The role of science in wildlife management: From grizzly bears in British Columbia to hunted species across Canada and the United States

by

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Ethics Statement

Abstract

Agencies often claim, and societies often assume, a scientific basis to natural resource management. Science does have potential for informing management, for example by providing rigorous approaches for advancing understanding of managed systems and predicting management outcomes. However, the extent to which science informs real-world management is rarely tested. I offer a simple conceptualization of the management process and show how it identifies multiple focal points for testing the scientific basis of management systems. I illustrate this first with hunt management of grizzly bears (*Ursus arctos horribilis*) in British Columbia (BC), Canada. I find that the number of kills often exceeds agency-defined sustainable limits, associated with unaddressed uncertainty. I refine approaches from fisheries management to illustrate how uncertainty could be buffered against when setting hunting targets. I then assess the ecology of grizzly bear-human conflict in BC. I find limited support for the common hypotheses that conflict- and hunt-related kills reduce subsequent conflict rates, despite both being management responses. Instead, I find that food availability is correlated with conflict rates, suggesting that more effective management might focus on protecting natural foods. I then focus on protected areas. I use a spatial capture-recapture approach to characterize spatial patterns of grizzly bears in the Great Bear Rainforest and find that existing protected areas do no better, or worse, than random at capturing areas with high densities of grizzly bear activity centres, suggesting protected areas shortcomings. Finally, I explore the process of management itself across Canada and the USA, where hunting is guided by a model which asserts that management is ‘science-based’. However, in 667 management plans from agencies across the continent, I find key hallmarks of science (evidence, measurable objectives, transparency, independent review) largely lacking, raising doubts about a scientific basis. These chapters illustrate how shortcomings at various stages of the management process might undermine the ostensible scientific basis of an overall management system. I argue that assessing the role of science in management is important not only for enabling the evolution of management systems, but also for honest and transparent governance, by clarifying where science begins and ends in decision-making.

Keywords: wildlife management; science-based management; conservation; human-wildlife conflict; spatial capture-recapture; North American Model of Wildlife Conservation

Dedication

To Jill Greer and Steve Artelle, my mom and dad – you guys were comically incompatible, but thanks very much for making poor choices decades ago that ultimately led to me. Thank you for supporting me every step of the way, for introducing me to a love for nature, a curiosity, and a deep sense of right and wrong, for encouraging me to pursue whatever I needed to, even if it pulled me thousands of kilometers away, for modeling a hard work ethic, and for always being there for me no matter what. That I was privileged enough to even pursue a thesis is more a result of your hard work than it could ever be of mine.

And to Uncle Gord, who showed me from an early age that biology is cool, that science is actually an option, even for us non-hoity-toity folk, and that having letters before or after your name can be helpful professionally but nothing to be a knob about otherwise. Most importantly, his example to not take yourself (or anyone else) too seriously is one that I think the world would do well to take to heart. You were always supportive, and shared congratulations for each science step I took, even if you described the statistics of quantitative ecology as “matters best debated among shamans and mystics”. Should the shamans and mystics in charge of my fate give me a passing grade, you would have been the first to offer me a large glass of beer – Gord, this thesis is a metaphorical large glass of beer to you!

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Many of the ideas and work I discuss in Chapters 1 and 6 comprise or are inspired by very collaborative work; first-person singular is used here for consistency, thesis tradition, and to not speak on anyone's behalf, but the totality of the work offered here has been strongly inspired, shaped, and moulded by countless teachers, collaborators, and co-conspirators.

Thank you so much Marlene Nguyen, Sandra Vishloff, and Laurie White at SFU, and Diane Braithwaite at UVic, who have all been incredibly helpful through the years. And

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Chapter 1.

Introduction

“Clark defends grizzly bear hunt, says B.C.’s wildlife policies based on science ” (Hume and Hunter 2015).

This 2015 headline from the Globe and Mail newspaper, quoting British Columbia’s then-Premier Christy Clark, provides insight into the intersection of science and politics that often defines wildlife management. Within the article she is quoted further: "We have a record number of grizzly bears in the province, a huge and growing population, and the hunt is scientifically managed” (Hume and Hunter 2015). These are strong scientific assertions. Although this example of scientific claims being invoked to defend policy is particular to a single species in a single jurisdiction, it raises broader questions with wide-reaching implications: What is the role of the natural sciences in wildlife management? What could it be? What are its limitations? And why should we care? These questions form the context of this thesis, which demonstrates how the role of science might be assessed in real-world systems, illustrated with examples ranging from the conservation and ecology of grizzly bears in the Great Bear Rainforest of British Columbia, Canada, to a continental-scale hunt management model used across Canada and the United States.

Historical context

The current practice of wildlife management in Canada and the US has its roots in the early 1900s. Following a period of excessive hunting which saw drastic reductions and extinctions of some species, there was a shift towards a ‘wise use’ approach to managing environmental resources (Gill 1996, Clark and Milloy 2014). This philosophy, based on optimizing the extraction of animal populations’ reproductive ‘surpluses’, followed from the European model of scientific forestry, where forests were treated as crops, tended and managed for maximum yields (Hilborn et al. 1995). Aldo Leopold, often seen as the godfather of modern wildlife management, was himself a trained professional forester and applied this philosophy to the new field of wildlife management (Gill 1996, Clark and Milloy 2014). Unregulated access to wildlife was replaced with a system that treated wildlife as optimizable renewable resources, with extraction rates controlled and administered by a central agency (Clark and Milloy 2014). A professional society was developed, wildlife agencies adopted the model, and universities began training wildlife managers in the management approaches borrowed from scientific forestry (Gill 1996). Many decades later, the main thrust of this approach is still largely unchanged (Clark and Milloy 2014), now formally described as the "North American Model of Wildlife Conservation" (Geist et al. 2001, Organ et al. 2012, Clark and Milloy 2014). This model both describes how management is conducted across Canada and the US, and it is the model to which management agencies across provinces and states in these countries ascribe. This model is predicated on seven tenets: that wildlife 1) is a public trust, 2) is not subject to market forces, 3) is 'allocated' (to hunters) by law, 4) can only be killed for legitimate purposes, 5) is considered an international resource (*e.g.* migratory species), 6) with science being the proper tool to discharge wildlife policy, and 7) hunting should be democratic (*i.e.* available to everyone; Geist et al. 2001, Organ et al. 2012, Clark and Milloy 2014).

The development of conservation, especially via protected areas, occurred somewhat in parallel to (though often apart from) the development of wildlife management. The first protected areas in both Canada and The US (*e.g.* Banff and Yellowstone) were initially created to protect scenic vistas and other areas of recreational importance (Dearden and Berg 1993), belying human-focused origins. Through time the focus shifted towards biocentrism, with a primary objective of protecting biodiversity itself (Soulé 1985). Whereas the emphasis of protecting biodiversity has defined conservation biology through much of its modern history, there is now substantial debate about conservation as an intrinsic act vs. one geared towards serving humans (Kareiva et al. 2011, Kareiva and Marvier 2012, Soulé 2013, Levin 2014, Doak et al. 2015).

The lines between wildlife management and conservation are often blurred (Soulé 1985). As views towards predators shift (*e.g.* from seeing wolves as vermin to ecologically important species [Nelson et al. 2011]), their management in some cases has expanded to consider and protect their role as broader ecological actors, not just competitors for human prey. Similarly, conservation is often either targeted towards, or at least involves, focal wildlife species (Fleishman et al. 2000, Carroll et al. 2001, Braid and Nielsen 2015). Some blurring might be intentional, an adaptation of organizations to evolving cultural mores that place a high value on conservation. For example, the Boone and Crocket club, the world's first hunting club, is self-described as pioneers in conservation (Boone & Crockett Club 2017), and the aforementioned wildlife model that guides hunting across Canada and the US (Chapter 5) is titled as the North American Model of Wildlife *Conservation*.

Whereas these two approaches to resource management might come from different worldviews and histories, driven by different values and goals that might be at odds with each other (*e.g.* in the case of managing predators that also prey on prized game species [Nelson et al. 2011, Clark and Milloy 2014, Marshall et al. 2016]), they do share important commonalities of particular relevance to this thesis: they attempt to abate or stop the global decline of biodiversity and animal populations, goals for which the costs of failure could be substantial.

Agencies tasked with wildlife management and conservation deal with complex issues in the face of substantial uncertainty. They are often required to make decisions with incomplete data and to address often controversial issues with complex causation. Accordingly, rigorous decision-making might be particularly important, to ensure rigorous decisions can be made with the best data possible.

Potential of science for management

Science has much to offer wildlife management. It provides rigorous means of weighing evidence (Chamberlin 1890, Platt 1964). Science incorporates and addresses uncertainty, treating uncertainty not as ignorance but instead as important information on the bounds of knowledge (Bradshaw and Borchers 2000). Science is also self-correcting; an approach based on continually confronting hypotheses with new data implies that our understanding of how the world works today will likely get disproven and improved upon tomorrow (Chamberlin 1890, Platt 1964, Mangel 2016). By providing an empirical, self-correcting basis to understand how the world works and what the likely outcomes of a suite of policy options are, science might have substantial potential for helping to resolve disagreements about natural resource management. Indeed, incorporation of scientific information can lead to better decision-making with better outcomes (Sutherland et al. 2004). Although political undermining of scientific integrity has been well-documented (*e.g.* governments cutting science funding, muzzling scientists, or politically interfering with the work of scientists; Goldman et al. 2017, Carroll et al. 2017), scientific information can provide the public with objective insight on key issues facing societies. Accordingly, agencies often strive for or claim to have a science-based approach to management. While a scientific basis seems sensible, what that entails is rarely defined, and tests for it are mostly absent (though see Horwitz and Calver 1998, Mangel 2011).

Idealized role of natural sciences in environmental management

Figure 1.1 builds on previous conceptualizations of how natural sciences and other factors influence wildlife management (Ehrlich and Daily 1993, Peterman 2004, Vucetich and Nelson 2012) to describe how natural sciences might ideally inform the practice of wildlife management. Wildlife management (including conservation) might be conceived of as a process that begins with the managed environment itself. An agency tasked with its management creates prescriptions (designed to reach pre-determined goals, *e.g.* limits and quotas [Lackey 1998]) which structure managed interventions (*e.g.* hunting, logging, fishing) on the managed environment. This cycle repeats, with agencies iteratively prescribing or conscribing additional interventions on the managed environment.

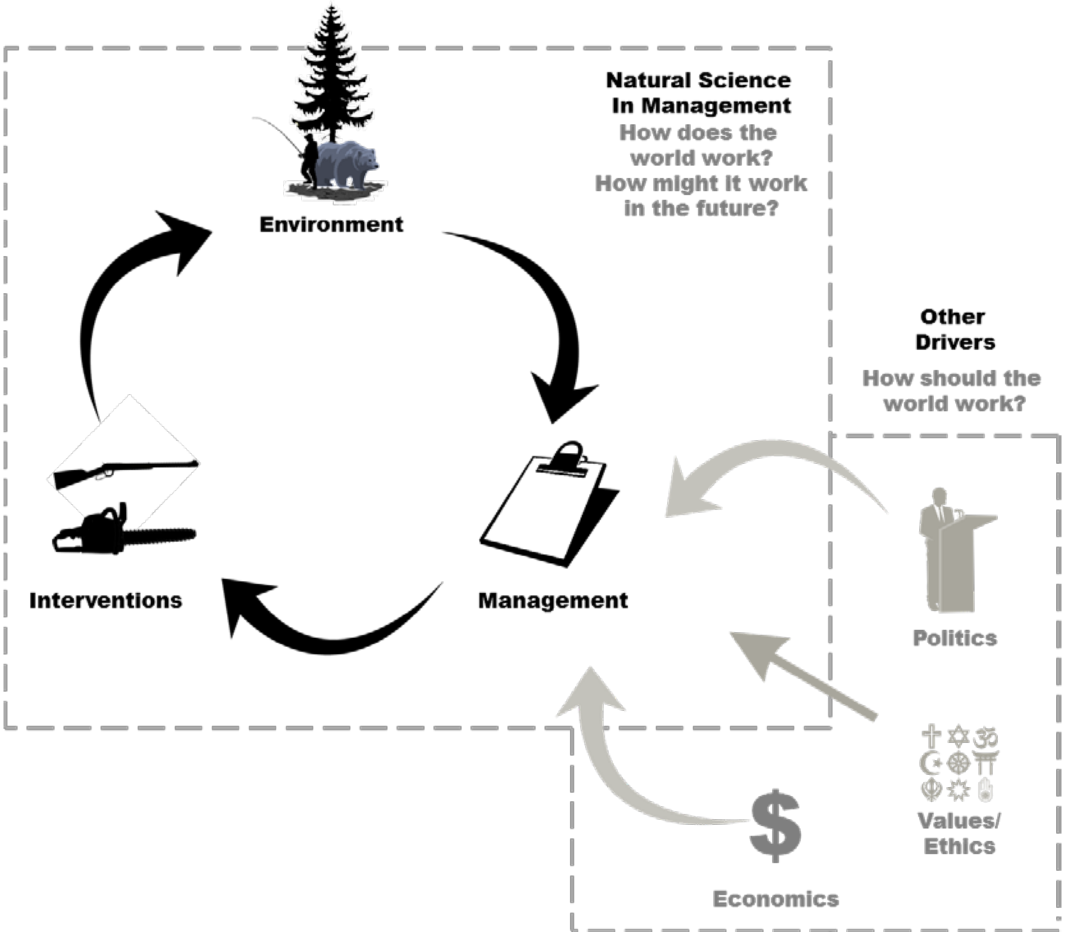

Figure 1.1 Simplified conceptualization of how natural sciences might inform environmental management.

The contents of upper left box represent the primary areas where natural science might specifically inform management (the focus of this thesis) by informing how the world works, and how it might be expected to work in the future. The 'other drivers' in the lower right box represent other considerations that necessarily affect management but are beyond the scope of this thesis. Notably, these other elements are crucial for determining management's objectives, for example by dictating how the world should work. Lines are dashed around both boxes to indicate that these borders are permeable, with elements interacting in additional ways that are beyond the scope of this thesis (*e.g.* other drivers might affect perceptions of the environment and interventions).

Natural sciences can inform each of these steps by providing an understanding of: a) the environment itself, the foundation on which prescriptions are built (Lackey 1998); b) how prescriptions translate to realized interventions (Lackey 1998, Holt and Peterman 2006), and c) how those interventions in turn affect the managed environment. Information at any of these steps could provide valuable insight on whether management is meeting its objectives while avoiding unanticipated or undesirable effects.

Process of science as a model for management

In addition to providing empirical knowledge on which well-informed decisions can be based, the process of science itself might be a useful model for management. The mechanisms of scientific publishing that ensure rigour while correcting against bias might provide particular benefit for management that often deals with considerable uncertainty, incomplete knowledge, and controversy. Hallmarks from science with specific relevance to management include: well-defined **objectives** for management prescriptions aimed at achieving well-defined goals (Platt 1964, Sullivan et al. 2006, Conservation Measures Partnership 2013); consideration, collection, and application of **evidence** to support well-informed decisions (Meffe et al. 1998, Dicks et al. 2014, Walsh 2015, Walsh et al. 2015) and provide baselines against which to assess management effectiveness (Meffe et al. 1998, Doremus 2007); **transparency**, to ensure the public is aware of how management is occurring on their behalf (Jasanoff 2006, Treves et al. 2017, Carroll et al. 2017); and **independent review**, to ensure that approaches are defensible, transparent, and support objectives, and to identify any potential shortcomings that might be addressed to improve management performance (Meffe et al. 1998, Horwitz and Calver 1998, Sullivan et al. 2006, Conservation Measures Partnership 2013).

Management might also follow from science by crafting management prescriptions as multiple competing hypotheses, enabling improved understanding through time (Chamberlin 1890, Platt 1964, Hilborn and Mangel 1997, Mangel 2011). This approach to management suggests that 'the best way to implement ecosystem management may be to learn from past mistakes and also systematically make some new but different ones' (Lackey 1998). Chamberlin (1890) and Platt (1964) discuss how in the sciences, a danger with single hypothesis approaches is that specific hypotheses might become researchers' 'babies', and can become deeply tied to their ego. Evidence contradicting a researcher's single hypothesis might be seen as a direct threat to the researcher's capabilities. They note that multiple hypotheses provide a solution to this, where data are used to compete among alternative hypotheses, not among researchers. A multiple hypothesis framework might similarly allow for evolving management: as the weight of evidence supporting a dominant hypothesis is surpassed by evidence supporting another, management could adapt based on this evolving understanding of the world. Such an approach can allow learning (*e.g.* management as experimentation [Walters and Holling 1990, Hilborn et al. 1995, Lackey 1998]), with newly acquired information informing future and improved prescriptions. This is in contrast to management without clearly defined alternative hypotheses, where the default might simply be an ill-defined assumption of "sustainability", and where evidence to the contrary might be interpreted as failure.

Limits of sciences in environmental management

Importantly, considerations beyond the natural sciences necessarily impact management (Meffe et al. 1998, Lackey 1998, Sullivan et al. 2006, Vucetich and Nelson 2012, Levin and Anderson 2016). Whereas science provides rigorous tools for understanding how the world works, and predicting the effects of interventions on a natural system, it cannot determine how the world should work (Nelson et al. 2011, Vucetich and Nelson 2012). Science can inform how a given objective might be achieved, but other factors ultimately determine the objectives themselves. Figure 1.1 shows some of these factors, including values, economics, and politics. Ethics and values might inform what is right and wrong, whereas economics and politics might determine what is possible (or, more cynically, beneficial to the agency).

Whereas the issues outside the dashed line in Figure 1.1 are beyond the scope of this thesis, clearly delineating the layout of that dashed line – *i.e.* understanding where the role of science begins and ends – is important for understanding the ultimate drivers of management decisions (Levin et al. 2015, Carroll et al. 2017). Moreover, other sciences, such as social and political sciences, provide important insights on these other dimensions. Although this thesis focuses on natural sciences specifically, the potential benefits of a science-based approach are not exclusive to this specific branch of the sciences.

Testing for a scientific basis

I propose that Figure 1.1 highlights focal points for assessing a management system's incorporation of natural science. Assessments might occur at linkages between each of the elements (*e.g.* where knowledge of environment guides management prescriptions, where prescriptions translate to interventions, and where interventions affect the environment), or they might focus on the management process itself (*e.g.* by testing for a rigorous process). Because the components combined constitute a continuous cycle, a break anywhere could undermine the overall system.

There are considerable benefits of directly testing the supposed scientific basis of management given a) assumptions or claims of a rigorous, scientific basis in management, b) the potential for a scientific basis to provide improved management outcomes, and, c) that there are risks imbued by scientific shortcomings. For example, a clear characterization of the extent to which approaches are supported by strong evidence, and the extent to which management itself follows a rigorous approach, might provide clarity to the public for whom natural resources are ostensibly managed and by whom this service is paid. Identified shortcomings might also inform potential improvements. Moreover, approaches modeled on the process of science might allow benefits to accrue across systems, as evidence and knowledge is transferred among practitioners. Finally, clearly defining the extent of scientific knowledge in a given management system and the mechanisms by which it influences decision-making could help to crystalize which aspects of decision-making are ultimately not determined by science, allowing societal discussions to focus on more fundamental areas of disagreement that are often muddled together with scientific questions (*e.g.* arguing over how many wolves are on a landscape when the more fundamental area of disagreement might regard views towards wolves in general).

Overview of chapters

This thesis examines the role of science in real-world management systems. I use various focal points identified by Figure 1.1 to assess the scientific knowledge (Chapters 2-4) and practice (Chapter 5) in a number of management systems.

In Chapter 2, I focus on aspects of environmental understanding and the link between management prescriptions and realized interventions by exploring the risks imbued by unaddressed uncertainty in hunt management of grizzly bears in British Columbia, Canada

(Figure 1.2). Specifically, I test how biological uncertainty in population sizes, population growth rates, and poaching rates; and outcome uncertainty, the discrepancy between targeted and realized mortality (Holt and Peterman 2006); might translate to risk of overkills in hunted populations. I use grizzly bears as a model species for this assessment because their management typically occurs with limited demographic information (Miller 1990, Mattson et al. 1996, McLoughlin 2003), they have life-history characteristics that make them particularly vulnerable to management error (Miller 1990), and because their mortality is primarily human-caused (Peek et al. 1987, Miller 1990, Treves 2009). I focus specifically on hunted grizzly bear populations of British Columbia, Canada, where this hunt is particularly controversial, and, as epitomized by the example from the beginning of this chapter, is frequently defended by hunt advocates and politicians as being based on sound science (though others have cautioned that more cautious management might be warranted [McLoughlin 2003, Peek et al. 2003]). I use the official data on hunting rates and hunting quotas across the province from 2001-2011 to assess the risks imbued by unaddressed uncertainty. In each area and time period, I characterize outcome uncertainty by comparing the prescribed number of bears hunt managers set to be killed to how many were actually killed. I then use simulation modeling to assess the effects that biological uncertainty around parameters used to set hunt quotas might have on overmortality probabilities. Finally, I demonstrate how outcome and biological uncertainty could be addressed in a transparent and repeatable method for setting hunt targets robust to both types of uncertainty.

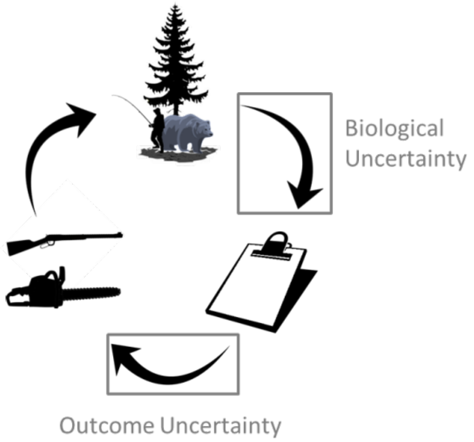

Figure 1.2 **Chapter 2: Assessment of biological and outcome uncertainty in hunt management of grizzly bears (*Ursus arctos horribilis*) in British Columbia Canada from 2001-2011.**

In Chapter 3, I focus on environmental understanding and the effectiveness of interventions in grizzly bear-human conflict in British Columbia, Canada, from 1960-2014 (Figure 1.3).

Conflicting anecdotal explanations have been offered for what drives substantial inter-annual and spatial variation in conflict frequency patterns. I condense these explanations into three distinct hypotheses with direct and quantitative predictions. These hypotheses alternatively state that variation in conflict frequency is driven by a) changes in grizzly bear population size (‘regional saturation hypothesis’), which might lead to an overabundance of bears and a depletion of per-capita food availability, leading in turn to increased risk-taking by individuals, b) prevalence of problem bears in a population (‘problem individual hypothesis’), and c) annual fluctuations in natural food availability. I follow a multiple hypothesis approach (Chamberlin 1890, Platt 1964) and use ecological data and records of bear-human conflict to weigh support for each. Current management responses (interventions) to conflict are more in line with the first two hypotheses: increases in conflict have been used to justify increases in hunt, and individuals involved in conflict are often killed to prevent subsequent conflict. By contrast, natural food availability is generally outside the scope of conflict management.

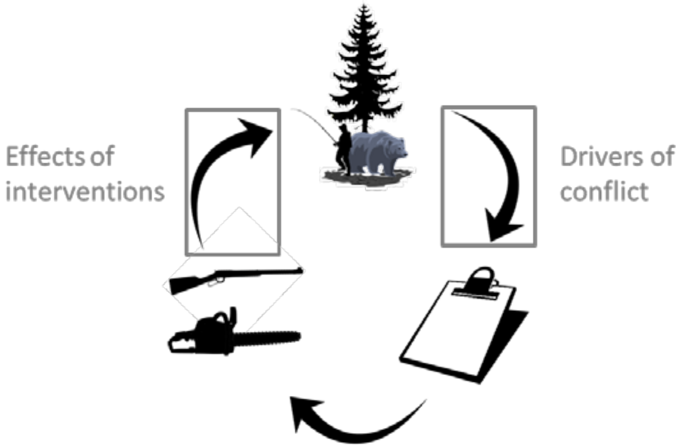

Figure 1.3 **Chapter 3: Assessment of ultimate drivers of human-grizzly bear (*Ursus arctos horribilis*) conflict, and effects of interventions, in British Columbia Canada between 1960-2014.**

In Chapter 4, I focus again on ecological knowledge underpinning management by comparing the layout of a protected areas network to density estimates of a focal species that the network was, in part, designed to protect (Figure 1.4). British Columbia’s Great Bear Rainforest is an area that has garnered considerable interest worldwide both for its ecological and cultural richness, and for a lengthy battle over land use that culminated in a recent extensive conservation and management strategy, known as the Great Bear Agreement. Although this development has been widely celebrated, and scholarship has been devoted to the unique circumstances that led to the negotiated cessation of conflict (Affolderbach et al. 2012, Clapp et al. 2016), empirical assessments of the realized layout of protected areas are largely lacking. I use data from a non-invasive hair sampling program across a large swath of the region to assess spatial patterns of grizzly bears from 2013-2016. I identify spatial hotpots as a) grizzly bear activity centre densities in the 90th percentile per unit area, and b) statistically meaningful hotspots defined by the Getis-Ord G_i^* test. I then assess the extent to which these hotspots occur in protected areas. I discuss how this approach could be used to rapidly assess realized use of habitat by focal species of interest, providing empirical data that might be used to optimize protected areas placement, monitor effectiveness through time, identify gaps in protection, and identify potential improvements.

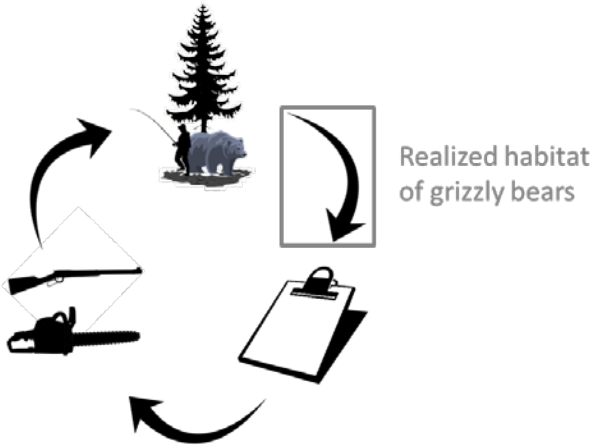

Figure 1.4 **Chapter 4: Ecological context of a protected areas network in the Great Bear Rainforest of British Columbia Canada, assessed by comparing realized densities of grizzly bear (*Ursus arctos horribilis*) activity centres from 2013-2016 with placement of protected areas.**

In Chapter 5, I focus on the process of management itself (Figure 1.5), using wildlife management plans of hunted species across Canada and the US. Practitioners and advocates of the North American Model of Wildlife Conservation, which guides hunt management throughout the region, often claim a scientific basis to management, through for example, the Model's tenet that "science is the proper tool to discharge wildlife policy" (Geist et al. 2001, Organ et al. 2012, Clark and Milloy 2014). Not only has this claim to my knowledge never been tested at a large scale (though see for example Chapter 2 and Morell 2014 where we and others have raised doubts at a more local scale), a definition of what is meant by 'scientific' is generally lacking. I look for four hallmarks that might be expected of science in general, but which might also be particularly relevant for rigour in management: measurable objectives, evidence, transparency, and independent review. Specifically, I test for criteria related to each hallmark in

667 wildlife management plans for 27 groups of species across 62 US states and Canadian provinces.

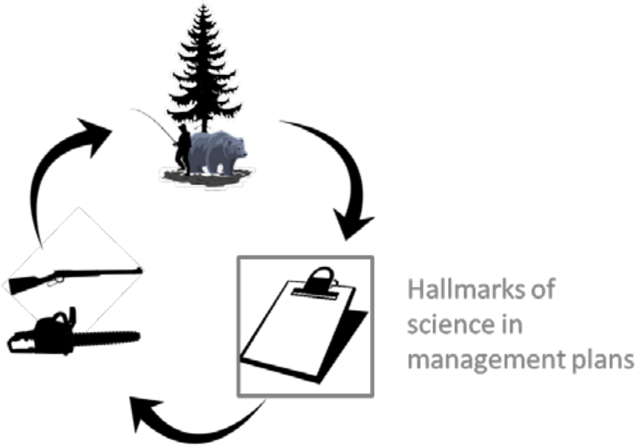

Figure 1.5 **Chapter 5: Assessing hallmarks of science (evidence, measurable objectives, transparency, and independent review) in US and Canadian wildlife management plans guided by the North American Model of Wildlife Conservation.**

Applied scholarship

Given the applied topic, this thesis, in line with the call from Ehrlich and Daily (1993), focuses on providing practical insight into questions of direct management importance. In this vein, I approach the research questions not only theoretically, but also offer suggestions in each case to address any identified shortcomings, and to offer more general insights that might be used in other applications. I also work to make insights from this research accessible to practitioners and the public alike.

The responses of agencies to insights from the published chapters also provide qualitative insight into the adaptiveness of the management systems examined. The response of agencies to newly available scientific evidence provides qualitative insight into their adaptability, and, more broadly, into the extent to which science guides their management. Accordingly, the results of these chapters and similar directed inquiries can be conceptualized as perturbations on the management system itself, qualitatively assessing their adaptiveness by their response to newly emerging scientific information.

Chapter 2.

Confronting uncertainty in wildlife management: Performance of grizzly bear management[1]

Abstract

Scientific management of wildlife requires confronting the complexities of natural and social systems. Uncertainty poses a central problem. Whereas the importance of considering uncertainty has been widely discussed, studies of the effects of unaddressed uncertainty on real management systems have been rare. We examined the effects of outcome uncertainty and components of biological uncertainty on hunt management performance, illustrated with grizzly bears (*Ursus arctos horribilis*) in British Columbia, Canada. We found that both forms of uncertainty can have serious impacts on management performance. Outcome uncertainty alone – discrepancy between expected and realized mortality levels – led to excess mortality in 19% of cases (population-years) examined. Accounting for uncertainty around estimated biological parameters (*i.e.* biological uncertainty) revealed that excess mortality might have occurred in up to 70% of cases. We offer a general method for identifying targets for exploited species that incorporates uncertainty and maintains the probability of exceeding mortality limits below specified thresholds. Setting targets in our focal system using this method at thresholds of 25% and 5% probability of overmortality would require average target mortality reductions of 47% and 81%, respectively. Application of our transparent and generalizable framework to this or other systems could improve management performance in the presence of uncertainty.

Introduction

Confronting uncertainty poses a central problem in the management of wildlife. Decisions made without proper consideration of uncertainty can have undesirable consequences, and have been

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[1] A version of this chapter appears as Artelle, Kyle A., Sean C. Anderson, Andrew B. Cooper, Paul C. Paquet, John D. Reynolds, and Chris T. Darimont. 2013 Confronting uncertainty in wildlife management: performance of grizzly bear management. PLOS ONE 8(11): e78041.

implicated, for example, in widespread overfishing (Harwood and Stokes 2003). Although often poorly accounted for or ignored, uncertainty exists about the “true” value of estimated biological parameters (Reckhow 1994, Hilborn and Mangel 1997, Regan et al. 2005, Armitage et al. 2009). Parameter uncertainty propagates to uncertainty in important management estimates, including the magnitude of mortality a population can withstand without experiencing long-term declines or other deleterious effects (hereafter “mortality limit uncertainty”; Caddy and McGarvey 1996, Prager et al. 2003). Management performance can also be compromised by outcome uncertainty, defined as the difference between targeted and realized (*i.e.* known after the period of exploitation) mortality levels (Holt and Peterman 2006). Remarkably, however, scholarly and independent retrospective examination of wildlife or fisheries management performance – in the presence of uncertainty, or, in general – is rarely conducted (but see Ross et al. 1996, Holt and Peterman 2006, Linnell et al. 2010).

Several methods can account for and incorporate uncertainty into decision-making, estimating a priori the probability that specific scenarios will lead to over-exploitation (Reckhow 1994, Harwood and Stokes 2003). Key to implementing these approaches is distinguishing between targets (mortality levels management aims to achieve) and limits (mortality levels management should never exceed). Given that there is always some chance of exceeding a target, management should avoid setting targets as high as limits, or conflating the two (Caddy and McGarvey 1996, Prager et al. 2003).

Grizzly bears (*Ursus arctos horribilis*) provide an ideal model species for assessing uncertainty in the management of wildlife. Management of most populations occurs with limited demographic information (Miller 1990, Mattson et al. 1996, McLoughlin 2003). Moreover, grizzly bears have life-history characteristics – including long lifespans, low reproductive rates, delayed reproductive maturity, and slow population growth rates (Miller 1990) – that cause high vulnerability to population declines in many other taxa (Reynolds 2003). Finally, as with many vertebrate taxa (Collins and Kays 2011), mortality is primarily human-caused (Peek et al. 1987, Miller 1990, Treves 2009). As such, management decisions can have considerable influence on population viability (McLoughlin 2003, McLoughlin and Messier 2004).

Management of grizzly bear mortality in British Columbia (BC) provides a particularly useful case study for examining effects of uncertainty on management performance. Most populations are managed for sustained yield whereby, in theory, a maximum number of bears (“mortality limit”) can be killed each year by humans, mostly by hunting (Figure 2.1), without causing population declines (Hamilton and Austin 2002, Lunn and Ethier 2007, British Columbia Ministry of Environment, Fish, Wildlife and Habitat Branch 2010). However, uncertainty in mortality limits is only partially addressed by managers in BC; biological parameters and calculated mortality limits are treated as point estimates, with uncertainty adjustments dictated by professional judgement (Hamilton and Austin 2004), not probabilistic assessments. As such, “true” mortality limits might be lower than suggested (Mattson et al. 1996, McLoughlin 2003). Furthermore, outcome uncertainty is not incorporated; mortality limits are used as mortality targets (Austin et al. 2004, Lunn and Ethier 2007) thereby conflating targets with limits.

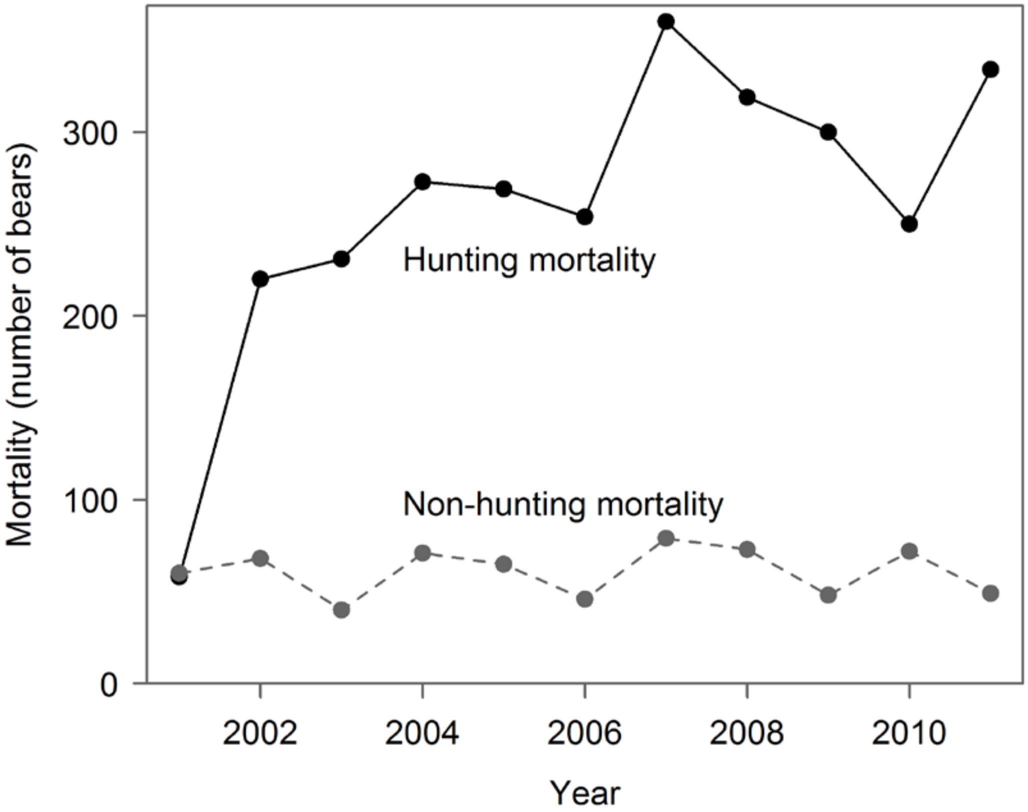

Figure 2.1 Total grizzly bear (*Ursus arctos horribilis*) mortality from hunting (solid-black line) and non-hunting sources (dashed line) in British Columbia, Canada, from 2001–2011.

A province-wide moratorium on the trophy hunt during one of two hunting seasons caused lower hunting mortality in 2001.

Debate about large carnivore management is often contentious and the situation with BC grizzly bears is no exception. Independent scientists have recommended more conservative management (McLoughlin 2003, Peek et al. 2003). Grizzly bears have been extirpated from a large portion of the province, and, citing sustainability concerns, the European Union has banned the import of BC grizzly bear parts since 2002 (Peek et al. 2003, Knapp 2007). Despite concerns, and concurrent with an increasing number of populations gaining threatened status, hunting mortality increased across the province from 2001–2011 (Figure 2.1; Ministry of Forests, Lands and Natural Resource Operations 2012, unpublished data).

We use grizzly bear management in BC from 2001–2011 to explore the potential effects of unaddressed uncertainty on management performance (in our case, the ability to maintain mortality below acceptable limits) and to illustrate general methods for confronting uncertainty in management. Others have highlighted the need to quantitatively address various aspects of uncertainty in management (McLoughlin 2003, Peek et al. 2003, McLoughlin and Messier 2004); we add empirical insight by retrospectively assessing historical management. Specifically, we assessed outcome uncertainty by comparing known human-caused mortality with targeted levels. We then used simulation modeling to estimate the biological uncertainty around mortality limit point estimates based on parameter uncertainty and assessed how mortality limit uncertainty might affect overmortality probabilities. Finally, we incorporated outcome and mortality limit uncertainty into a generalizable and transparent method for identifying mortality targets that maintain the probability of overmortality below pre-determined thresholds. We discuss how this general approach might help inform population management of other exploited species.

Methods

We conducted our analyses at the Grizzly Bear Population Unit (hereafter “population unit”) spatial scale, thought to reflect ecologically and demographically relevant sub-populations (British Columbia Ministry of Environment, Fish, Wildlife and Habitat Branch 2010). We divided our study period into the same multi-year allocation periods (2001–2003, 2004–2006, and 2007–2011) used by the British Columbia Ministry of Environment (hereafter “government”; British Columbia Ministry of Environment, Fish, Wildlife and Habitat Branch 2010). We calculated known mortality for each population unit and each allocation period using a government database (“Compulsory Inspection Database”) of all known human-caused mortality including licensed hunting, animal control kills, road and rail accidents, and known poaching (British Columbia Ministry of Environment, Fish, Wildlife and Habitat Branch 2010). Additionally, we followed government procedures for calculating mortality limits (in units of bears per allocation period) based on estimates of population size, annual allowable mortality (AAM; proportion of a population that can theoretically be removed without causing population declines), and unreported mortality (from rates observed in one population unit and extrapolated to other population units based on four variables thought to correlate with unreported mortality; see Appendix A.2). In our outcome uncertainty analyses we applied the government's "uncertainty correction factors" to population estimates, whereas in subsequent analyses we used an empirical and probabilistic approach to address uncertainty. In most population units, the correction factors used by BC managers are deterministic values, based on expert judgement, that are inversely proportional to estimated population sizes (Appendix A.2, Austin et al. 2004). Our analyses followed the government practice of calculating mortality limits for the entire population (Eq 2.1) and for females separately (Eq 2.2) to account for the sensitivity of populations to female mortality (Harris 1986, Hamilton and Austin 2002, British Columbia Ministry of Environment, Fish, Wildlife and Habitat Branch 2010). We also calculated female mortality as a percentage of total mortality. The government subtracts predicted non-hunt mortality (*e.g.* road kill, animal control kills, and illegal hunting) estimates from mortality limits and allocates the remaining mortality to hunting. We note, however, that by allocating mortality right up to mortality limits, BC managers treat limits as targets, conflating the two; we hereafter refer to true targeted mortality levels (whether or not they are conflated with mortality limits by managers) as "targets" and true, biologically-determined mortality limits as "limits". Details on mortality limit calculations, and on how they differed among periods, are provided in Appendices A.2 and A.3, respectively.

$$\begin{aligned}&\text{total mortality limit} = \text{population estimate x uncertainty correction factor}\\&\text{x (annual allowable mortality} - \text{estimated unreported mortality)}\\&\text{x period length} - \text{previous period total overmortalities}\end{aligned}\tag{2.1}$$

$$\begin{aligned}&\text{female mortality limit} = 0.3\text{ x population estimate}\\&\text{x uncertainty correction factor x (annual allowable mortality}\\&-\text{estimated unreported female mortality) x period length}\\&-\text{previous period female overmortalities}\end{aligned}\tag{2.2}$$

Outcome uncertainty and mortality patterns

We assessed outcome uncertainty across population units and across study periods by calculating the difference between known mortality (from the Compulsory Inspection Database) and targeted mortality:

$$\text{percent difference} = 100 \times \frac{\text{known mortality} - \text{targeted mortality}}{\text{targeted mortality}}\tag{2.3}$$

We further explored patterns of mortality types associated with overmortality events.

We characterized outcome uncertainty as a function of targeted mortality. Using maximum likelihood estimation, we fit Michaelis-Menton curves to model known mortality as a function of targeted mortality, for each period, and for total and female mortality:

$$known\ mortality_i = a + \frac{b(targeted\ mortality_i)}{(c + targeted\ mortality_i)} + \varepsilon_i, \qquad (2.4)$$
$$\varepsilon_i \sim \mathrm{Negbin}(0, k)$$

where i represents a population unit-period; a, b, c, are estimated parameters of the curve; ε_i represents residual error; and k is the estimated size parameter of a negative binomial error distribution with a mean of 0. We used this error distribution because targets must be positive integer values. We fit the models using optim in R 2.14.1 (R Core Team 2012, R Foundation for Statistical Computing) with the Nelder-Mead method and with estimated parameters in log space.

Mortality limit uncertainty and probability of overmortality

Whereas current management procedure (above) treats mortality limits as point estimate, we propagated biological parameter uncertainty to estimate cumulative uncertainty around mortality limits using simulation modeling (Milner-Gulland et al. 2001, Peterman 2004) and assessed how this uncertainty might affect the probability of overmortality. We focused on three key parameters currently treated as point estimates by managers. Because empirically derived uncertainty estimates are lacking for most BC populations, we derived parameter uncertainty estimates from a literature review (Appendix A.4). For each parameter, we took random draws from a continuous uniform distribution centred on existing point estimates. The distributions were bounded by: population estimates: +/−40% of point estimate; AAM: +/−2% of population estimate (because AAM is a percentage of population estimate); and unreported mortality: from 50% (*i.e.* half) to 200% (*i.e.* double) of the point estimate (Appendix A.4). We calculated simulated female and total mortality limits by substituting randomly drawn parameter values into Equation 2.1 and Equation 2.2. We did not incorporate the government's estimated uncertainty correction factors in these calculations. We repeated these simulations 1000 times in each population unit and period to construct a distribution of realistic mortality limits (the simulated breadth of mortality limit uncertainty). We used the percentage of simulations in which simulated mortality limits fell below known mortalities as a proxy for overmortality probability (Figure 2.2, Video A.1).

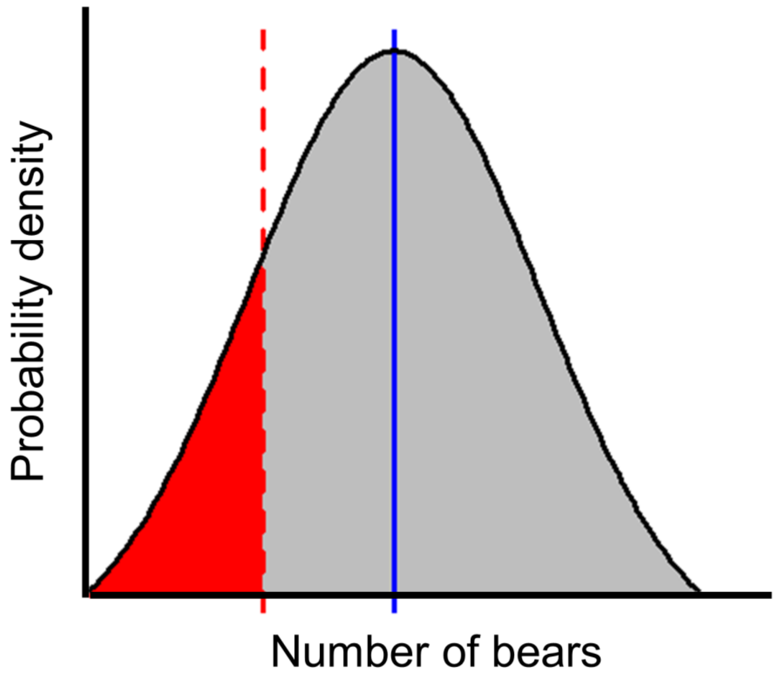

Figure 2.2 Illustration of method for estimating the probability of overmortality in an individual Grizzly Bear (*Ursus arctos horribilis*) Population Unit (“population unit”) and period.
Blue vertical line represents the mortality limit point estimate used by government. Entire distribution (in this example a hypothetical normal distribution used for simplicity) represents the distribution of mortality limit uncertainty, or the distribution of simulated mortality limits. Red dashed line represents the known mortality for the same population unit-period. Red portion of the distribution represents the proportion of simulated mortality limits that fell below known mortality levels in the population unit-period. The percent area of the overall distribution occupied by the red portion provides a proxy for the probability that overmortality occurred. See also Video A.1.

Identifying Targets that Incorporate Outcome and Mortality Limit Uncertainty

We used derived distributions of outcome and mortality limit uncertainty to calculate targets for each population unit that maintained the probability of overmortality below 5% (low risk-tolerant, conservation-prioritizing scenario) or 25% (higher risk-tolerant, exploitation-prioritizing scenario), using data from 2007–2011. For a given target, we used a “plug-in” approach (Bolker 2011) to estimate outcome uncertainty. This approach estimates outcome uncertainty from the stochastic component (the negative binomial error) of Equation 2.4, assuming that the deterministic component (the Michaelis-Menten curve) was fixed at the maximum likelihood estimate. For each population unit, we calculated the intersection of the resultant outcome uncertainty and mortality limit distributions for all possible target values, keeping mortality limit distributions fixed, to find the highest target for which the resultant outcome uncertainty distribution intersected with less than the maximum area (the given thresholds, 5% or 25%) of the mortality limit distribution (Video A.2). We performed all analyses with R 2.14.1 (R Core Team 2012, R Foundation for Statistical Computing).

Results

Outcome uncertainty and mortality patterns

Outcome uncertainty varied across population units and periods, with discrepancies between targeted and known mortality being more pronounced for female mortalities than total mortalities (Figure 2.3, A.1.1, A.1.2). Because government procedures conflated targets with limits, cases in which targets were exceeded also constituted overmortalities. While mortality fell mostly below targets, overmortalities occurred in at least one period in 26 of the approximately 50 population units open for hunting, and most frequently in southern and eastern BC (Figure 2.4). Overmortalities (18 total cases and 33 female cases from 2001–2011) occurred more frequently in population units with smaller targets (Figure 2.3, A.1.1, A.1.2, A.1.3). In seven population units, overmortality events occurred in two periods, whereas in three population units they occurred in all three periods (Figure 2.4). Overmortality events ranged from one to 24 bears. Finally, targets were also frequently approached but not exceeded (Figure A.1.3).

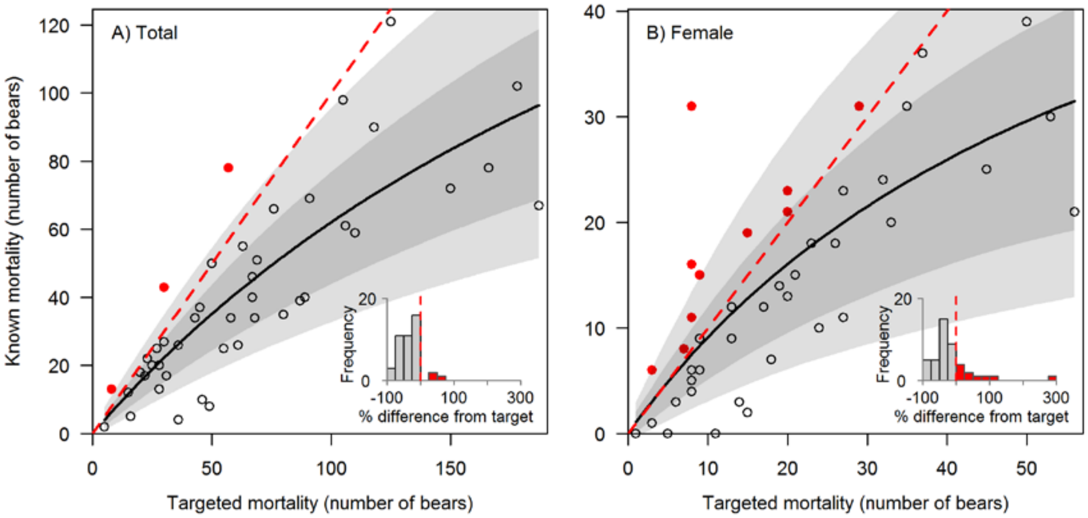

Figure 2.3 Outcome uncertainty for A) total and B) female mortality in Grizzly Bear (*Ursus arctos horribilis*) Population Units ("population units") in British Columbia, Canada, 2007–2011 (see SI for additional periods).

Black curve is a Michaelis-Menten curve fitted by maximum likelihood, assuming a negative binomial error distribution. Red dashed line indicates a 1:1 relationship; solid red dots above this line signal population unit-level overmortality events. Dark and light grey-shaded regions encompass the 50% and 80% prediction intervals, respectively (smoothed for visual purposes). Inset histograms show the distribution of GBPU-level percent difference between known mortalities and mortality targets (conflated with limits under mortality management policy); red bars to the right of red dashed lines indicate overmortality events.

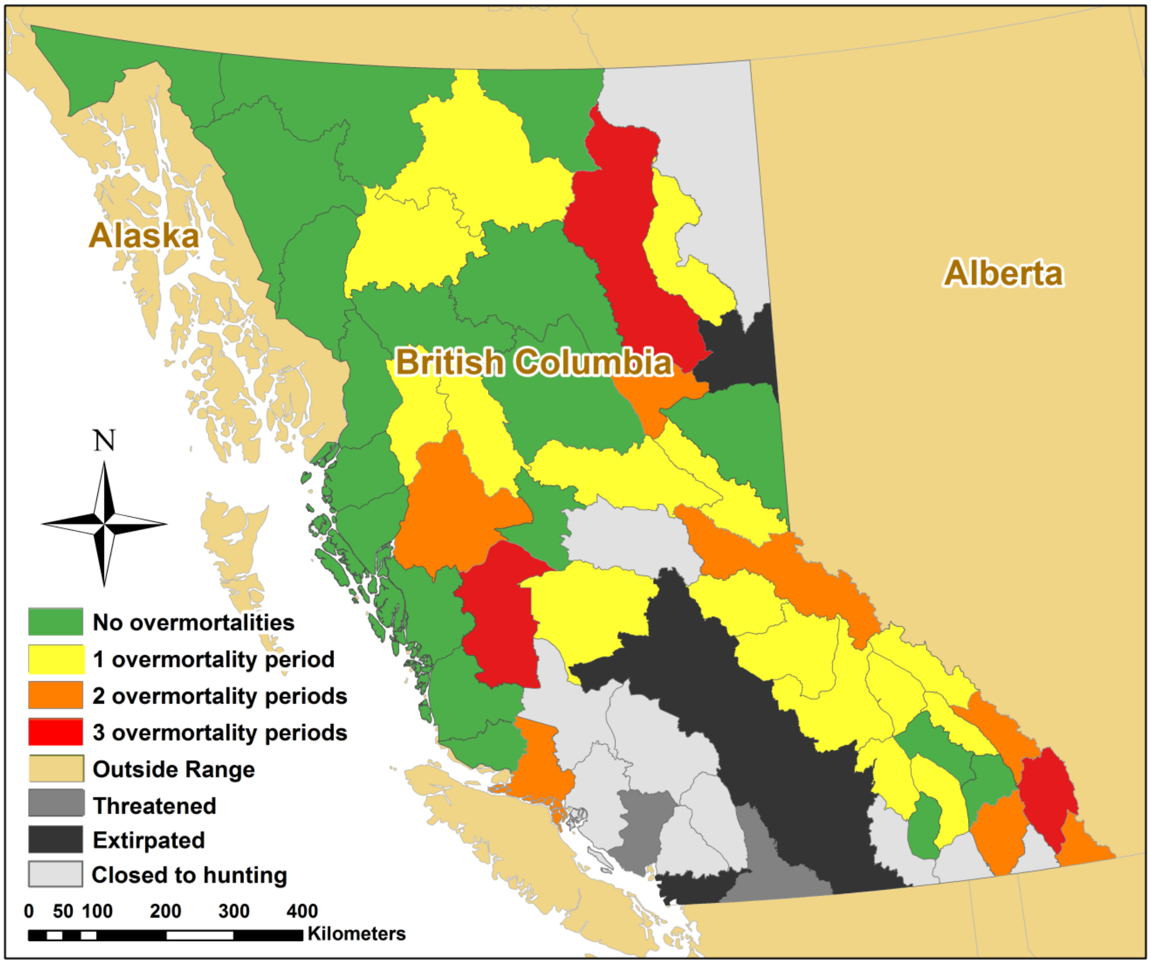

Figure 2.4 Number of allocation periods (2001–2003, 2004–2006, or 2007–2011) in which female or total overmortality occurred in Grizzly Bear (*Ursus arctos horribilis*) Population Units ("population units") of British Columbia, Canada.

Shown are 2009 population unit boundaries. Hunting is not allowed in areas denoted as "threatened", "extirpated", or "closed to hunting". One additional population unit (Blackwater-West Chilcotin) has been reclassified as threatened as of 2012.

The most common factor associated with total overmortalities was unpredicted non-hunting mortality. However, most of the total overmortalities from 2001–2011 (17 of 18, or 94%) could have been avoided with reduced hunting mortality (Figure A.1.3). The most common factor associated with female overmortalities was hunting mortality. Most female overmortalities (25 of 33, or 76%) could have been avoided with reduced hunting mortality (Figure A.1.3).

The female component exceeded 30% of *total* mortality (from hunting and non-hunting sources combined) in 55% of all cases and in 94% of all female overmortality events (Figure 2.5 A and B, respectively). The female component exceeded 30% of *total hunting* mortality in 50% of all cases and in 82% of all female overmortality cases (Figure 2.5 C and D, respectively).

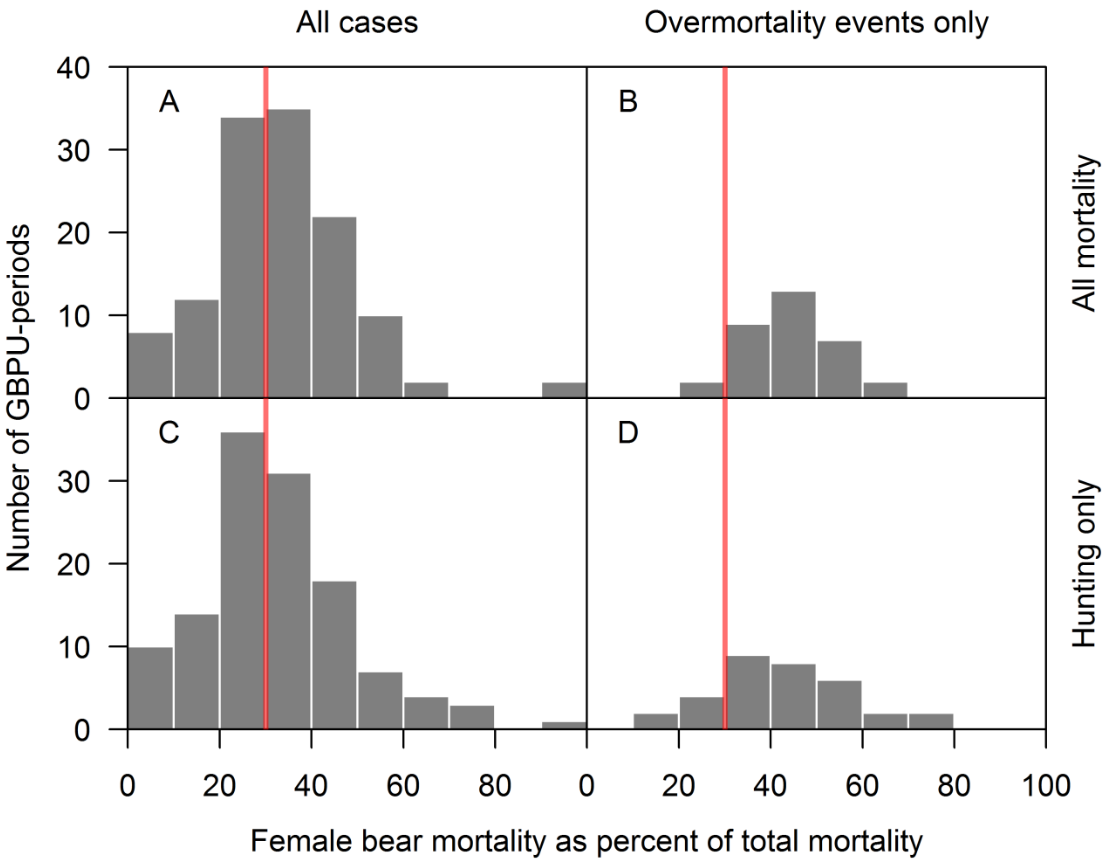

Figure 2.5 Female mortality as percent of total mortality across Grizzly Bear (*Ursus arctos horriblis*) Population Units ("population units") in British Columbia, Canada, and allocation periods (2001–2003, 2004–2006, and 2007–2011). (A) female mortality as percent of all mortality, (B) female mortality as percent of all mortality in female overmortality events, (C) female hunting mortality as percent of all hunting mortality, and (D) female hunting mortality as a percent of all hunting mortality in female overmortality events. Vertical red lines indicate 30%, the threshold below which female mortality must remain for total mortality limits to be theoretically sustainable according to the BC government's mortality management procedure.

Mortality limit uncertainty and probability of overmortality

Accounting for components of biological uncertainty revealed that overmortalities might have occurred in 90 of 127 (71%) examined female cases and 89 of 127 (70%) examined total cases. This comprised an additional 45% of female cases and 56% of total cases relative to overmortality assessments that did not consider uncertainty (Figure 2.6 A and B, A.1.4 A and B, and A.1.5 A and B). Even in the face of uncertainty, reducing hunting by half would have reduced the probability of overmortality by an average of 85% for total and 75% for female overmortality cases (Figure 2.6 C, A.1.4 C, and A.1.5 C), whereas completely eliminating hunting would have reduced the probability of overmortality by an average of 96% for total and 89% for female overmortality cases (Figure 2.6 D, A.1.4 D, and A.1.5 D).

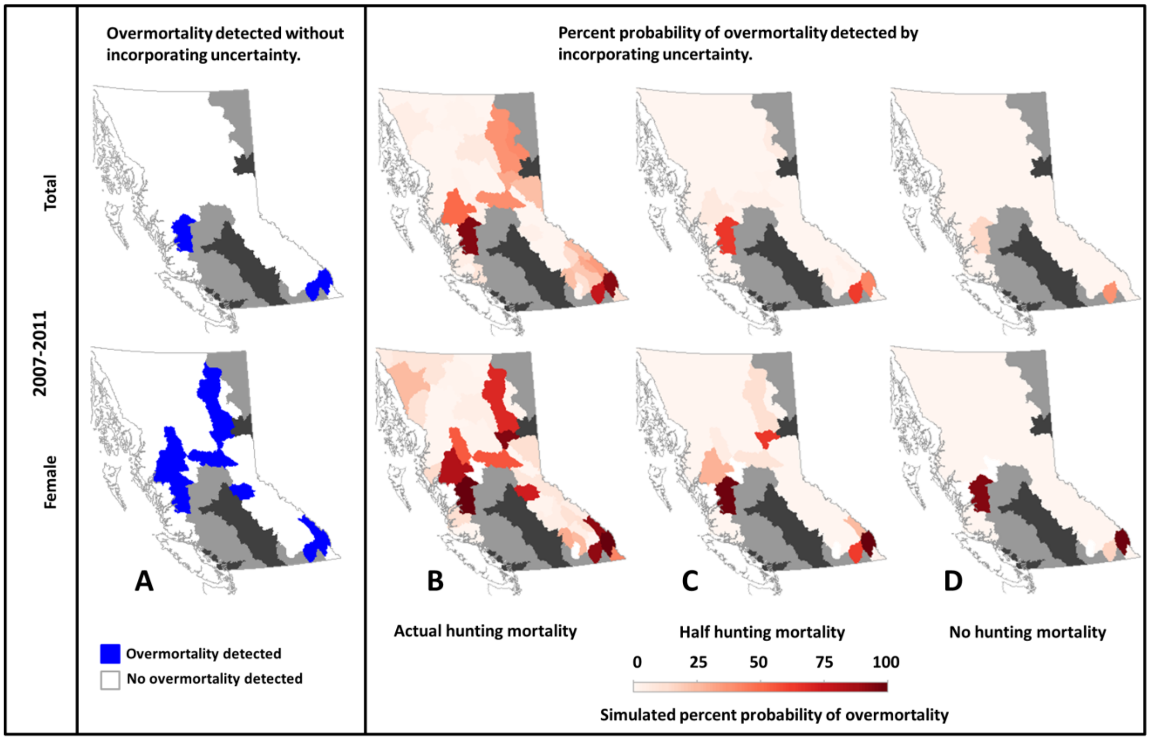

Figure 2.6 Total and female overmortalities of Grizzly Bear (*Ursus arctos horribilis*) Population Units ("population units") of British Columbia, Canada, from 2007–2011 (see SI for additional periods).

A) Overmortalities detected given known hunting mortality levels and without consideration of mortality limit uncertainty. Blue indicates population units with detected overmortality whereas white indicates population units without. B–D) Simulated probability of total or female overmortality, incorporating uncertainty around mortality limits. Panel B shows simulated probability of overmortality given known mortality rates; panels C and D show what the probability of overmortality would be had hunting mortality been reduced by 50% or 100%, respectively, assuming other sources of mortality remained unchanged. Increasingly dark red indicates an increasing probability of overmortality in a given period. Grizzly bears have been extirpated from dark-grey areas. Light-grey areas indicate population units in which populations are either threatened or were closed to hunting during the study period.

Identifying targets that incorporate outcome uncertainty and mortality limit uncertainty

To maintain the probability of overmortality below a 5% threshold, mortality targets would need to be reduced by an average of 81% across all population units relative to 2007–2011 targets, and by 100% in 15 (Figure 2.7 A, B and E). For the exploitation-prioritizing 25% threshold, mortality targets would still need to be reduced by an average of 47% across all population units, and by 100% in four population units (Figure 2.7 C, D, and F).

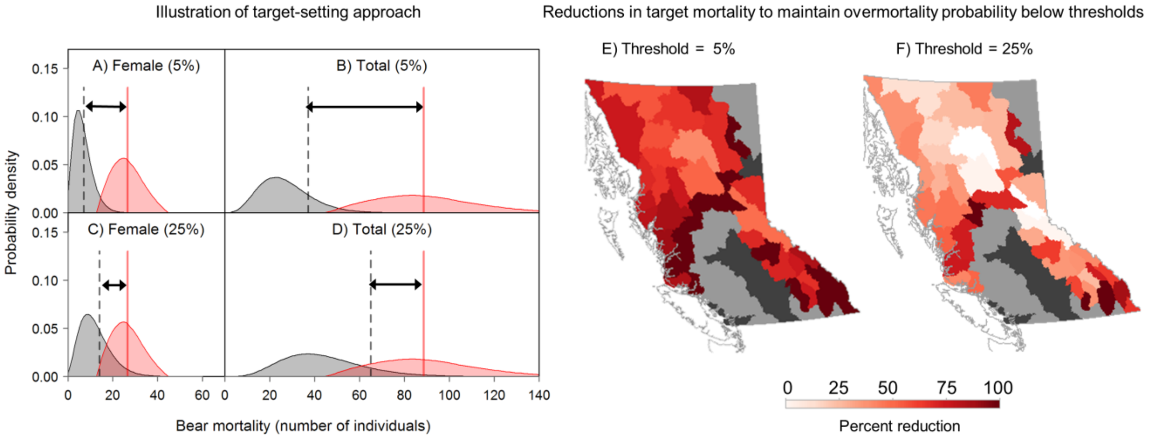

Figure 2.7 Illustration of our method for setting female (A and C) and total (B and D) mortality targets, with maximum probability of overmortality of 5% (A and B) or 25% (C and D) by integrating outcome uncertainty (grey distribution) and mortality limit uncertainty (red distribution), using the Stewart Grizzly Bear (*Ursus arctos horribilis*) Population Unit as an example.

Targets (dashed black lines) from this approach are set so that the resulting outcome uncertainty distribution (grey distribution) overlaps with a maximum of 5% or 25% of the mortality limit uncertainty distribution (red distribution). Red vertical lines represent mortality limits (conflated with targets in previous periods under mortality management policy) set by the government in 2007–2011. Magnitudes of recommended target reductions are shown by black double-headed arrows. E-F) Reduction in mortality targets, relative to 2007–2011 targets (conflated with limits under mortality management policy), required to maintain the probability of both female and total overmortality below E) 5% or F) 25%. Increasingly dark red indicates increasing target reductions identified.

Discussion

Our analysis illustrates the importance of assessing management performance and uncertainty. Specifically, we found that unaddressed uncertainty could compromise management performance by leading to excessive mortalities in hunted species. We found that grizzly bear overmortalities in British Columbia, Canada, were spatially widespread, occurred repeatedly, and were more frequent in females. Considering biological uncertainty around mortality limits revealed that many additional populations might have experienced overmortalities. A target-setting framework that incorporates outcome and mortality limit uncertainty shows that considerable reductions in targeted mortality would be required to improve management performance.

Considerations

We used grizzly bears to illustrate general issues applicable to many other taxa, rather than prescribing specific management actions for this particular species. Moreover, mortality limit simulations used uniform distributions with ranges considerably narrower than the full extent suggested in the literature (see Appendix A.4 for full ranges). We had insufficient data to determine clearly which particular distribution best approximated such parameters; however, the use of such limited ranges of uncertainty suggests our estimates of overmortality risks and target reductions were underestimated even if the true error structure followed a different distribution (*e.g.* normal or log-normal). Importantly, estimated probabilities of overmortality and reductions in targeted mortalities would change if empirically derived and area-specific ranges and distributions of uncertainty were known for each population unit. Similarly, given that the outcome uncertainty was estimated from management performance over a short time, our derived distributions likely underestimated the true range of uncertainty. Additionally, the relationship between targeted and known mortality changes through time (as might be expected given the fluidity of political, social, and ecological contexts, for example), which potentially affects the ability to predict the future using historical data. However, by frequently and iteratively re-evaluating management performance, managers adopting this approach could detect such changes and respond by updating outcome uncertainty distributions. Finally, our analyses did not address assumptions used by management in setting specific parameter point estimates for each area, or in adjusting estimates among periods, which could have affected our ability to detect overmortalities (Appendix A.3). Given these considerations, our results could provide minimal requirements for improving performance in this particular system; we recommend that management systems adapting this approach obtain geographically-explicit data, and characterize and incorporate uncertainty. We also recommend that management be re-evaluated, updated, and refined iteratively to account for possible changes in dynamics in targeted species and hunter behaviour.

Additional sources of uncertainty

Our analyses addressed only a subset of uncertainty in the management of wildlife. For example, there is additional uncertainty about the appropriateness of models used in setting limits (“model selection error” [Harwood and Stokes 2003]); genetic, phenotypic, or social effects of exploitation on hunted populations (*e.g.* [Swenson et al. 1997, Wielgus et al. 2001, Darimont et al. 2009]); time required for population recovery (Reynolds 2003); effects of declining food availability (Levi et al. 2012); and the cumulative effect of other anthropogenic disturbances such as logging, mineral extraction, roads, and development (Mattson et al. 1996, Weaver et al. 1996, Peek et al. 2003) Despite examining only a subset of uncertainty, our work empirically illustrates potential effects on management performance, and suggests methods management agencies could consider.

Management performance and outcome uncertainty

Multiple processes may contribute to outcome uncertainty. For instance, in the case of grizzly management, hunting mortality, especially in females, was often higher than targeted. Guidelines that encourage hunters to avoid females seem inadequate given that female mortality consistently exceeded the 30% threshold dictated by government procedures (Harris 1986, Austin et al. 2004, British Columbia Ministry of Environment, Fish, Wildlife and Habitat Branch 2010). Similar barriers to limiting female mortality might also apply to other wildlife species in which sexes are not particularly dimorphic, with similar concerns about population dynamics (*e.g.* caribou *Rangifer tarandus* [Festa-Bianchet et al. 2011]). Additionally, although most total and female overmortality events could have been prevented through hunting reductions, mortality sources beyond management control might also contribute to outcome uncertainty. In our analysis road kill, animal control kills, and illegal hunting were important, highlighting that measures beyond hunt reductions are likely required to safeguard populations. Importantly, not explicitly incorporating outcome uncertainty into procedures for management of wildlife could result not only in sporadic and isolated, but also chronic and repeated, overmortality events, as highlighted in our study period in which overmortalities occurred repeatedly in many areas.

Mortality limit uncertainty

In addition to outcome uncertainty, uncertainty not explicitly accounted for in estimating biological parameters, such as mortality limits, can also lead to excessive mortality. For example, by accounting for mortality limit uncertainty, our simulations revealed that overmortality events might have occurred in many cases in which mortality did not exceed government-determined mortality limits. We found that the probability of overmortality would have decreased considerably had hunting been reduced or eliminated, as expected for any system in which hunting constitutes most mortality. This result provides management a direct and easily controlled route to reducing the probability of over-exploitation.

Identifying targets that incorporate uncertainty

Our framework for transparently incorporating uncertainty identified targets that reduce the probability of over-exploitation. This approach is a considerable improvement from the deterministic and ad hoc “uncertainty correction factors” used in previous management. In our approach, uncertainty is incorporated in a repeatable, quantitative and transparent fashion, and can readily include new data as they become available. Of particular relevance to managers, the public, and decision-makers is how mortality management might change if this approach were implemented. Our simulations revealed that careful management would require considerable target reductions, consistent with the conservative ‘bet-hedging’ recommended for cautious management (Reckhow 1994, Mattson et al. 1996). Importantly, given that female mortality seems difficult to control independently of total mortality, a given population unit’s total target mortality would need to be reduced sufficiently to maintain total and female overmortality probabilities below thresholds. Recommended targets changed considerably depending on the threshold used, highlighting the importance of careful consideration and engagement of stakeholders when setting targets. Although the acceptable probabilities of overmortality used in our approach (5% or 25%) were arbitrary, they might represent thresholds for a low risk-tolerant, conservation prioritizing scenario and a higher risk-tolerant, exploitation-prioritizing scenario, respectively. Notably, hunting reductions would be required even in the exploitation-prioritizing scenario.

Identifying targets in other scenarios

Our case study illustrated an approach for reducing the risk of overmortality of species managed for long-term population viability. This approach could also be used for reducing the risk of undermortality of species managed for population reduction or elimination, such as in the control or eradication of invasive species (*e.g.* control of invasive lionfish through exploitation [Akins 2012]). In such cases targets would be set sufficiently high to ensure they do not fall below levels needed to obtain population reductions required. This approach provides the first steps to a full decision analysis framework, a quantitative approach for weighing various management options that might be appropriate in future management deliberations (Reckhow 1994, Peterman 2004).

Importance of incorporating best-practices from other disciplines

This study illustrates the merit of incorporating approaches from other disciplines and taxa into wildlife management. Whereas BC grizzly bear management incorporates data and management techniques from grizzly bear management in other jurisdictions (Hamilton and Austin 2002, British Columbia Ministry of Environment, Fish, Wildlife and Habitat Branch 2010), it does not incorporate some promising methods from other disciplines. For example, our approach, which relies on the principle that targets should be set sufficiently low to account for uncertainty (and lower than most of the estimated range of mortality limits; Reckhow 1994, Caddy and McGarvey 1996, Prager et al. 2003) is used in fisheries but far less commonly in wildlife management, highlighting the need for better integration of best practices across taxa and disciplines.

Conclusion

Science can provide valuable insight into management issues often mired in heated debate. Management often occurs within contentious social environments, with interest groups advocating strongly for different scenarios, informed by varying ethical perspectives and philosophies (Lackey 1998, Paquet and Darimont 2010, Linnell et al. 2010, Darimont and Paquet 2012, Phillis et al. 2012). Science can inform such debate by assessing the ability of management to achieve objectives and by transparently communicating risks associated with various scenarios. We suggest that many management systems might benefit from retrospective and empirical examinations that can inform present and future management. These could be conducted as a part of the management process or, as in this study, by third parties. Results and predictions from such examinations in any system could help to communicate likely outcomes while simultaneously improving future management performance.

Chapter 3.

Ecology of conflict: marine food supply affects human-wildlife interactions on land[2]

Abstract

Human-wildlife conflicts impose considerable costs to people and wildlife worldwide. Most research focuses on proximate causes, offering limited generalizable understanding of ultimate drivers. We tested three competing hypotheses (problem individuals, regional population saturation, limited food supply) that relate to underlying processes of human-grizzly bear (*Ursus arctos horribilis*) conflict, using data from British Columbia, Canada, between 1960–2014. We found most support for the limited food supply hypothesis: in bear populations that feed on spawning salmon (*Oncorhynchus* spp.), the annual number of bears/km^2 killed due to conflicts with humans increased by an average of 20% (6–32% [95% CI]) for each 50% decrease in annual salmon biomass. Furthermore, we found that across all bear populations (with or without access to salmon), 81% of attacks on humans and 82% of conflict kills occurred after the approximate onset of hyperphagia (July 1st), a period of intense caloric demand. Contrary to practices by many management agencies, conflict frequency was not reduced by hunting or removal of problem individuals. Our finding that a marine resource affects terrestrial conflict suggests that evidence-based policy for reducing harm to wildlife and humans requires not only insight into ultimate drivers of conflict, but also management that spans ecosystem and jurisdictional boundaries.

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[2] A version of this chapter appears as Artelle, K. A., S. C. Anderson, J. D. Reynolds, A. B. Cooper, P. C. Paquet, and C. T. Darimont. 2016. Ecology of conflict: marine food supply affects human-wildlife interactions on land. Scientific Reports 6:25936.

Introduction

Human-wildlife conflicts are widespread, occurring when resource use by human and non-human animals overlap. Interactions can endanger the safety and well-being of humans and wildlife alike, lead to economic loss, and affect the conservation of species by negatively altering public perceptions (Treves and Karanth 2003, Distefano 2005, Woodroffe et al. 2005, Treves et al. 2006, Clark and Slocombe 2011, Fernández-Gil et al. 2016). Animals typically avoid humans (Smith et al. 2005), raising the question of what ultimately causes conflicts to occur when and where they do. We propose that investigating the broader ecological context of conflict (hereafter the 'ecology of conflict') might help to explain variation in conflict patterns, leading to a better mechanistic understanding and improved prediction and management (Treves et al. 2004, von der Porten 2010, Teichman et al. 2013).

We conceive of conflict as a process emerging from proximate and ultimate drivers. Research usually focuses on the former, including human group sizes and behaviours, attractant management, and behaviour of humans and wildlife involved (but see Stringham 1986, Linnell et al. 1999, Beckmann and Berger 2003, Treves et al. 2004, Fernández-Gil et al. 2016). Proximate inquiry provides important insights for understanding specific conflicts and how to avoid them (Herrero 1985, Ciarniello 1997, Gore et al. 2006), but renders limited insight into the timing, location, and causes of broader conflict patterns. Moreover, proximate investigations rarely yield insights generalizable across taxa.

Herein we use a generalizable, ecological approach to explore patterns of human-wildlife conflict, assessing three potential hypotheses of ultimate drivers of conflict. The 'Problem Individuals' hypothesis posits that conflict frequency is driven by the number of conflict-prone (risk-tolerant/bold) individuals in populations (Wilson et al. 1994, Linnell et al. 1999, Wolf and Weissing 2012), and predicts that removing such individuals should reduce subsequent conflict (Linnell et al. 1999). Consistent with hunger-mediated risk-taking observed across taxa (Lima and Dill 1990, Godin and Crossman 1994, Damsgird and Dill 1998, Morton and Chan 1999), the 'Regional Population Saturation' hypothesis posits that conflict patterns are driven by wildlife populations exceeding regional carrying capacities, causing nutritionally stressed individuals to take increased risks, leading to increased conflicts with humans. This hypothesis predicts that population reductions (*e.g.* by increased hunting) should decrease subsequent conflict. Finally, via a similar reduction in per capita food supply (and hunger-mediated pathway), the 'Food Supply' hypothesis posits that conflict patterns are driven by changes in regional food supply. It predicts that periods of high conflict should coincide with shortages of natural foods (Gunther et al. 2004, Baruch-Mordo et al. 2014, Johnson et al. 2015). Although not exhaustive, this list of hypotheses allows comparisons of different ultimate ecological processes that might commonly drive conflict in many systems.

We assessed the extent to which conflict between humans and grizzly bears (*Ursus arctos horribilis*) in British Columbia (BC), Canada, might be explained by the three proposed ultimate drivers of conflict. Considerable inter-annual variation exists in patterns of conflict, represented here by human injury and death from, and conflict kills of, grizzly bears from 1960–2014. Similarly, considerable variation exists in patterns of annual human-caused mortality (mostly by hunting [Artelle et al. 2013]), and in annual food availability, especially of spawning Pacific salmon (*Oncorhynchus* spp.), which, in areas where it is available to bear populations, provides a high-caloric and disproportionately important food source to which abundance and fitness are directly related (Hilderbrand et al. 1999a, Mowat and Heard 2006, Van Daele et al. 2013). The peak of spawning salmon biomass also coincides with hyperphagia, the pre-hibernation period of intensive energetic demand (Nelson et al. 1983, Robbins et al. 2004, McDonough and Christ 2012, Schindler et al. 2013). Our assessment, which identifies food supply as the hypothesis with most support, illustrates how using a multiple-hypothesis ecology of conflict framework can discriminate among alternate ecological explanations of conflict patterns. Moreover, it illustrates that human-wildlife conflict might be affected by ecological processes that are broadly applicable across space, time, and taxa, and that might extend well beyond administrative and ecological boundaries.

Methods

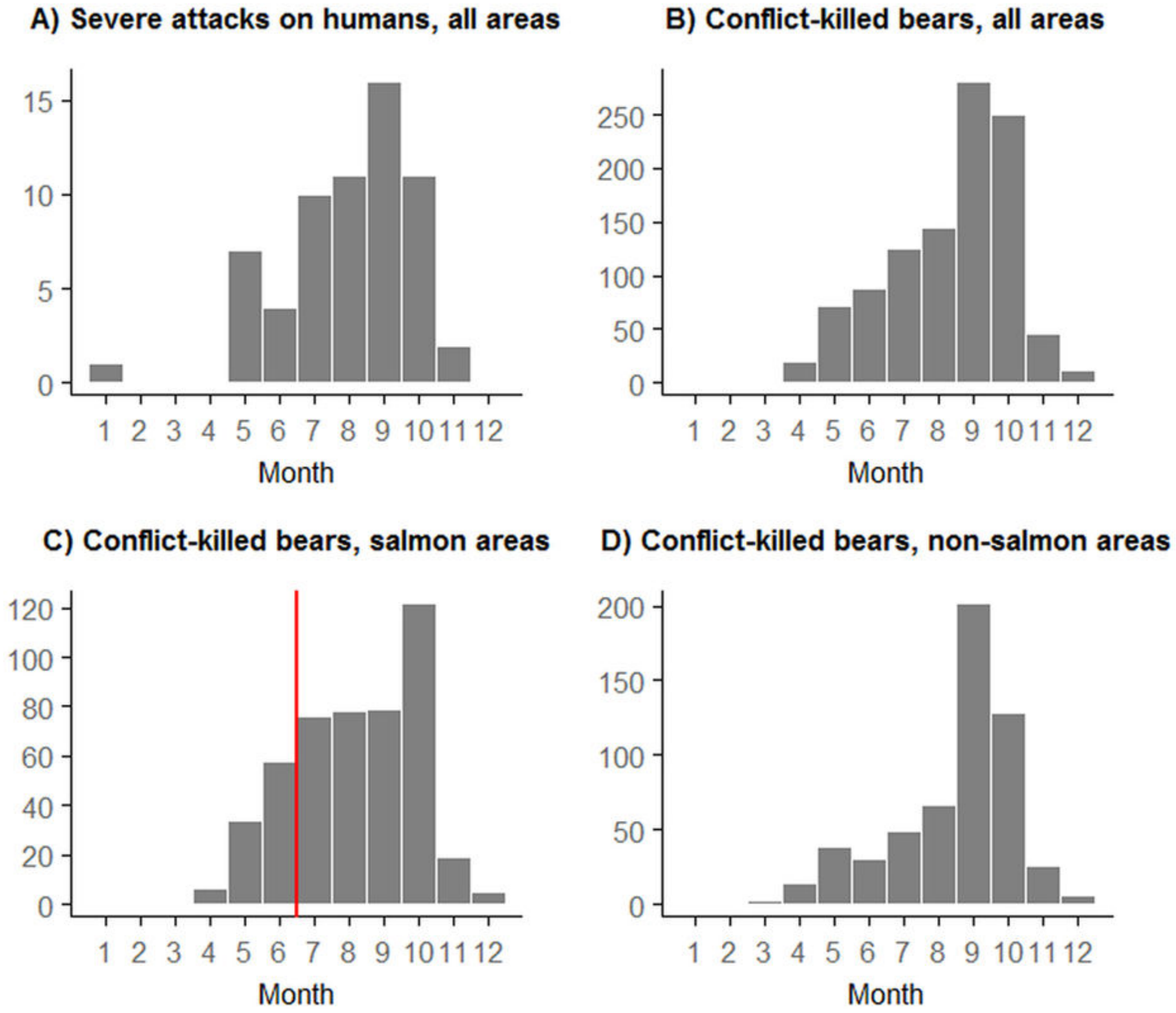
We assessed patterns in timing, location, and age of grizzly bears involved in human-wildlife conflict, represented by conflict kills of bears and attacks on humans in British Columbia (BC), Canada. We modeled the association between annual variation in ecological variables and human-bear conflict frequency. Whereas we were primarily interested in inter-annual patterns for assessing the relative support for our three hypotheses, we included spatial variables in our model to account for ecological differences among populations.

All analyses were performed at the scale of Grizzly Bear Population Unit (hereafter ‘population’), which is designated by the provincial government of BC and is thought to correspond with geographically and genetically relevant sub-populations (British Columbia Ministry of

Environment, Fish, Wildlife and Habitat Branch 2010; Appendix B.1). The ‘habitable area’ (area excluding glaciers and water bodies, Figure B.1) of these populations ranges from 2,698 km^2 to 49,268 km^2 (mean = 13,316 km^2).

Conflict kills

We compiled the annual number of conflict-killed grizzly bears from the ‘Compulsory Inspection Database’ (hereafter ‘CID’), which contains the date, location, and cause (*e.g.* hunt, conflict kill, road accident) of all known human-caused grizzly bear deaths in BC, from 1977–2014 (British Columbia Ministry of Environment, Fish, Wildlife and Habitat Branch 2010; Appendix B.1; Figure B.2). We also extracted age estimates from the database, which were available for 75% of human-caused kills. We used entries only from 1980-onwards because data quality improved considerably after this point (T. Hamilton pers. comm.). We excluded conflict kills from areas where grizzly bears are considered extirpated or threatened ($n = 37$; Appendix B.1) because such kills are anomalies, whereas we were interested in generalizable patterns. We included only late-season conflict (occurring from July 1st onwards; 79% of recorded conflict kills; Figure 3.1) as a response in our models, because abundance of spawning salmon (a predictor in our model) and bear predation on salmon peak from summer through autumn (Hilderbrand et al. 1999c). We used the ArcGIS (ESRI 2013) spatial analyst kernel density estimator, which uses a quadratic kernel function as described in (Silverman 1986) to visualize the spatial density (number per km^2) of conflict kills.


A) Severe attacks on humans, all areas

B) Conflict-killed bears, all areas

C) Conflict-killed bears, salmon areas

D) Conflict-killed bears, non-salmon areas

Figure 3.1 Number of conflicts between grizzly bears (*Ursus arctos horribilis*) and humans by month in British Columbia, Canada

(A) monthly number of severe grizzly bear attacks on humans from 1960–2014 (n = 64), monthly number of conflict-killed grizzly bears from 1980–2014 for (B) the whole province combined (n = 1145), (C) for areas with salmon (n = 546), and (D) those without salmon (n = 599). Red vertical line indicates approximate onset of most salmon runs.

Attacks

We combined a database of all known dates and locations of attacks in BC from 1960 to 1997 provided by Stephen Herrero (Herrero and Higgins 1999) with a database of attacks from 1998 to 2014 provided by the BC Ministry of Environment. We included only 'severe' attacks for both time periods (for which details on hospitalization differed: pre-1998 severe attacks included fatalities, and injuries requiring >24 hours of hospitalization, whereas from 1998 onwards, when data on hospitalization duration were absent, severe attacks included fatalities, and injuries of a severity requiring hospitalization [*e.g.* dismemberment and broken bones]) when examining trends through time. We did this because all severe attacks are recorded by the provincial government, whereas the proportion of ‘minor’ attacks (those not requiring medical attention) recorded is unknown (but see Figure B.3 for timing of all recorded attacks).

Spatial correlates

We accounted for geographic variation in climate (temperature and precipitation), grizzly bear and human population densities, and presence or absence of spawning salmon. To assess climatic differences among populations we used the program ClimateBC (Wang et al. 2015), which downscales climatic variables obtained from weather stations across the province to an 800 m × 800 m resolution with high accuracy (R2 >> 0.9 between most predicted and weather-station measurements (Spittlehouse and Wang 2014, Wang et al. 2015). We created a 4 km × 4 km grid of points across each population’s habitable area (Figure B.1) and calculated the log-transformed mean of climate normals (mean spring and summer temperatures and log total spring and summer precipitation from 1981–2010) extracted at each point. To assess differences in grizzly bear densities among populations, we divided 2012 population estimates (British Columbia Ministry of Environment, Fish, Wildlife and Habitat Branch 2010) by habitable area in each population and log-transformed the quotient. We used the 2011 Canadian census (Statistics Canada 2011) for spatial assessments of human densities. We attributed human population counts from the finest spatial scale available (census subdivisions) to each bear population unit based on percent overlap of the two spatial scales, divided by habitable area of the bear population unit. For a bear population unit with k subdivisions the calculation was:

$$\mathbf{human\ density} = \left(\frac{\sum \left(\begin{array}{c} \mathbf{human\ population\ of\ census\ subdivision_k} \\ * \dfrac{\mathbf{area\ of\ census\ subdivision_k\ overlapped\ by\ population\ unit}}{\mathbf{total\ area\ of\ census\ subdivision_k}} \end{array} \right)}{\mathbf{habitable\ area\ of\ population\ unit}} \right) \tag{3.1}$$

We used a province-wide database of spawning salmon enumerations (FOC 2014) to attribute presence/absence of spawning salmon to each population.

Annual correlates

Within each population, we assessed inter-annual variation in number of recent conflict kills, number of recent hunting kills, mean spring and summer temperature and precipitation, and annual salmon availability to evaluate the relative support for our three hypotheses (problem individuals, regional population saturation, food supply). We used climate as a coarse but broadly applicable proxy for terrestrial bear food availability because estimates of terrestrial food across BC do not exist, though climate has been linked to food availability and human-wildlife conflict elsewhere (Zack et al. 2003). Specifically, given their broad association with net productivity (Del Grosso et al. 2008), we used measures of temperature and precipitation, during the growing season (spring and summer) of vegetative grizzly bear foods, including shoots, sedges, and berries (Welch et al. 1997, Robbins et al. 2004, Krebs et al. 2009, Holden et al. 2012). We calculated annual values of mean spring and summer temperature and log-transformed total precipitation from ClimateBC values extracted from a 4 km × 4 km grid of points across each population. We calculated the number of hunting and conflict kills in recent years using a 3-year rolling window, *e.g.*:

$$\textbf{Recent hunting kills}_{\textbf{year i}} = \sum_{\textbf{year i}-\textbf{3}}^{\textbf{year i}-\textbf{1}} \textbf{yearly number of hunting kills} \qquad (3.2)$$

Within each population, recent hunt and conflict kills were scaled by 2 standard deviations with the mean subtracted, providing a measure of inter-annual variation scaled to the magnitude and variability of these measures in each population. We did not include human population as an annual predictor because such data do not exist annually, and there was little temporal variation among censuses in this period. Similarly, we did not include inter-annual variation in grizzly bear densities because such data do not exist in BC (Artelle et al. 2013). We assessed inter-annual variation in spawning salmon biomass across the province from 1980 to 2013, using the Fisheries and Oceans Canada nuSEDS database (Appendix B.1; FOC 2014, but see Price et al. 2008, Bryan et al. 2014 for caveats). At each salmon count location (Figure B.4), we calculated the annual biomass of each species individually, omitting species-stream time series with data missing for more than eight years total, or for three or more consecutive years. We estimated missing counts in the remaining time series by multiple imputation with a Ricker-logistic model fitted to each stream and species (Appendix B.1; Figure B.5). We attributed each stream salmon count location to a bear population unit and calculated the total annual salmon biomass for each population as the geometric mean of annual stream biomasses of all salmon species combined (Appendix B.1). Within each bear population, annual biomass was scaled by 2 standard deviations with the mean subtracted, providing a measure of inter-annual variation scaled to the abundance and variability of salmon in each population.

Analyses

We assessed associations between ecological correlates and conflict patterns using the R (R Core Team 2016) package glmmADMB, which estimates parameters by maximizing likelihood (Skaug et al. 2013). We used a hierarchical modeling approach combining variables that vary spatially among populations with those that vary temporally within each population (Equation 3.3). We centred and scaled all predictors (subtracted the mean from each observation and divided by 2 standard deviations) to facilitate meaningful comparisons of effect sizes among predictors (Gelman 2008). We ran 'full region' models that included all populations, and 'salmon areas' models restricted to populations with estimated salmon availability. We visually inspected residuals plotted against each predictor and the fitted values and did not detect any remaining strong patterns. Similarly, we visually assessed autocorrelation in residuals and observed little spatial autocorrelation, and substantial temporal autocorrelation in only one population (excluding this population had no qualitative effect on our results), so we did not include autocorrelation terms for model simplicity.

We modelled the number of conflict-killed bears (y) per unit area (km^2) in year i and population unit j as

$$\begin{aligned} \mathbf{y}_{\mathbf{i[j]}} &\sim \textbf{Negative binomial}\left(\boldsymbol{\mu}_{\mathbf{i[j]}}, \boldsymbol{\phi}\right) \\ \log \boldsymbol{\mu}_{\mathbf{i[j]}} &= \log \textbf{area}_{\mathbf{j}} + \boldsymbol{\alpha} + \boldsymbol{\alpha}_{\mathbf{j}} + \mathbf{X}_{\mathbf{i[j]}} \boldsymbol{\beta}_{\textbf{annual}} + \mathbf{Z}_{\mathbf{j}} \boldsymbol{\beta}_{\textbf{spatial}} \\ \boldsymbol{\alpha}_{\mathbf{j}} &\sim \textbf{Normal}(\mathbf{0}, \boldsymbol{\sigma}_{\boldsymbol{\alpha}}^{\mathbf{2}}), \end{aligned} \tag{3.3}$$

where $\mu_{i[j]}$ and ϕ represent the mean and size parameters of the 'NB2' parameterization of the negative binomial distribution (Hilbe 2011) in glmmADBM, which was used because our data were over-dispersed (ϕ in fitted model estimated as 0.72 for salmon areas and 0.62 for full region model); $X_{i[j]}$ represents a vector of annual predictors (salmon biomass, recent conflict kills, recent hunt kills, mean spring and summer temperature, total spring and summer precipitation) with associated β_{annual} coefficients; and Z_j represents a vector of spatial predictors (grizzly population density, human population density, mean spring and summer temperature, mean total spring and summer precipitation, salmon present [yes/no]) with associated $\beta_{spatial}$ coefficients. The α_j term represents random deviations from the overall intercept α that vary with population unit and have variance σ_α^2. The term $\log \text{area}_\text{j}$ is an offset term representing the habitable area of each population.

We used an information theoretic approach (Burnham and Anderson 2002), whereby we assessed relative variable importance to weigh support for our hypotheses, and conducted model averaging across two sets of candidate models ('full region' and 'salmon areas'; Table B.1). Spatial predictors were used to account for spatial differences in conflict patterns and allow for inference about our temporal hypotheses. We assessed support for our three hypotheses using coefficient estimates and variable importance of temporal predictors in the two model-averaged models. For the problem individuals hypothesis we assessed previous 3 years of conflict kills, for the regional population saturation hypothesis we assessed previous 3 years of hunting kills, and for the food supply hypothesis we assessed marine-derived food using salmon availability (salmon areas model only), and terrestrial food using climatic variables (annual precipitation and mean temperature; both models) combined. All analyses were performed using R 3.1.2 (for code and source data see github.com/kartelle/ecology-of-conflict/).

In describing overall patterns of conflict, we used all data available (spanning 1960 to 2014), whereas we were limited to data from 1980 to 2013 for modeling purposes because the salmon database and climate data we used did not extend beyond 2013, and reliable conflict-killed bear data were only available from 1980-onwards.

Results

Temporal and spatial patterns of conflict

Between 1960–2014, severe attacks on humans were rare (mean of 1.18/year). Although their frequency increased slightly through time, attacks were episodic, with considerable inter-annual variation (from 0–4/year; Figure 3.2A). Most (50 of 62; 81%) occurred late in the year (from July-onwards; Figure 3.1A). Similarly, between 1980–2014 conflict kills of grizzly bears (involved in human-wildlife conflict and killed as a result, either by private citizens or provincial agents) were episodic, increasing somewhat over time (Figure 3.2B), and primarily occurred late in the year, peaking in autumn (857 of 1042, 82% occurred from July-onwards; Figure 3.1B). This seasonal pattern was consistent in areas with and without spawning salmon (379 of 479, 79% occurred from July-onwards in areas with salmon, Figure 3.1C; 478 of 563, 85% occurred from July-onwards in areas without salmon, Figure 3.1D). Conflict-killed bears were typically younger than hunter-killed bears (median age of 2 and 5 years, respectively; Figure B.6A), and occurred closer to towns (median distance of 17 km for conflict-killed and 44 km for hunter-killed; Figure

B.6B). Conflict kills were clustered in hotspots, mostly where high estimated densities of grizzly bears overlapped with human habitation (Figure 3.3).

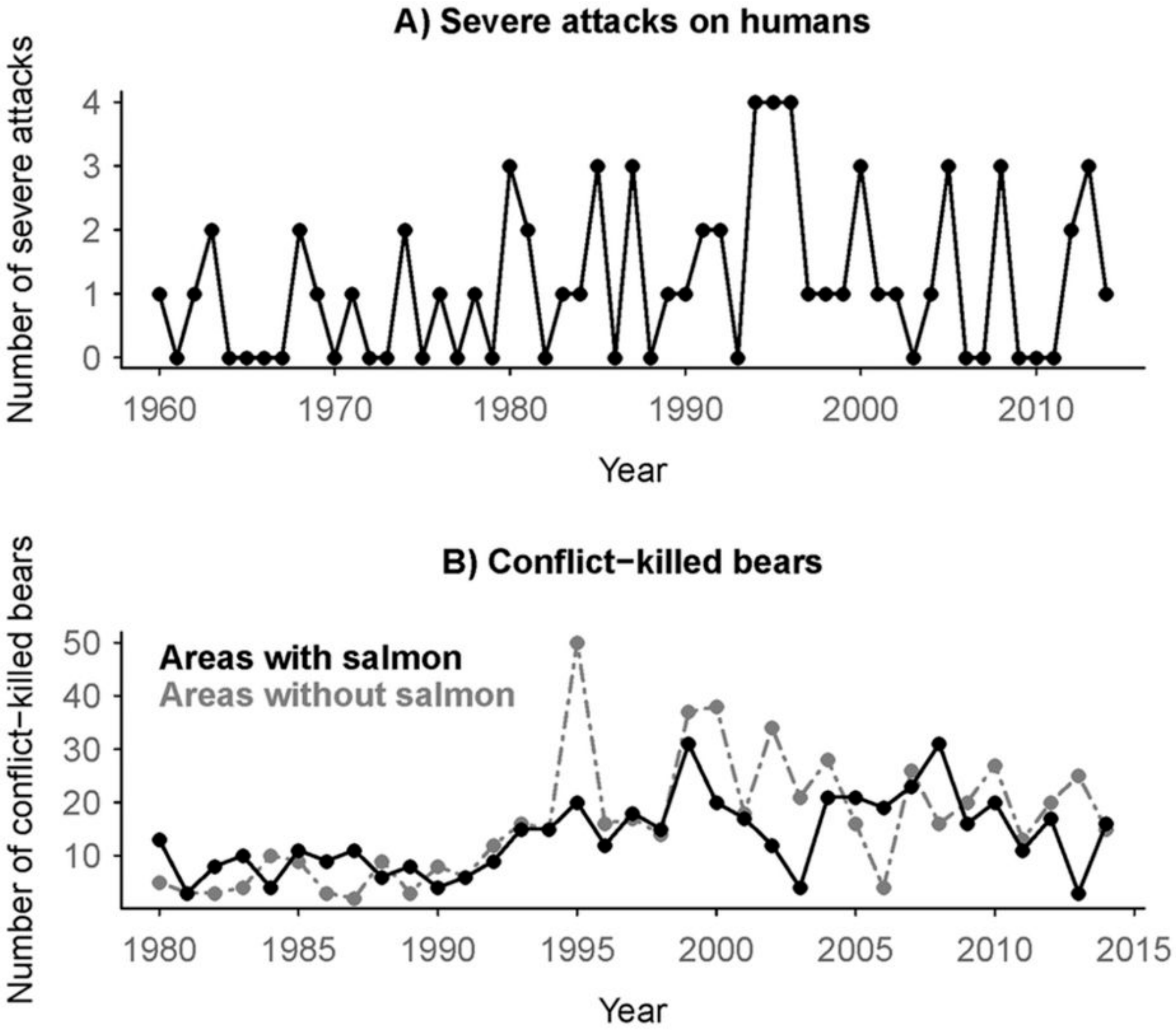


Figure 3.2 Number of grizzly bear (*Ursus arctos horribilis*)-human conflicts by year in British Columbia, Canada

A) Annual number of severe (causing hospitalization) grizzly bear attacks on humans for the whole province combined, 1960–2014 (top), and (B) annual number of conflict-killed grizzly bears in areas with (black lines) and without (grey lines) spawning salmon, 1980–2014.

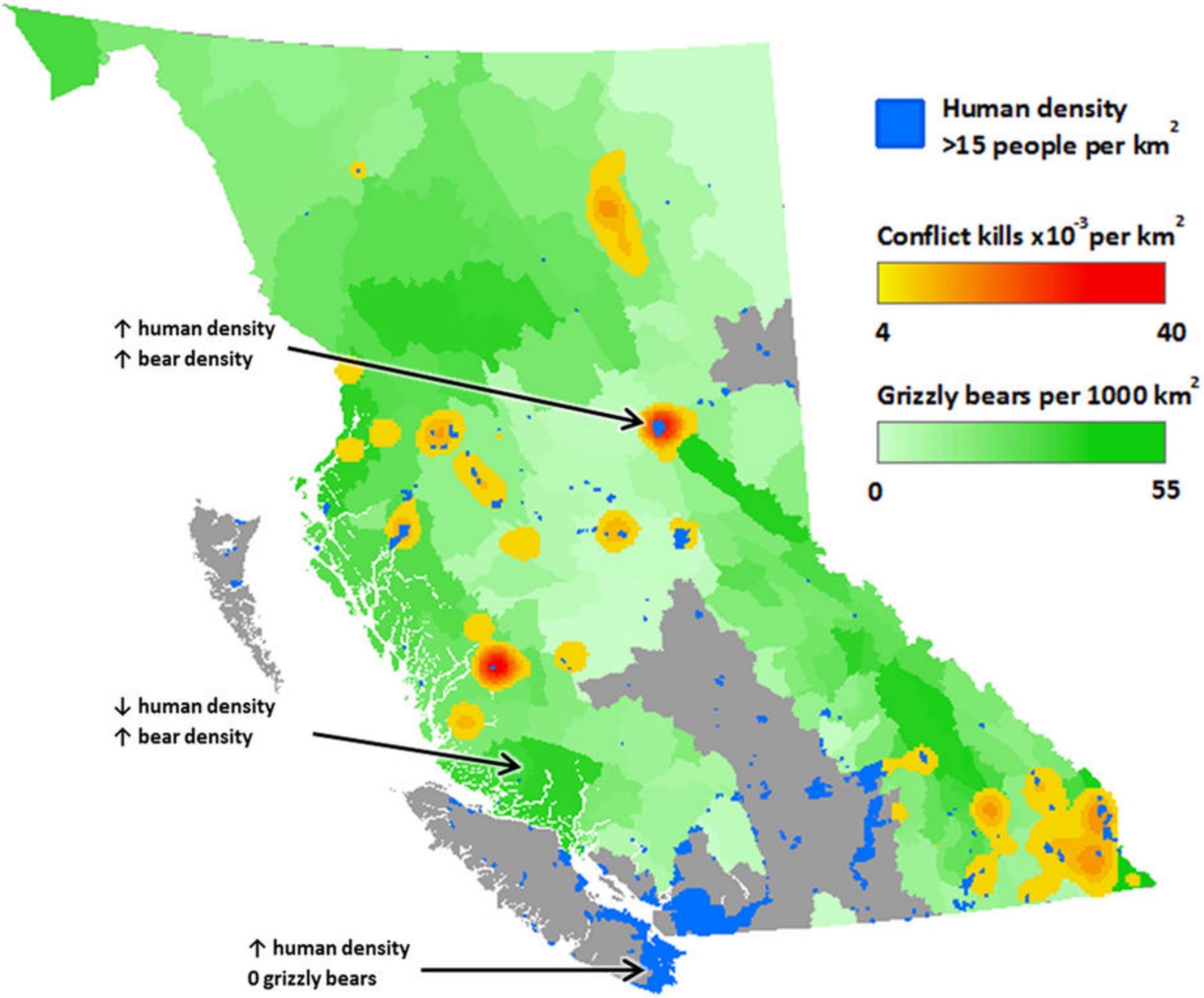


Figure 3.3 **Hotspots of grizzly bear (*Ursus arctos horribilis*) conflict kills in British Columbia, Canada, 1978–2014.**
Increasingly 'hot' colours (yellow to red) represent an increasing density of conflict kills across the study period. Darker green areas have higher estimated grizzly population densities (grey areas have no grizzly bears). Blue areas are those with a human density ≥15 people per km^2. Generated with ArcMap 10.2, www.esri.com.

Predictors of conflict kills

We used model-averaged, hierarchical models to identify associations between patterns of conflict (*i.e.* annual number of conflict-killed bears per km^2) and spatial and temporal variation in ecological predictors, and to assess the relative support for our three hypotheses (problem individuals, regional population saturation, food supply). Because salmon only spawn in some areas, we fitted two separate model-averaged models: a 'salmon areas' model that included temporal variation in salmon availability, limited to areas with spawning salmon, and a 'full region’ model that included the full province but excluded salmon availability as a predictor. Both models had moderate fit to the data (*e.g.* Figure B.7).

Spatial predictors accounted for considerable regional differences in conflict patterns in both models (Figure 3.4A). Areas with larger estimated bear densities had more conflict in the full region model, as did areas with larger human densities. We did not find an effect of spatial differences in precipitation and temperatures on conflict in either model. Similarly, we did not detect a difference in conflict prevalence between areas with and without salmon.

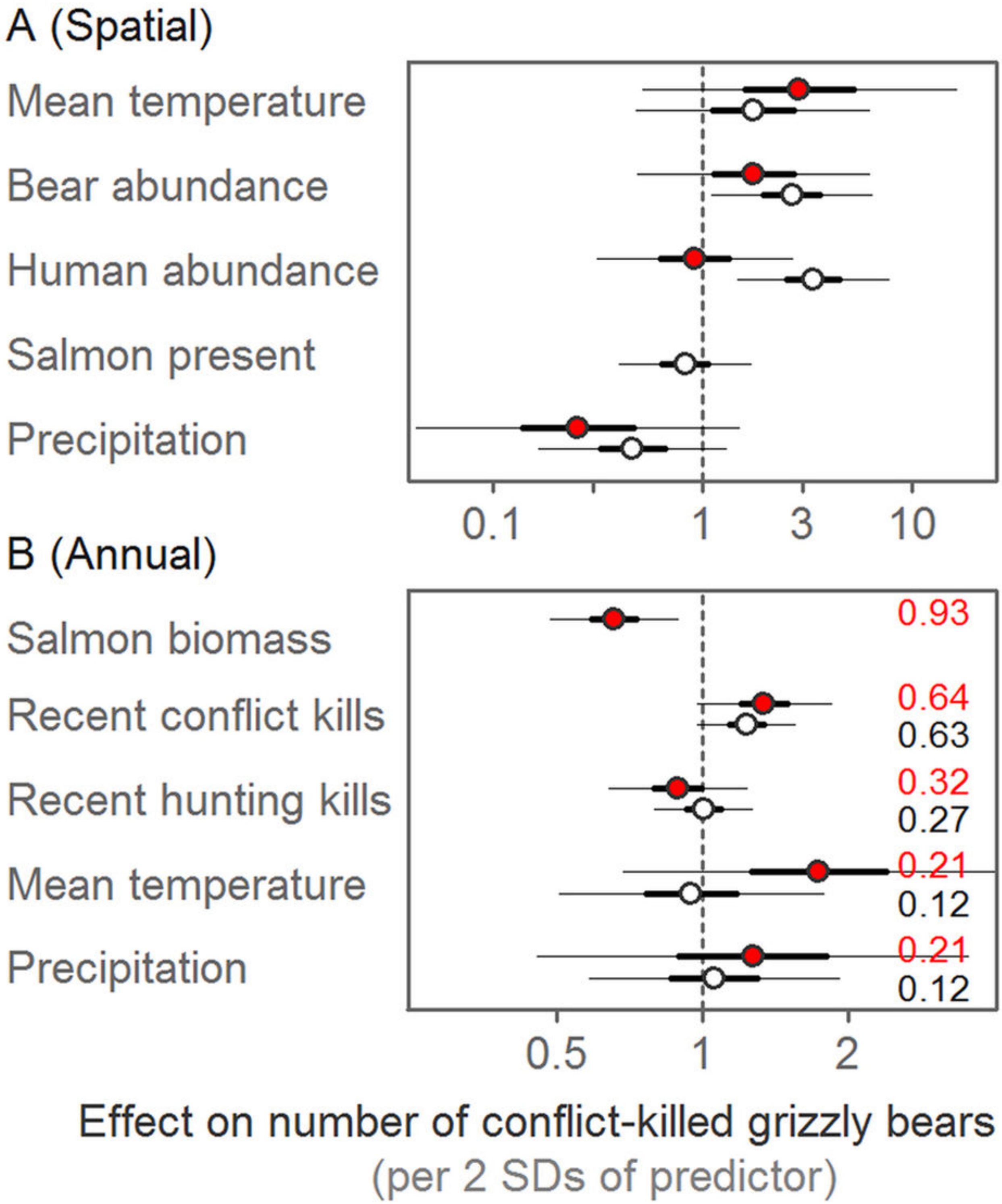


Figure 3.4 Effect of ecological variables on annual number of conflict-killed grizzly bears (*Ursus arctos horribilis*) in British Columbia, Canada, 1980–2013. Dots represent centred (mean-subtracted) and scaled (divided by 2 SD) parameter estimates and thick and thin bars represent the 50% and 95% confidence intervals, respectively, from salmon areas (red, with filled circles) and full region (black, with hollow circles) models. Relative variable importance values are shown in panel B. Results shown are model-averaged across candidate model sets (Tables B.1 and B.2).

Temporal variables revealed support only for the food supply hypothesis. Contrary to the problem individuals hypothesis, we did not find that previous conflict kills were associated with subsequent conflict levels, with 95% confidence intervals of coefficients that overlapped zero, and with moderate relative variable importance (‘RVI’; 0.63 for full region and 0.64 for salmon areas model; Figure 3.4B, Table B.2). Contrary to the regional population saturation hypothesis, we found little evidence of an effect of previous hunting levels on conflict, and low RVI (0.27 for full region and 0.32 for salmon areas; Figure 3.4B, Table B.2). Although we found little evidence of an effect of terrestrial food supply on conflict, with 95% confidence intervals of coefficients for annual climatic proxies for terrestrial food availability (temperature and precipitation) that overlapped zero, and low RVI (0.12 for full region and 0.21 for salmon areas; Figure 3.4B), we found the most support for marine-derived food supply affecting conflict: annual variation in salmon biomass had the highest RVI of all annual variables in the salmon areas model (0.93, Figure 3.4B, Table B.2). Years with lower salmon abundance were associated with increased conflict (Figure 3.4B, Table B.2). For example, conflict increased by 20% (6%–32% [95% CI]) for each 50% decrease in the geometric mean of salmon biomass for a grizzly bear population with average salmon variability (Figure B.8).

Discussion

Discriminating among hypotheses

Of the three hypotheses assessed, we found most support for the food supply hypothesis. Contrary to the predictions of the problem individuals hypothesis, we did not find a reduction, but instead a suggestive trend of an increase, in conflict kills following periods with high conflict removal of bears. Apparent increases in conflict following increased kills might be explained by a number of mechanisms, including, but not limited to, social effects on the hunted populations (*e.g.*Treves 2009, Fernández-Gil et al. 2016), reduced tolerance of humans towards wildlife following recent periods of conflict, or the presence of persistent anthropogenic attractants across multiple years. However, in this particular case the suggestive trend was not substantiated statistically, and hence did not constitute evidence of any discernible effect of conflict kills on subsequent conflict. That we did not detect an effect is perhaps not surprising because most conflict involved younger individuals (Elfström et al. 2014). If conflict-proneness decreases with age, then removing young individuals might not reduce future conflict because individuals would become less conflict-prone as they age, with or without management intervention.

Similarly, we did not find support for the regional population saturation hypothesis. Whereas areas with higher estimated densities of grizzly bears and humans experienced more conflict, annual hunting intensity had no measurable effect on subsequent conflict, suggesting attempted population reduction via hunting might not be effective in mitigating conflict (see also Treves et al. 2010, Obbard et al. 2014, Baruch-Mordo et al. 2014). Moreover, as in other wildlife systems where hunting is used in part to mitigate conflict (Treves 2009), individuals killed by hunters differed from those typically involved in conflict: in our system, hunter-killed bears were older and lived farther from human habitation.

We found the most support for the food supply hypothesis, with salmon availability being the annual variable with the greatest measured importance for explaining conflict prevalence. However, the use of coarse measures might have obscured other effects related to food supply. For example, estimated spawning abundance is a crude proxy for salmon availability (Boulanger et al. 2004, Housty et al. 2014). In addition, whereas we did not find a strong association with annual climate measures (temperature and precipitation), these measures might have limitations as proxies for terrestrial food availability. Whereas changes in climate and weather would be expected to affect terrestrial food availability, responses among plant species vary considerably (Krebs et al. 2009), and weather-related events such as late frosts (*e.g.* Krebs et al. 2009) or acute weather events might have an effect not detectable with the available data. Similarly, climate-driven changes in phenology of food sources have been observed in Alaska, with foods that once occurred sequentially co-occurring temporally instead, resulting in concurrent changes in brown bear diets (Deacy et al. 2017). Similar phenological data were not available for our analyses. Finally, given the size and bioclimatic diversity of British Columbia, a generalizable effect of climate on food availability might not be realistic across this large and varied region. We suggest that monitoring of terrestrial food availability, at least where possible at finer scales, might help to elucidate food-related mechanisms further and provide considerable improvements over the proxies we used. Despite not detecting a relationship with terrestrial foods, most conflict kills in all areas occurred in the latter part of the year and peaked in autumn, coincident with hyperphagia. This suggests that additional food-related causation might be important, even in areas without salmon (*e.g.* Obbard et al. 2014, Johnson et al. 2015). Although attacks were too rare to model, they similarly peaked during hyperphagia, additionally suggesting food-related causation. Although the particularities of hyperphagia's effects on human-bear conflict are not generalizable to all conflict systems, it provides an illustrative example of how the timing of resource need, resource availability, and human-wildlife conflict might offer insight into potential ecological associations.

Management considerations

Our findings suggest that reconsidering lethal removals and hunting, approaches commonly prescribed by management to reduce conflict (Treves et al. 2006, Treves 2009, Peebles et al. 2013, Fernández-Gil et al. 2016) might be warranted. Removal of individuals might be considered necessary in some circumstances, such as when individuals exhibit predatory behaviour towards humans (Beckmann and Berger 2003, Costello et al. 2014, Baruch-Mordo et al. 2014), or when specific individuals are involved in repeated livestock predation (Woodroffe et al. 2005, Treves 2009). However, as we observed, increasing overall rates of removal might not affect subsequent rates of conflict. This seemingly counter-intuitive result, given support for the food supply hypothesis which implies per-capita food limitation, might be explained by the fact that the variation in salmon abundance far exceeds variation in human-caused mortality. For example, assuming linear relationship between salmon availability and salmon consumption, a 90% reduction in salmon availability in a given year might require a 90% reduction in bear populations to abate the sudden per-capita loss. The considerably smaller removals observed might have little noticeable effect in such a situation, whereas larger removals might have deleterious consequences to grizzly bear populations. Improved conflict management might instead include addressing underlying ecological stressors, such as protecting or restoring natural food (*e.g.* from overharvest or habitat destruction). Additionally, a focus on understanding the underlying ecology of conflicts could focus limited resources on mitigation efforts (including education and attractant management) when and where conflicts are most likely to occur. Predicting conflicts could enable a proactive, non-lethal approach to prevention, reducing the impetus for the reactive, often lethal responses that might offer only limited benefit in the long term.

Broadly, management conducted without consideration of underlying ecology could lead to errors, and in some instances, harm. For example, in cases where increases in conflicts are driven by reduced food supply but are assumed to be caused by increasing wildlife population densities (*i.e.* regional population saturation hypothesis), managers might fail to address the underlying issue and instead subject populations already facing stress and potential declines to increased lethal control or hunting.

Moreover, in many jurisdictions worldwide, including BC, wildlife populations (and the processes that affect them) transcend ecological and/or jurisdictional boundaries, yet are managed by agencies that do not (Darimont et al. 2010, Ruttenberg and Granek 2011). This ecological mismatch limits the ability of agencies to address important ecological drivers of conflict like those detected here. For example, in BC, grizzly bears (and human-bear conflict) are managed by the provincial government of British Columbia, whereas the spawning salmon on which many populations depend are managed by Fisheries and Oceans Canada. The provincial government has the ability to destroy grizzly bears, but not to manage their food, whereas our results suggest the former might be less effective than the latter. Additionally, whereas the importance of nutrient subsidies in ecology is well-studied, including in this region (*e.g.* Darimont et al. 2010, Hocking and Reynolds 2011, Field and Reynolds 2013, Schindler et al. 2013), to our knowledge it has never before been assessed as a driver of human-wildlife conflict. Effective prevention and mitigation of human-conflict might require agencies to manage at more ecologically relevant scales, and manage not only conflict-implicated species, but also the foods on which they rely. Similarly, encouraging agencies responsible for prey species (*e.g.* salmon) management to also consider dependent communities of wildlife consumers might help to mitigate the current disconnect. Canada's 'Wild Salmon Policy', which requires ecosystem considerations in fisheries allocations (Fisheries and Oceans Canada 2005), provides an example of a potential mechanism, though it has yet to be implemented (Levi et al. 2012). Applying this policy for mitigating human-wildlife conflict might provide a tractable test case for cross-biome ecosystem management while benefiting both ecosystem conservation and human safety.

Ecology of conflict

Our study illustrates a generalizable multiple-hypothesis-testing approach for assessing ultimate ecological drivers of human-wildlife conflict. Instead of presenting a single hypothesis for observed patterns, we concurrently weighed support for multiple hypotheses within a single system (Chamberlin 1890). This approach not only provides greater confidence in the associations detected, but also is amenable to various taxa, geographies, and ecological contexts. For example, whereas food supply seemed to have the greatest impact on conflict patterns in our study system, additional mechanisms, including but not limited to our alternate hypotheses, might be at play here or elsewhere, might interact with one another, and might be context-dependent. Applying this approach broadly might help to increase the understanding of ultimate drivers of human-wildlife conflict in any system, while identifying commonalities among human-wildlife conflict systems worldwide.

Chapter 4.

Spatial capture-recapture analysis reveals deficiencies of a globally-renowned protected areas strategy: grizzly bears in the Great Bear Rainforest of Canada[3]

Abstract

Protected areas are often used to abate global declines in biodiversity. Quantitative methods are available for optimizing protected area placement and post-hoc assessment; however, given frequent data deficiencies, these methods often rely on modeled predictions of habitats as substitutes for empirical information. Estimating spatial patterns in densities of organisms provides a tractable approach of assessing realized habitat use, providing empirical insight into conservation gaps of planned or existing conservation networks. Here, we describe how spatial capture-recapture (SCR) can be used to compare the spatial distribution of organisms to the spatial distribution of protected areas. We illustrate this approach using grizzly bears (*Ursus arctos horribilis)* in the Great Bear Rainforest region of British Columbia, Canada. We conducted SCR modeling on capture data from a non-invasive bear monitoring project to characterize the density of grizzly bear activity centres (estimated centroids of space use) from 2013-2016. We identified hotspots using two methods: 1) identifying areas with activity centre densities in the 90th percentile of those across the region, and 2) using the Getis-Ord G_i^* statistic, to identify statistically significant spatial congregations of high activity centre densities. We found poor congruence between hotspots and protected areas: whereas 45% of the approximately 18,000 km^2 area studied was comprised of protected areas, these only overlapped with 1) 34% of male and 44% of female upper percentile hotspot area and 2) 42% of male and 41% of female G_i^* hotspot area. These results identify potential conservation gaps, and inform potential improvements to the protected areas network. More broadly, this work illustrates the potential of SCR for empirically assessing potential gaps in understanding of spatial ecology and gaps in protected areas networks.

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[3] A version of this chapter is in preparation and is co-authored by M. Bourbonnais, J.D. Reynolds, P.C. Paquet, and C.T. Darimont

Introduction

Extinctions of animal populations are occurring at unprecedented rates globally (Ceballos et al. 2017). Protected areas are intended to abate such losses. Recent expansions in protected areas worldwide have been hailed as a major conservation success (Ervin 2003), with many calling for additional increases (Wilson 2016). However, concerns exist about the efficacy of current protected areas, including whether they are large enough to meet their objectives (Newmark 1987, Bruner et al. 2001, Ervin 2003) and whether they are located in areas of particular importance to resident species and biodiversity (Margules and Pressey 2000, Ervin 2003).

Quantitative methods are often used to optimize reserve designs for maximal conservation benefit (Margules and Pressey 2000). These approaches can identify spatial configurations that maximize the achievement of pre-determined objectives while minimizing costs (*e.g.* financial, stakeholder conflict; Margules and Pressey 2000). For example, the program MARXAN (Ball et al. 2009) has been widely used to optimize the designs of marine reserves (Fernandes et al. 2005, Ball et al. 2009) and terrestrial protected areas networks (Ceballos et al. 2005, Ball et al. 2009, Loos 2011).

Quantitative approaches can similarly be used to assess the configurations of existing protected areas networks (*e.g.* Gonzales et al. 2003, Ban et al. 2014). For example, gap analyses compare layouts of protected areas to the spatial distributions of organisms or biogeographic zones of interest to determine whether further protection might be warranted (Jennings 2000). Such approaches could be used to iteratively modify protected areas networks, allowing management evolution and learning through time. This would be in line with the adaptive management paradigm whereby prescriptions are modified as new knowledge is gained about a system of interest (Walters and Holling 1990, Lackey 1998),.

In any modeling exercise, however, the quality of predictions is linked directly to the quality of data used. Because of data limitations, biological inputs (*e.g.* ideal habitat for species of interest) in optimization approaches and assessments are often derived from models that estimate habitat suitability or predict landscape value. Whereas such approaches might often constitute important first steps in assessing conservation priorities, in the absence of empirical data their reliability in a given application is unknown. Here, we illustrate a complementary approach to inform conservation planning and assessments. We use empirical spatial assessments of organisms' use of the landscape to assess potential gaps in protection areas.

Estimating spatial variation in densities of organisms provides an empirical and tractable approach for assessing realized habitat use, with important insights for conservation. For example, realized habitat use might identify potential conservation gaps identified by large concentrations of animals occurring outside of protected areas. Large concentrations of organisms outside of modeled high value habitat might also identify where models might require refinement. Empirical assessments of organism density might also be used for monitoring population demographics and to assess the outcomes of protected areas, information that might inform adaptive management. Finally, in the absence of more refined data on demographic information of organisms, areas of high use might have disproportionately high conservation value simply by encompassing disproportionately large proportions of the population of interest.

Although the use of focal species as proxies for broader biodiversity has limitations (Caro and O'Doherty 1999, Roberge and Angelstam 2004), they can provide useful information pertinent to other species, which might be especially helpful when empirical data on other species are limited (Fleishman et al. 2000, Braid and Nielsen 2015). Importantly, conservation of individual species often matters in its own right - for example, species that are of disproportionate cultural (Garibaldi and Turner 2004), ecological (Paine 1969, Simberloff 1998), or economic importance (Lemelin et al. 2015, Honey et al. 2016).

Spatial Capture-Recapture (SCR) is well-suited for comparing the spatial distribution of species to the spatial distribution of protected areas. Its predecessor, non-spatial capture-recapture, is an approach whereby capture histories of individuals that are detected initially (*i.e.* "captured", either by physical capture, with a mark added to identify individuals, or by genetic identification of sampled tissues), and then subsequently re-detected (recaptured) are used to estimate capture probabilities and to infer population sizes and/or densities. SCR additionally models capture probability as a function of distance between individuals' estimated activity centres (analogous to home range centres) and trap locations (Efford 2004, Borchers and Efford 2008, Royle et al. 2013). This approach is inherently spatial, estimating not only numbers and/or densities of organisms, but also how these measures vary across a landscape of interest. This empirical approach thereby provides an assessment of the realized use of landscapes. The potential of SCR for identifying areas of high conservation value has been noted (Morin et al. 2017), but, to our knowledge, has yet to be applied to real-world assessments.

The Great Bear Rainforest of British Columbia, Canada, has garnered international attention given its significance as part of the world's largest remaining temperate rainforest, and recent conflicts and negotiations over land use (Price et al. 2009, DellaSala et al. 2011, Affolderbach et al. 2012). Stretching from the British Columbia, Canada, mainland just North of Vancouver Island to the southern tip of Southeast Alaska (Figure 4.1), this area still hosts most of the species that were present prior to European colonization, including notably intact assemblages of terrestrial large carnivores (DellaSala et al. 2011). It is composed mostly of the unceded territories of First Nations who have inhabited and shaped the region for millennia (Price et al. 2009, Turner and Bitonti 2011, Housty et al. 2014). Whereas the area is still largely forested, many of the most productivity valleys, with the highest value timber, have already been logged (Prescott-Allen 2005, Green 2007, Price et al. 2009). In the 1990s, ongoing concerns over industrial activities led to increasing conflict over land use, sparking a prolonged negotiation period among the British Columbia provincial and local First Nations governments, environmental groups, and industry. Negotiations culminated in designating a patchwork of protected areas across approximately 33% of the overall land base, with so-called 'ecosystem-based management', in this case a moniker for modified industrial forestry, prescribed for the remaining matrix of unprotected areas (Price et al. 2009, Affolderbach et al. 2012, Clapp et al. 2016). The current protected areas include: provincial parks (hereafter 'parks'), which prohibit any industrial activities (BC Parks 2016); conservancies, which prohibit industrial activities while allowing for traditional uses such as harvesting cedar, hunting, and fishing (Turner and Bitonti 2011, Stronghill et al. 2015, BC Parks 2016); Biodiversity, Mining and Tourism Areas (BMTAs), which prohibit industrial logging and large-scale power generation but allow mining, tourism, recreational activities, and 'limited power developments' (Province of British Columbia 2009, 2016a); and Special Forest Management areas (SFMAs), which prohibit commercial forestry but allow for hydroelectric generation, mining, and tourism (British Columbia Ministry of Forests, Lands and Natural Resource Operations 2016, Province of British Columbia 2016a). The remaining EBM matrix is now subject primarily to rotational logging, with the exception of areas of highest quality modeled grizzly bear habitat ("Class 1 EBM reserves"; Appendix C.1) in which logging is prohibited (except where permitted through exemptions described in Province of British Columbia 2016b).

Although some have questioned the efficacy of the approach used for designing the current protected areas network (Gonzales et al. 2003), proponents of the process have celebrated it as a success, and it has been promoted internationally. However, empirical examinations of the ecological context of this current protected areas strategy are largely absent.

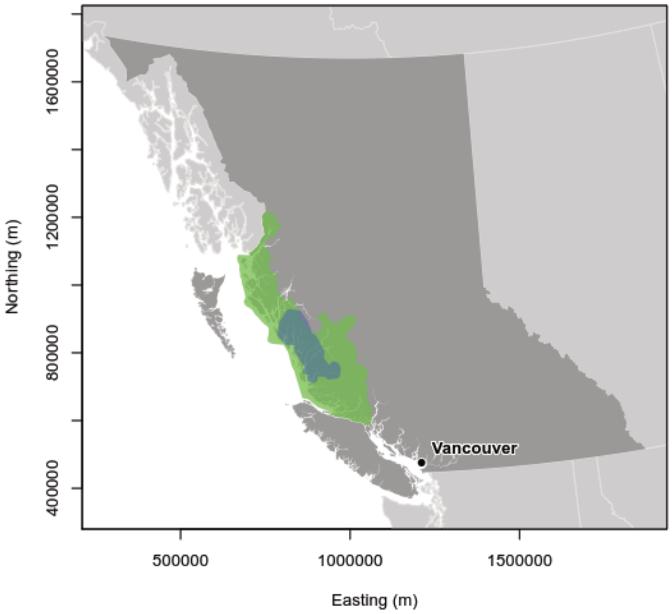

Figure 4.1 Focal study region.
The province of British Columbia, Canada, is shown in grey, with the region of coastal temperate rainforest commonly referred to as the "Great Bear Rainforest" (specifically the North and Central Coast land use planning areas) highlighted in green and the study area in blue.

Grizzly bears, the namesake of this region, serve as its de facto flagship species. Their conservation featured prominently in the conflict leading up to, and during the negotiation of, the current conservation strategy (*e.g.* Rumsey et al. 2004, British Columbia Ministry of Environment 2008, Horn et al. 2009, Grizzly Bear Habitat Mapping Technical Review Team 2010). Their modeled habitat was one of the primary ecological considerations in negotiations (Central Coast LRMP completion table 2004, Rumsey et al. 2004, map 11) and they are one of five focal indicator species of ecological health for the region (Province of British Columbia 2016c).

The choice of grizzly bears as a focal species for this region is perhaps fitting. The life history of grizzly bears makes them partial proxies for broader habitat needs (Rumsey et al. 2004, Horn et al. 2009): they have large home ranges, require a diversity of habitats across large landscapes, are sensitive to human impacts, and have high caloric requirements that necessitate productive (or, alternatively, vast) environments (Noss et al. 1996, Carroll et al. 2001, Darimont et al. 2010, Adams et al. 2017). Moreover, conservation of grizzly bears is of considerable importance in its own right – they play diverse and important ecological roles through, for example, transfer of nutrients (Hilderbrand et al. 1999b, Holtgrieve et al. 2009, Darimont et al. 2010), transfer of seeds (Noss et al. 1996), and disturbance of soils (Tardiff and Stanford 1998, Doak and Loso 2003). They are of central importance to many of the First Nations whose territories comprise the region (Housty et al. 2014), and provide important revenue for a burgeoning ecotourism industry (Lemelin et al. 2015, Honey et al. 2016). As a result of a multi-year and multi-national collaboration (Bryan et al. 2013, 2014, Service et al. 2014, Adams et al. 2017), grizzly (and black) bears are also the terrestrial taxon for which there is now by far the most information, an exception in a region where monitoring of terrestrial taxa is mostly lacking (Price et al. 2009).

Here, we use spatial variation of grizzly bear land use from 2013-2016, as estimated by density of activity centres derived from spatial capture-recapture modeling, with the current layout of protected areas. We use this system to consider more broadly how empirical data on focal species' realized landscape use might be applied to rapidly assess potential gaps in protected areas network, provide baseline measures of population distribution at the onset of a protected areas strategy, and identify gaps in knowledge of an organism's spatial ecology.

Methods

We used hair samples (from N = 106 males and N = 57 females) collected non-invasively (Woods et al. 1999, Proctor et al. 2010) from 2013-2016 for our empirical assessment of grizzly bear populations. We sampled across an approximately 18,000 km^2 subset of the Coastal British Columbia, centred in the villages of Bella Bella, Wuikinuxv, and Klemtu, in territories of the Heiltsuk, Wuikinuxv, and Kitasoo/Xai'xais First Nations, respectively (Figure 4.2; Bryan et al. 2013, 2014, Service et al. 2014, Adams et al. 2017). In early May of each year, we assembled an average of 185 sampling sites (min = 159, max = 196; hereafter 'traps') across the study area. Traps consisted of a 'bait pile' of vegetation on which a liquid non-reward lure of dogfish or fermented salmon fertilizer was poured, encircled by a barbed wire corral. To reach the pile, bears needed to step over or crawl under the corral, which snagged clumps of their shedding hair. We revisited each site for sampling sessions 2-3 times each year at intervals of approximately 10 days. We collected snagged hair and rebaited each site by pouring additional lure onto the bait pile. After each May-June field season, all samples were sent to Wildlife Genetics International, where individual identity, sex, and species of the bear to whom each hair sample previously belonged were determined genetically using seven microsatellite markers (plus a sex marker; Paetkau 2003).

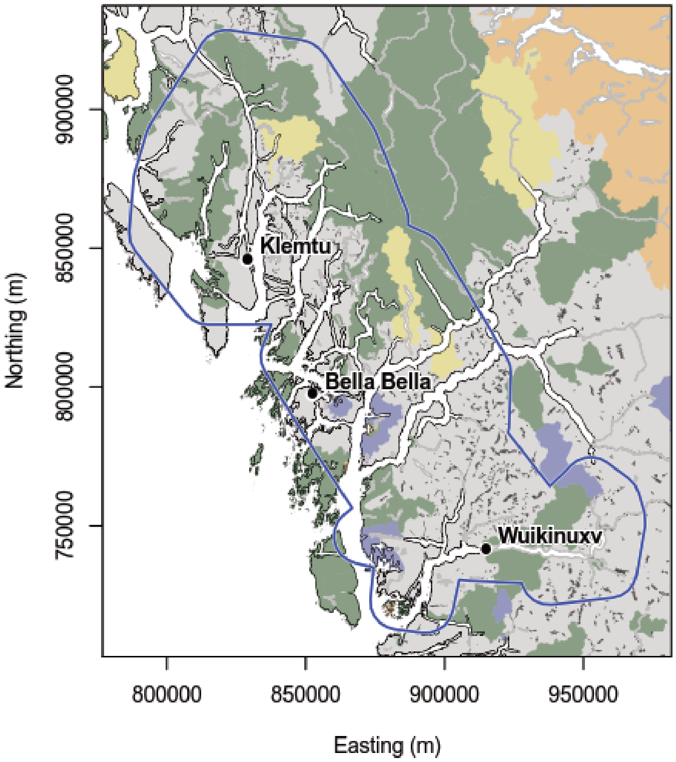

Figure 4.2 Protected areas and reserves included in our spatial analyses.
British Columbia provincial parks are shown in Orange, Conservancies in green, Biodiversity, Mining, and Tourism Areas (BMTAs) in blue, Special Forest Management Areas (SFMAs) in yellow, and Class 1 EBM reserves (small scattered polygons) in dark grey. Area of study is delimited by blue boundary line. Map is in BC Albers Projection.

Spatial capture-recapture modeling

We used an SCR approach (Royle et al. 2013) to assess spatial variation in population densities annually from 2013-2016. We modeled detection of a given individual at a given trap in a given sampling session as a function of a) that individual's estimated activity centre (the centroid of their estimated space use in the season sampled), b) baseline capture probability (*i.e.* at a distance of d=0 between activity centres and trap locations), c) decay in detection probability with increasing distance between traps and activity centres, and d) whether the individual had already been captured at that trap in that sampling session (local behavioural response; to account for trap-happiness and/or shyness). We used data augmentation to account for individuals that were in the population but not encountered: ‘augmented’ individuals, those with all-zero capture histories (*i.e.* y_{ijk} is entirely 0), were added to the set of detected individuals. We then modeled which of the augmented individuals were structural 0s (non-individuals) vs. sampling 0s (individuals in the population that were not detected; Royle et al. 2013).

The simplified hierarchical model used was:

$$y_{ijk} \sim \text{Binomial}\left(1, p_{ijk}\right)$$

$$p_{ijk} = z_i * p_{0ijk} * e^{-\propto_1 \|\mathrm{x}_j - s_i\|^2}$$

$$\text{logit}\left(p_{0ijk}\right) = \propto_0 + \propto_2 C_{ijk}$$

Where y_{ijk} is a binary indicator of whether individual i was encountered at trap j during session k,

p_{ijk} is the encounter probability of individual i at trap j in session k,

z_i is a binary indicator of whether individual i is a member of the population or not. This variable is estimated for augmented individuals, and set to 1 for all observed individuals.

p_{0ijk} is the probability of detecting an individual at a distance of *d*=0 between its activity centre and a trap

$\propto_1$ is a scale parameter for how quickly detection probability decays with distance (proportional to home range size) between a trap and an individual’s activity centre.

$\|\mathrm{x}_j - s_i\|$ is the distance between individual i’s estimated activity centre and trap j

x_j is trap j’s location (in 2D space)

s_i is individual i’s activity centre (in 2D space; a latent estimated variable)

$\propto_0$ is the baseline encounter probability (in this case, of an individual that has not yet been captured in the given session, at a distance of d=0 between its activity centre and the trap)

$\propto_2$ is the effect of previous capture on encounter probability

C_{ijk} is a 3d array describing whether individual i has been detected at trap j prior to session k

We fit separate models for each year (from 2013-2016) and for each sex to allow modeled parameters to vary by year and sex. The ‘state-space’ – the full candidate area across which activity centre locations could be estimated – was a rectangular area defined by the full extent of the trap arrays, with an additional 10-km buffer added. This approach ensured that the state-space was large enough to account for activity centres of detected individuals that might have occurred outside of the trapping array.

We used a Bayesian approach with Markov Chain Monte Carlo (MCMC) estimation to analyze the models (Royle et al. 2009), implemented with the dclone and rjags packages in R. We ran 3 separate MCMC chains for each model with a thinning rate of 1 for 5250 iterations, discarding the first 1250 iterations as burn-in. We used the Gelman-Rubin diagnostic to test for convergence (Brooks and Gelman 1998).

Characterization of population size and density

We estimated annual sex-specific population sizes by summing the annual activity centre posteriors of all individuals of a given sex within the study area boundary (Appendix C.1), and dividing by the length of the posterior (number of MCMC iterations; Royle et al. 2013). We estimated total annual population sizes first by adding the male and female components together. Given poor performance of female models (see results) and the approximately 1:1 sex ratio often observed in grizzly bear populations (Schwartz et al. 2003), we also estimated total annual population sizes estimates alternatively by doubling the male estimates.

We constructed annual sex-specific activity centre density surfaces by summing the annual activity centre posteriors per unit of area (state-space divided into 4 km^2 pixels), and dividing by the length of the posterior. This characterization of density is based on each individual's estimated activity centre across a given sampling episode (season in a year; Royle et al. 2013), which differs from the number of individuals at a given instant in time. This characterization of density surfaces also differs from more derived spatial characterizations of predicted density based on modeled parameter estimates of spatial covariates (Royle et al. 2013, Efford 2017).

To assess areas of consistently high use across years, we calculated cumulative activity centre densities by averaging the value of each pixel across 2013-2016. Hotspots were defined first as pixels with activity centre densities in the top 90th percentile. We then defined hotspots based on spatial clustering of high density values using the Getis-Ord G_i^* statistic (Getis and Ord 1992), which evaluates both the spatial intensity of hot (and cold) spots and tests whether observed values are more divergent than would be expected for a random process. This statistic proportionally compares the observed summed values of a cell and its neighbours with all those of the study area. A statistically significant (at $\alpha = 0.05$) Z-score (above + 1.96 and below -1.96) indicates observed values greater (or lower) than expected. We used a 4 km moving window (representing queen's case spatial contiguity [Getis and Ord 1992]) to define the spatial neighbourhood of each cell.

Spatial comparisons

We compared the locations of activity centre hotspots identified using the 90th percentile and G_i^* approaches with the layout of existing protected areas. Whereas density surfaces and G_i^* hotspots were estimated across the full state-space, we performed spatial comparisons only in an area within 10 km of the study area trap array (Appendix C.1), and only for pixels over land (*i.e.* marine pixels were omitted).

Results

SCR models

Male models converged reasonably well, with gelman diagnostic scores (a measure of chain convergence) all <1.02 (and most <1.01). Baseline probabilities of detection for an individual's first detection in a given trap and year ranged from 0.08-0.10. There was evidence of trap-happiness, with subsequent detection probabilities of an individual at a given site and year increasing to 0.14-0.44. The average annual number of males (*i.e.* male activity centres) estimated within the study boundary was 84 (min = 74, max = 94; Figure 4.3)

Convergence of female models varied considerably. Female models for 2013 converged particularly poorly, with gelman diagnostic point estimates of up to 2.1 (and upper C.I of 4.2); however, removal of this year from the cumulative density estimates had no qualitative effect on subsequent spatial analyses (Figure C.4). Convergence of models for years 2014-2016 was better but still poor, with mean gelman diagnostic estimates of 1.04 (range 1.00-1.14). Baseline probabilities of detection for individuals' first detection in a given trap and year varied substantially, from 0.005-0.09. There was evidence of substantial trap-happiness in most years: in years 2014, 2015, and 2016, probabilities increased from 0.05, 0.07, and 0.09, respectively, to 0.5, 0.7, and 0.3, respectively, following initial detection, though no difference was detected in 2013. The number of females estimated within the study area varied substantially among years (mean = 148, min = 100, max = 173; Figure 4.3) and the posteriors were wide and relatively flat, consistent with the poor model performance (Figure 4.3). The scale parameter was substantially smaller in all years for females compared to males (females ranged from 0.02 to 0.09, males from 0.3 to 0.6), suggesting that detection probability decays substantially faster with distance in females.

Total average annual population size estimated by a) combining annual means of the male and female components was 232 (min = 174, max = 257, mean density = 12.7 bears per 1000 km^2), and by b) doubling the male component was 168 (min = 148, max =187, mean density = 9.2 bears per 1000 km^2).

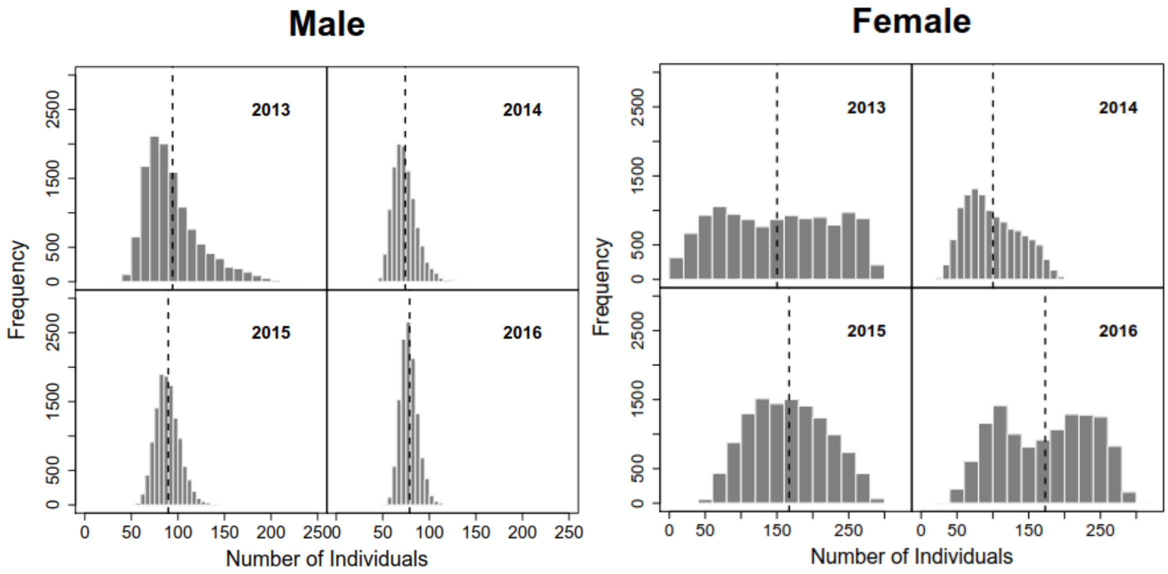

Figure 4.3. Posterior distributions of grizzly bear (*Ursus arctos horribilis)* estimated population sizes within study area boundary, out of 12,000 iterations (3 chains of 4,000 iterations each) of the SCR model.
Dashed black lines represents the mean estimated populations.

Spatial comparisons

We found poor congruence between protected area placement and areas of high grizzly bear activity centre densities. Whereas 45% of the landscape within the study boundary is comprised of protected areas (Figure 4.2), these areas were found disproportionately outside grizzly bear hotspots, as delineated by either 90th percentile or G_i^*approaches.

Males

We found that only 34% of male upper percentile hotspot area fell within protected areas: 26% within conservancies, none in SFMAs, 4% in BMTAs, 4% in Class 1 EBM reserves, and none in parks, with 66% unprotected (Figure 4.4, Figure 4.5). We found that 42% of male hotspot area identified by G_i^* fell within protected areas: 35% in conservancies, 0.3% in SFMAs, 3% in BMTAs, 3% in Class 1 EBM reserves, and 0% in parks, with 58% unprotected (Figure 4.4, Figure 4.6). Unprotected areas identified by both methods were strongly concentrated in the mainland region in the south-east corner of the study area (Figure 4.5, Figure 4.6).

Females

For females, we found that 44% of upper percentile hotspot area fell within protected areas: 31% within conservancies, 8% in SFMAs, 3% in BMTAs, 2.5% in Class 1 EBM reserves, and <0.1% in parks, with 56% unprotected (Figure 4.4 Figure 4.5). We found that 41% of female hotspot area identified by G_i^* fell within protected areas: 28% in conservancies, 7% in SFMAs, 4% in BMTAs, 3% in Class 1 EBM reserves, and <0.1% in parks, with 59% unprotected (Figure 4.4, Figure 4.6). Unprotected hotspot locations identified by both methods were more diffuse for females than males. Although many occurred in the same south-east region of the study boundary as unprotected male areas, there were additional unprotected hotspots elsewhere (Figure 4.5, Figure 4.6).

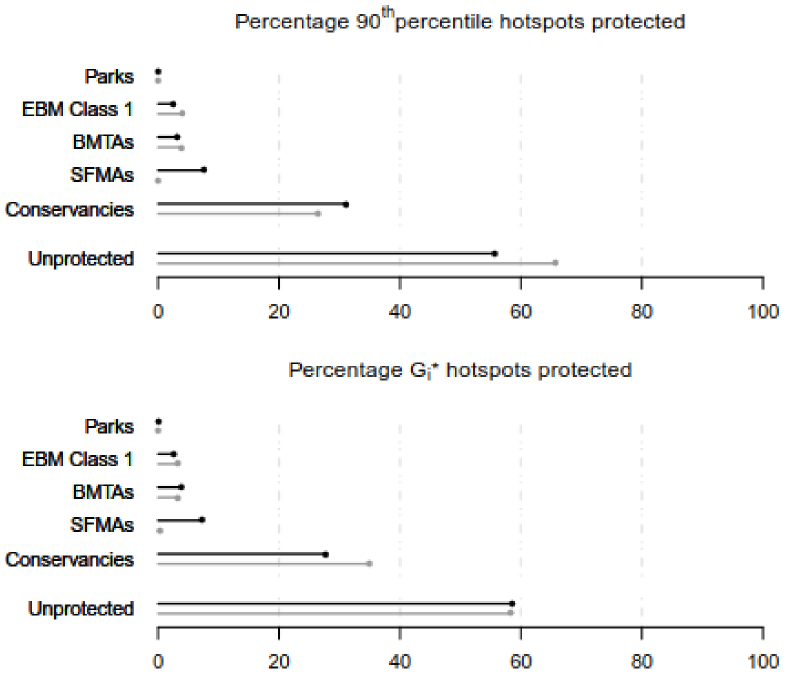

Figure 4.4 **Percentage of female (black lines) and male (grey lines) grizzly bear (*Ursus arctos horribilis*) hotspot area identified by 90th percentile hotspots (top) and Getis-Ord G_i^* (bottom) captured within Parks, EBM Class 1 reserves, BMTAs (Biodiversity, Mining, and Tourism Areas), SFMAs (Special Forest Management Areas), and Conservancies.**

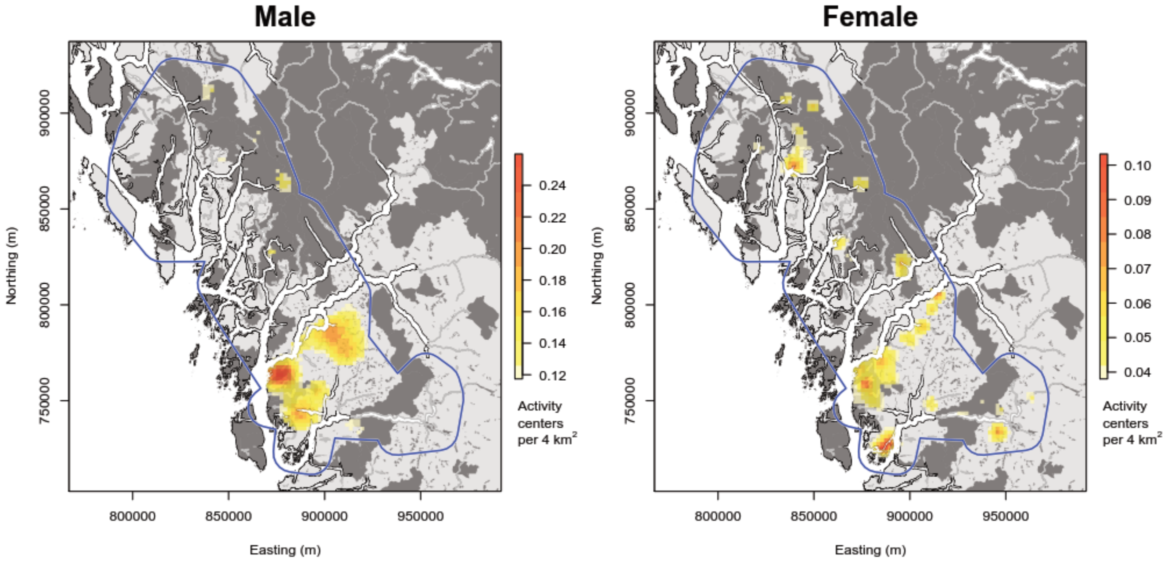

Figure 4.5 **Spatial comparison of areas of with high estimated activity centre density of male (left) and female (right) grizzly bears (*Ursus arctos horribilis)* with current protected areas in the Great Bear Rainforest of British Columbia, Canada.**

Dark gray areas represent protected areas (conservancies; biodiversity, tourism, and mining areas [BMTAs]; special forest management areas [SFMAs], and EBM class 1 reserves). “Hot” (yellow to red) colours indicate areas of relatively high grizzly bear activity centre densities (plotted are pixels with the 90th percentile estimated densities), with densities reported per 4 km^2. Maps are in BC Albers projection.

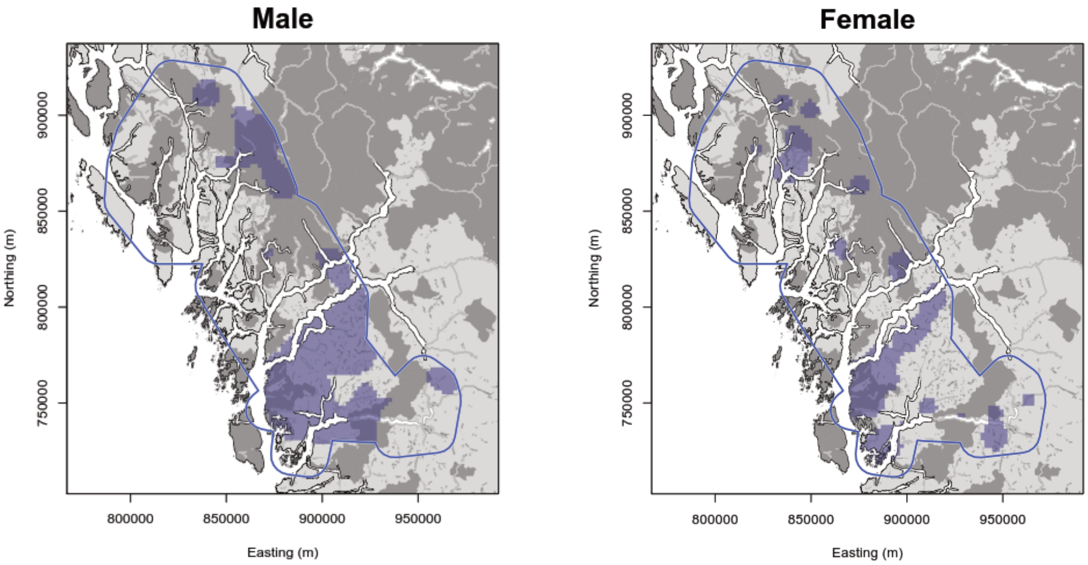

Figure 4.6 Spatial comparison of male (left) and female (right) high grizzly (*Ursus arctos horribilis*) G_i^* hotspots with current protected areas in the Great Bear Rainforest of British Columbia, Canada.

Dark gray areas represent protected areas (conservancies; biodiversity, tourism, and mining areas [BMTAs]; special forest management areas [SFMAs], and EBM class 1 reserves). Blue areas represent G_i^* hotspots (spatially auto-correlated congregations of areas with activity centre densities higher than expected from random chance). Maps are in BC Albers projection.

Discussion

We used a spatial capture-recapture approach to assess how well protected areas encompass high use areas of a focal species. We found only partial overlap between protected areas and areas with high concentrations of grizzly bear activity centres, with variation between sexes and among years. Our results have implications for the Great Bear Rainforest mosaic of land use. More generally, they illustrate how SCR can be used to characterize organisms' realized landscape use, providing empirical insight into gaps in protected area networks or models of landscape use, and baseline information on populations of interest.

We observed considerable differences between sexes. Models for males converged substantially better than those for females, potentially due to larger sample sizes, resulting in more precise population estimates. This suggests that the overall population sizes derived from doubling male populations might be more accurate than those derived from adding male and female components together. However, departures from a 1:1 sex ratio have been observed elsewhere, usually biased towards females (Schwartz et al. 2003), suggesting that this approach risks underestimating total population sizes. The poor convergence of female models might have also led to sampling error. Given how quickly female detection decayed with distance (as expected, given females' smaller home ranges [Schwartz et al. 2003]), this is unlikely to have qualitatively affected the locations of hotspots that were identified. However, it might have resulted in some hotspots being missed. A cautious approach would be to treat the identified hotspots as a minimum characterization and to continue monitoring for hotspots that might have been missed.

That we found apparent trap-happiness in both sexes was somewhat surprising. Whereas behavioural effects are common in capture-recapture studies (Royle et al. 2013), the lures we used do not offer a nutritive reward. However, remote cameras at a subset of sites have often filmed grizzly bears rolling in the bait piles, suggesting these sites might offer a non-nutritive reward.

Our results illustrate the benefits of using complementary approaches to identify hotspots (see also Harvey et al. 2017). Defining hotspots using upper percentiles involves tangible quantities, for example specific minimum densities of organisms. However, the cut-off value chosen is arbitrary, and this approach does not provides a statistical assessment of whether identified hotspots (and coldspots) differ from the rest of the landscape by more than might be expected from chance alone, a shortcoming specifically addressed by the Getis-Ord G_i^* approach. In our example, both methods provided mutually reinforcing results: the Getis-Ord G_i^* hotpots corresponded reasonably well with the more tangible 'hottest' areas, defined as those in the upper 90th percentile of densities, while the upper 90th percentile hotspots were reciprocally affirmed by spatial congruence with the statistically meaningful Getis-Ord G_i^* hotspots.

The results of this study offer insight into potential improvements of the current protected areas network. The south-east mainland corner of the study area in particular seems disproportionately used by grizzly bears, but has very little protection, suggesting that increasing protection there might offer disproportionate conservation potential. That the current configuration of protected areas overall covers *less* high-use area than expected by random chance alone suggests that addressing gaps in protection could be done relatively efficiently; *e.g.* doubling protection of areas of high grizzly bear use could be accomplished *without* doubling total protected area.

Finally, these results illustrate how SCR might be used to establish baselines against which future monitoring might be compared. Future changes in patterns of landscape use or numbers of individuals might signal demographic changes, informing future research and management directions that might identify the causes of such changes and the management responses that could address them.

Consideration of temporal scope

Important for applying this approach is a consideration of the temporal scope of inference provided. For example, we identified regions with high incidence of activity centres that are not currently protected, but did *not* conversely identify areas of little value in general because the data used were specifically from spring captures. In other seasons, bears might be found in high concentrations in areas not identified herein (though in the limited data we have for individuals detected in >1 season [n = 55 individuals], individuals' mean locations [*e.g.* geographic centre of all detections] in summer and fall were typically in the same general area as those of their spring detections [median distance of 5 km, min = 0, max = 35; Figure C.5]).

Additional variation in spatial patterns might be expected among and beyond years of a particular study. In our example some inter-annual variation of hotspots was observed (Figure C.6, Figure C.7). That hotspots can vary among years suggests that areas not identified as high use in one time period (*e.g.* this limited study period) might be important in others.

Consideration of spatial scale

Attention to spatial scale is also warranted when applying this approach. Activity centres describe the estimated centroid of an individual's realized space use, not their full home range. By definition, activity centres might not even occur in usable habitat (*e.g.* an extreme example would be a parking lot surrounded by high quality habitat, Royle et al. 2013). Broad regions with high densities of activity centres and low coverage of protected areas (*e.g.* the south-east corner of this study area) would suggest large-scale conservation gaps; however, comparisons or conservation prescriptions at very small scales would be less appropriate for this method because they might place undue influence on areas at the centre of home ranges while missing important habitats located further towards home range peripheries. Notably, this issue would be most relevant with species and/or individuals with large home ranges relative to the scale of prescription. In our particular example, females had considerably smaller home ranges, suggesting that their home range posteriors would provide a closer characterization of realized landscape use compared to males, whose larger home ranges would suggest inference is more appropriate at larger scales.

Caution might also be warranted in interpretation of non-sampled habitats. Whereas our sampling occurred primarily in habitats identified as seasonally important (*i.e.* spring habitats; Grizzly Bear Habitat Mapping Technical Review Team 2010), used non-reward bait to attract individuals from afar (Woods et al. 1999), and occurred throughout the study area, if individuals occurred in other habitats distal to sampled patches, they might have had a disproportionately low probability of detection.

Landscape use vs. habitat importance

Our results demonstrate how realized landscape use by organisms can be used to assess gaps in protected area configurations. This approach could similarly be employed to test models used in conservation planning, by identifying gaps in modeled habitats. However, the realized density of organisms does not necessarily correlate directly with habitat quality and vital rates (Braid and Nielsen 2015). For example, areas with lower estimated use might represent areas whose importance to a population is disproportionate to the amount of time they are occupied. Alternatively, high-quality habitats might be temporarily unpopulated or have lower densities of organisms because of external factors such as recent mortality events or loss of connectivity from other habitats, suggesting that unoccupied areas are not necessarily of low quality habitat. As such, a cautious approach would treat gaps in conservation or modeled habitat identified by this approach as minima, acknowledging that additional gaps might have been missed, and might further warrant investigation.

Implications for Great Bear Rainforest

There has been considerable scholarship focussed on the Great Bear Rainforest, describing the successes of the negotiation process, with ‘success’ synonymous with the cessation of conflict (Affolderbach et al. 2012), and of the changing political landscape that has emerged (Clapp et al. 2016). Others, particularly during the negotiation process, have provided assessments of broad protection by landscape type or modeled habitat representations (*e.g.* Wells et al. 2003, Gonzales et al. 2003). However, our work constitutes a rare empirical examination of the realized layout of this region’s protection. In particular, our results identify potential shortcomings in grizzly bear protection with the current configuration of protected areas. The gaps might be of concern, given the species' high conservation value and its designation as a focal species for this region. Although the transition to "EBM" logging in unprotected areas has been described as analogous to traditional protected areas (*e.g.* the region being described as 85% protected, Langer 2016), we found that modeled class 1 EBM reserves, the only 'hard' protection outside the protected area matrix in this management scheme, encompass very little of the estimated hotspot area. The paucity of protection within the EBM matrix highlights how modified extraction approaches are not analogous to, and should likely not be considered together with, true protected areas (Locke and Dearden 2005). These potential shortcomings are consistent with previous criticisms about this implementation of EBM, including a lack of species-specific protection for focal species (Rainforest Solutions Project 2010) and a lack of follow-through on recommendations of the original scientific panel, including larger areas off-limit to logging and larger buffers around riparian features (Price et al. 2009). Importantly, although we were not able to directly predict the effects that industrial activities would have on the identified protected gaps, logging has been identified as a primary threat to biodiversity in general (Betts et al. 2017), and likely to grizzly bears specifically (McLellan and Shackleton 1988, MacHutchon et al. 1993). Others have cautioned that spring (the season we investigated) grizzly bear habitats might be particularly vulnerable, with a paucity of substitute foods available at that time of year (Horn et al. 2009). Given the recentness of the current protected areas configuration, its effects on resident species and biodiversity have likely not yet manifest, suggesting that gaps in protected areas could be addressed before most potential deleterious effects occur.

Although we illustrated how this spatial approach might be used to assess protection as it relates to a focal species, its usefulness towards achieving a broader spectrum of realized biodiversity protection might be improved if applied across several species. For example, elsewhere, using the full large predator guild has provided better overall biodiversity proxies than individual species alone (Carroll et al. 2001, Roberge and Angelstam 2004), by representing a broader niche-space. In this system, whereas we did not find outer coastal areas to be important for grizzly bears, they are home to an ecologically unique 'evolutionarily significant unit' of wolves (Darimont et al. 2004, Muñoz-Fuentes et al. 2009), suggesting that inclusion of even this one additional large predator in assessing conservation gaps might prove particularly useful.

Whereas our analysis identified gaps in the current protected areas strategy, it does not constitute an endorsement of current or past approaches to protected areas. For example, many approaches to date have been damaging to local people, with a colonial history of displacing Peoples from their lands when areas become "protected", and to non-human species, by justifying exploitation in non-protected areas (Wilson 2016). In the Great Bear Rainforest in particular, benefits to human well-being have yet to be realized from protected areas and EBM implementation (Green 2007, Price et al. 2009). However, the new designation of conservancies provides promise by explicitly allowing for continued use by local Peoples, while excluding larger scale industrial impacts, and while maintaining conservation as a primary objective (Turner and Bitonti 2011, Stronghill et al. 2015). Tribal Parks elsewhere offer similar promise (Murray and King 2012). Finally, Nation-level stewardship might provide an important mechanism - driven by local values - for protection above and beyond that negotiated in the current protected areas network. We suggest that increasing the distribution of these kinds of protected areas, which explicitly consider humans as part of the ecosystem while preventing against industrial degradation, holds considerable promise for achieving multiple converging objectives.

Gaps within protected areas

In addition to identifying spatial gaps in protected areas, conservation effectiveness also benefits from assessing the realized protections offered by protected areas themselves (Bruner et al. 2001, Ervin 2003). For example, species vary substantially in the degree to which they are threatened by modern land-use changes (McKinney 1997, Cardillo et al. 2005), suggesting the effects of protected areas might vary taxonomically. Moreover, the degree to which protected areas offer conservation benefits depends on which activities are allowed within them (Bruner et al. 2001, Darimont et al. 2010), and the degree to which agencies can control those (Bruner et al. 2001).

The protected areas we examined protect habitat by preventing industrial logging, and most of them prohibit mining. At the time of writing, protected areas in this region offer no direct protection from hunting (*e.g.* the trophy hunt), the largest source of mortality of grizzly bears in the province (Artelle et al. 2013). However, reducing potential forestry activities in the region might mitigate forestry-mediated vulnerability of populations to hunting (caused by human access via forestry roads, *e.g.* McLellan and Shackleton 1988, Boulanger and Stenhouse 2014), though the extent to which this indirect protection might affect vital rates of resident populations is unknown. A moratorium will soon be placed on the hunt in the region, but this might be reversed by future governments. Specific hunt prohibitions within protected areas, similar to “no-take” zones that have proven highly effective in the marine realm (Hooker and Gerber 2004, Lester et al. 2009, Ban et al. 2014), might provide a more permanent means of protection.

Similarly, protected areas in our focal region do not offer protection of food, in particular, spawning salmon, which are disproportionately important for coastal grizzly bears (Darimont et al. 2010, Levi et al. 2012). Given gaps described above, the realized effect of these protected areas on vital rates, independent of their size and location, are unknown. Regardless of potential shortcomings of the protected areas we examined, they comprise the only concrete protection for grizzly bears (and broader terrestrial biodiversity in the region) offered by the current protected areas strategy, suggesting gaps in their placement and scope might have important implications that warrant further investigation.

Test of adaptiveness

The gaps addressed herein might be seen not as an indictment of the protection in this region, but instead as a test of the adaptive ability of the current management regime. The spatially-explicit, empirical information on grizzly bears presented herein were not available at the time of the planning. These new data might provide a valuable test of the management’s adaptiveness, by highlighting current shortfalls but also suggesting potential improvements.

Moreover, the approach we have highlighted might prove crucial for detecting and adapting to future changes. Realized distributions of bears might change through time, *e.g.* in response to habitat degradation or recovery, climate change, or changes in natural food availability. The population sizes and densities described herein provide a baseline against which future distributions might be compared. Continued monitoring following the approach described herein might reveal future emergent gaps in protection or changes in populations, and could form an important pillar of well-informed adaptive management moving forward.

This approach in general

We showed how SCR can be used to assess the spatial configuration of a recently developed protected areas network, providing insight into how its configuration might be improved to better capture focal species of interest, while also providing baseline information against which future changes might be measured. We note, however, that caution is required in interpretation of results from this approach. Activity centre densities are *not* directly interpretable as densities of organisms, nor of high quality habitat. Instead, activity centres describe the estimated centroids of space use. Activity centre hotspots therefore indicate not the specific areas used by many individuals, but instead the centroids of such areas. Estimated hotspots might indicate general areas of high space use, but not specific locations. Further investigation would be necessary to identify which specific patches of nearby habitat are used, which are of particular conservation concern, and how these might relate to current protected areas configurations.

In addition to identifying broad areas of conservation importance, we suggest that using SCR continually to monitor focal populations might facilitate adaptive conservation approaches that could respond to changes in population demographics and spatial configuration. This approach might prove useful here and elsewhere for assessing potential, or existing, conservation and management strategies, including those of protected areas or areas subject to ecosystem-based management.

Chapter 5.

Hallmarks of science missing from North American wildlife management[4]

Abstract

Natural resource management policy is often controversial and defended by agencies claiming adherence to science-based approaches. For example, proponents of the 'North American Model of Wildlife Conservation', which guides hunting policy across the United States and Canada, claim that science plays a central role in shaping policy. We tested for the presence of fundamental hallmarks of science (*objectives, evidence, transparency, and independent review*) across 667 wildlife management plans by 62 provincial, territorial, and state agencies. We found that most (68%) plans contained fewer than half of the indicator criteria assessed, with more criteria detected in plans that were independently reviewed, that pertained to 'big game' taxa, and for jurisdictions at increasing latitudes. These results raise doubt about the purported scientific basis of a continental-scale approach to management. Our framework provides guidance towards adopting an authentically science-based approach to safeguard not only wildlife but also agencies from potential social, legal and political conflict from unsupported policy.

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[4] A version of this chapter is in revision and is co-authored by J.D. Reynolds, A. Treves, J.C. Walsh, P.C. Paquet, and C.T. Darimont

Introduction

Governments often assert, and society often assumes, that science comprises the foundation of natural resource management. In the United States and Canada, for example, agencies responsible for managing bird and mammal hunting commonly assert that they adhere to the North American Model of Wildlife Conservation (hereafter the Model). This model is predicated on seven central tenets, one of which is that ‘science is the proper tool to discharge policy’ (Geist et al. 2001, Organ et al. 2012, Clark and Milloy 2014).

Despite widespread use and endorsement of the Model, however, its advocates rarely articulate what science-based management entails. Additionally, no one has comprehensively assessed whether claims of science-based management are supported. That knowledge gap is troubling, given the ‘science-based’ justifications for policy decisions commonly offered by agencies, the substantial public investments that support these agencies, and the considerable influence that hunting has on otherwise self-regulating wildlife populations; in many taxa, adult mortality from hunting exceeds mortality from all other predators combined (Darimont et al. 2015).

To address this gap, we identified four fundamental, inter-related hallmarks (*measurable objectives*, *evidence*, *transparency*, and *independent review*) that might be expected of a science-based wildlife management *process* (*e.g.* management using not only the products of science but also operating with a similar rigour). We identified 13 specific criteria as indicators of the hallmarks (*e.g.* “Is the technique for setting hunting quotas explained?” for our *transparency* hallmark; Table 5.1, Appendix D). These consisted of both criteria that a) we suggest as core requirements for a given hallmark (*e.g.* their absence might signal a substantial scientific deficit) and b) we suggest as desirable (*e.g.* their presence might bolster support for the presence of a given hallmark, but a scientific approach is still conceivable in their absence; Table 5.1). We assessed how many of these criteria appeared in 667 management plans (produced by agencies to describe how hunted species are managed) for 27 groups of species across 62 provinces, territories, and states in the U.S. and Canada (File D.1).

Table 5.1 Hallmarks and their related indicator criteria assessed in management plans (N = 667) produced by 62 wildlife agencies across Canada and the United States. Criteria with an asterisk are those we suggest as desirable, not necessarily required, for a science-based approach.

Hallmarks	Indicator criteria
Measurable objectives	Provide measurable objectives
Evidence	Report quantitative information about populations
	Report uncertainty in population parameter estimates
	Estimate realized hunting rates
	Cite external evidence *
	Collaborate with external scientists *
Transparency	Explain technique for setting hunting quotas
	Explain how population parameters are estimated
	Explain how realized hunting rates are estimated
	Provide publicly-available management information
	Respond to public inquiry
Independent Review	Subject management plans to any review
	Subject management plans to external review

Methods

We evaluated the presence of scientific hallmarks across 62 provincial, territorial, and state jurisdictions in wildlife management plans for 27 species (or species groups, *e.g.* 'upland birds'; File D.1). One informed non-specialist (research technician; MVR) searched agency websites for all available management-relevant information, including online sources, wildlife management plans, and other available documents (herein referred to collectively as 'management plan' or simply 'plan'; N = 667), for all hunted species (or groups of species). Whereas plans varied in content, the description from the Oregon [State] Furbearer Program Report (2011, pg 4) is representative: "The purpose of this report is to provide information not only to trappers and hunters, but to all interested in furbearer management in Oregon. This report contains harvest management information, current and recent research and management projects, and monitoring efforts throughout the state, and primarily with ODFW partners." Whereas most information we found online might have been intended for a lay audience less interested in some of the more technical information we sought, the documents scored constituted all available information, including any additional documents sent to us by agencies.

To identify appropriate hallmarks, we reviewed a broad literature spanning the process and theory of science to applied management approaches and identified four recurrent inter-dependent components that together create a comprehensive approach to science: *measurable objectives*, *evidence*, *transparency*, and *independent review*. Within each management plan, we searched for the presence of 13 criteria, each in the form of a basic question related to a hallmark (*e.g.* "Is the technique for setting quotas explained?" for the *transparency* hallmark; Table 5.1; Appendix D).

We scored generously; for example, if a management plan covered multiple populations and/or species and we found support for a particular criterion in any population/species, we scored it as present. Similarly, we tested only for the presence of criteria, not their rigour (*e.g.* 'do they estimate realized hunting rates', instead of 'do they *reliably* estimate realized hunting rates'). We evaluated the quality of our data using two approaches. First, we provided agencies the opportunity to identify errors (or forward any relevant documents we might have missed) by emailing them our assessments. After 24 months, we received 272 of 624 potential responses (*i.e.* regarding plans for which we were able to find an agency email address). Of these, agencies indicated that no changes were required in 15% (n = 42 plans), that they were unwilling or unable to review 18% (n = 48), and provided suggested changes for 8% (n = 22), with corroborating evidence for most, resulting in an average of 1.1 criteria revised per suggested plan (Appendix D). We also assessed inter-observer agreement by providing two additional observers with non-overlapping random subsets of 5% of management plans (n = 28 each) to independently re-score. We compared how often rescores matched original assessments across criteria and found agreement 87% of the time on average (range: 75-96; Table D.1). Two criteria were excluded from this inter-observer assessment: 'Provide publicly-available management information', because only cases with available documents were rescored, and 'Respond to public inquiry' because this was not a scored criterion but was instead a measure of whether our emails to agencies received a response.

We used a multilevel modeling approach to test for associations between number of criteria present in a given management plan and 1) whether the managed taxa were 'big game', or 2) native; the jurisdiction's 3) country (Canada vs. US), 4) latitude, 5) longitude, and 6) human population; 7) whether large carnivores (grizzly bears, cougars, or wolves) exist anywhere in the jurisdiction; and 8) whether a plan was independently reviewed. We used the *glmmADMB* (Skaug et al. 2013) package in R (R Core Team 2016) to run the model with a Poisson distribution and with deviations to intercepts varying randomly with jurisdiction (US state or Canadian province). We centred all predictors (subtracted the mean from each observation) and scaled (divided by 2 standard deviations) all continuous predictors (latitude, longitude, size of human population) using the *arm* package (Gelman 2008, Gelman and Su 2016). Because we included independent review as a predictor in this model, it was excluded from the response (which did not qualitatively affect other coefficient estimates, c.f. Figure 5.1B and Figure D.2).

Determining suite of taxa hunted in each jurisdiction

We reviewed hunting synopses to determine if there were species hunted in a given jurisdiction for which we lacked management plans. Hunting synopses, typically released annually, inform hunters of the rules and regulations regarding all hunted species. In cases where hunting synopses indicated that a species was hunted in a given jurisdiction, but management plans were not found on the website, we sent emails to relevant agency contacts whose contact information was found in management plans or on agency website. In cases where no relevant email addresses were found, we emailed any other available agency contacts that we found online, requesting them to suggest appropriate contacts (see Appendix D: Emails to agencies).

Cases excluded

We limited our assessments to management of hunted species that fall under the jurisdiction of US states and Canadian territories and provinces, which comprise most hunted species and areas in both countries. As such, we excluded polar bears, waterfowl, and migratory birds (except in 14 plans where doves were mixed in with other, non-migratory taxa), because their management differs from most terrestrial species by being governed through a mix of federal and state/province/territory-level laws and regulations. We similarly excluded assessment of hunting on parcels of federal and tribal lands. We excluded the Canadian province of Québec from our analyses because management plans were not available in English.

Species were categorized as native or non-native, with mixed-species plans designated based on the majority of species therein (*e.g.* we classified 27 management plans that included mostly native bird species, but also non-native pheasants, as native). We did not exclude non-native species because, despite perhaps being guided by different objectives (*e.g.* reducing or eliminating populations) than management of native species, the same science-based hallmarks might be expected in either case.

Results and Discussion

Our results contradict assertions that wildlife management in North America is guided by science. Plans often lacked the basic hallmarks of a scientific approach to management we proposed. Although some plans contained many of the assessed criteria (*e.g.* 2 plans [of 667, 0.3%] contained 12 [92% of total] of the 13 total criteria and 5 plans [0.7%] contained 10 [91% of total] of the 11 ‘required’ criteria [*e.g.* excluding desirable, but not required criteria], and 40 plans [6%] contained at least 10 of the total criteria [77% of total]), most contained fewer than half of criteria examined [*e.g.* 448 of 667; 67% had less than half of total criteria, and 402 (60%) had less than half of the required criteria]: the average number of total and required criteria present per plan was 5 (38%; range: 0 – 12; Figure D.1) and 4.6 (42%; range 0-10, Figure D.2), respectively. Moreover, 62% (8) of the examined criteria were found in fewer than 50% of plans (Figure 5.1A). We detail shortcomings found across all four hallmarks next.

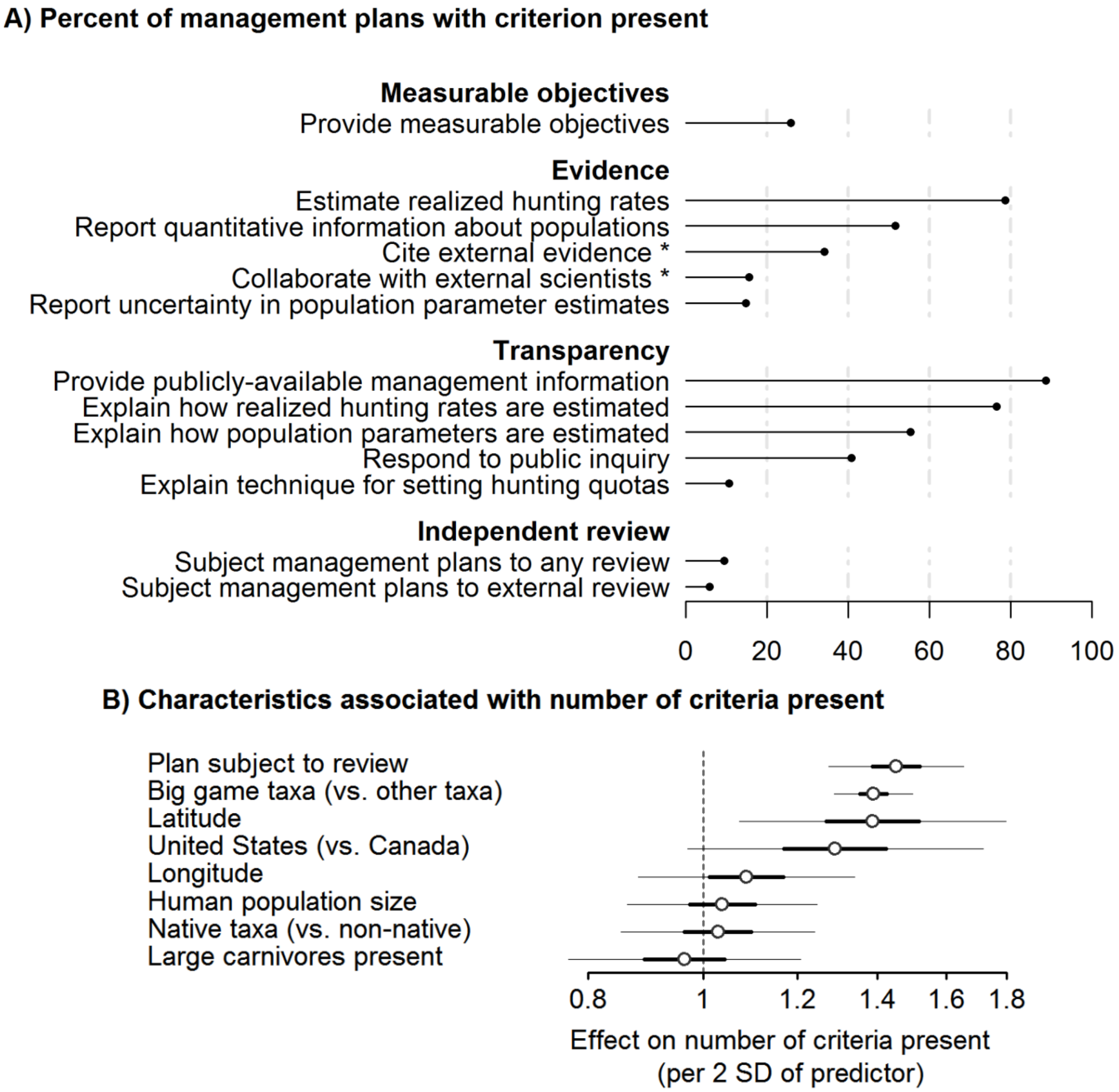

Figure 5.1 **A) Percent of management plans across Canadian provinces/territories and US states (N = 667 plans) in which indicator criteria for hallmarks of scientific management (measurable objectives, evidence, transparency, and independent review) were present. Criteria with an asterisk are those we suggest as desirable, not necessarily required, for a science-based approach. B) Associations between management plan characteristics and number of criteria present (out of 11, with independent review hallmark criteria excluded as part of the response [c.f. Figure D.3]) Coefficients shown are odds ratios from a multi-level model, with thick and thin bars representing 50% and 95% confidence intervals, respectively, and plotted on a log scale, with all criteria included (c.f. Figure D.4).**

Use of measurable objectives

Measurable objectives were detected in only 26% of plans (Figure 5.1A). Without a benchmark against which to measure performance, neither agencies nor the public that trusts them to manage wildlife can assess the efficacy of management or the associated value of their investments in this public service. Moreover, a lack of objectives might lead to management procedures (surveys, data collection, use of technical equipment) becoming the focus of agency activities, instead of strategic approaches designed to accomplish well-defined goals (Platt 1964, Sullivan et al. 2006, Mangel 2011).

Use of evidence

Indications that evidence is employed were largely lacking. Whereas data on estimated hunting rates were present in 79% of plans, quantitative information about populations (*e.g.* abundances, trends) were present in only half (52%; Figure 5.1A).Only 34% of plans cited external sources of evidence (*e.g.*, literature on focal taxa). Fewer (15%) provided measures of uncertainty in population estimates, and only 16% revealed collaboration with external scientists (Figure 5.1A). These results might warrant attention, given the myriad roles of evidence in management, *e.g.* in determining reliable baselines, assessing population dynamics and management outcomes (Meffe et al. 1998, Doremus 2007), and buffering against inherent uncertainties (Reckhow 1994). Moreover, in the apparent absence of evidence, the bases for policy decisions by agencies are not clear (see below).

Presence of transparency

Whereas 89% of plans had some publicly-available information (*e.g.* any hunt-related documents, regardless of their content, on agency websites), and 76% explained how realized hunting rates were estimated, only 55% of plans described how population parameters (trends, abundances) were estimated (and even fewer disclosed these data [*i.e.* quantitative information disclosed in evidence hallmark above]; Figure 5.1A). Only 11% of plans described how hunting quotas were set (Figure 5.1A). Regarding accessibility of agencies to the public, responses to our email inquiries were received in only 41% of cases (Figure 5.1A). Finally, the moderate inter-observer variation in our assessments (mean of ~13% across all criteria; Table D.1) might in part be explained by lack of clarity (itself an important component of transparency) in plans. Deficits in transparency might have affected our ability to properly assess the presence of other hallmarks – *e.g.* we would not have been able to detect if agencies have measurable objectives for a given species, subject its plan to independent review, and its estimate population parameters, but do not describe this publicly. Relatedly, the observed deficits in transparency reduce opportunities for scrutiny by independent parties, and the associated constructive criticism that could inform improvements in management. Indeed, in a review of global fisheries, degree of transparency had a strong positive association with measures of sustainability, even outweighing the effect of jurisdictions' wealth (Mora et al. 2009).

Use of independent review

Only 9% of plans reported any form of review. Fewer (6%) involved external referees (Figure 5.1A). This deviates substantially from scientific research, where verification by external experts is a core requirement, addressing potential issues with impartiality, rigor, and intelligibility (Ruhl and Salzman 2006, Mangel 2011). Those with scientific literacy are well positioned to evaluate agency science; their involvement in agency reviews could help protect not only the integrity of the term 'scientific', but also the trust and interest of the public for whom management is ostensibly conducted (Doremus 2007).

Associations with presence of criteria

We found positive associations between the number of criteria present in a plan and it pertaining to big game, being independently reviewed, and with increasing latitude of the jurisdiction (Figure 5.1B). Critics of the North American model have previously noted that management agencies tend to focus disproportionately on taxa most valued by hunters, and pay little attention to those that are not (Nelson et al. 2011, Clark and Milloy 2014). A similar mechanism might explain why a greater number criteria were found in hunting plans for big game, given their significance to hunters (Darimont et al. 2017). The positive association with independent review, itself a criterion rarely found across plans, in part might explain the general deficiency of other hallmarks; lack of external scrutiny reduces opportunities for identifying management errors and offering avenues for improvement. We do not know what drives the positive association with latitude, but suggest that it might be an interaction of taxonomic, political, and societal variation with latitude that warrants further investigation.

Broader implications

Our findings suggest that the assumed scientific basis of wildlife management in North America might warrant significant reconsideration. More broadly, our results highlight the importance of honestly disclosing the relative contribution of science compared to other considerations (*e.g.* political, economic; Meffe et al. 1998, Sullivan et al. 2006) in management decision-making, and the limitations, uncertainties, and related risks inherent in the data and approaches used (Reckhow 1994, Sullivan et al. 2006, Artelle et al. 2013). We do not suggest that science alone should shape management decisions; science is an important tool for predicting management outcomes and understanding how the world works, but it cannot determine how the world *should* work. Accordingly, social dimensions of management (as articulated in community based management (Gutiérrez et al. 2011) [including, for example, Indigenous practice (Turner 2014)]) and ethics (Nelson et al. 2011) can and should play prominent roles, but in a transparent manner.

We offer the proposed hallmarks herein to encourage developing a common understanding of what might be expected of scientific wildlife management. We also illustrate how such an approach might be tested for at a large scale, illustrated using proposed candidate criteria and hunt management across North America. We note that the criteria we used are not exhaustive, and that the results we described would be subject to change had different criteria been chosen or weighed differently. Moreover, the inter-dependence of these hallmarks warrants caution in interpretation. For example, management plans with low detected transparency might be expected to score poorly for other hallmarks by simple virtue of not having sufficient information for them to be scored. Future scholarship might improve upon the framework presented herein, and apply it iteratively to real-world management systems to better understand their scientific basis at any given point in time, while also assessing how that changes through time.

We suspect that agencies might respond to this external audit and associated evaluations (File D.1) with either a) disagreement or criticism of our framework, b) more judicious defense of policy invoking science-based claims, and/or c) steps to build and maintain a more scientific approach. The hallmarks provided herein are not exhaustive, but provide a foundation for building a science-based approach and for agencies and others to assess organizational change throughout time. In particular, we suggest that implementation of external review would be important for facilitating the adoption of other aspects of a scientific approach. For example, deficiencies in use of evidence, clear objectives, and transparency might be easier to detect --

and avenues for improvement more likely to emerge -- if management approaches were subjected to independent review. Examples from other management regimes have shown how such scrutiny could be integrated into management, including reviews by external organizations (Mora et al. 2009), by academic journals (Wilson et al. 2014), and by independent committees, as in the approach to endangered species assessments in Canada (Waples et al. 2013).

While acknowledging constraints faced by agencies, and that our assessment comes from an academic perspective, many of the aspects (*e.g.* transparently describing approaches already used) of our framework would not be expensive to implement. Other hallmarks might require greater financial investment (*e.g.* reliable estimates of population dynamics to improve evidence). However, we speculate that the greatest barrier to implementing our hallmarks, or a scientific approach in general, is political. Others have cautioned that so-called ‘agency capture’ – undue influence on agency decision-making by special interest groups, such as hunters – might shape policy in an unacknowledged fashion, as might traditions or social pressures within management agencies (Gill 1996, Clark and Milloy 2014). Approaches founded on the hallmarks described herein might help protect against this phenomenon, as well as safeguard agencies from related accusations (Mora et al. 2009) and the associated social, legal and political conflict.

Chapter 6.

Discussion

My thesis assesses the role of science in wildlife management. Across various systems I explore a) the ecological foundation of wildlife management, b) the understanding of how management prescriptions translate to interventions, c) how interventions in turn affect the managed system, and d) the rigour of the management process itself.

In Chapter 2, I assessed the risks imbued by unaddressed uncertainty in the management of hunted grizzly bears in British Columbia, Canada. I found that unaddressed outcome uncertainty led to more bears dying than deemed sustainable (‘overkills’) by provincial biologists in half of the populations examined, that unaddressed uncertainty in biological parameters might have led to even more overkills occurring, and that these would not have been detectable with the current management approach. I refined a target-setting approach more commonly used in fisheries management and applied it to this system, illustrating a generalizable method that could be used to quantitatively incorporate the uncertainties identified to set targets that buffer against overmortality risks. This chapter provided insight not only into risks faced by hunted populations, but also provided a quantitative approach for addressing that risk.

In Chapter 3, I used a multiple hypothesis approach to weigh support for competing explanations of human-grizzly bear conflict in British Columbia, Canada. I found relatively little support for the effectiveness of current approaches to conflict mitigation, including conflict kills of grizzly bears or legal hunts. Instead, I found the most support for natural food availability being associated with levels of conflict, with reduced food associated with increased conflict. These results offer transformative insight into the current approach to management, identifying an ecological mismatch where lethal approaches available to agencies tasked with bear-human conflict have seemingly limited benefit, whereas the availability of spawning salmon, a resource managed by a different agency, seemed strongly linked. I pointed to an existing policy mechanism, the Wild Salmon Policy, which could be used to address this mismatch and to provide more ecologically-coherent approaches to bear management.

In Chapter 4, I compared the configuration of protected areas in the Great Bear Rainforest of British Columbia to hotspots of grizzly bears, the area’s namesake focal species. Using spatial capture-recapture and hair samples from a non-invasive monitoring my colleagues and I coordinate across the area, I identified hotpots based on estimated grizzly bear activity center densities in the 90th percentile of the study area, and statistically using the Getis-Ord G_i^* test. I found that protected areas cover hotspots no better, or worse, than random. Whereas this provides only a preliminary understanding of realized landscape use, it suggests that a considerable portion of realized grizzly bear habitat currently falls outside of protected areas, while providing spatial insight into where protected areas gaps might occur and where they might be addressed.

In Chapter 5, I assessed role of science in wildlife management across states and provinces across the US and Canada. Despite a scientific basis being a central tenet in the model of wildlife management across these jurisdictions, what this means is rarely defined and has never been tested. I searched for indicators of hallmarks of science – evidence, measurable objectives, transparency, and independent review – in hunt management plans across Canada and the US – and found a surprising paucity of them. Whereas others have noted conceptual inadequacies of the model (Nelson et al. 2011, Clark and Milloy 2014), this represented the first broad-scale empirical assessment of its scientific basis. These results challenge a deeply-rooted management paradigm, and raise questions about the extent to wildlife management in these jurisdictions bears any resemblance to science.

Testing for a scientific basis

Beyond insights into the specific ecological and management contexts of the individual chapters, my thesis offers insights into the broader role of science in management. The strong inference provided by rigorous approaches to inquiry have long been recognized, as articulated by Chamberlin (1890) and Platt (1964). Others have described the benefits and importance of applying rigorous evidence and scientific approaches to conservation and management broadly (White 2001, Sutherland et al. 2004). Accordingly, agencies are often assumed, or directly claim, to have a science-based approach to management. However, such claims are rarely tested, an important gap that my thesis addresses. The chapters within illustrate how an idealized model of the management process suggests focal points for assessing the role of natural sciences in real-world management systems (Figure 6.1). For example, Chapters 2, 3, and 4 assess the ecological understanding underpinning the management of grizzly bear hunting, conflict management, and conservation. Chapter 2 focuses on the translation of management prescriptions into interventions by assessing outcome uncertainty, or the discrepancy between the two. Chapter 3 focuses on the link between interventions and the environment, by assessing the effects of hunting and conflict kills on subsequent bear-human conflict patterns. Finally, Chapter 5 assesses the process of management itself, testing for hallmarks of science in hunt management. In each of these cases, shortcomings at different focal points were revealing, providing insight into the rigour of the overall management process: each identified ‘break’ had the potential to undermine the integrity of the overall process by misleading either managers or the public. Whereas understanding the broad role of science in wildlife management might at first seem a daunting and nebulous goal, I illustrated how breaking the process down into smaller, more tractable components (a common approach for addressing complex natural sciences problems [Platt 1964]), allows for directed inquiry, with results relevant both to the specific phenomena studied and to the broader management process itself.

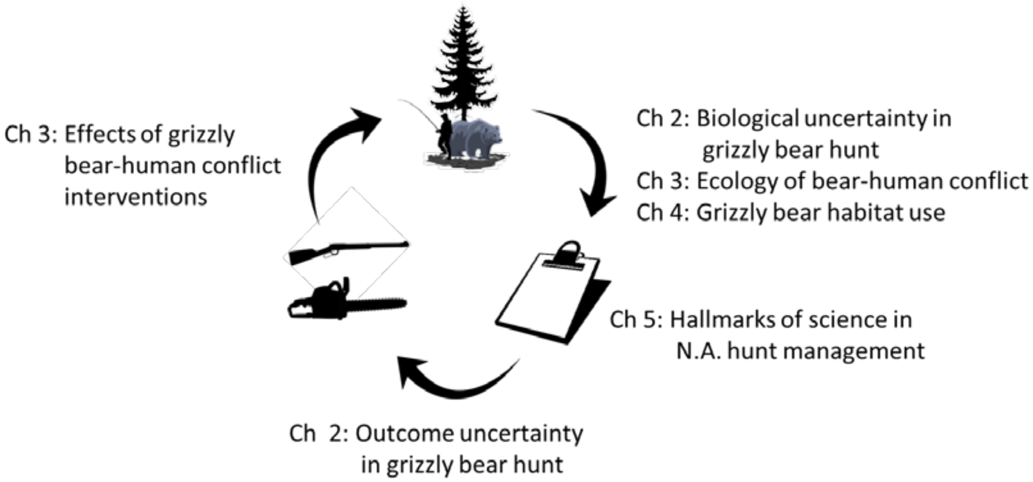

Figure 6.1 **Simplified conceptualization of the management process, depicting which focal points each chapter addressed**

Benefits of assessing the role of science in management

Scientific capture

Examples provided herein highlight the importance of testing scientific assumptions of real-world management to identify shortcomings and suggest solutions. More broadly, these examples hint at the importance of defending scientific integrity itself. The risk of ‘agency capture’ – the undue influence of special interest groups on direction of agencies – is well-known (Gill 1996, Clark and Milloy 2014). Similarly, overt attacks on science by governments have occurred recently, resulting in strong pushback from society and a renewed push to protect scientists from political interference (Goldman et al. 2017, Carroll et al. 2017). Perhaps more pernicious though is the risk of what might be termed ‘scientific capture’ – where the mantle of science-based claims are used to defend a preferred policy option, in contrast to science aimed at empirical assessments that can provide the foundation for honest and informed decisions. In contrast to agency capture, which involves capturing agencies, scientific capture involves capturing the term itself, occurring any time the term ‘science’ is invoked to bolster a given argument without credible scientific backing. Other fields have mechanisms to prevent misappropriation - for example, selling a product as ‘organic’ requires third-party certification. However, although science *does* have mechanisms (*e.g.* peer-review) to protect the integrity of legitimate science, there are few repercussions for ostensibly ‘science-based’ claims that sidestep such mechanisms. Captured science might act as the crooked cop of the management realm by misleading the public, taking advantage of the trust currently held in science (*e.g.* Goldman et al. 2017). Scientific capture might be concerning not only for specific real-world applications, but for the trust in science as a whole. In a worst-case scenario, if the public is misled about the true state and purpose of science, they might begin to see science as just another political tool. This risks the loss of an important means of presenting empirical, rigorous information on which to base decisions. I do not suggest that the results presented herein constitute evidence of intentional scientific capture, but the shortcomings uncovered suggest that it cannot be ruled out.

The process of science itself might also provide specific insight into buffering against the possibility of, or perception of, scientific capture. In particular, employing the hallmarks of evidence, measurable objectives, transparency, and independent review described in Chapter 5 could imbue to management the rigour and self-correction attributed to science, providing an approach that is more robust to both malfeasance and to the appearance of it.

Adaptiveness

The response of agencies to newly generated scientific evidence, *e.g.* from directed approaches such as those described by this thesis, provides qualitatively insight into a management system’s adaptiveness. As mentioned above, shortcomings in ostensibly science-based management processes do not necessarily indicate scientific capture. They might instead be honest mistakes, *e.g.* from misunderstandings of how the world works, research capacity gaps, or from systems changing at rates too fast for management to adapt. Instead, the way in which management agencies respond to new information might be most revealing about the extent to which agencies actually base decisions on scientific information, and, relatedly the extent to which they are adaptive.

When shortcomings are uncovered, an open and transparent response, including enacting appropriate improvements, might be indicative of a truly science-based approach. Importantly, if agencies use an adaptive, multiple hypothesis approach, new information that suggests limited support for a single hypothesis among many does not need to be perceived as failure, but instead provides an opportunity for learning. If, by contrast, agencies do not incorporate or properly address new scientific evidence as it arises, this might suggest a lack of adaptability in the system, and raise questions about the role of science in decision-making.

Role of scientists

I think it is imperative for scientists to act as advocates – not necessarily for individual issues, but instead to protect the integrity of science itself. Others have noted that to defend scientific integrity, scientists must communicate and demonstrate the importance of scientific inquiry to society (Lubchenco 2017, Goldman et al. 2017, Carroll et al. 2017). Whereas this is undoubtedly important for defending against overt attacks on scientific integrity, I think we additionally need to protect against the more covert threats posed by scientific capture. Whenever science-based claims are used to defend a preferred policy options, scientists, especially independent scientists more isolated from risks of political interference (Doremus 2007, Carroll et al. 2017), ought to see this as a bat-signal calling them to assess whether the claims offered might be described as “Beautiful Science”, or BS of a different sort. For example, agencies defending preferred policy options with scientific claims might trigger inquiry by experts in the relevant field to test the credibility of those claims, and to ensure that the contributions of science and politics are not conflated or obfuscated. Clarifying both the limits of what science could offer towards a given management issue (*e.g.* is the issue about how the world works, or is it more about how it should work?), and the limits of current relevant scientific knowledge, could be critical for transparent societal discussions, by clarifying which issues are truly science-based and by protecting against obfuscation of scientific and non-scientific considerations. Scientists are uniquely positioned to police not only one another, but also those who choose to use science to defend their preferred policy options.

Agency response to published work from this thesis

In some ways I found the insight gleaned from responses to the previously published work (*e.g.* Chapters 2 and 3) to be as interesting as the results of the published work themselves.

Of the published chapters, Chapter 2 has provided perhaps the greatest insight because it received the most attention, spurring a concerted response from the relevant management agency. It was the most directly critical of an agency, by identifying a substantial risk of current approaches, while providing insight into how the identified shortcomings could be addressed. After publication, Chapter 2 received substantial public attention, was discussed in the provincial legislature, and played a large part in sparking an audit by the provincial government's office of the auditor general. However, the concerns raised were not addressed by the management agency, nor were the suggested solutions to set lower targets that buffered against uncertainty enacted. Instead, the agency announced an expansion of the hunt, presumably increasing the risks previously identified. This sparked our 2014 self-descriptively titled letter to Science, "When Science-Based Management Isn't" (Appendix E). Remarkably, the then-Premier's aforementioned quote, "We have a record number of grizzly bears in the province, a huge and growing population, and the hunt is scientifically managed", was made the following year. This quote combines a strong assertion of science, directly preceded by comments that are not defended scientifically (*e.g.* by then it was well-known that the total population size is highly uncertain and population trends across the province are largely unknown).

Perhaps of greater concern with respect scientific integrity was a subsequent paper in the Journal of Wildlife Management authored by provincial biologists (Mclellan et al. 2017), which was ostensibly a response to previously raised hunt management concerns, including those we raised in 2013. The authors looked for signs "that the hunt is unsustainable" and, finding only mixed evidence of this, suggested this inferred that the hunt was sustainable overall. Beyond a fundamental issue of confusing absence of evidence with evidence of absence, this was also concerning because in the PLOS ONE publication we noted that population inventories had only been conducted in approximately 14% of hunted populations, with far fewer monitored, and that even among these populations uncertainty was sufficiently high that overmortalities could occur without detection. In other words, given the paucity of data, a lack of evidence of overkills would be the base expectation, regardless of true population trajectories.

To my colleagues and me, the varied responses raised the question of whether science was being done in this case not to clarify how the world works, but instead to bolster preferred policy options. Had the shortcomings we identified been directly addressed, by highlighting methodological issues in our assessment, by offering contradicting evidence, or by offering alternative solutions, this might have led to constructive evolution of scientific understanding and of the management itself. Instead, the publishing of unrelated metrics was analogous to us discovering a hole in a figurative boat hull and providing the means to patch it, with the agency responding that there was no issue with the boat, because the figurative engine still ran and the marine radio still functioned. As a public relations exercise this has been effective by giving the impression of scientific disagreement about whether there are risks imbued by the hunt. However, it was a missed opportunity, where science could have been used to honestly disclose the state of knowledge, characterize true areas of disagreement, and allow an honest discussion of values ultimately driving management decision, but instead might have obfuscated the risks currently imbued.

Interestingly, with the election of a new provincial government, the hunt in parts of the province (the Great Bear Rainforest) will be suspended, with likely reductions in hunting elsewhere. The provincial government noted that this shift was not due to science, but instead in response to societal values and ethics on trophy hunting. Whereas this elicited pushback from some scientists, it is arguably the most honest admission by the provincial government of the true reasons guiding their hunt policy. For the first time in recent memory, the government is not using science to justify their actions, and are being very clear about the true drivers of this recent policy decision.

The response to Chapter 3 was markedly different. Whereas there was some coverage by media, the manuscript has resulted in neither improvements nor pushback from the management agencies. In part I did not offer as concrete a policy criticism or solution as those from Chapter 2. Whereas I discussed the mismatch in scales between the ecology of conflict in this system and the jurisdictions of agencies that aim to address it, the suggested solution of simply employing the existing “Wild Salmon Policy” might have been too glib. In hindsight a better communication of the inefficiencies of current lethal approaches might have been useful, and might have led to more actionable suggestion. Translating the more fundamental finding of the study, regarding the importance of addressing natural food shortages, into directly actionable improvements to management is something that still evades me.

Although Chapters 4 and 5 are not yet published, they similarly offer specific solutions to potential management shortcomings and could provide additional qualitative tests of how insight management agencies respond to new evidence.

Outlook

Science has considerable potential for providing credible evidence to inform management, and for imbuing rigour to the management process itself. However, the extent to which this potential is currently realized in management systems is often unknown. This thesis has provided insights into specific management systems ranging from hunt and conflict management to protected areas placement, from the Great Bear Rainforest to the continental scale, and from grizzly bears to hunted species across the continent. More broadly, it has illustrated how direct scientific inquiry, confronting management assumptions with data at focal points in the management process, offers a means of providing much-needed insight into the role of science in real-world management, and, by important corollary, insight into the extent to which other issues necessarily drive decision-making. Whereas science can and does provide an important tool for understanding how the world works and understanding the likely outcomes of management interventions, scientific capture is often a distinct possibility that might erode not only the rigour of applied management systems, but also of science itself. Scientists are uniquely equipped to assess the veracity of science-based claims and to offer critical interventions and improvements. This thesis illustrates a broad approach towards attaining that goal.

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Appendix A.

Supporting information for Chapter 2

A.1 Supplementary Figures

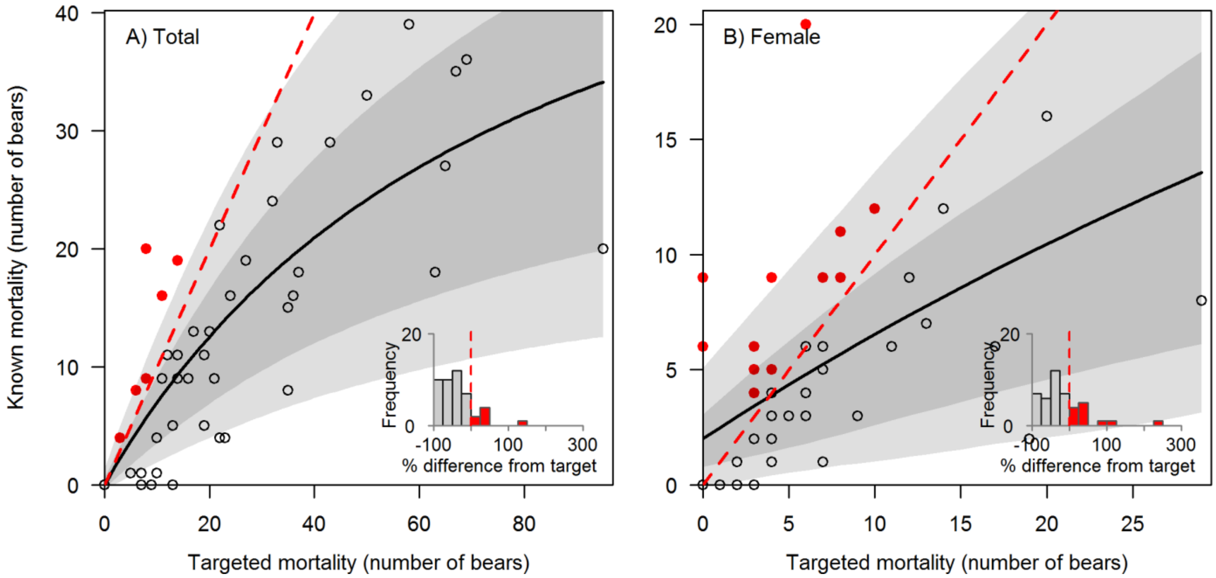

Figure A.1.1 Outcome uncertainty for A) total and B) female mortality in Grizzly Bear (*Ursus arctos horribilis*) Population Units ("population units") in British Columbia, Canada, 2001–2003 (see SI for additional periods).

Black curve is a Michaelis-Menten curve fitted by maximum likelihood, assuming a negative binomial error distribution. Red dashed line indicates a 1:1 relationship; solid red dots above this line signal population unit-level overmortality events. Dark and light grey-shaded regions encompass the 50% and 80% prediction intervals, respectively (smoothed for visual purposes). Inset histograms show the distribution of GBPU-level percent difference between known mortalities and mortality limits (conflated with limits under mortality management policy); red bars to the right of red dashed lines indicate overmortality events.

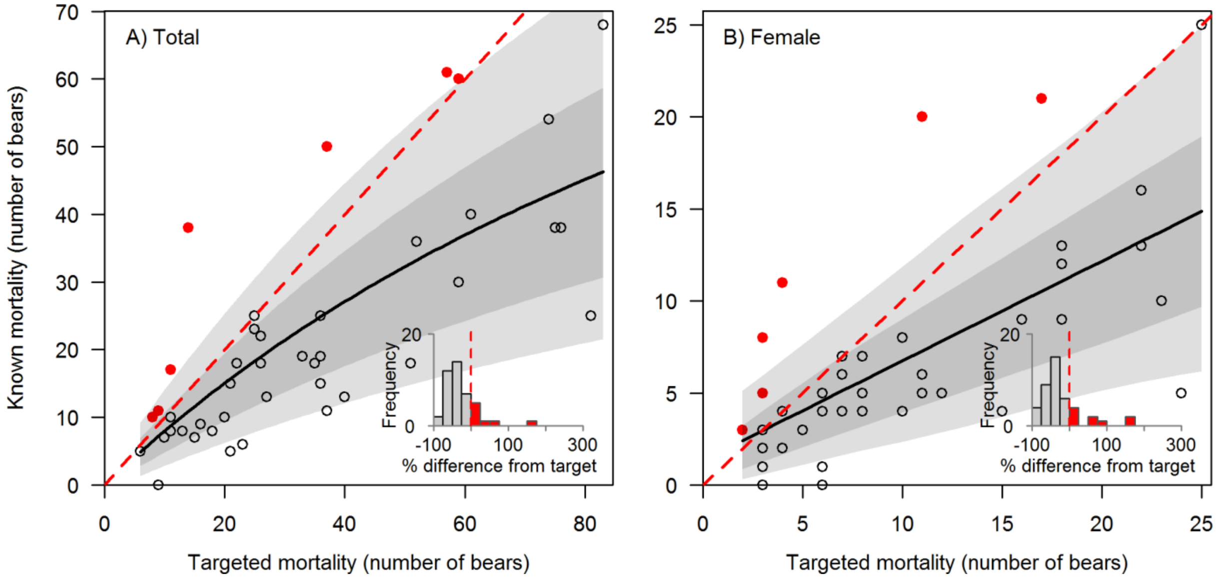

Figure A.1.2 Outcome uncertainty for A) total and B) female mortality in Grizzly Bear (*Ursus arctos horribilis*) Population Units ("population units") in British Columbia, Canada, 2004–2006

Black curve is a Michaelis-Menten curve fitted by maximum likelihood, assuming a negative binomial error distribution. Red dashed line indicates a 1:1 relationship; solid red dots above this line signal population unit-level overmortality events. Dark and light grey-shaded regions encompass the 50% and 80% prediction intervals, respectively (smoothed for visual purposes). Inset histograms show the distribution of GBPU-level percent difference between known mortalities and mortality targets (conflated with limits under mortality management policy); red bars to the right of red dashed lines indicate overmortality events.

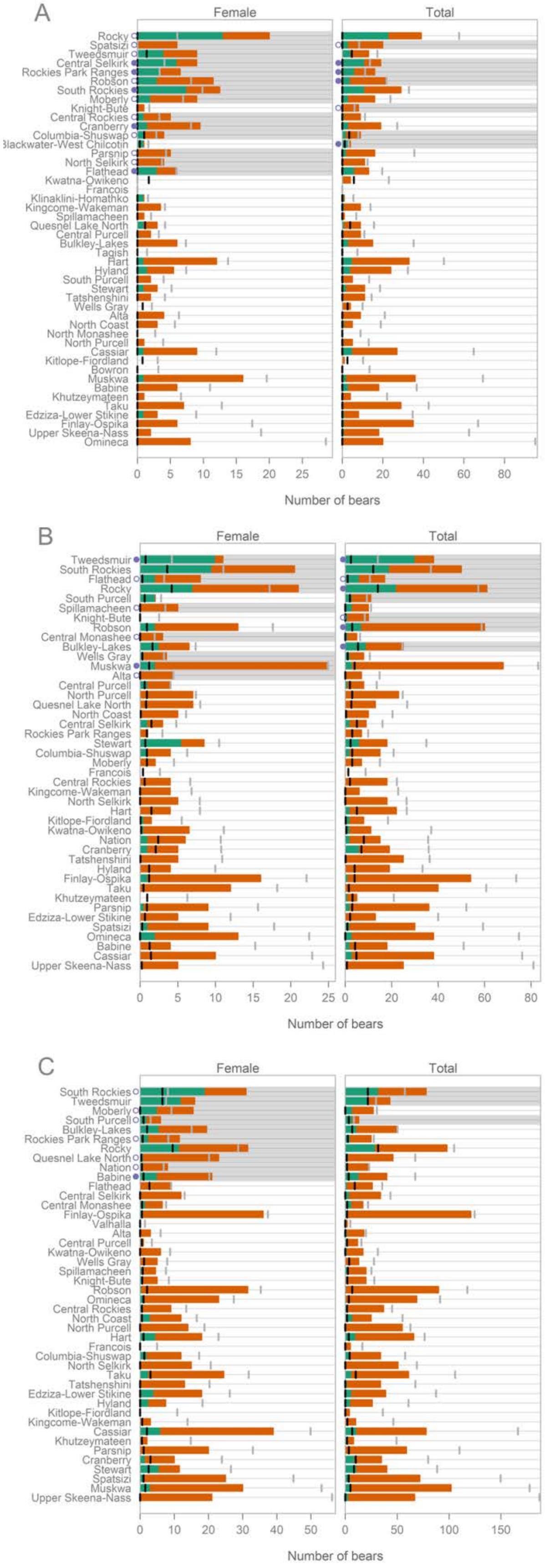
A
Female
Total
Rocky
Spatsizi
Tweedsmuir
Central Selkirk
Rockies Park Ranges
Robson
South Rockies
Moberly
Knight-Bute
Central Rockies
Cranberry
Columbia-Shuswap
Blackwater-West Chilcotin
Parsnip
North Selkirk
Flathead
Kwatna-Owikeno
Francois
Klinaklini-Homathko
Kingcome-Wakeman
Spillamacheen
Quesnel Lake North
Central Purcell
Bulkley-Lakes
Tagish
Hart
Hyland
South Purcell
Stewart
Tatshenshini
Wells Gray
Alta
North Coast
North Monashee
North Purcell
Cassiar
Kitlope-Fiordland
Bowron
Muskwa
Babine
Khutzeymateen
Taku
Edziza-Lower Stikine
Finlay-Ospika
Upper Skeena-Nass
Omineca
0
5
10
15
20
25
0
20
40
60
80
Number of bears
B
Female
Total
Tweedsmuir
South Rockies
Flathead
Rocky
South Purcell
Spillamacheen
Knight-Bute
Robson
Central Monashee
Bulkley-Lakes
Wells Gray
Muskwa
Alta
Central Purcell
North Purcell
Quesnel Lake North
North Coast
Central Selkirk
Rockies Park Ranges
Stewart
Columbia-Shuswap
Moberly
Francois
Central Rockies
Kingcome-Wakeman
North Selkirk
Hart
Kitlope-Fiordland
Kwatna-Owikeno
Nation
Cranberry
Tatshenshini
Hyland
Finlay-Ospika
Taku
Khutzeymateen
Parsnip
Edziza-Lower Stikine
Spatsizi
Omineca
Babine
Cassiar
Upper Skeena-Nass
0
5
10
15
20
25
0
20
40
60
80
Number of bears
C
Female
Total
South Rockies
Tweedsmuir
Moberly
South Purcell
Bulkley-Lakes
Rockies Park Ranges
Rocky
Quesnel Lake North
Nation
Babine
Flathead
Central Selkirk
Central Monashee
Finlay-Ospika
Valhalla
Alta
Central Purcell
Kwatna-Owikeno
Wells Gray
Spillamacheen
Knight-Bute
Robson
Omineca
Central Rockies
North Coast
North Purcell
Hart
Francois
Columbia-Shuswap
North Selkirk
Taku
Tatshenshini
Edziza-Lower Stikine
Hyland
Kitlope-Fiordland
Kingcome-Wakeman
Cassiar
Khutzeymateen
Parsnip
Cranberry
Stewart
Spatsizi
Muskwa
Upper Skeena-Nass
0
10
20
30
40
50
0
50
100
150
Number of bears

Figure A.1.3 (previous page) Mortality targets (conflated with limits under mortality management policy) and known mortalities for each Grizzly Bear (*Ursus arctos horribilis*) Population Unit (population unit) in British Columbia, Canada, during A) 2001–2003, B) 2004–2004, and C) 2007–2011 allocation periods.

Green and orange bars represent number of bears killed by non-hunting and hunting sources, respectively. Vertical grey lines denote mortality targets and vertical black lines denote predicted non-hunt mortality for each period. Population unit rows in which known mortality exceeded mortality targets (‘overmortality’) are shown with grey highlighting. Open blue circles denote population units in which hunting mortality alone exceeded the mortality targets for all sources combined; filled blue circles denote areas in which the unpredicted non-hunting mortality (difference between known and predicted non-hunting mortality) exceeded the excess mortality.

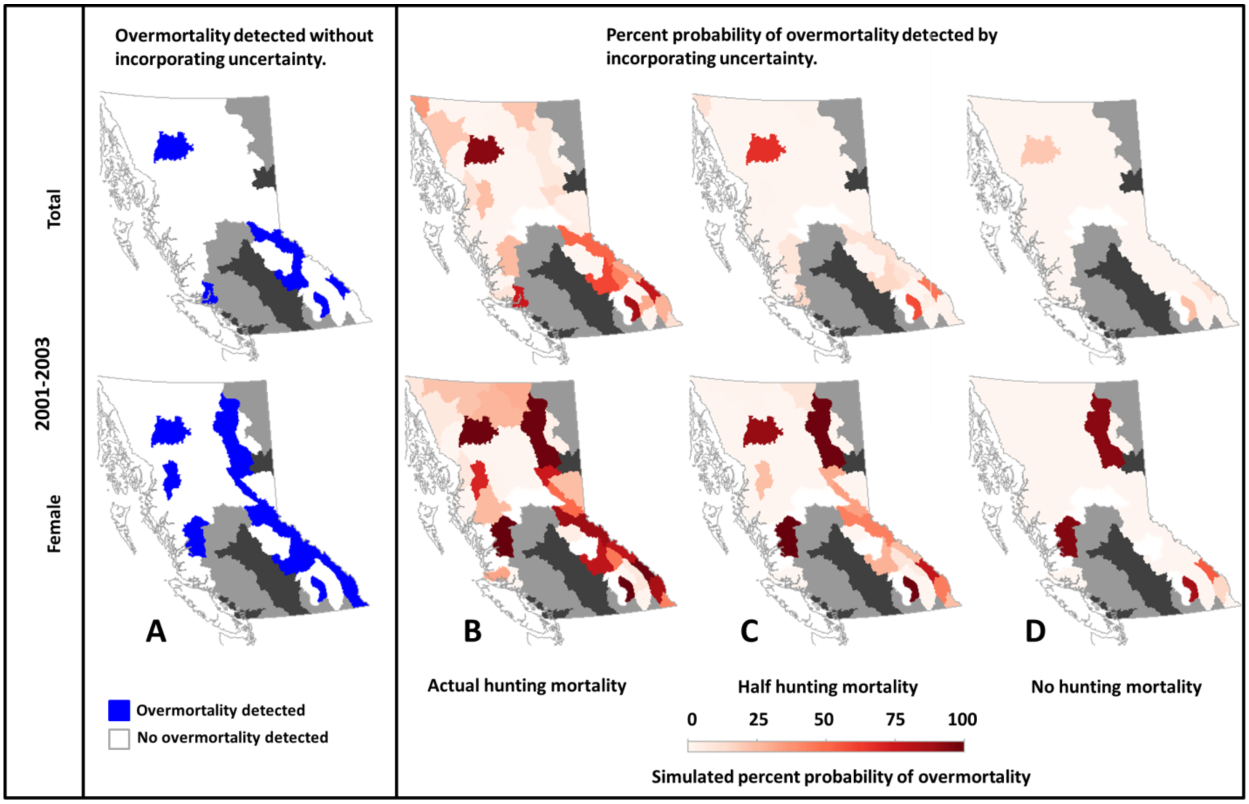

Figure A.1.4 Total and female overmortalities of Grizzly Bear (*Ursus arctos horribilis*) Population Units ("population units") of British Columbia, Canada, from 2001–2003.

A) Overmortalities detected given known hunting mortality levels and without consideration of mortality limit uncertainty. Blue indicates population units with detected overmortality whereas white indicates population units without. B–D) Simulated probability of total or female overmortality, incorporating uncertainty around mortality limits. Panel B shows simulated probability of overmortality given known mortality rates; panels C and D show what the probability of overmortality would be had hunting mortality been reduced by 50% or 100%, respectively, assuming other sources of mortality remained unchanged. Increasingly dark red indicates an increasing probability of overmortality in a given period. Grizzly bears have been extirpated from dark-grey areas. Light-grey areas indicate population units in which populations are either threatened or were closed to hunting during the study period.

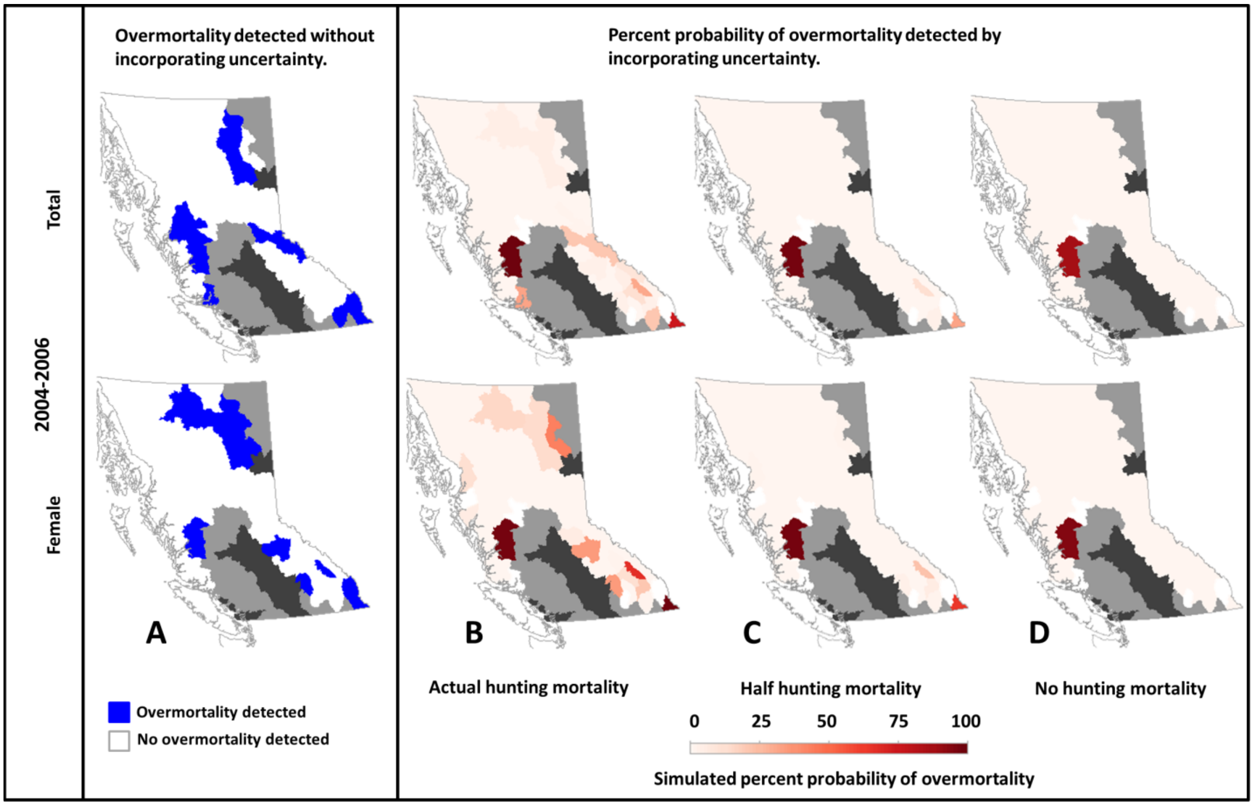

Figure A.1.5 Total and female overmortalities of Grizzly Bear (*Ursus arctos horribilis*) Population Units ("population units") of British Columbia, Canada, from 2004–2006

Overmortalities detected given known hunting mortality levels and without consideration of mortality limit uncertainty. Blue indicates population units with detected overmortality whereas white indicates population units without. B–D) Simulated probability of total or female overmortality, incorporating uncertainty around mortality limits. Panel B shows simulated probability of overmortality given known mortality rates; panels C and D show what the probability of overmortality would be had hunting mortality been reduced by 50% or 100%, respectively, assuming other sources of mortality remained unchanged. Increasingly dark red indicates an increasing probability of overmortality in a given period. Grizzly bears have been extirpated from dark-grey areas. Light-grey areas indicate population units in which populations are either threatened or were closed to hunting during the study period.

A.2 Parameters for setting mortality limits

The government estimates parameters at both the Grizzly Bear Population Unit ("population unit") and Management Unit ("MU") scales. We performed all analyses first at the finer MU scale, then scaled up to the population unit scale which is thought to reflect ecologically and demographically relevant sub-populations [1].

Population estimates

The government sets population estimates using a variety of methods including: (1) DNA capture-recapture surveys [2] (approximately 14% of population units as of 2010 [3], [4]); (2) model estimates based on habitat suitability regression analyses (56% of population units as of 2010); and (3) expert opinion (30% of population units as of 2010).

Uncertainty factor

Uncertainty factors are multipliers used by the government that reduce the population estimate in some population units and periods (0% of population units in 2001-2003, 98% in 2004-2006, and 14% in 2007-2011) to account for uncertainty. These corrections, applied by provincial managers, are based on uncertainty in population estimates and acceptable levels of risk [5]. In population units inventoried with DNA, uncertainties estimated from mark-recapture were used; elsewhere, corrections were assigned according to the ratio between the current estimated density of bears and the potential habitat capability (density the habitat could support before post-contact anthropogenic landscape changes), with lower densities being assigned a higher correction factor [5]. The magnitude of corrections has been reduced in the most recent period (Appendix A.3). The data used in setting factors for each individual MU or population unit are not publicly available, and if methodology has changed since 2004 it has not been publicized

Annual allowable mortality (AAM)

Annual allowable mortality is the annual proportion of the population for which human-caused mortality is assumed sustainable by the government, informed by Harris's [6] work in Montana that estimated maximum AAM (rate with a 10% or less probability of causing chronic declines) in highly productive populations to be somewhere between 6.35% and 6.6%. AAM values used were highest in 2007-2011 (Appendix A.3).

Period length

Period length is three years for 2001–2003 and 2004–2006, and five years for 2007–2011.

Estimated unreported mortality

Estimated unreported mortality is an estimated proportion of the population killed annually by humans through sources including poaching, illegal kills, and unreported road accidents. Sufficient data to directly assess unreported mortality exist only for the Flathead population unit. In the study period managers extrapolated unreported mortality rates to other population units by increasing or decreasing based on four factors believed to be correlated to unreported mortality: 1) human hunter density, 2) large ungulate human hunter density, 3) proportion of habitat capability in areas with roads, and 4) proportion of habitat capability in areas with human populations exceeding 5,000 within a 50 km radius [5].

Previous period overmortalities

Previous period (total or female) overmortalities account for the number of bears killed in excess of mortality limits in the previous period. Note that the government did not carry overmortalities forward from the 2001–2003 to 2004–2006 period.

Supporting references for A.2

1. British Columbia Ministry of Environment, Fish, Wildlife and Habitat Branch (2010) Grizzly bear hunting: frequently asked questions.

2. Hamilton AN, Austin M (2004) Estimating grizzly bear (*Ursus arctos*) population size in British Columbia using an expert-based approach. British Columbia Ministry of Water, Land and Air Protection. Available: http://www.env.gov.bc.ca/wld/documents/gb_est_pop_size.pdf. Accessed 25 September 2012.

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6. Harris RB (1986) Modeling sustainable harvest rates for grizzly bears. Unpublished manuscript.

A.3 Factors affecting detectability of overmortality

The government tests for overmortality events by comparing calculated mortality limits to recorded (*i.e.* actual) mortality. As such, detected frequency of overmortalities can be affected by changes to recorded mortality rates or, importantly, by changes to how mortality limits are calculated (Equation 2.1 and Equation 2.2). Additionally, the temporal scale at which these comparisons are made can affect results. Specifically, longer periods might conceal overmortality events that occur over shorter periods. Accordingly, we examined two aspects that could influence detectability of overmortality events.

First, we examined the distribution of AAM estimates, unreported mortality estimates, uncertainty correction factors, and total mortality limits across allocation periods. Second, we tested the effect of allocation period length on detectability of overmortality events. We compared period overmortality to average yearly overmortality. **Period overmortality** was the number of overmortalities in a given period. **Yearly overmortality** was assessed by comparing *annual* mortality limits (period limit divided by period length) to *annual* known mortality for population unit. For each period, we also compared counts of how many population units experienced a period overmortality to counts of how many population units experienced at least one yearly overmortality.

Detection of overmortality events was likely influenced by harvest management procedures that differed among periods. We found that: i) AAM estimates increased across periods (Figure A3.1), ii) estimates of unreported mortality decreased between 2001-2003 and subsequent periods (Figure A3.2) and, iii) uncertainty correction factors, introduced in period 2, were considerably reduced in period 3 (Figure A3.3). Accordingly, resultant mortality limits also increased across periods (Figure A3.4). Whereas these changes may have reflected the inclusion of more accurate data, we note that apparent reductions in overmortality frequencies may have been due to adjusted parameters, not reduced mortality.

We also found evidence that assessing overmortality across entire periods had the effect of concealing inter-annual variation in mortality rate (Figure A3.5); years in which mortality was unusually high were balanced by years in which it was unusually low. This concealment increased with the longer (*i.e.* five year) duration introduced in period 3, resulting in an apparent reduction of overmortality frequency compared to previous two periods, each of which were three years in length. This effect was most pronounced with total overmortality measures;

whereas counts of whole period and yearly female overmortalities followed a similar pattern across periods, counts of whole period total overmortalities decreased considerably in period 3 whereas counts of yearly overmortalities did not (Figure A3.6).

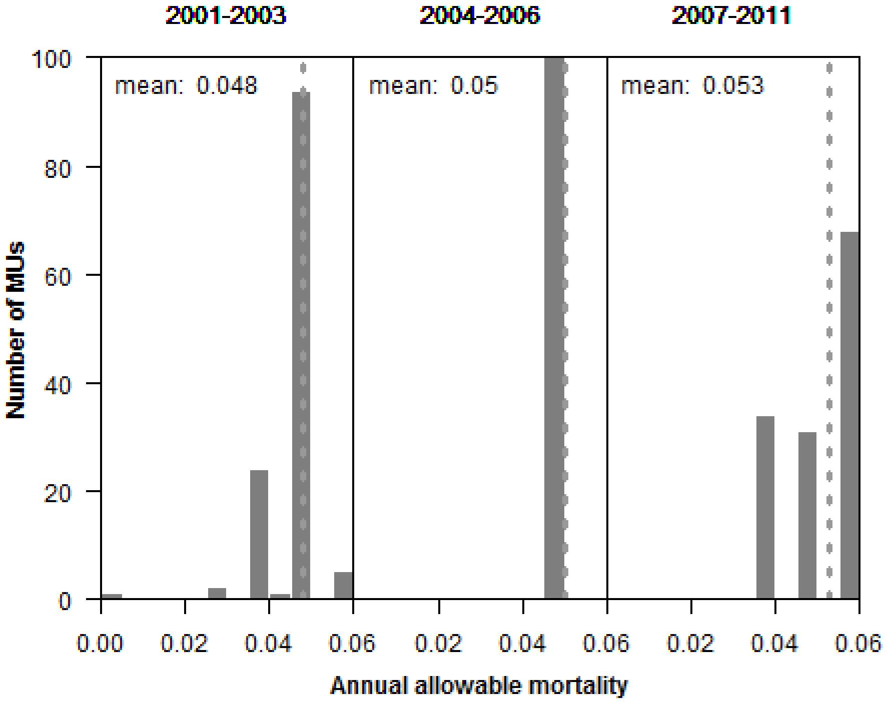


Figure A3.1 Management unit annual allowable mortality estimates used in grizzly bear (*U. arctos horribilis*) management, British Columbia, Canada, 2001-2003, 2004-2006, and 2007-2011. Dashed line represents the period mean value.

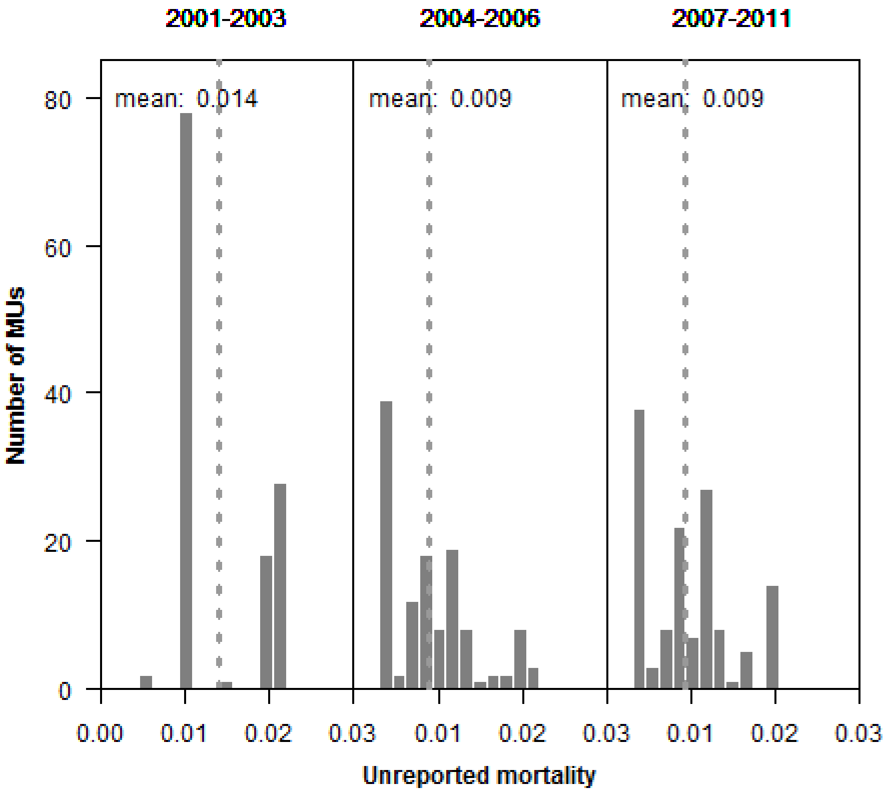


Figure A3.2 **Management unit unreported mortality estimates used in grizzly bear *(U. arctos horribilis)* management, British Columbia, Canada, 2001-2003, 2004-2006, and 2007-2011. Dashed line represents the period mean value.**

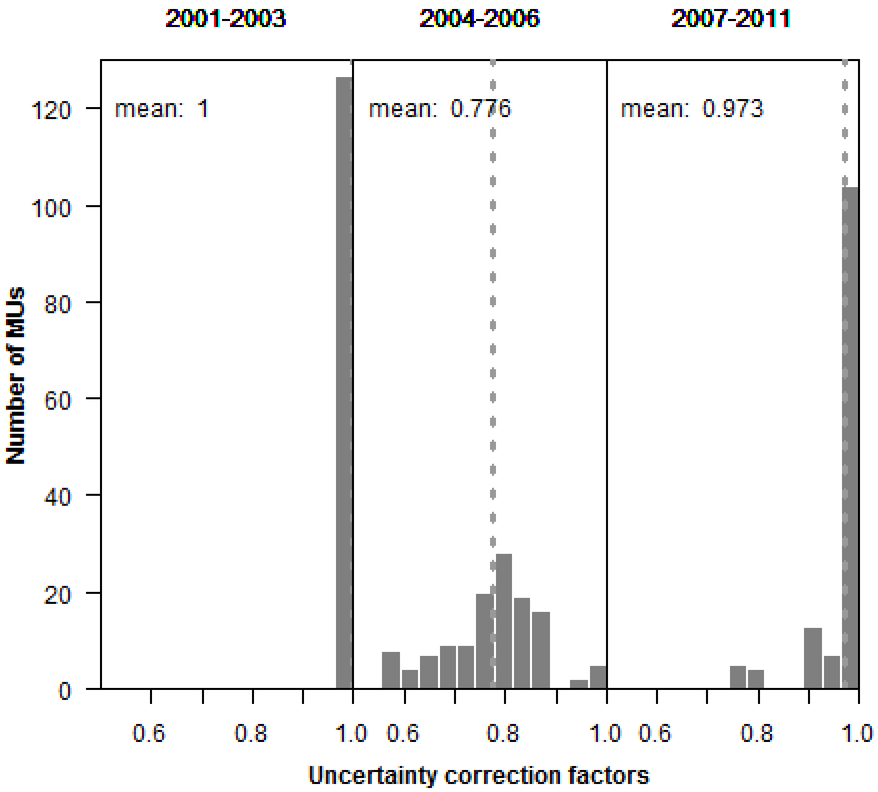


Figure A3.3 **Management unit uncertainty correction factors used in grizzly bear *(U. arctos horribilis)* management, British Columbia, Canada, 2001-2003, 2004-2006, and 2007-2011. Dashed line represents the period mean value.**

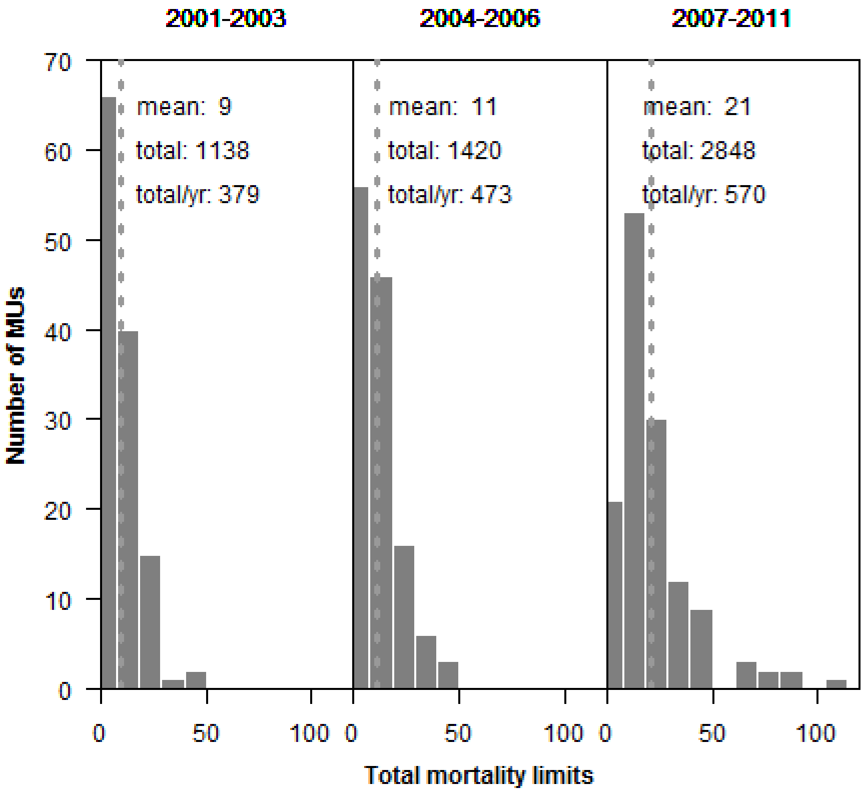
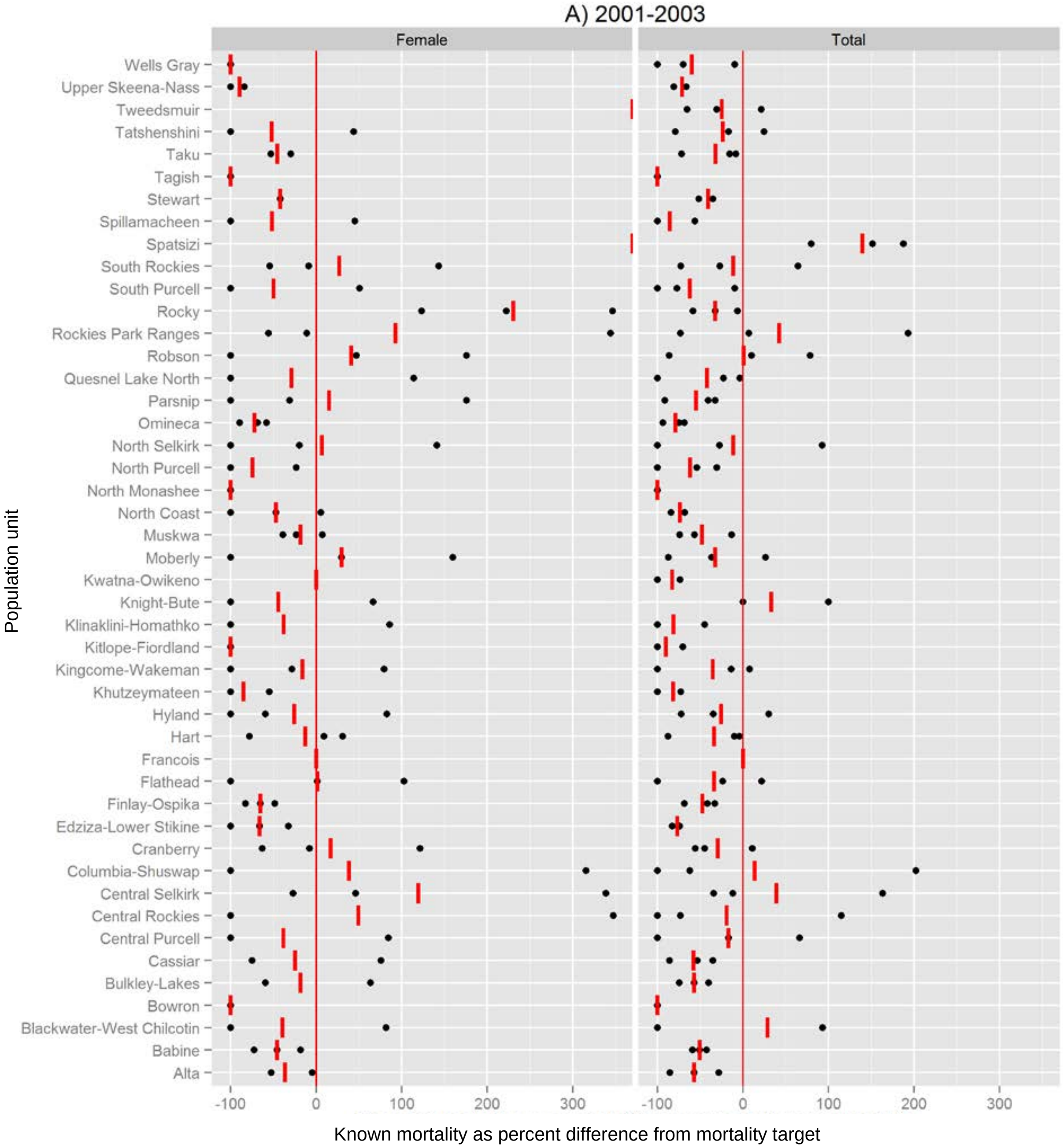
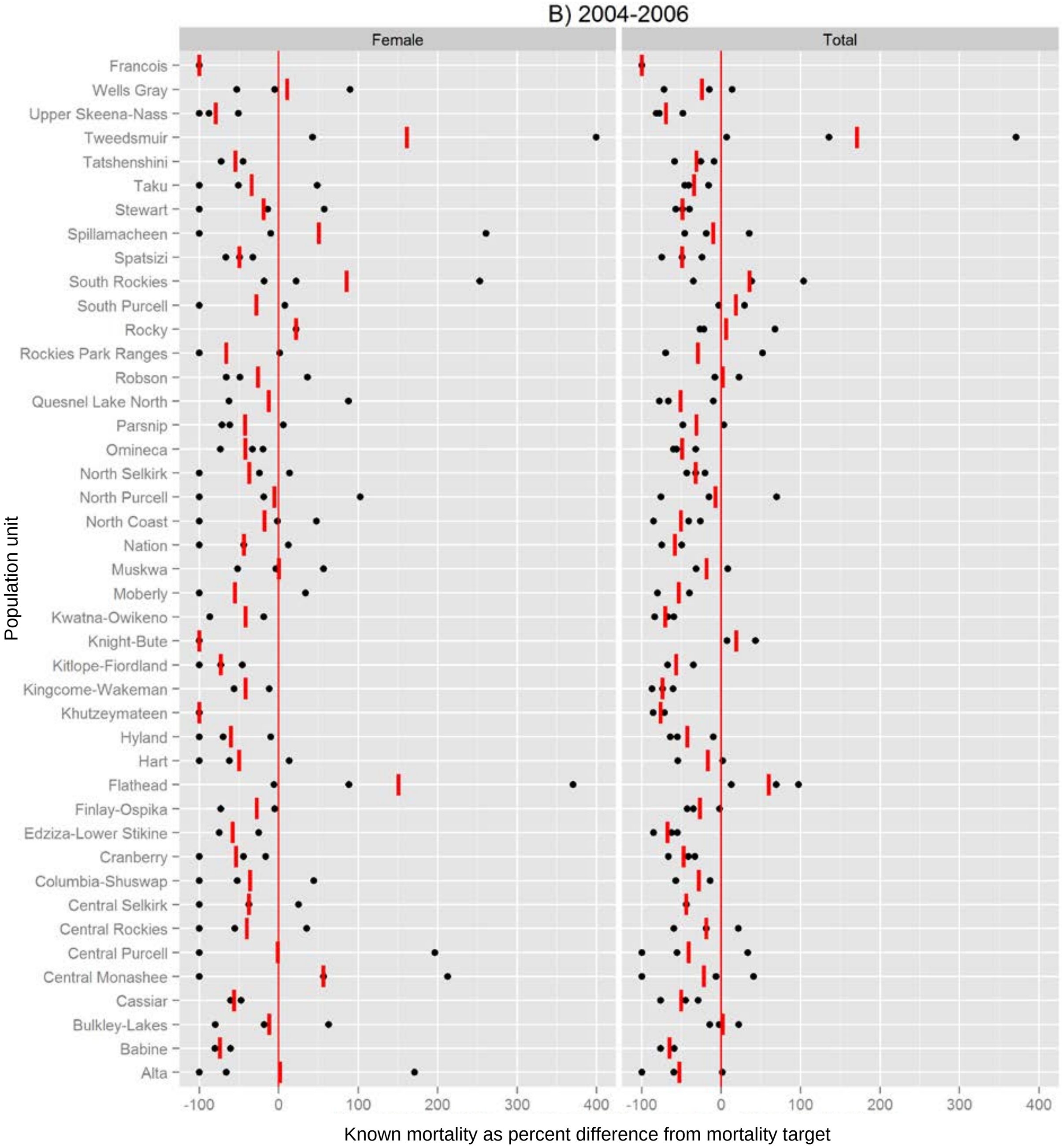


Figure A3.4 **Management unit total mortality limit estimates used in grizzly bear *(U. arctos horribilis)* management, British Columbia, Canada, 2001-2003, 2004-2006, and 2007-2011. Dashed line represents the period mean value.**


A) 2001-2003
Female
Total
Population unit
Wells Gray
Upper Skeena-Nass
Tweedsmuir
Tatshenshini
Taku
Tagish
Stewart
Spillamacheen
Spatsizi
South Rockies
South Purcell
Rocky
Rockies Park Ranges
Robson
Quesnel Lake North
Parsnip
Omineca
North Selkirk
North Purcell
North Monashee
North Coast
Muskwa
Moberly
Kwatna-Owikeno
Knight-Bute
Klinaklini-Homathko
Kitlope-Fiordland
Kingcome-Wakeman
Khutzeymateen
Hyland
Hart
Francois
Flathead
Finlay-Ospika
Edziza-Lower Stikine
Cranberry
Columbia-Shuswap
Central Selkirk
Central Rockies
Central Purcell
Cassiar
Bulkley-Lakes
Bowron
Blackwater-West Chilcotin
Babine
Alta
-100
0
100
200
300
-100
0
100
200
300
Known mortality as percent difference from mortality target


B) 2004-2006
Female
Total
Population unit
Francois
Wells Gray
Upper Skeena-Nass
Tweedsmuir
Tatshenshini
Taku
Stewart
Spillamacheen
Spatsizi
South Rockies
South Purcell
Rocky
Rockies Park Ranges
Robson
Quesnel Lake North
Parsnip
Omineca
North Selkirk
North Purcell
North Coast
Nation
Muskwa
Moberly
Kwatna-Owikeno
Knight-Bute
Kitlope-Fiordland
Kingcome-Wakeman
Khutzeymateen
Hyland
Hart
Flathead
Finlay-Ospika
Edziza-Lower Stikine
Cranberry
Columbia-Shuswap
Central Selkirk
Central Rockies
Central Purcell
Central Monashee
Cassiar
Bulkley-Lakes
Babine
Alta
-100
0
100
200
300
400
-100
0
100
200
300
400
Known mortality as percent difference from mortality target

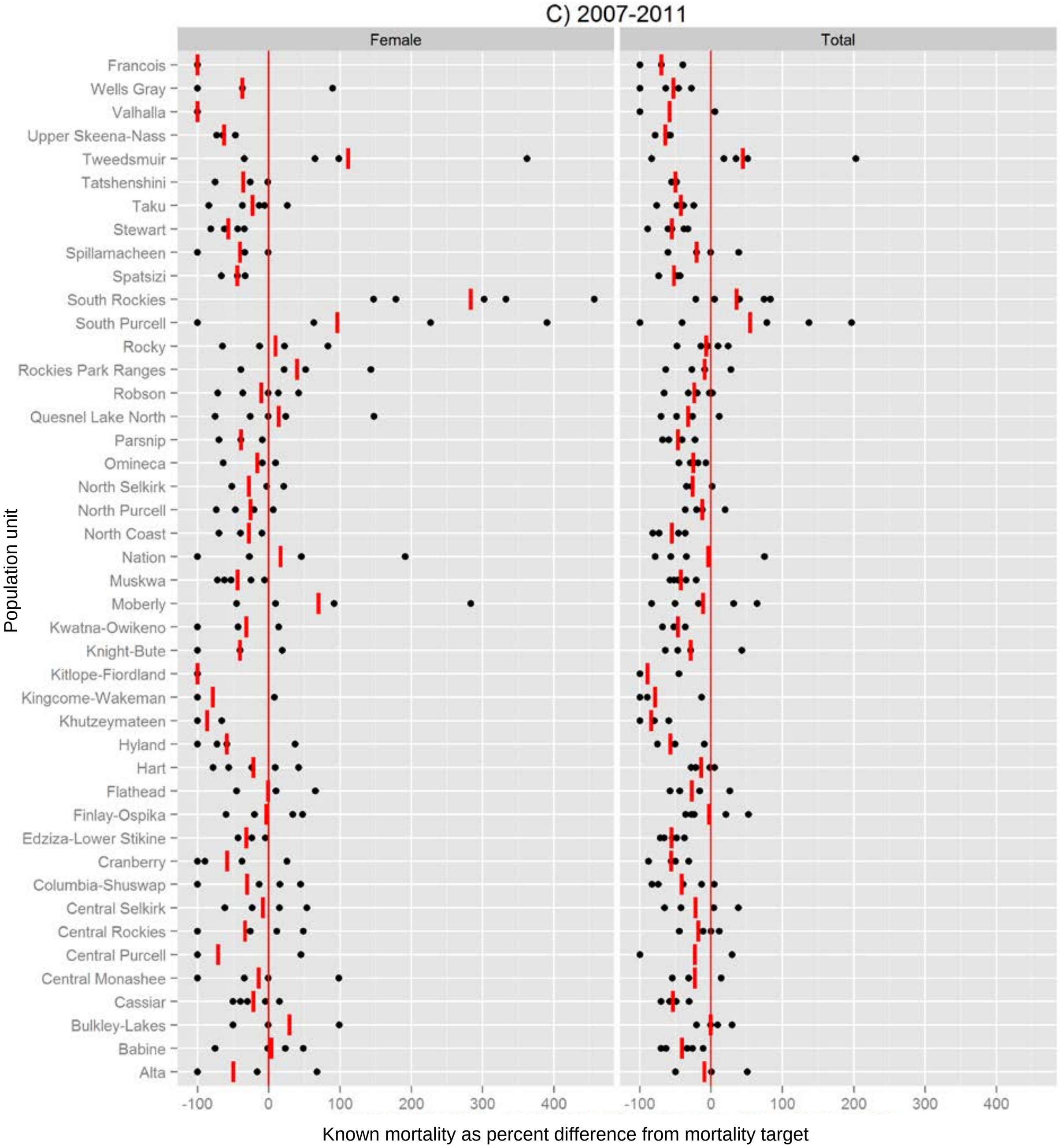


Figure A3.5 **Comparison of percent difference between known mortality and mortality limits in Grizzly Bear *(U. arctos horribilis)* Population Units (population units) of British Columbia, Canada, 2001-2011, at the yearly scale (black dots) and the period scale (red dashes). Vertical red line indicates a percent difference of 0 (known mortality was equal to mortality limits). Periods examined are A) 2001-2003, B) 2004-2006, and C) 2007-2011**

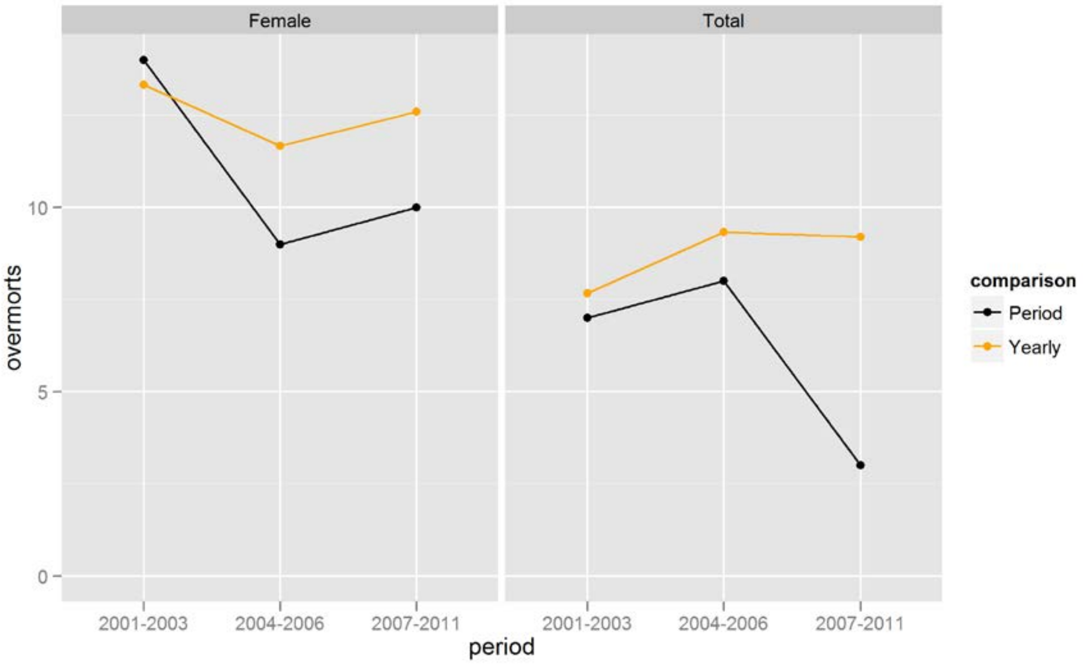


Figure A3.6 Comparison of detected Grizzly Bear (*U. arctos horribilis)* Population Unit (population unit) female and total overmortalities in British Columbia, Canada, from 2001-2003, 2004-2006, and 2007-2011. Black lines are number of population units with detected period overmortalities (known mortality for period exceeding mortality limits for period). Orange lines are number of population units with detected yearly overmortalities (known yearly mortality exceeded period mortality/period length at least once in given period).

A.4 Parameter uncertainty ranges

Population estimate

In our simulation model scenarios, we randomly increased or decreased population estimates by up to 40%. Overall, the average change in government population unit population estimates between 2004 and 2012 was approximately -10%, though adjustments ranged from -89% to 130% (Figure A.4.1A; [1], [2], and [3]). These adjusted values reflected modifications to population estimates, such as inclusion of new capture-recapture data or model refinement, not changes in the population [3]. DNA inventories (used in the estimation of approximately 14% of population units as of 2010), the most rigorous population estimates used by the government, still contain considerable uncertainty. The 95% confidence interval widths around estimates range from 33% to 152%, with an average of 70%, of the magnitude of the point estimate (Figure A.4.1B; [1], [4], and [5]). Moreover, the magnitude of uncertainty for population estimates derived from models and/or from expert opinions is untested and unknown. In summary, the ±40 % range used in our simulations is considerably narrower than that suggested by the wide confidence intervals in DNA capture-recapture estimates, large fluctuations in the government's population unit population estimates throughout the study period, and the heavy reliance on model-derived and/or expert-based estimates.

Annual allowable mortality

Annual allowable mortality (AAM) values are not empirically derived for each population unit. Instead, estimates are based on a sliding scale dictated by government estimates of a given population unit's habitat quality and estimates of population vital rates [6], [7], with a maximum possible value of 6% (above; [8]). Importantly, this rate assumes that female mortality comprises 30% or less of the total mortality. However, published estimates of maximum AAM values vary widely. Data from Bunnel and Tait [9] modeling suggested maximum AAM for "maximally productive populations" to be 5.7%, though others considered their estimates of reproductive rates and survivorship were "very generous" [10]. Sidorowicz and Gilbert [11] estimated AAM to be 2-3% in a Yukon population, whereas simulation by McLoughlin [12] estimated maximum AAM values of 4.9% for good habitat, 2.8% for moderate, and 0% for poor habitat within BC. In the Northern Continental Divide area, Mace et al. [13] calculated vital rates suggesting an AAM of approximately 3%. In Yellowstone, Schwartz et al. [14] estimated up to 9% of female mortality could occur without population decline; however, this estimate included natural mortality, whereas the BC government AAM parameter represents only human-caused mortality. Hovey and McLellan [15] estimated maximum finite rates of increase approximately 8.5% (95% CI of 3.2-13.6%), though, similar to Schwartz et al. [14] this estimate is only relevant in terms of all mortality. Similarly, simulation modeling found a total mortality (human and natural) of 10 bears per year to be sustainable in an initial population of 100 bears modelled after the Yellowstone populations [16], [17], but this estimate depended on strong density-dependence for which there is mixed evidence [10]. Pease et al. [18] found that survival in Yellowstone grizzly populations was food-dependent, with finite rates of increase of up to 7% in years with abundant food (white-bark pine mast years), and -5% in non-mast years. Overall, population growth was likely positive, though given uncertainty in estimates the authors recommended cautious management. In our simulation model scenarios, we increased or decreased annual allowable mortality (AAM) values by up to 2% of the population estimate, resulting in maximum provincial AAMs ranging from 4% to 8%, centred on the maximum AAM point estimate of 6% currently used, a range considerably narrower than that suggested by the literature.

Unreported mortality

We increased or decreased unreported mortality estimates, ranging from half to twice the current point estimate for each population unit. Currently, unreported mortality estimates used by the province range from 0.3% to 2.2% of population unit populations (unpublished data). Even when explicitly studied, however, unreported mortality is notoriously difficult to estimate [19], [20]. Data from BC and beyond suggest that in many cases it could be considerably higher than estimates currently used. For example, in northwestern Alaska, less than half of grizzly bear hunting pre-1990 was thought to be reported [10], whereas wounding loss of black bears was found to account for 9% of human-caused kills on Alaska's Kenai Peninsula from 1982-1987 [21], losses that might have occurred unknown even to the hunters. In a study of radio-collared grizzly bears in the Selkirk mountains that straddle southeastern BC, northeastern Washington, and northwestern Montana, Knick and Kasworm [22] found that the only source of death (27% of 11 bears collared) from 1983 to 1987 was illegal mortality. A meta-analysis by McLellan et al. [23] of grizzly mortality in the Canadian and American Rockies, 1975-1997, found that 26% of kills were illegal. These data supported the estimate reported by Peek et al. [19] that illegal kill of grizzlies comprised 25% of all human-caused mortality from 1970-1977. Our simulated uncertainty range, from half to twice the value of currently used estimates of unreported mortality, is therefore considerably narrower than the range suggested by the literature.

We excluded one population unit (South Rockies) from these analyses in 2004–2006 because the mortality limit for this period was set manually by the government, without record of relevant parameters. No mortalities were detected for Bowron, North Monashee, or Tagish in 2001-2003, or Francois in 2004-2006, so these were also excluded from simulated overmortality assessments.

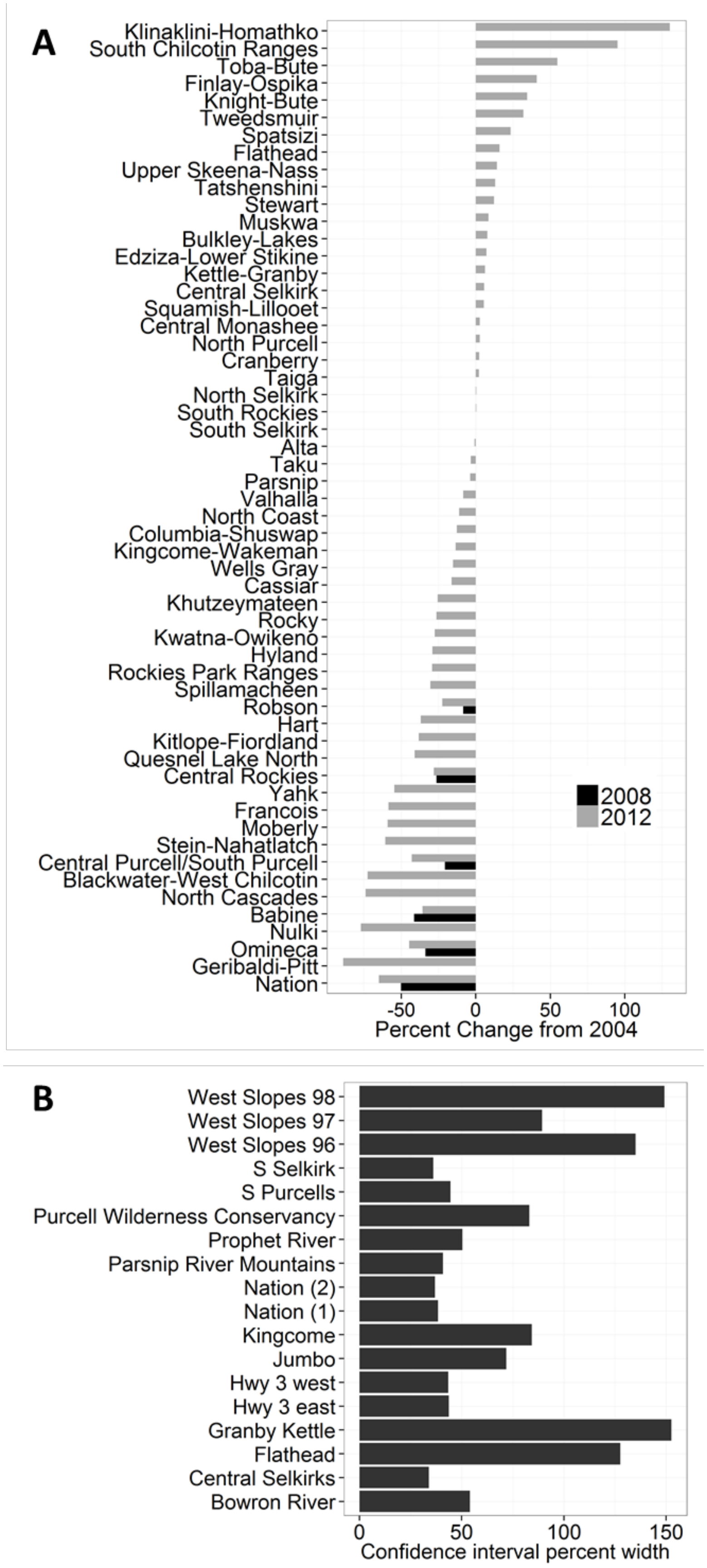

A
Klinaklini-Homathko
South Chilcotin Ranges
Toba-Bute
Finlay-Ospika
Knight-Bute
Tweedsmuir
Spatsizi
Flathead
Upper Skeena-Nass
Tatshenshini
Stewart
Muskwa
Bulkley-Lakes
Edziza-Lower Stikine
Kettle-Granby
Central Selkirk
Squamish-Lillooet
Central Monashee
North Purcell
Cranberry
Taiga
North Selkirk
South Rockies
South Selkirk
Alta
Taku
Parsnip
Valhalla
North Coast
Columbia-Shuswap
Kingcome-Wakeman
Wells Gray
Cassiar
Khutzeymateen
Rocky
Kwatna-Owikeno
Hyland
Rockies Park Ranges
Spillamacheen
Robson
Hart
Kitlope-Fiordland
Quesnel Lake North
Central Rockies
Yahk
Francois
Moberly
Stein-Nahatlatch
Central Purcell/South Purcell
Blackwater-West Chilcotin
North Cascades
Babine
Nulki
Omineca
Geribaldi-Pitt
Nation
-50
0
50
100
Percent Change from 2004
2008
2012
B
West Slopes 98
West Slopes 97
West Slopes 96
S Selkirk
S Purcells
Purcell Wilderness Conservancy
Prophet River
Parsnip River Mountains
Nation (2)
Nation (1)
Kingcome
Jumbo
Hwy 3 west
Hwy 3 east
Granby Kettle
Flathead
Central Selkirks
Bowron River
0
50
100
150
Confidence interval percent width

Figure A.4.1 **(previous page) A) Magnitude of confidence intervals as percent of point estimate for DNA capture-recapture inventories of Grizzly Bears (*U. arctos horribilis*) in British Columbia, Canada. Data from [1], [4], and [5]. B) Percent change in estimated population size of Grizzly Bear (*Ursus arctos)* Population Units (population units) in British Columbia, Canada, from 2004 to 2008 (black bars) and 2004 to 2012 (grey bars) Data from [1], [2] , and [3].**

Supporting references for A.4

1. Hamilton AN, Heard DC, Austin MA (2004) British Columbia Grizzly Bear (Ursus arctos) Population Estimate 2004.

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Appendix B.

Supporting information for Chapter 3

B.1 Supplementary Methods

Spatial scale

We used the 2012 grizzly bear population units (hereafter 'populations'; [1]; http://catalogue.data.gov.bc.ca/dataset/grizzly-bear-population-units) as our spatial scale of analysis. The publicly-available shapefile depicting these contains some 'donut holes' – areas between polygons not assigned to any population. We deleted and excluded these from calculations of 'habitable area' and other spatial variables. Kills were attributed to nearest population in most cases (see below). Of the 57 populations (as delimited in 2012), 46 were viable throughout 1980-2013, and 21 of these had salmon. Across viable populations, grizzly bear densities ranged from 1.9×10^{-3} to 5.26×10^{-2} bears per km^2, with a mean of 2.54×10^{-2} and sd of 1.22×10^{-2}.

Preparation of database containing human-caused kills of grizzly bears

We compiled conflict and hunt kills of grizzly bears from the Compulsory Inspection Database[2]. For modelling purposes, each kill between 1980-2013 was assigned spatially to a population. Hunt and conflict kills in extirpated (hunt n=17; conflict n=35) and threatened (hunt n=133; conflict n=89) regions were excluded from models because hunting was excluded for at least part of the study period in these areas, likely resulting in dynamics that differ from the rest of the province. There were 217 hunt and 37 conflict kills that were excluded because they lacked spatial information. There were 8 hunt and 17 conflict kills with spatial data that occurred outside the limits of populations. Most of these were due to GIS errors – they were immediately adjacent to populations or in "donut holes" between populations – and were assigned to the nearest population. Four cases of human-caused kills on Vancouver Island (3 conflict kills and 1 hunt) were grouped (and excluded from models) with kills in extirpated regions because grizzly bears are present there only occasionally. All remaining hunt and conflict kills were used for modeling: within viable populations, the annual number human-caused kills from conflicts ranged from 0 to 48 (mean = 6.2, sd = 6.1), and from hunts ranged from 0 to 27 (mean = 0.6, sd = 1.6).

Salmon biomass calculations

The Fisheries and Oceans Canada nuSEDS salmon database[3] comprises spawning enumerations of all five species of Pacific salmon in the province. Salmon biomass in each stream was calculated by multiplying raw counts with average species-specific weights of individuals, assuming a 1:1 sex ratio. Values per fish used, in kilograms, were: Chinook: 13.6, Chum: 5.2, Coho: 3.2, Pink, odd years: 2.4, Pink, even years: 1.7, Sockeye: 2.7[4].

Data gaps were common in the dataset, with species-specific counts of salmon missing from many streams in many years[5,6]. We excluded from the analyses species-stream times series with counts missing for more than 8 years in total, or more than 3 consecutive years. We imputed missing annual biomass values in remaining species-streams with a Ricker-logistic model fit to the number of salmon counted of each species in each stream:

$$\mathrm{x_t = x_{t-1} + r_{max}\left(1 - \frac{N_{t-1}}{K}\right) + \epsilon_t}$$

$$\mathrm{\epsilon_t \sim Normal(0, \sigma^2)},$$

where $\mathrm{N_t}$is the number of salmon counted at year t, $\mathrm{x_t = lnN_t}$, $\mathrm{r_{max}}$ represents the theoretical maximum per capita growth rate that is obtained as $\mathrm{N_t}$ approaches 0, K represents the carrying capacity, and ϵ_t represents the normally distributed random process noise (the stochastic jumps between time-steps that are not explained by the Ricker-logistic model) with mean 0 and standard deviation σ. Any years with missing values were estimated as additional parameters.

To fit the Ricker-logistic models, we set the prior on K as uniform between zero and the maximum observed abundance (as in [7]). We set the prior on $\mathrm{r_{max}}$ as uniform between 0 and 5. We set a weakly informative prior of Half-Cauchy(0,2.5) [8,9] on the process noise standard deviation.

We fit our imputation models with Stan [10–12]. We initially sampled from our models with 10,000 iterations across 4 chains, discarding the first half of the iterations on each chain as warmup, for a total of 20,000 samples. We checked if $\hat{\mathrm{R}}$ (a measure of chain convergence) was less than 1.05 and if $\mathrm{n_{eff}}$ (the number of effective uncorrelated samples) was greater than 100. For all streams that did not meet these criteria, we resampled from the models with 200,000 iterations (100,000 warmup), 4 chains, and saved every 5th iteration. We then fit the remaining three streams that had not yet converged according to our criteria of $\hat{\mathrm{R}}$ <1.05 and $\mathrm{n_{eff}}$ >100 with 1 million iterations (discarding the first half), 4 chains, and saving every 10th iteration. We also visually inspected the chains of each final model for convergence. We used the median posterior imputed values for our primary analysis.

To test whether our conclusions were sensitive to uncertainty in the posterior distribution, we drew 8 samples from the posterior of imputed values of each time series to run as a multiple imputation sensitivity test (Figure B.5A). We fit the full model (not the model-averaged model) to each of these 8 replicate datasets to illustrate how the model would perform under alternative plausible imputation scenarios, and found that results did not change qualitatively.

To test how well the Ricker model imputed missing data points we randomly removed one data point (biomass in a given year) from each complete time series (time series of a given species in a given stream without any missing years). Comparing the imputed values from this simulation to actual values revealed that the Ricker model approximated the missing data reasonably well (Figure B.5B)

When attributing stream salmon counts to bear population units we used the geometric mean of annual stream biomasses to give more weight to smaller streams, given their disproportionate importance for bear predation on salmon [13]. Running the analyses with total biomass instead of geometric mean did not qualitatively change the results.

B.2 Supplementary Figures and Tables

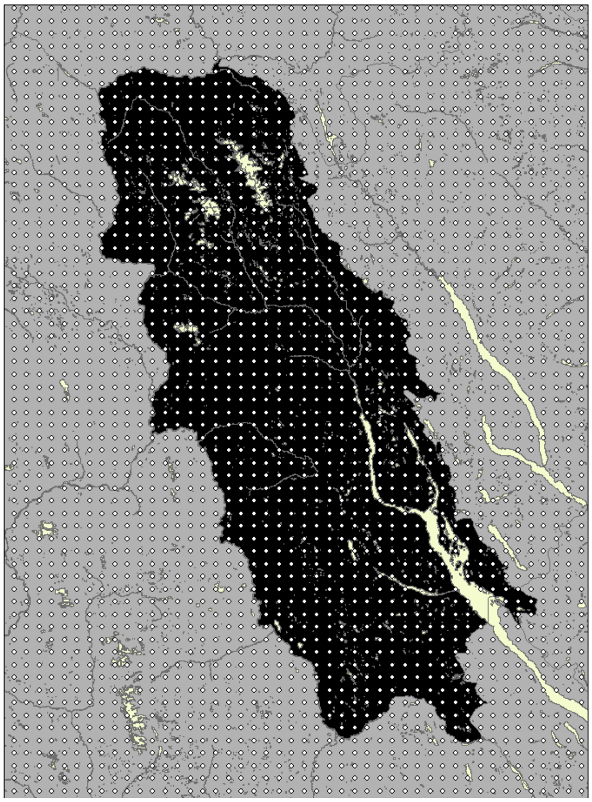
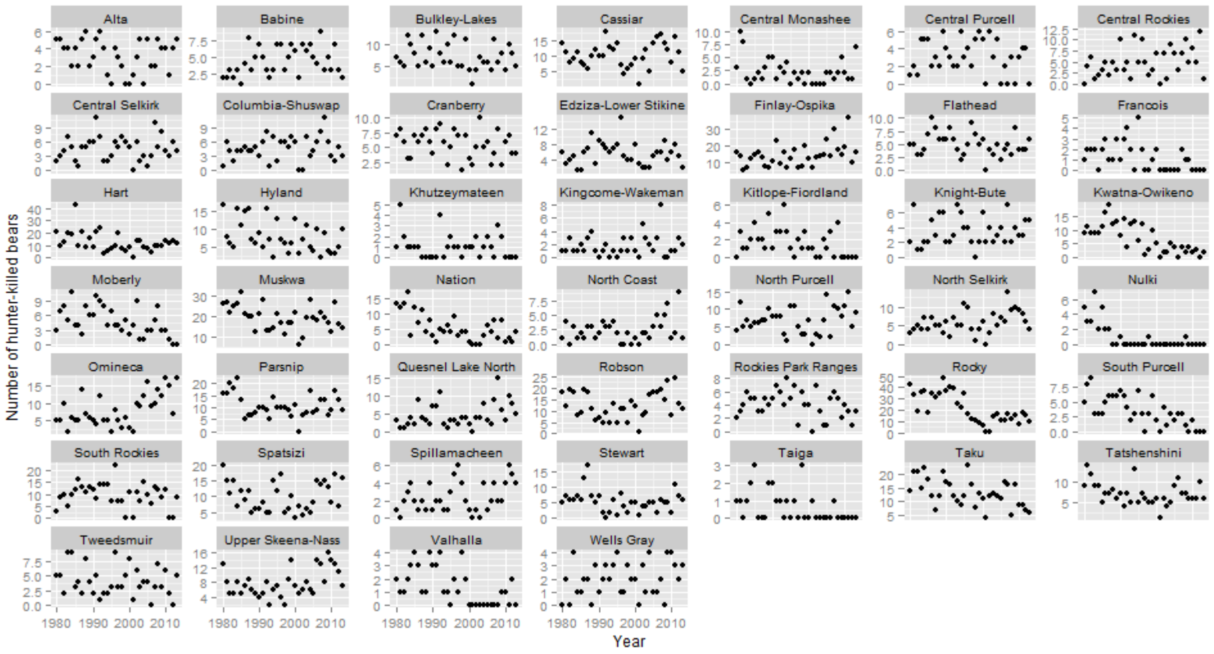


Figure B.1 Example of approach used to estimate habitable area of a population and to extract population-level climate indices.

Habitable area of the Babine grizzly bear (*Ursus arctos horribilis*) population unit is shown in black. Glaciers and waterbodies (lakes and rivers) are shown in white, and excluded from habitable area. Each dot represents a location from which climate normals (typical temperature and precipitation from 1981-2010) were extracted. Generated with ArcMap 10.2, www.esri.com.

A) Hunt kills



B) Conflict kills

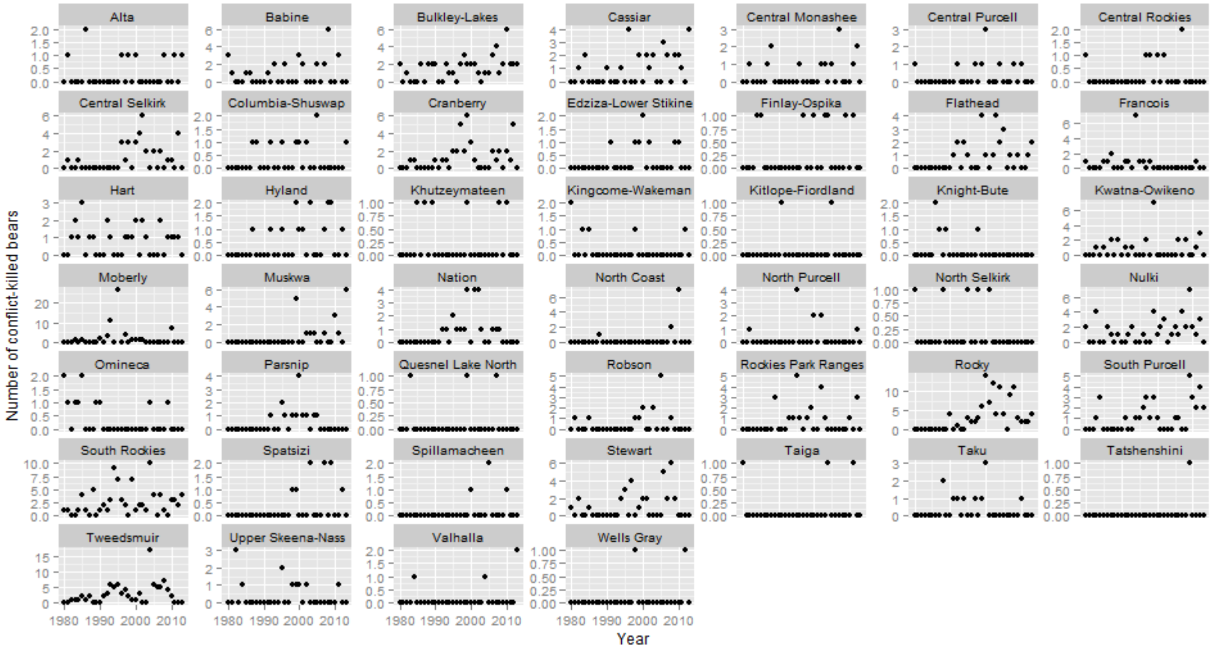


Figure B.2 **Number of A) hunter-killed and B) conflict-killed grizzly bear (*Ursus arctos horribilis*) by year in each Grizzly Bear Population Unit in British Columbia, Canada, used to model grizzly bear-human conflict from 1980-2013.**

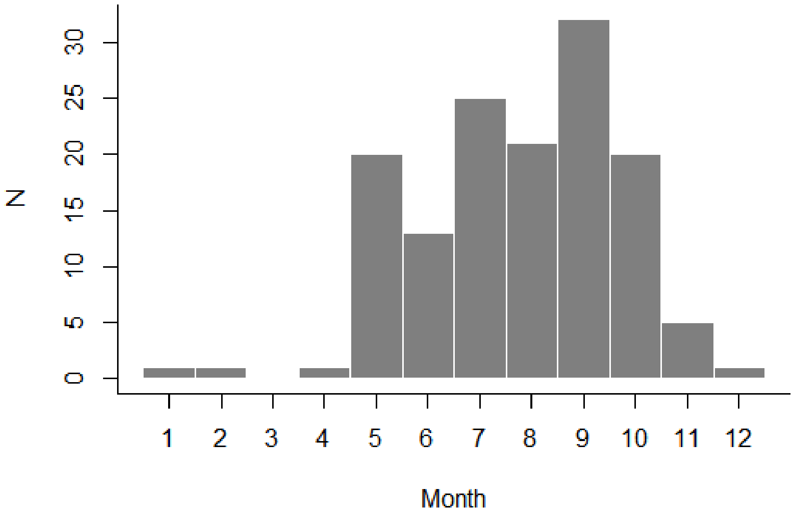


Figure B.3 **Number of grizzly bear (*Ursus arctos horribilis*) attacks (including attacks that did not cause injury and/or require hospitalization) on humans by month in British Columbia, Canada from 1960 to 2014 (n = 82).**

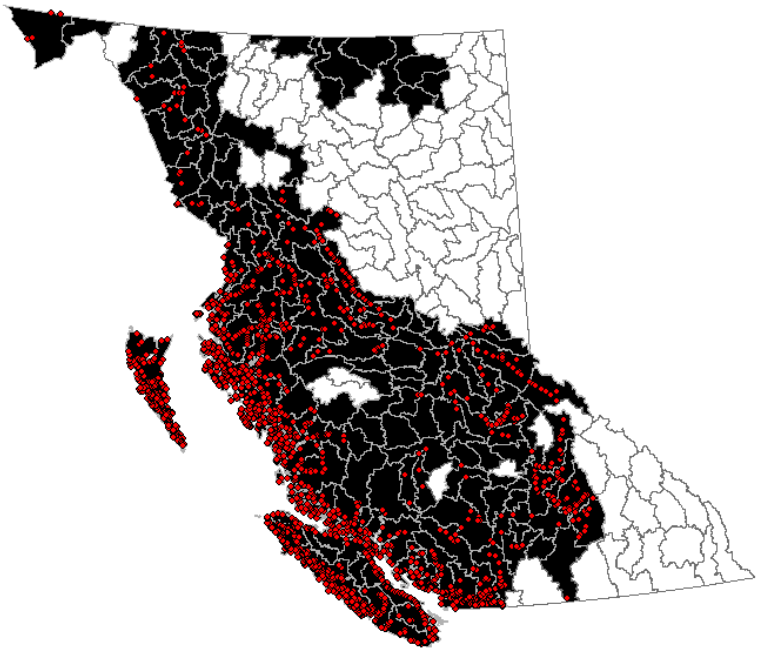


Figure B.4 **Locations of spawning salmon counts within British Columbia, Canada.** Polygons shown are watershed groups as defined by the BC watershed atlas [14,15]; spawning salmon (*Oncorhynchus* spp.) have been observed [16] in black watersheds, red dots are point locations where spawning salmon were enumerated [3]. Generated with ArcMap 10.2, www.esri.com.

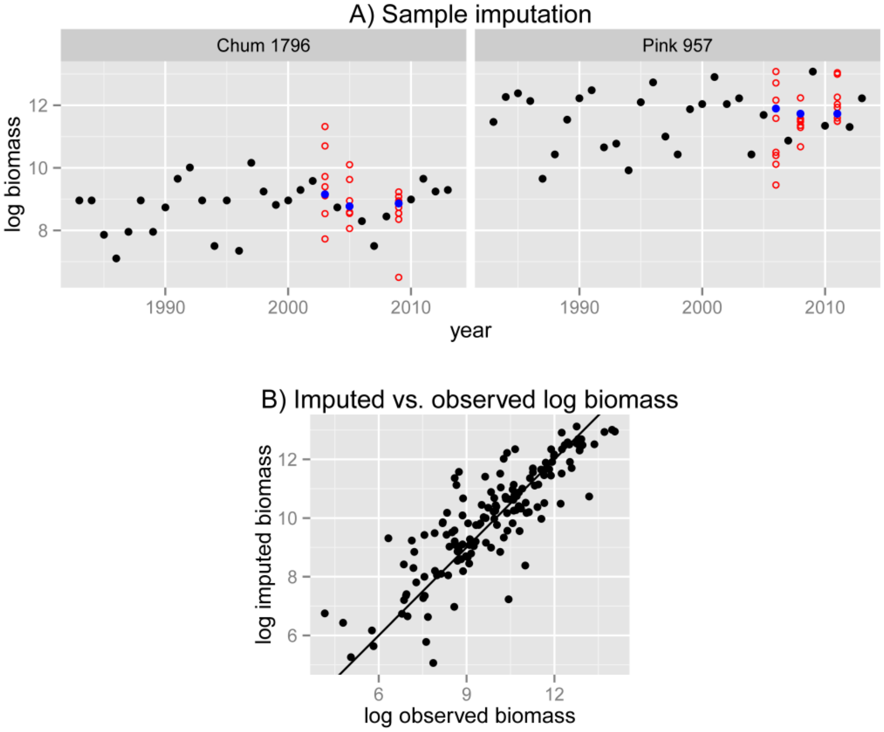


Figure B.5 A) Sample imputed time series for two salmon (*Oncorhynchus* spp.) count time-series in the Kwatna-Owikeno grizzly bear (*Ursus arctos horribilis*) population unit.

Black dots represent log biomass from count data. Red dots represent eight draws from, and blue dots represent median value of, posterior distributions of values from a logistic Ricker-model used to impute biomass for years with missing count data. B) Comparison of median imputed versus observed log biomass, calculated by randomly removing and imputing one year of data from all complete time series (species counts in streams without any missing annual counts). Black line is the 1:1 line.

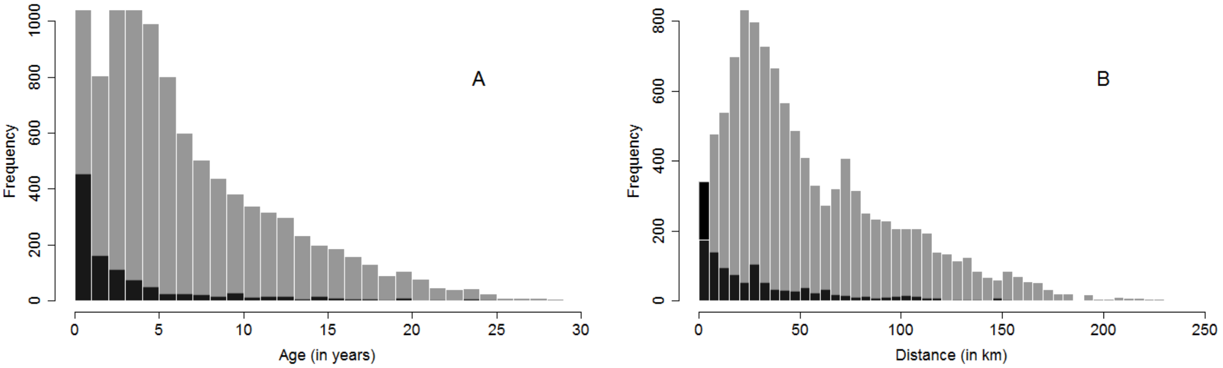


Figure B.6 A) Age and B) distance from nearest city, town, or community of conflict-killed (black bars) and hunter-killed (grey bars) grizzly bears (*Ursus arctos horribilis*) in British Columbia, Canada, 1978-2014.

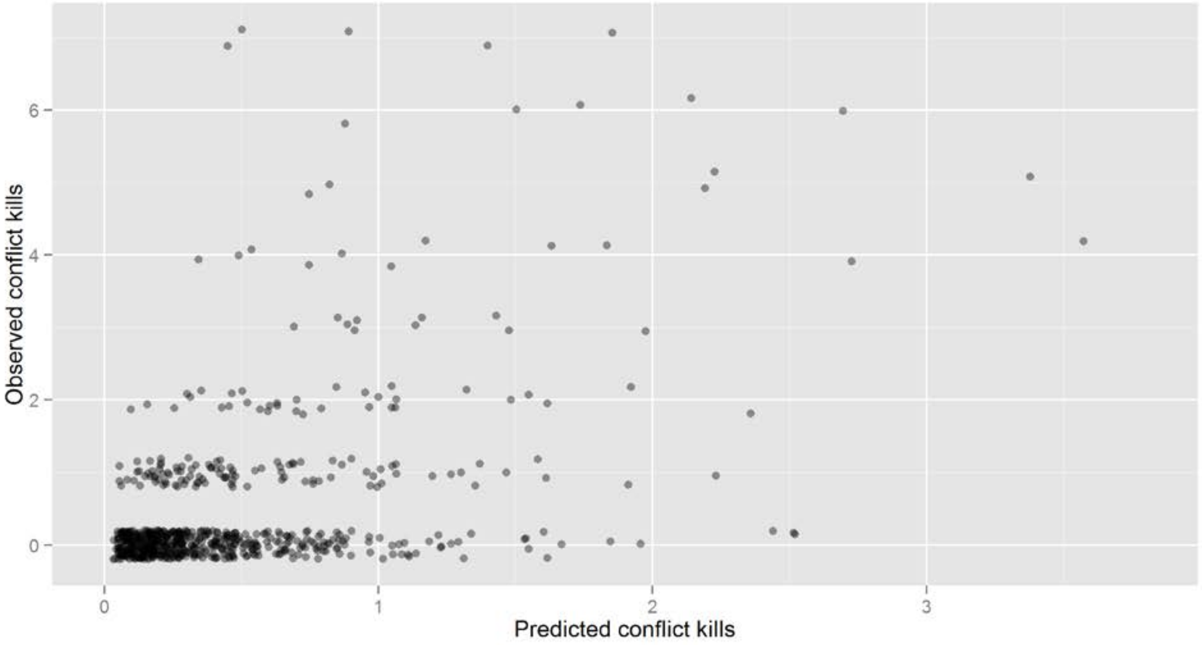


Figure B.7 Observed versus predicted annual number of conflict-killed grizzly bears (*Ursus arctos horribilis*) in British Columbia, Canada, 1980-2014, from the model-averaged salmon areas model.

Predictions shown are based on fixed effects only added to random effect estimates for each grizzly bear population unit. Two points were omitted (predicted conflict kills > 4), and positions of points on y-axis were jittered, to better show the bulk of data.

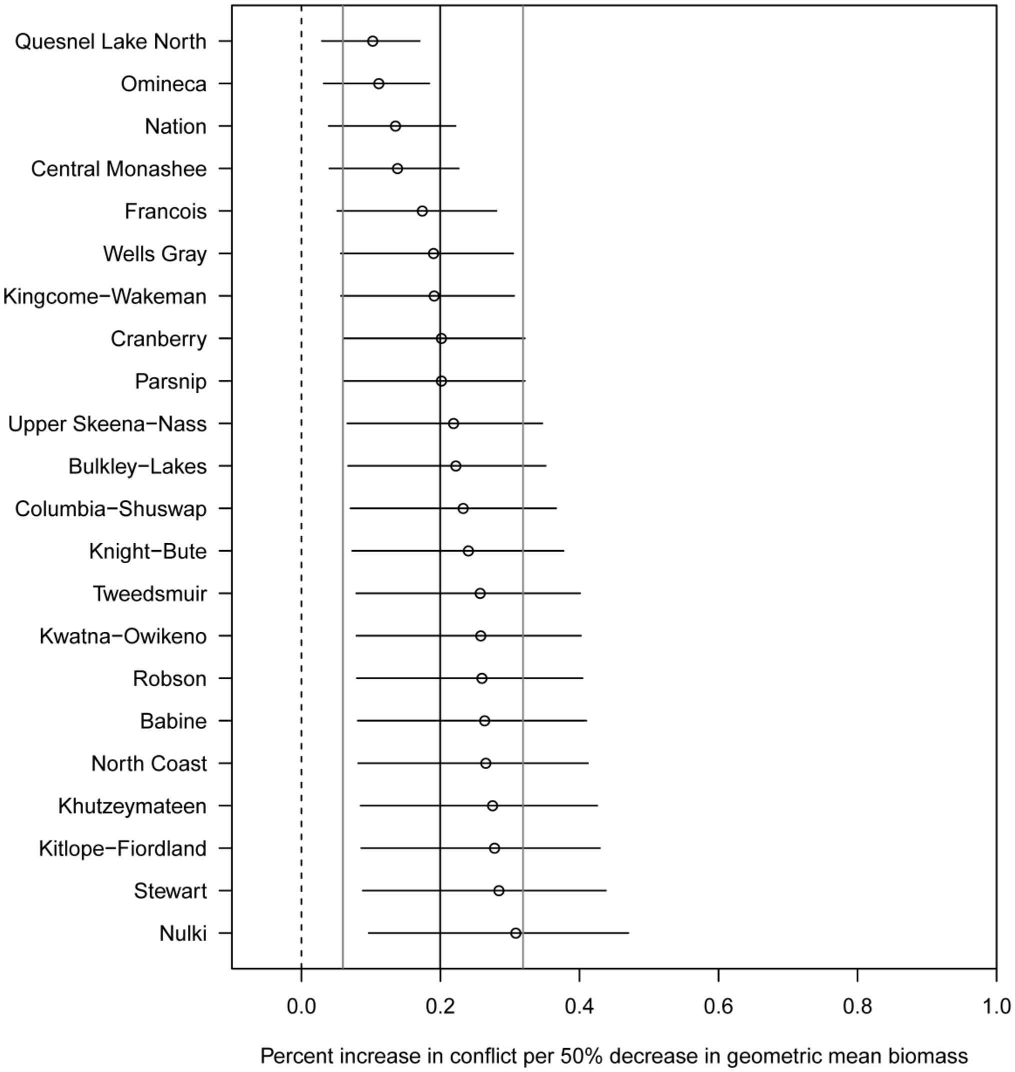


Figure B.8 Effect of salmon availability on annual number of conflict-killed grizzly bears (*Ursus arctos horribilis*) for each grizzly bear population unit analyzed in British Columbia, Canada, 1980-2013.

Open circles represent percent increase in conflict per 2-fold (50%) decrease in geometric mean of salmon biomass and bars represent the 95% confidence intervals. Black solid vertical line and dark grey solid lines indicates the percent increase in conflict-killed bears and 95% CI, respectively, per two-fold (50%) decrease in the geometric mean of salmon biomass for a population with average variability of salmon. The back-transformed effect sizes vary by population because the salmon predictor was scaled within each population.

Table B.1 **Candidate model set used to assess the effect of ecological variables on annual number of conflict-killed grizzly bears (*Ursus arctos horribilis*) in British Columbia, Canada, 1980-2013. Salmon represents annual geometric mean of salmon biomass, Precip and Temp represent mean spring and summer temperature and total spring and summer precipitation, Hunt and Conflict represent the total number of hunter-killed and conflict-killed bears, respectively, in the previous three years, Grizzly pop represents estimated grizzly bear densities, and Human pop represents estimated human population densities.**

	Model	Annual Variables	Spatial Variables
Salmon Areas	1	salmon+temp+precip+hunt+conflict	temp+precip+human pop+grizzly pop
	2	salmon+temp+precip+hunt	temp+precip+human pop+grizzly pop
	3	salmon+temp+precip	temp+precip+human pop+grizzly pop
	4	salmon	temp+precip+human pop+grizzly pop
	5	salmon+hunt+conflict	temp+precip+human pop+grizzly pop
	6	salmon+temp+precip+conflict	temp+precip+human pop+grizzly pop
	7	salmon+hunt	temp+precip+human pop+grizzly pop
	8	salmon+conflict	temp+precip+human pop+grizzly pop
	9	temp+precip	temp+precip+human pop+grizzly pop
	10	temp+precip+hunt+conflict	temp+precip+human pop+grizzly pop
	11	temp+precip+hunt	temp+precip+human pop+grizzly pop
	12	temp+precip+conflict	temp+precip+human pop+grizzly pop
	13	hunt	temp+precip+human pop+grizzly pop
	14	hunt+conflict	temp+precip+human pop+grizzly pop
	15	conflict	temp+precip+human pop+grizzly pop
	16	no annual variables	temp+precip+human pop+grizzly pop
Full Region	1	temp+precip	temp+precip+human pop+grizzly pop+salmon present
	2	temp+precip+hunt+conflict	temp+precip+human pop+grizzly pop+salmon present
	3	temp+precip+hunt	temp+precip+human pop+grizzly pop+salmon present
	4	temp+precip+conflict	temp+precip+human pop+grizzly pop+salmon present
	5	hunt	temp+precip+human pop+grizzly pop+salmon present
	6	hunt+conflict	temp+precip+human pop+grizzly pop+salmon present
	7	conflict	temp+precip+human pop+grizzly pop+salmon present
	8	no annual variables	temp+precip+human pop+grizzly pop+salmon present

Table B.2 **Candidate models used to assess the effect of ecological variables on annual number of conflict-killed grizzly bears (*Ursus arctos horribilis*) in British Columbia, Canada, 1980-2013. Salmon represents yearly geometric mean of salmon biomass, Precip and Temp represent mean spring and summer temperature and total spring and summer precipitation, Hunt and Conflict represent number of hunter-killed and conflict-killed bears, respectively, in the previous three years, Grizzly pop represents grizzly bear densities, Human pop represents human population densities, Delta represents delta-AIC, and Weight represents model weight.**

				Annual variables				Spatial variables						
	Model	Intercept	Salmon	Precip	Temp	Previous conflict	Previous hunts	Precip	Temp	Grizzly pop	Human pop	Year	Delta	Weight
Salmon Areas	8	-24.36	-0.42			0.29		-1.41	1.14	0.63	-0.08	0.02	0.00	0.32
	4	-24.36	-0.41					-1.43	1.14	0.64	-0.08	0.03	1.21	0.18
	5	-24.36	-0.43			0.28	-0.11	-1.40	1.13	0.63	-0.07	0.02	1.61	0.14
	6	-24.37	-0.42	0.25	0.57	0.31		-1.20	0.79	0.32	-0.13	0.02	2.54	0.09
	7	-24.36	-0.43				-0.14	-1.42	1.13	0.63	-0.06	0.03	2.56	0.09
	3	-24.36	-0.41	0.29	0.49			-1.32	0.83	0.36	-0.12	0.03	4.04	0.04
	1	-24.37	-0.43	0.21	0.58	0.30	-0.11	-1.15	0.77	0.30	-0.12	0.02	4.17	0.04
	15	-24.34				0.28		-1.36	1.12	0.57	-0.09	0.03	5.29	0.02
	2	-24.36	-0.43	0.24	0.51		-0.14	-1.25	0.81	0.35	-0.11	0.03	5.41	0.02
	16	-24.34						-1.38	1.12	0.58	-0.09	0.03	6.17	0.01
	14	-24.34				0.28	-0.06	-1.35	1.11	0.56	-0.08	0.02	7.21	0.01
	12	-24.35		0.11	0.62	0.30		-0.97	0.74	0.22	-0.15	0.03	7.75	0.01
	13	-24.34					-0.09	-1.37	1.11	0.57	-0.08	0.03	7.95	0.01
	9	-24.34		0.15	0.54			-1.10	0.79	0.27	-0.14	0.03	8.97	0.00
	10	-24.35		0.08	0.62	0.30	-0.07	-0.94	0.72	0.22	-0.14	0.03	9.66	0.00
	11	-24.34		0.12	0.55		-0.09	-1.05	0.77	0.26	-0.13	0.03	10.72	0.00
Full Region	7	-24.24				0.21		-0.76	0.55	0.98	1.22	0.03	0.00	0.41
	8	-24.24						-0.76	0.55	0.98	1.22	0.04	1.07	0.24
	6	-24.24				0.21	0.01	-0.76	0.56	0.98	1.22	0.03	2.03	0.15
	5	-24.24					0.00	-0.76	0.55	0.98	1.22	0.04	3.10	0.09
	4	-24.24		0.04	-0.04	0.21		-0.82	0.58	0.99	1.22	0.03	4.03	0.05
	1	-24.24		0.08	-0.08			-0.88	0.59	1.01	1.23	0.04	4.99	0.03
	2	-24.24		0.05	-0.04	0.21	0.01	-0.82	0.58	0.99	1.22	0.03	6.06	0.02
	3	-24.24		0.08	-0.08		0.00	-0.88	0.60	1.01	1.23	0.04	7.03	0.01

Supplementary References for Appendix B

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Appendix C.

Supporting information for Chapter 4

C.1 Supplementary Methods

Study area boundary

We constructed an overall study area boundary using buffered convex hulls (Figure C.1). For the HT and KT subprojects we defined study boundaries using one convex hull around each project's trap arrays. Because the WT project has an irregular shape, its study boundary was defined using 3 separate adjoining convex hulls, one each around the western portion of the subproject, a southern lobe, and an eastern lobe. A buffer of 10 km was added to all convex hulls – an arbitrarily-chosen distance, but one where individuals would have a reasonable chance of encountering a baited trap – and the overlapping sub-project sub-boundaries were merged into the broader study area boundary. This boundary successfully captured most of the activity centre variation driven by observed data, while omitting areas further from the study area which represent average densities of activity centres of augmented individuals (Figure C.2, Figure C.3).

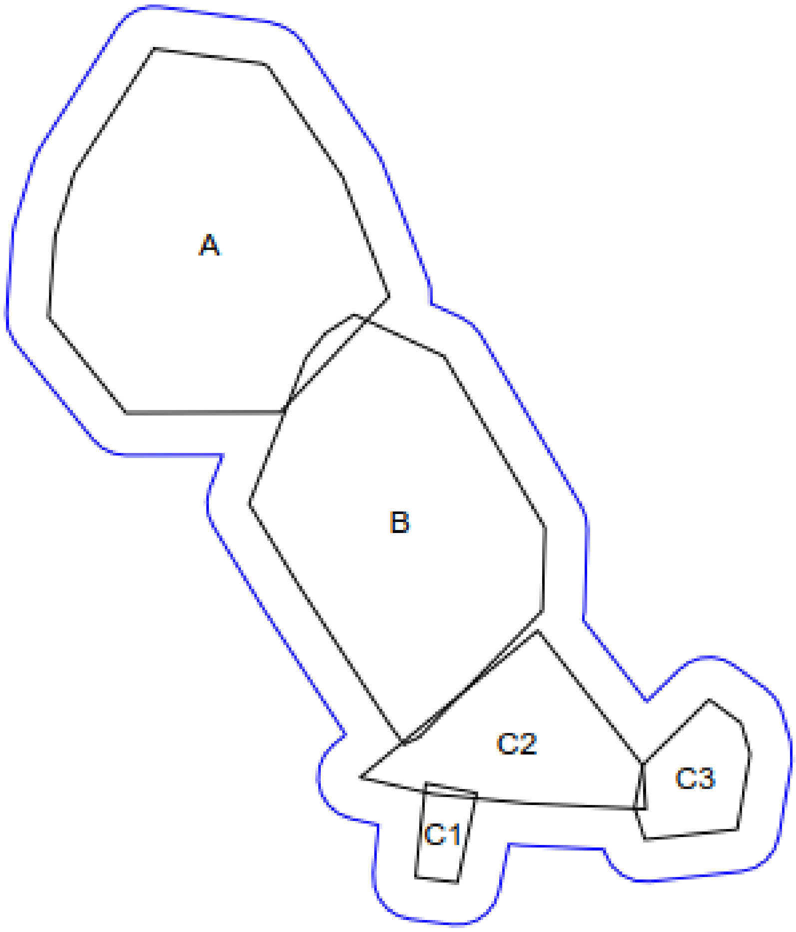

Figure C.1 Construction of combined study area.
A is the convex hull for the Kitasoo/Xai'xais project area, B for the Heiltsuk project, and C1, C2, C3 combined for the Wuikinuxv project, which was described using separate convex hulls given the project area's irregular shape. The outer blue polygon is the combined study area, consisting of all 5 polygons combined, with a 10-km buffer added.

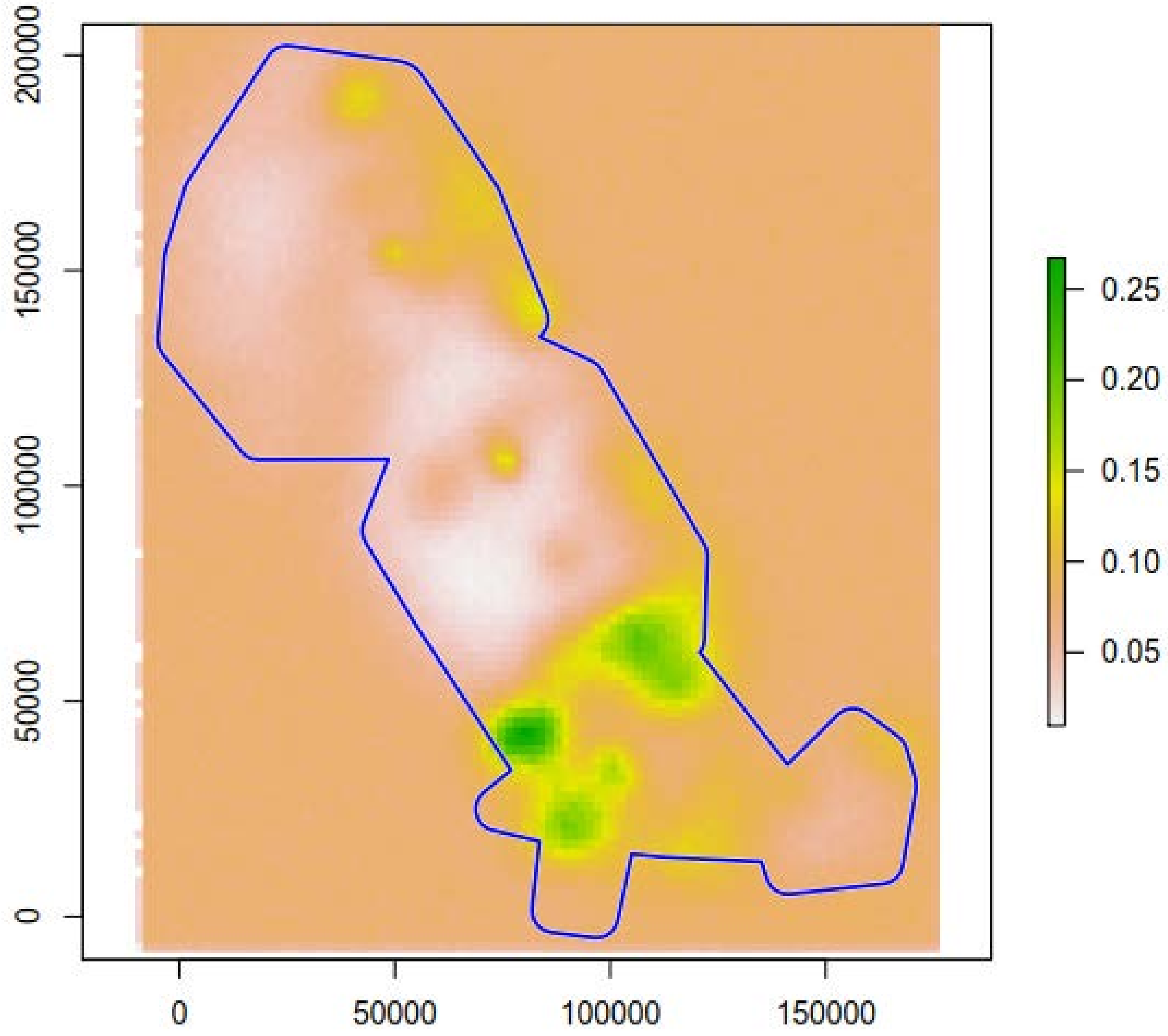

Figure C.2 Density of estimated male activity centres, with increasingly green colours indicating pixels of higher density.

The blue polygon is the study area boundary, a combination of convex hulls surrounding trap arrays, with a 5 km buffer.

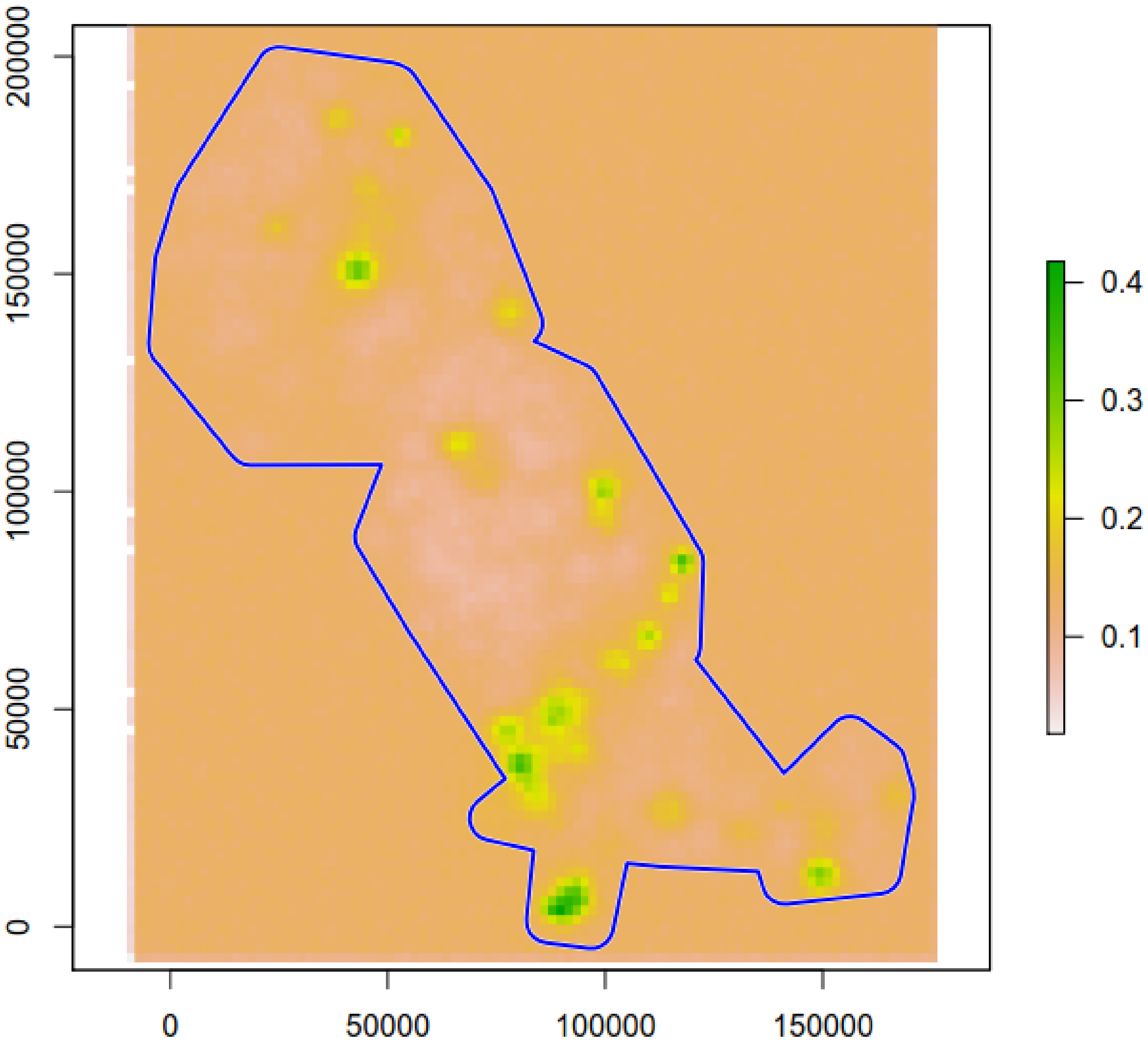

Figure C.3 Density of estimated female activity centres, with increasingly green colours indicating pixels of higher density.

The blue polygon is the study area boundary, a combination of convex hulls surrounding trap arrays, with a 5 km buffer.

EBM polygons

For our analyses we omitted class 1 EBM reserves that overlapped SFMAs, areas newly designated in 2016 that are no longer subject to rotational logging and are therefore not relevant to the EBM calculations herein.

C.2 Supplementary Results

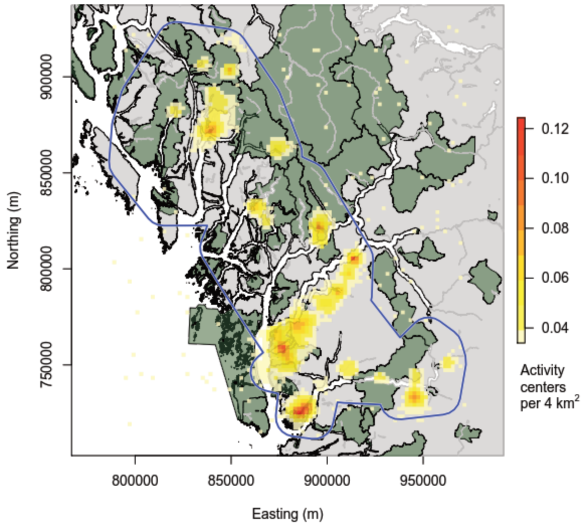

Figure C.4 **Spatial comparison of areas of with high estimated female grizzly bear (*Ursus arctos horribilis*) density from 2014-2016 (*i.e.* probability of occurrence of activity centres estimated from spatial-capture recapture) with current protected areas in the Great Bear Rainforest of British Columbia, Canada.**

Green areas represent protected areas (conservancies; biodiversity, tourism, and mining areas; and special forest management areas). "Hot" (yellow to red) colours indicate areas of relatively high activity centre densities (plotted are pixels with the 90th percentile estimated densities), with densities of estimated grizzly bears reported per 45 km^2. Map is in BC Albers projection.

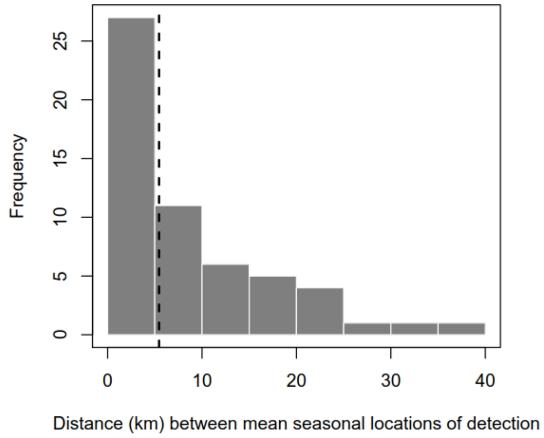

Figure C.5 Distance (in km) between mean seasonal locations of detection for all grizzly bears (*Ursus arctos horribilis*) captured across >1 seasons (spring vs. summer and fall) in the study area between 2009-2016.

Mean seasonal location was the mean of x and y coordinates of all sites of detection for a given individual in a given season across years, and distance was the straight-line distance between seasonal mean locations. Dashed black line indicates the median inter-seasonal distance across individuals.

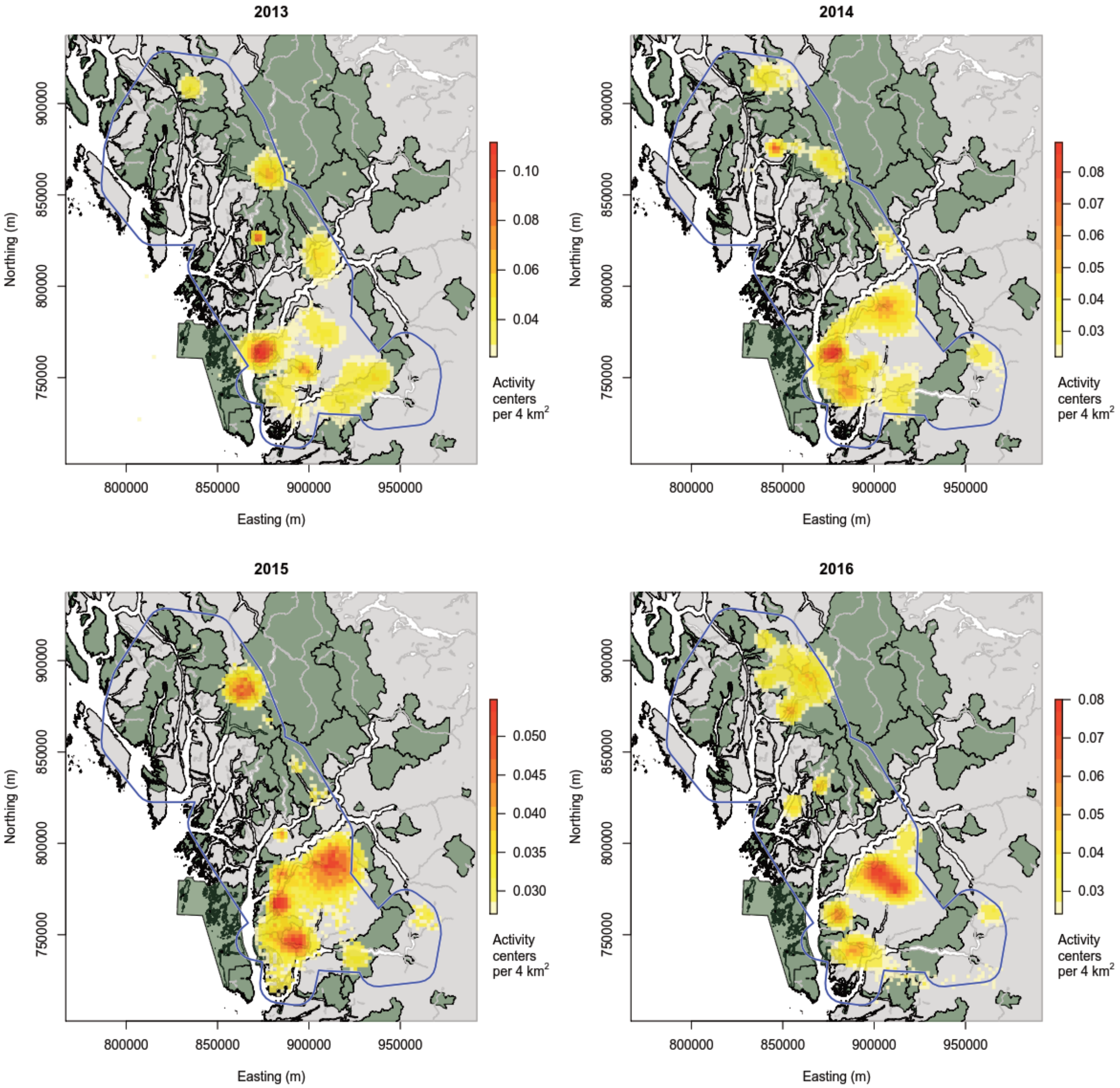

Figure C.6 **Yearly spatial comparison of areas of with high estimated male grizzly bear (*Ursus arctos horribilis*) density (*i.e.* probability of occurrence of activity centres estimated from spatial-capture recapture) with current protected areas in the Great Bear Rainforest of British Columbia, Canada.**
Green areas represent protected areas (conservancies; biodiversity, tourism, and mining areas; and special forest management areas). "Hot" (yellow to red) colours indicate areas of relatively high grizzly bear densities (plotted are pixels with the 90th percentile estimated densities), with densities of estimated activity centres reported per 4 km^2. Maps are in BC Albers projection.

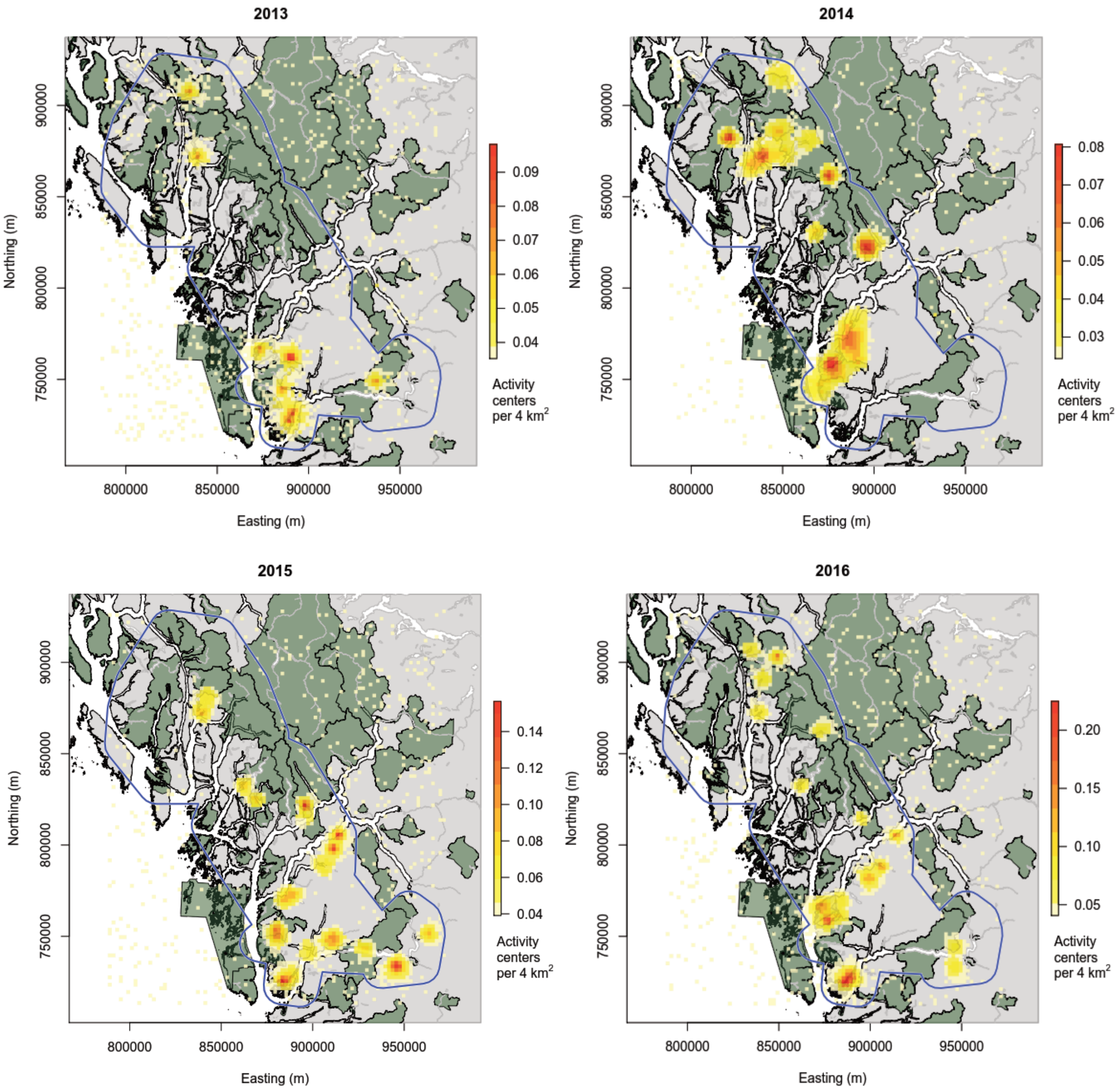

Figure C.7 Yearly spatial comparison of areas of with high estimated female grizzly bear (*Ursus arctos horribilis*) density (*i.e.* probability of occurrence of activity centres estimated from spatial-capture recapture) with current protected areas in the Great Bear Rainforest of British Columbia, Canada. Green areas represent protected areas (conservancies; biodiversity, tourism, and mining areas; and special forest management areas). "Hot" (yellow to red) colours indicate areas of relatively high grizzly bear densities (plotted are pixels with the 90th percentile estimated densities), with densities of estimated activity centres reported per 4 km^2. Maps are in BC Albers projection.

Appendix D.

Supporting information for Chapter 5

Emails to agencies

We sent emails to all agencies with available email addresses (n = 624 of 667 plans; 94%). These emails were sent by our primary scorer on behalf of the lead author (KAA; see 'Template communications with agencies'). In all cases, we requested corrections if applicable, contact information of agency contacts that we had not found, and any publicly-available documents that we had not identified.

These emails served not only to evaluate the quality of our data, but also as a proxy for how responsive agencies are to public inquiry using a common (as evidenced by email addresses being available for most plans) communication channel. As such, they provided another method to assess agency transparency.

Of the 624 cases (management plans) where agency contacts were found and emails sent, we received responses regarding 272 (44% of total; no responses were received for the remaining 56%).

Of the 272 plans with a response, agencies:

- indicated that no changes were needed in 42 (15%),
- indicated they were unwilling or unable to review 48 (18%),
- answered emails but did not provide relevant information on assessments (*e.g.* provided general statements about management without new documents or specific changes to scoring, but did not specifically state they were unwilling to participate) in 130 (48%)
- provided feedback, but only for draft criteria that were not analyzed herein in 2 (0.01%),
- suggested changes in 22 (8%), providing corroborating evidence for most individual scorings, leading us to revise 24 among them (average of 1.1 criteria per plan), though revisions were not made for changes to 12 individual scorings that were provided without any corroborating evidence (average of 0.5 criteria per plan), 4 that were corroborated only by internal, not publicly-available documents (average of 0.2 criteria per plan), and 2 whose submitted evidence did not support the suggested

change (average of 0.1 criteria per plan). Evaluation of documents provided as part of the response for these 22 plans resulted in additional (unrequested) changes to an additional 13 individual scorings (average of 0.6 per plan; all such scores revised from ‘absent’ to ‘present’, as new documents provided evidence of previously undetected criteria)

- suggested no changes in scorings of analyzed criteria, but provided additional documents that triggered re-evaluation of 28 (10%) plans, resulting in changes to 7 (17 individual scorings among them, or an average of 2.4 criteria per plan; all such scores revised from ‘absent’ to ‘present’, as new documents provided evidence of previously undetected criteria).

Template communications with agencies

Letter requesting management plans

Dear [Agency Representative]

I am writing you today about research we’re doing with the Applied Conservation Science lab at the University of Victoria and the Reynolds Lab at Simon Fraser University. We are collecting information on approaches to wildlife management across North America, with a special focus on hunt management. We have been amassing publicly-available documents that describe management objectives, approaches used for setting hunt quotas, descriptions of population monitoring, and descriptions of how science and other sources of knowledge contribute to decision-making. For each jurisdiction and taxon we have used publicly-available documents to characterize hunt management based on a set of categorical criteria.

We have not been able to find any information about [Species Name] in [Jurisdiction]. If relevant information is available, would you mind please forwarding the relevant documents, and an appropriate link if they are already available on a website? Alternatively, if there is someone else we should ask for these documents, could you please forward their contact information?

It would be very helpful if we could please receive this information, by October 23rd, 2014, which is when we will analyze the data.

Thank you very much for your help.

Yours sincerely,

Kyle Artelle

Letter requesting review of assessments

Dear [agency representative],

I am writing you today about research we're doing with the Applied Conservation Science lab at the University of Victoria and the Reynolds Lab at Simon Fraser University. We are collecting information on approaches to wildlife management across North America, with a special focus on hunt management. We have been amassing publicly-available documents that describe management objectives, approaches used for setting hunt quotas, descriptions of population monitoring, and descriptions of how science and other sources of knowledge contribute to decision-making. For each jurisdiction and taxon we have used publicly-available documents to characterize hunt management based on a set of categorical criteria.

I have attached our categorization of [Species Name] management in [Jurisdiction], with reference to the publicly-available documents used in our assessments. We were wondering if you could please let us know if there are any errors in how we have categorized this management. If there are documents that describe management differently than we have categorized here, could you please reference the relevant sections and documents so we can re-assess the information?

Alternatively, if there is someone else we should ask for these documents, could you please forward their contact information?

It would be very helpful if we could receive this information, by October 23rd, 2014, please, which is when we will analyze the data.

Thank you very much for your help.

Yours sincerely,

Kyle Artelle

Hallmarks of science-based anagement: Expanded descriptions

Measurable objectives

Setting measurable objectives guides management, ensuring approaches are consistent with reaching pre-determined outcomes for wildlife populations being managed (Platt 1964, Sullivan et al. 2006, Conservation Measures Partnership 2013). Clear objectives provide concrete baselines against which to assess efficacy (Kleiman et al. 2000, Riley et al. 2003): ecological data are particularly useful if they inform an underlying objective (Mangel 2011), or, in research, a hypothesis (Platt 1964). We focused on objectives for the wildlife populations being managed, not social objectives such as increasing hunter participation or maintaining public support for wildlife management.

Criterion evaluated

Provide measurable objectives: Are measurable objectives provided in the plan (*e.g.* limiting probability of extinction below a threshold, maintaining desired population sizes and sex ratios)?

Evidence

Considering and applying scientific evidence can help to support well-informed decision-making (Meffe et al. 1998, Dicks et al. 2014, Walsh 2015, Walsh et al. 2015). The importance of incorporating scientific information and other forms of evidence into conservation practice is now broadly recognised (Sutherland et al. 2004, Legge 2015). Moreover, effective wildlife management requires baselines to evaluate success in meeting objectives: knowledge on how many individuals comprise populations, population status and trends, and the impacts of human-caused mortality are fundamental to managing hunted populations effectively (Meffe et al. 1998, Doremus 2007). Seeking external evidence, whether from publications, or through collaboration with scientists (*e.g.* academic researchers), can also improve the use of scientific evidence in management decisions (Sutherland et al. 2004, Keene and Pullin 2011). Finally, careful consideration and communication of the uncertainty inherent to most scientific evidence is necessary to safeguard against errors arising from the precision, quality, or limitations of the data (Reckhow 1994, Sutinen et al. 2004, Regan et al. 2005, Ruhl and Salzman 2006, Sullivan et al. 2006, Doremus 2007, Artelle et al. 2013).

Criteria evaluated

Report quantitative information about populations: Is quantitative information provided for the managed populations (*e.g.* densities, trends)?
Report uncertainty in population parameter estimates: Are estimated population parameters reported with confidence intervals or as ranges?
Estimate realized hunting rates: Is the total hunting mortality in the population measured and reported?
Cite external evidence: Are scientific studies or other data sources (*e.g.* peer-reviewed articles, grey literature) cited within documents, or listed within a reference list?
Collaborate with external scientists: Is there mention of collaboration with scientists (*e.g.* academic researchers)?

Transparency

Describing all evidence, methods, assumptions, and prior knowledge in a replicable and cogent fashion allows external verification of the reliability, credibility, and relevance of approaches used (Jasanoff 2006). Ensuring this information (and access to agencies) is available and interpretable to the public might similarly be expected for resource management that is publicly funded (Treves et al. 2015). Similarly, transparency of decision-making might shed light on the necessary involvement of factors other than science (Ruhl and Salzman 2006, Sullivan et al. 2006, Adams and Sandbrook 2013). Beyond good governance, such transparency might also lead to better management outcomes (Mora et al. 2009).

Criteria evaluated

Explain technique for setting hunting quotas: Is there a description of the approach used to set quotas?
Explain how population parameters are estimated: Is the technique used to estimate population parameters (*e.g.* abundance, density, trend) specified (*e.g.* aerial surveys/genetic tagging/ expert opinion/camera trapping)?
Explain how realized hunting rates are estimated: Is there an explanation of how hunting rates are measured (*e.g.* hunter survey/mandatory reporting/check-in stations/hunting tags)?
Provide publicly-available management information: Is the species management plan (or similar wildlife management documents) publicly available?

Respond to public inquiry: Did the management agency respond to our emails asking for verification of scorings and/or further information?

Independent review

Reviews allow approaches to be assessed for potential shortcomings, errors, and general rigor, as well as to ensure that approaches are defensible, transparent, appropriate for achieving goals, informed by relevant evidence, and that evidence presented supports conclusions reached (Meffe et al. 1998, Horwitz and Calver 1998, Mangel 2011, Sullivan et al. 2006, Conservation Measures Partnership 2013). Independent (external) review might better ensure impartiality in the assessment (Doremus 2007).

Criteria evaluated

Subject management plans to any review: Does the plan mention being subjected to any form of review?
Subject management plans to external review: If the plan was reviewed, were reviewers external (*e.g.* from the public, an outside organization, or a university)?

Non-exhaustive indicators

The criteria we examined were not exhaustive, but might instead be considered indicators of identified hallmarks. For example, although beyond our scope, assessing whether management objectives are being met, with appropriate responses planned for when they are not, might be an important component for achieving *measurable objectives* (Conservation Measures Partnership 2013). Moreover, a clear accounting of how decisions flow logically from evidence to management prescriptions would be an important component of *transparency*, and assessments of the *quality* of *evidence* being used might be important for conveying the level of risk involved with a given management prescription (Chapron and Treves 2016).

Supplementary Figures and Tables

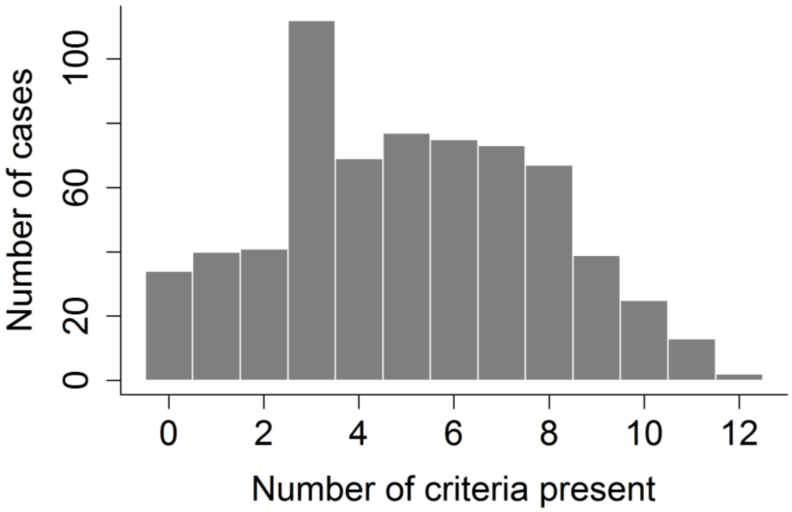

Figure D.1 Number of criteria (out of possible 13) present in wildlife management plans across Canadian provinces/territories and US states (N = 667)

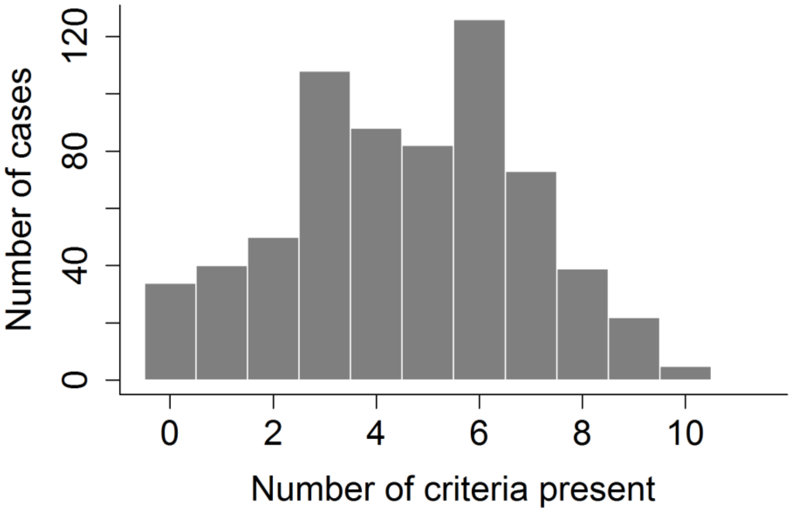

Figure D.2 Number of criteria criteria (out of possible 11), excluding desirable, but non-required present in wildlife management plans across Canadian provinces/territories and US states (N = 667)

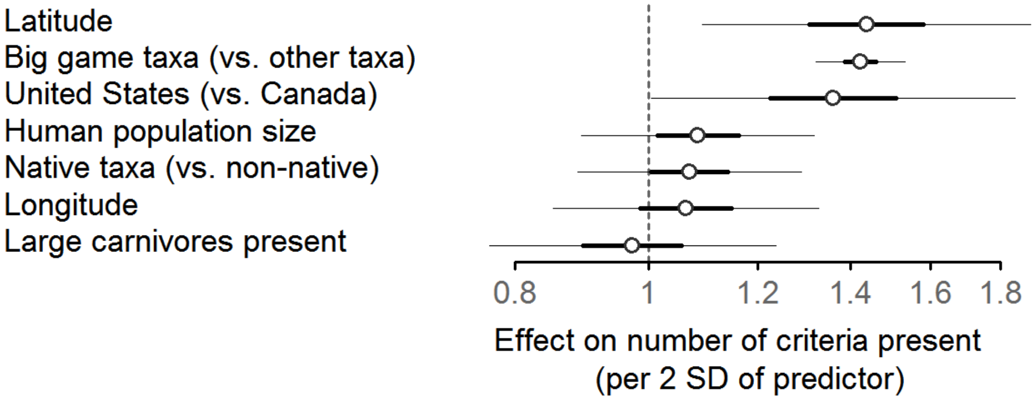

Figure D.3 **Effect of management characteristics on number of criteria present (out of 13, including the independent review hallmark criteria as responses [c.f. Figure 5.1B]) across plans.**

Coefficients shown are odds ratios from a multi-level model, with thick and thin bars representing 50% and 95% confidence intervals, respectively, and plotted on a log scale

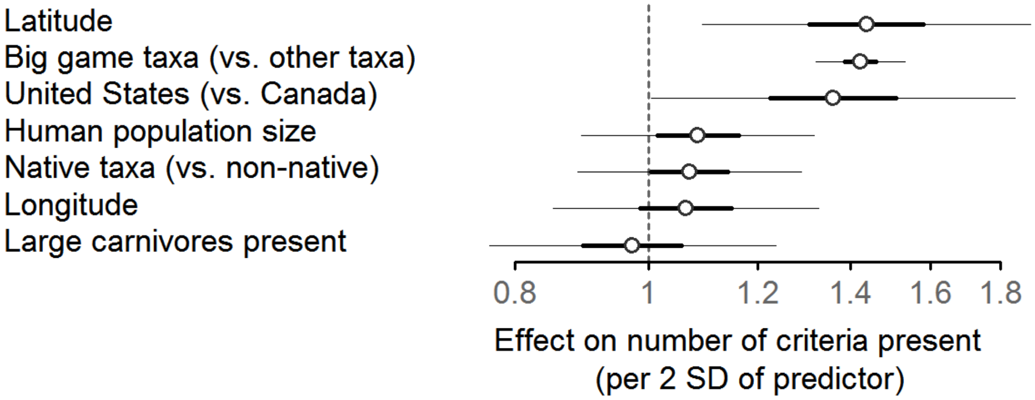

Figure D.4 **Effect of management characteristics on number of required criteria present (out of 13, including the independent review hallmark criteria as responses [c.f. Figure 5.1B]) across plans.**

Coefficients shown are odds ratios from a multi-level model, with thick and thin bars representing 50% and 95% confidence intervals, respectively, and plotted on a log scale

Table D.1 **Inter-observer agreement between initial scorings (by MVR) and rescores (by KAA and KF), calculated as the percentage of rescores that matched initial scorings**

Hallmark	Criterion	Inter-Observer Agreement (%)
Measurable objectives	Provide measurable objectives	86
Evidence	Estimate realized hunting rates	93
	Report quantitative information about populations	88
	Cite external evidence	84
	Collaborate with external scientists	84
	Measure uncertainty in population parameter estimates	86
Transparency	Provide publicly-available management information	96
	Explain how realized hunting rates are estimated	80
	Explain how population parameters are estimated	75
	Explain technique for setting quotas	88
Independent review	Subject management plans to any review	89
	Subject management plans to external review	96
		Mean: 87%

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Appendix E.

When Science-based Management Isn't[5]

In December 2013, the provincial government of British Columbia, Canada, approved the expansion of a controversial trophy hunt of at-risk grizzly bears. This decision raises doubts about the rigor of wildlife management and government policy in the region. Similar concerns have been raised in the United Kingdom (1) and the United States ("Science behind plan to ease wolf protection is flawed, panel says." V. Morell, News & Analysis, 14 February, p. 719).

We recently found that between 2001 and 2011, in half of all hunted populations, human-caused death of grizzlies exceeded mortality rates deemed sustainable by government biologists. In addition, failure to properly account for uncertainty in estimates of population sizes, poaching rates, and population growth parameters meant that hunting targets might have been too high (2). Surprisingly, despite the ensuing media attention, the government reopened hunting in previously overhunted populations, stating, "[b]ecause we recognize inherent uncertainty in our population and harvest rate estimates, conservative mortality targets are used" (3). Although the government's justification borrowed our recent study's language about uncertainty, their decision ran counter to its conclusions. Moreover, the government came under fire during debate in the provincial legislature (4, 5) for claiming in a press release that another recent study (6) confirmed management sustainability, when in fact the paper made no such claims.

Such outcomes reflect a wider problem that often arises when scientific evidence exposes flaws in preferred government policies. Governments can make "science-based" claims without being held to the same standard of transparency and scrutiny expected from scientific researchers. Similar shortcomings were recognized in the proposed delisting of gray wolves from the U.S. Endangered Species Act (Morell's News & Analysis) and badger culling in Great Britain for disease control (1). Given the substantial economic and ecological costs of management failure, it is alarming that purported scientific management often proceeds without the hallmarks of science—transparency, intelligibility, and rigorous evidence.

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[5] A version of this appendix appears as K.A. Artelle, J.D. Reynolds, P.C. Paquet, and C.T. Darimont. 2014. When Science-Based Management Isn't. *Science.* 343(6177):1311–1311.

We propose that wildlife managers be held to the same level of scrutiny as research scientists through independent oversight similar to the peer-review process. This would incorporate science into management, ensure that the best available evidence is used in management decisions, and improve accountability to the public for whom wildlife are ostensibly managed.

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3. S. MacDonald, “Province proposes grizzly hunting around Kimberley, Fernie, Sparwood and Elkford,” Free Press (26 December 2013); www.thefreepress.ca/news/237171991html.
4. 2014 Legislative Session: Second Session, 40th Parliament, Committee A Blues (6 March 2014); www.leg.bc.ca/hansard/40th2nd/20140306pm-CommitteeA-Blues.htm.
5. 2014 Legislative Session: Second Session, 40th Parliament, Committee A Blues (10 March 2014); www.leg.bc.ca/hansard/40th2nd/20140310pm-CommitteeA-Blues.htm.
6. G. Mowat et al., PLOS ONE 8, e82757 (2013).

Appendix F.

Supplementary Files

Video A.1

Description:

This video is supplementary to Chapter 2. It animates how we used simulations to estimate overmortality probability based on biological uncertainty.

Filename: Mortality limit uncertainty calculations.zip

Video A.2

Description:

This video is supplementary to Chapter 2. It animates how we set targets that incorporate outcome and biological uncertainty while keeping probability of overmortality below a pre-determine threshold.

Filename: Identifying targets that incorporate outcome and mortality limit uncertainty.zip

File D.1

Description:

This spreadsheet is a supplement to Chapter 5. It contains the scorings for indicator criteria across all hunt management plans and references to the corroborating evidence supporting each scoring.

Filename: NA scorings database.xlsx