = 0.21; Figure 2, Appendix S3: Figure S1) indicates, however, that there remains considerable unexplained variation in black bear salmon consumption patterns. We are not surprised by this moderate explanatory ability. For behaviourally complex vertebrates, like black bears, numerous influences likely affect consumption patterns across a very large and heterogeneous landscape. Although beyond the scope of our analysis, these include an individual's age, body size, and position in its social hierarchy; time devoted to other activities; and especially the availability of other food resources over time and space (Deacy, Armstrong, Leacock, Robbins, & Gustine, 2017; Takimoto et al., 2009). In addition, our estimates of proportion of dietary salmon were inherently noisy, incorporating error from multiple sources (e.g., stable isotope measurement, dietary fractionation estimates; Moore & Semmens, 2008). Although our final model-averaged model demonstrated moderate fit, each individual parameter of interest in our top model explains a reasonable amount of variation. For example, removing the term for salmon diversity reduces our model R^2 by 0.10. Similarly, removing grizzly bear presence reduces R^2 by 0.13. Regardless of limitations in our approach, grizzly bear presence and salmon diversity are evidently important factors that influence black bear salmon consumption.

Several management implications emerge from these findings. The relevance of a diversified salmon portfolio for terrestrial consumers argues for considerations beyond previous ecosystem-based fisheries management recommendations that focussed solely on increasing salmon abundance available to consumers after exploitation by fisheries (Darimont et al., 2010; Levi et al., 2012)—at least for relatively low-density large mammals like bears that satiate (Armstrong & Schindler, 2011). This consideration may be especially relevant for consumers involved in widespread interactions via their roles as vectors of resources to other ecosystem recipients. For example, riparian benefits (e.g., greater insect diversity and biomass, increased songbird diversity and biomass, higher plant diversity) are associated with increased bear-mediated nutrient transfer into temperate rainforest ecosystems (Christie, Hocking, & Reimchen, 2008; Mathewson, Hocking, & Reimchen, 2003; Reimchen, Mathewson, Hocking, Moran, & Harris, 2003; Schindler, Armstrong, & Reed, 2015); these benefits are likely amplified with the increase in consumption associated with greater salmon diversity. Accordingly, if maintaining diversity is important to managers, habitat destruction and other human interference that can reduce salmon diversity should be minimized in riparian areas—the nexus of salmon resource waves. Importantly, these implications of salmon diversity are set against a background of extirpation and reduced phenological diversity of salmon populations (Price, Darimont, Temple, & MacDuffee, 2008; Price, English, Rosenberger, MacDuffee, & Reynolds, 2017; Quinn, McGinnity, & Cross, 2006), efforts to restore lost salmon runs (Lichatowich, Mobrand, Lestelle, & Vogel, 1995), and the conservation of bears that co-evolved with this marine resource.

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AUTHOR CONTRIBUTIONS

C.N.S., C.T.D., P.C.P., and T.E.R. conceived the ideas and designed the work; C.N.S., M.S.A. and K.A.A. collected the data; C.N.S. and A.W.B. analysed the data. C.N.S. and C.T.D. led the writing. All authors contributed to every draft and approved the final version for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.t474mn0 (Service et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Appendix C: Supporting Information for Chapter 4

Appendix S1:

Laboratory methods for mc1r genotyping

Wildlife Genetics International developed a test to access the polymorphism responsible for the white phenotype, as follows. Primers (5'- TET-TCC TGC ACC TCT CGC TCA TGG – 3' and 5' – G AGC TCC TGG CTG CGG AAG – 3') were designed to amplify a 142 bp fragment of the melanocortin 1 receptor (MC1R) gene (Genbank accession no. JN575070.1) (Ritland et al. 2001). The temperature profile and reaction conditions for polymerase chain reactions were as described (Player et al 2017 Table 1) and cycling was done on MJ Research PTC-100 thermocyclers. Single-track sequencing (Pavel et al. 2004) with the TET-labeled primer was then used to assess the presence or absence of adenosine residues at the polymorphic position (position 115 within the amplified sequence). The 'A-track' sequence reactions were resolved on an ABI Prism 310 genetic analyzer, and peak heights were measured using Genotyper software. The ratio of the adenosine peak height at the polymorphic position was compared to that of a non-polymorphic adenosine residue 20 bp upstream (position 95). The distribution of this ratio had 3 modes, at 0, 0.38 and 0.64, corresponding to white bears (no A at position 115), heterozygotes, and homozygous wild-type individuals. No samples produced ratios between 0.02 and 0.26, but the heterozygote and wild-type distributions were less well separated. Therefore, the 4% of sequence profiles that gave ratios between 0.4 and 0.5 were reanalyzed for confirmation. In addition, all white and heterozygous genotypes were confirmed by analyzing a second sample from the same individual or by reanalyzing the original sample when only one sample was available from the individual in question. To ensure that weak results didn't bias against the recording wild-type alleles, no result was recorded if the height of the position 95 peak was < 200 relative fluorescent units, and no heterozygous or white genotype was recorded based on sequence runs in which the height of that peak was < 300 units. In no case did different sequence profiles from the same individual, whether from the same sample or from different samples, produce ratios that implied different genotypes.

Appendix S2: SECR modelling

We used closed population spatially explicit capture recapture (SECR) models that assumed demographic closure during the sampling round for each spring sampling session (May-June). We constructed detection histories from binary records of non-detection or detection (0 or 1) from hair samples for each individual and sampling site. We had two to three sampling occasions in each year, with 10-14 days between each occasion. Across years (2016-2017) the average distance between sites was ~5km.

We used likelihood-based SECR models from the R package *secr* (Efford, 2018) to determine black bear densities for each sex and year combination (2016-2017). All models used a proximity detector and a half-normal detection function (Efford 2016). Our state-space was determined by building a 20km buffer distance around the sampling site array and excluding the ocean (total area=~15000 km^2). We chose this buffer distance by conservatively (approximately) quadrupling the result of the *suggest.buffer* function in *secr* (2016~7.1 km; 2017~5.5 km). We confirmed the conservative nature of this approach by also calculating the root pooled spatial variance (RPSV), a measure of detection dispersion around sampling sites that is often used to determine buffer distance (2016=3.2 km; 2017=2.6 km; Efford 2016). An additional line of evidence that our buffer distance was a conservative choice is that it corresponds to an area larger than that of a coastal black bear's home range (Hatler et al. 2008). *secr* models use a gridded mask to discretely define density across continuous habitat; we used a mask spacing of 1km^2 between grid centroids. We performed a sensitivity analysis on buffer distance (5, 10, 15, 20, 25, 30, 35 km) and mask spacing (250 m, 500 m, 1000 m,1500 m, 2000 m), which confirmed that our chosen values were suitable (minimal change in log-likelihood and density across the matrix of all values tested).

Because our study area consisted of natural barriers to movement (ocean), we used a model that considered static non-Euclidean habitat geometry (*userdist* in *secr*). Specifically, we constructed a cost-distance matrix using a 0.1km^2 pixel size, with ocean defined as unsuitable habitat. Although black bears can swim, this threshold was supported by our multi-year detection data showing that black bears are rarely detected moving across waterbodies any wider during our study period (Darimont et al. unpublished data) and prior genetic research on population structure (Marshall and Ritland 2002).

We attempted to estimate how density varies with the landmass spatial scale (see landmass definition in Chapter 4) by including landmass as a covariate in our model (Table S3). However, due to small sample sizes and connectivity between some of the landmasses, we simplified our approach by merging several landmasses together to improve model performance. Landmasses on the mainland were amalgamated as north mainland and south mainland respectively, but were estimated separately because they are not connected (separated by Douglas Channel). Due to Yeo island's small area, limited sample size, and proximity to the mainland it was grouped with the southern mainland landmasses. Pooley and Roderick island were grouped together for density estimation as they are separated by less than 100m (Figure S1). Our models that incorporated landmass as a covariate were exceptionally imprecise, restricting their utility for our purposes (Table S3). As such, we carried forward a global density estimate (D~1) averaged from year specific estimates (Table S4)

Due to our small sample size (n=33) and lower recapture rate for females' (average across year recaptures=1.13) (Figure S2), we calculated total population density by doubling the male estimate (derived from male n=175; average across year recaptures=1.23; Table S4). As this ratio estimate is plausible, but arbitrary, we also constructed estimates from other reasonable alternative ratios (60:40-40:60; Noyce and Garshelis 1997, Noyce and Garshelis 1997; Table S4). Accordingly, for our main analysis, we doubled the landmass specific male *D* (or grouped landmass male *D* value) to account for both males and females in the population and multiplied the value by the respective area of landmass.

Figures

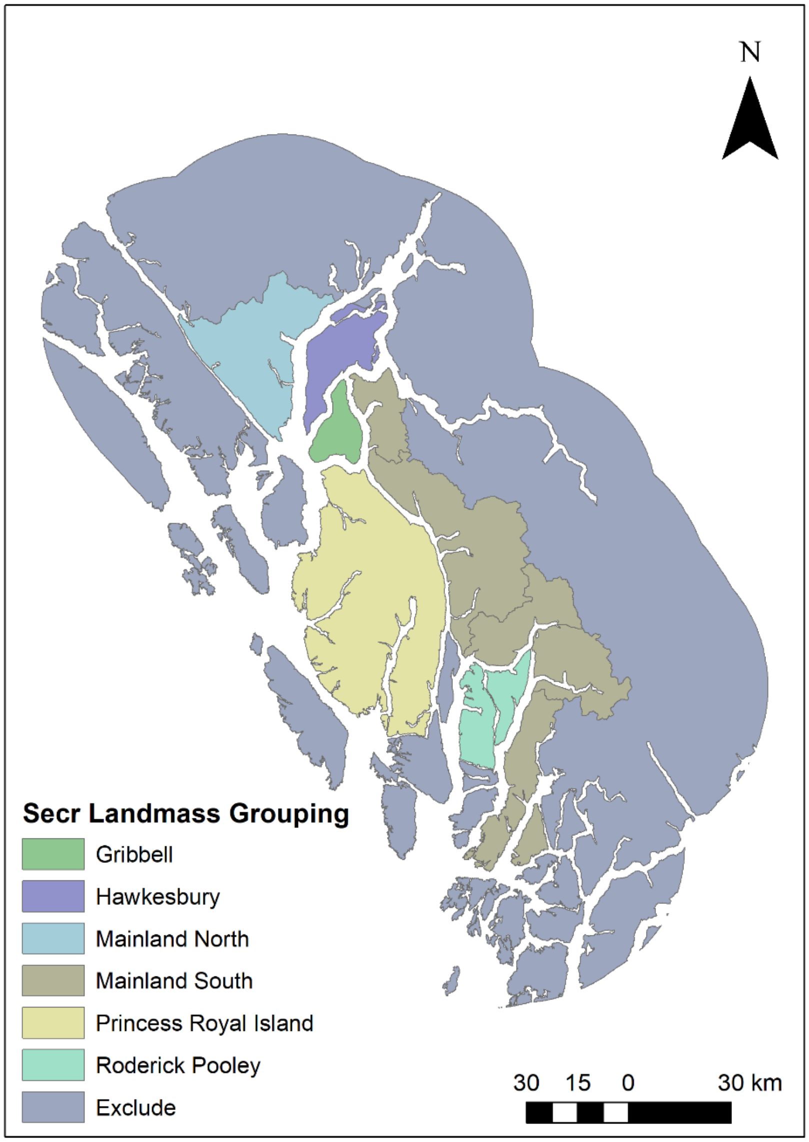

Figure S1: Landmass groupings for *secr* modelling of coastal black bear density.

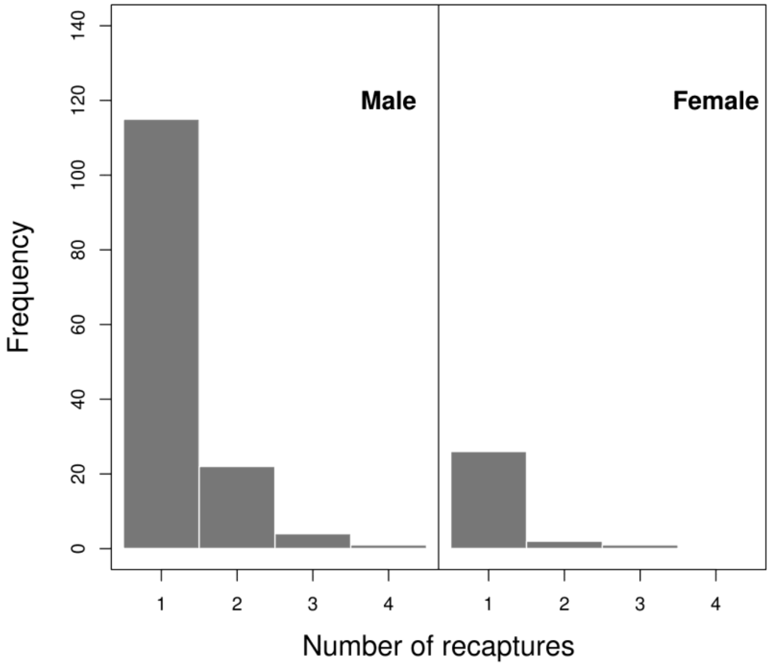

Figure S2: Average number of male (n=175) and female (n=33) coastal black bear (*Ursus americanus*) redetections across years (2016-2017).

Tables

Table S1: Model selection for spatially explicit capture-recapture models for male black bears in coastal British Columbia, Canada. Year:year of detection; model form: the structure of the secr model with and without g_0 varying by project; K: the number of parameters; LL: log likelihood; AIC: Akaike information criterion; weight: model weight.

year	***model form***	***K***	***LL***	***AIC***	***∆AIC***	***weight***
2016	D~1 g_0~project sigma~1	5	-6273.56	12557.61	0.00	1.00
2016	D~1 g_0~1 sigma~1	3	-8521.06	17048.32	4490.00	0.00
2017	D~1 g_0~project sigma~1	5	-5378.67	10767.35	0.00	0.64
2017	D~1 g_0~1 sigma~1	3	-5381.39	10768.77	1.16	0.36

Table S2: Estimates of black bear (*Ursus americanus*) population size (‘mean bb’ and lower and upper 95% confidence limit (‘LCL bb’ and ‘UCL bb’) by landmass based on spatial capture recapture modelling in coastal British Columbia, Canada. ‘Area’ represents the total area of each landmass. Population estimates are based on the global density estimate reported in the Table 3 (main manuscript).

Landmass	***Area (km^2)***	***mean bb***	***LCLbb***	***UCLbb***
Don Peninsula	427	52	38	70
East of Princess Royal	1121	135	99	185
Gribbell	207	25	18	34
Hawkesbury	368	44	33	61
Kynoch	483	58	43	80
North of Roderick	433	52	38	71
Pooley	163	20	14	27
Princess Royal Island	2279	275	201	376
Roderick	240	29	21	40
West of Hawkesbury	954	115	84	157
Yeo	95	11	8	16

Table S3: Estimates of black bear (*Ursus americanus*) population density (‘D bears/1000km^2’, and lower and upper confidence limits (‘LCL-UCL’)) based on spatial capture recapture modelling that includes landmass a covariate. ‘SECR grouping’ represents the amalgamated spatial unit that was used as a covariate for secr modeling (Appendix Figure S1).

Landmass	***SECR grouping***	***D bears/1000km^2 (LCL-UCL)***
Don Peninsula	Mainland South	85 (30-241)
East of Gribbell	Mainland South	85 (30-241)
East of Princess Royal	Mainland South	85 (30-241)
Gribbell	Gribbell	200 (59-676)
Hawkesbury	Hawkesbury	219 (65-747)
Kynoch	Mainland South	85 (30-241)
North of Roderick	Mainland South	85 (30-241)
Pooley	Roderick Pooley	163 (43-655)
Princess Royal Island	Princess Royal Island	89 (32 -244)
Roderick	Roderick Pooley	163 (43-655)
West of Hawkesbury	Mainland North	320 (105-1014)
Yeo	Mainland South	85 (30-241)

Table S4: Global mean density estimates (2016-2017) of coastal black bears based on male only *secr* models extrapolated to various plausible male:female sex ratios.

	50:50 M:F			***40:60 M:F***			***60:40 M:F***		
	mean	*LCL*	*UCL*	*mean*	*LCL*	*UCL*	*mean*	*LCL*	*UCL*
Density (bears/1000 km^2)	120	88	165	150	110	206	100	73	137