Applying predation risk theory to wildlife behaviour during non-consumptive ecotourism in Tweedsmuir Provincial Park, Nuxalk Territory: insights into risk, foraging, and conflict dynamics

by

Kate Alexandra Field
B.Sc., University of Victoria, 2016
M.Sc., University of Victoria, 2019

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Abstract

Managing to minimize human disturbance of wildlife populations and the individuals that comprise them can draw on theory and data related to non-consumptive effects of risk on wildlife. Predation risk theory is a behavioural-ecological framework that describes how the risk of predation influences the behaviour, physiology, and spatial distribution of prey. Interconnected with predation risk theory is a linkage to foraging behaviour. The asset protection principle (APP) predicts that variable food supply and its associated risks will affect antipredator behaviour; responses to predation risk should dominate when food reserves are high, whereas nutritional risk becomes more important when food reserves are limited. Additionally, the human shield hypothesis (HSH) describes how some individuals might seek human presence if it repels other and presumably more dangerous potential sources of risk. Owing to these contexts and more, tolerance of human-caused disturbance stimuli can vary among animals, often mediated by how individuals and demographic sub-groups perceive risk. My research applied these frameworks to community-driven research questions related to the potential effects of ecotourism on several dimensions of grizzly bear (*Ursus arctos horribilis*) behaviour in a protected area in Nuxalk Territory, British Columbia, Canada.

In my first data chapter (Chapter 2), we tested components of the APP and HSH where ecotourism co-occurs with grizzly bear foraging during hyperphagia. We used generalized linear mixed effects and multinomial regression models to understand how weekly detection rates (measured by camera traps) varied with food abundance (salmon and berries), ecotourist visitors, time of day, and age-sex class. When salmon abundance was high, bear activity (weekly detections) decreased by 13% with every 100 visitors/week. Under low salmon conditions, we observed the opposite pattern; bear activity increased with visitor numbers, creating 'high bear-high visitor' conditions. Consistent with HSH, detection data revealed an increased likelihood of detecting subordinate age-sex classes compared with adult males when visitor numbers were high. Our findings suggest that when salmon are low, managers might consider limiting visitors to mitigate disturbance. More broadly, understanding how wildlife allocate anti-predator behaviour as a function of risk and food can inform conservation science and practice.

In my second data chapter (Chapter 3), we approached the potential influence of ecotourism using different approaches, tools, and spatial scales. Specifically, we assessed whether and how a grizzly bear population might show among- and across-individual variation in tolerance to ecotourism activity using both spatial and behavioural lenses. Despite the high mobility of grizzlies and access to regionally-abundant salmon resources at ecotour sites, our genetic tagging approach revealed that only a small subset of individuals detected at least twice (n = 11 of 80) showed spatial detection histories that favoured areas of pronounced human activity. Most of these individuals (n = 9 of 11) were female, providing additional support for the human shield hypothesis. Our companion behavioural observations at ecotourism sites considered how ecotourism intensity (number of visitors, number of boats) and environmental variables (presence of other bears, salmon biomass) might affect fishing and alertness behaviour. Our findings revealed no evidence for an effect of measured ecotour metrics on grizzly behaviour. Instead, we found a negative association between salmon biomass and alertness, a pattern opposite to predictions based on predation risk theory. We speculate that reduced alertness at higher salmon densities related to (mostly female) bears, shielded from dangerous male bears, focusing their attention on hyperphagic behaviour during high salmon periods to maximize fitness gains related to reproductive potential. Collectively, our multi-lens approach illustrates how comprehensive insight into wildlife tolerance of human activity can emerge.

Finally, in my last data chapter (Chapter 4) we asked whether ecotour bears, which show tolerance to human activity, can lead to tolerating other presumably risky scenarios that lead to human-wildlife conflict in communities downstream of ecotourism sites. We screened for genetic matches between individuals that encountered conflict (n = 30) and 118 individuals detected upstream via hair snags (including 34 at ecotour sites). Of these 34, one encountered conflict. In analysis scenario 1, we considered all detected and undetected bears in the region as freely mixing, and used Bayes' theorem to account for imperfect detection of ecotour bears among conflict samples, deriving an estimate of 1.47 (rounded to 2). Accounting for this uncertainty, we used a probability approach to ask how large the unknown non-ecotour bear population would have to be to observe this frequency of conflict among ecotour bears (2/34) by chance. The resulting population level exceeded available estimates, suggesting ecotour bears are less likely to encounter conflict. In scenario 2, we assumed that downstream bears are not necessarily from the same population as those sampled upstream, and compared the proportions of known ecotour

and non-ecotour bears among conflict samples. We found no evidence of a significant difference. Collectively, these analyses suggest that tolerance to ecotourism did not predispose ecotourism bears to engage in risky scenarios, suggesting other human-caused drivers of conflict.

In general, my dissertation research contributes to our understanding of the contexts in which non-lethal human disturbance stimuli can affect wildlife behaviour. Specifically, I highlight that neglecting context-dependent decision-making, such as resource availability, limits the practical utility of measuring non-consumptive risk effects. I also highlight how this work can support local, system-specific management decisions related to ecotour management.

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Co-Authorship Statement

Chapters 2 through 4 of this dissertation were co-authored. The following outlines my contributions, and that of each of the authors. I also provide the publication status of each chapter.

Chapter 2

Field, K. A., Short, M. L., Moody, J. E., Artelle, K. A., Bourbonnais, M. L., Paquet, P. C., & Darimont, C. T. (2024). Influence of ecotourism on grizzly bear activity depends on salmon abundance in the Atnarko River corridor, Nuxalk Territory. *Conservation science and practice*, *6*(4), e13097.

K. A. F., C. T. D., J. E. M., and P. C. P. contributed to the inception and design of the study. Data collection and field program management and coordination was undertaken by K. A. F. and J. E. M. Data analysis was performed by K. A. F. with guidance in design, data preparation, analyses and/or visualization from C. T. D., M. L. S., K. A. A., and M. L. B. All authors were involved in drafting the manuscript or revising it critically.

Chapter 3

Co-authorship of this chapter for peer-review was still evolving at the time this dissertation was submitted. The current draft was written by Kate Field and Chris Darimont, with insights from Melanie Clapham, Douglas Clark, Persia Khan, Don Kramer, Taal Levi, and Paul Paquet.

Intrapopulation variation in space-use and behavioural states in a grizzly bear-ecotourism system: a multi-dimensional approach reveals spatial filtering of tolerance (*In preparation*)

Chapter 4

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KAF, JEM, CTD: conceptualization; KAF, TL, CTD: formal analysis; KAF, JEM, CTD: investigation; KAF, JEM, TL, CTD: methodology; KAF, JEM, CTD: project administration; JEM, CTD: resources; JEM, CTD: supervision; KAF, TL, CTD: validation; KAF, CTD: writing—original draft; KAF, JEM, TL, CTD; writing—review and editing.

Chapter 1. Introduction

Risk associated with human activity is now common for wildlife. Accurate assessment and response to risk is necessary for reproduction and survival (Brown, 1988; Lima, 1998; Lima & Dill, 1990). Whereas avoiding human-associated risk may reduce direct mortality, energetic costs of foregoing key foods in risky areas might reduce components of fitness, including reproduction and survival. In considering these apparent trade-offs, emerging evidence suggests that human-mediated risk can lead to persistent spatial or temporal avoidance behaviour at the individual and population level (Carter et al., 2012; Gaynor et al., 2019; Polfus et al., 2011; Tuomainen & Candolin, 2011). Risk avoidance is also likely mediated by sex and age classes (Nevin & Gilbert, 2005). Additionally, case studies show that animals may forage in risky habitats if human activities create opportunities for accessing rewarding foods (Lamb et al., 2017; Sitati et al., 2003), or if foods are constrained to, or concentrated in, human-disturbed areas (Gill et al., 2001). More detailed understanding might emerge by engaging multiple interconnected theories in systems in which risk varies, key foods occur in risky areas, and associated wildlife behaviour can be measured.

The human shield hypothesis, predation risk theory, asset protection principle, and wildlife tolerance are interconnected frameworks that can collectively describe how animals navigate risks and benefits in their environments. The human shield hypothesis (Berger, 2007) posits that prey animals may use humans as a buffer to reduce predation risk, aligning with the broader concepts of predation risk theory (Brown, 1988; Lima, 1998; Lima & Dill, 1990), which explains how animals balance the trade-off between foraging and avoiding predators. This balance often involves decisions that align with the asset protection principle (Clark, 1994), where animals with greater assets (e.g., offspring, access to resources) prioritize risk-averse behaviours to optimize fitness. Finally, shaped by the processes involved above and more, tolerance of human-caused disturbance stimuli can vary among animals, often mediated by how individuals perceive risk. On one hand, tolerating benign stimuli while maintaining the ability to respond to novel or risky stimuli can promote fitness by filtering out irrelevant stimuli and focusing selectively on important stimuli (Rankin et al., 2009). On the other hand, tolerance may lead wildlife to ecological traps, whereby individuals that develop a tolerance for benign human activity may be more vulnerable to lethal human activity (Darimont & Shukla, 2023; Geffroy et al., 2015). Collectively, these concepts highlight the complex interplay of processes that shape behavioural adaptation in human-altered ecosystems.

Wildlife management may benefit from an increased understanding of wildlife risk-perception and associated behavioural responses, including in systems influenced by seemingly benign human activity. Disturbance of wildlife by humans has been proposed as analogous to predation risk, whereby predation and non-lethal disturbance stimuli create similar trade-offs between avoiding perceived risk and pursuing behaviours that will enhance fitness (Frid & Dill, 2002). Accordingly, anti-predator behaviour in response to human disturbance can have direct fitness consequences. Commonly, ecotourism creates scenarios in which humans seek to encounter wildlife non-consumptively, yet its myriad influences have been identified across a range of taxa globally (Blumstein et al., 2017). Understanding how wildlife perceive and respond to human activity, particularly within the context of ecotourism, is essential for formulating evidence-based management strategies.

My PhD research questions drew on these bodies of work to examine responses by a culturally, ecologically and economically important wildlife species to non-consumptive human activity in a protected area in British Columbia, Canada. Specifically, I drew on the human shield hypothesis, predation-risk theory, asset protection principle, and tolerance frameworks for examining risk perception of grizzly bears (*Ursus arctos*) exposed to ecotourism along a gradient of spatial and temporal human activity in Tweedsmuir Provincial Park (South), which is located in the unceded Territory of the Nuxalk First Nation. Wildlife ecotourism in the park co-occurs with grizzly bears while in a pre-denning state of hyperphagia, and provides a system in which non-lethal human stimuli and key food (salmon) resources vary over space and time. The park also occurs adjacent to communities in which human-grizzly conflict is frequent. Accordingly, in addition to examining how ecotourism may affect grizzly bear behaviour, locally-driven interest led me to examine whether ecotourism affected the likelihood grizzly bears subsequently encountered conflict with humans in downstream human communities.

One central approach to this work was its community-driven nature. This project was a collaborative partnership among Indigenous, Provincial and academic teams. Managers from British Columbia Parks and the Nuxalk Nation solicited the study to inform their ecotourism management policy. Recognizing that grizzly bears are among the most popular species for ecotourism in North America and Europe (Fortin et al., 2016; Penteriani et al., 2017), managers sought evidence-based recommendations towards the effectiveness of their current bear viewing program. Indeed, long-term conservation outcomes can be signalled early by subtle behavioural changes that, if detected, provide managers with an opportunity to intervene. Accordingly, my work aimed to provide system-specific information for local management consideration, while also providing wider conceptual contributions to academic discourse.

Each chapter of my dissertation drew on diverse methods in wildlife behavioural ecology to answer research questions that examined different scales and processes. In Chapter 2, we drew on the asset protection principle and human shield hypothesis to examine variation in detection rates of grizzly bears as measured by camera traps. We asked how grizzly bear spatial–temporal activity varied and interacted across human and environmental contexts, as well as by age-sex classes. In Chapter 3, we drew on predation risk theory, human shield hypotheses, and tolerance frameworks to examine variation in behavioural states as measured by direct behavioural observation of grizzly bears, as well as space-use of genetically identified individuals within and beyond the ecotourism area. This multidimensional approach to examining wildlife tolerance that drew on more than modality of behaviour (space-use and behavioural states) asked whether there was intrapopulation (across- and among-individual) variation in spatial and behavioural tolerance. In Chapter 4, we used a probability approach to ask whether genetically identified grizzly bears that were exposed to ecotourism were more or less likely than predicted by chance to encounter subsequent conflict. Here, we screened for genetic matches between grizzly bears that were exposed to ecotourism and grizzly bears that encountered human conflict. Collectively, these approaches afforded diverse vantage points from which to examine drivers in variation of wildlife behaviour in a grizzly bear-ecotourism system.

Chapter 2. Influence of ecotourism on grizzly bear activity depends on salmon abundance in the Atnarko River corridor, Nuxalk Territory

Adapted from: Field, K. A., Short, M. L., Moody, J. E., Artelle, K. A., Bourbonnais, M. L., Paquet, P. C., & Darimont, C. T. (2024). Influence of ecotourism on grizzly bear activity depends on salmon abundance in the Atnarko River corridor, Nuxalk Territory. *Conservation Science and Practice*, *6*(4). https://doi.org/10.1111/csp2.13097

2.1 Introduction

Research approaches that incorporate animal behaviour (Berger-Tal et al., 2011; Blumstein & Fernández-Juricic, 2004) can lead to a better understanding of non-consumptive human-wildlife interactions that can support evidence-based management. Wildlife ecotourism - an industry built on purpose-driven human-wildlife encounters - continues to grow rapidly as demand by ecotourists increases (Balmford et al., 2015). Evidence for social merits of wildlife ecotourism is clear. Whereas the effects on species targeted for ecotourism vary (Penteriani et al., 2017), behavioural data can inform policy that seeks to reduce and minimize potential impacts. For example, ecotourism policies informed by behavioural research reduced rhinoceros (*Diceros bicornis*) displacement by 80% while maintaining 95% positive feedback from guests (Muntifering et al., 2019). Such evidence-informed outcomes rely in part upon a relevant theoretical background and data. Here we draw on a body of theory that identifies how wildlife can respond to human-caused disturbance in a similar way to how prey respond to predation risk.

The Asset Protection Principle (Clark, 1994) considers the reproductive asset (i.e., expected future lifetime reproduction) of organisms that forage under the risk of predation. Exposure to predation can subject the whole asset to risk (via mortality); on the other hand, accepting the risk (and benefiting from the available food resources) can preserve or enhance the asset. A central prediction is that foragers with lower energy reserves will accept greater predation risk than foragers that have adequate energy reserves. In this context, periods of low foraging success may drive an animal to temporarily use risky habitats that would normally be avoided (Clark, 1994). This scenario suggests a counterintuitive pattern whereby prey can be more active in risky environments, which does not match an optimality model (see Stephens & Krebs, 1986, Stephens et al., 2007). This paradox can be confronted, however, by considering context-dependent decision-making by animals (Beale, 2007), including those related to food resources, prey traits, and characteristics of the predator.

Food resources can be spatially and/or temporally constrained to risky environments, thereby potentially influencing the allocation of behaviours in the context of reproductive asset protection. Specifically, where and when resource waves (Armstrong et al., 2016) co-occur with risk, costs of predator avoidance are particularly acute if alternative access to resources are limited. In such a context, the net benefits of shifting habitats might not outweigh the costs of remaining at disturbed sites; on the other hand, if resources are also available in areas with lower risk, the decision of moving to other patches may be optimal (Gill et al., 2001). For example, Beale and Monaghan (2004) found that the distance at which turnstone (*Arenaria interpres*) took flight in response to human presence was greater for birds provided with supplementary food than for control birds, demonstrating that the provisioned birds were more able to respond earlier compared with birds with limited food resources.

In addition to the distribution of foods, traits of prey comprise another dimension that may interact with asset protection and associated responses to risk while foraging. For example, species vary in their foraging specialization. Whereas generalists can shift among foods to avoid risky areas or times associated with specific resources (e.g., Christianson & Creel, 2006), specialized feeders have less opportunity to employ a similar response (Creel & Ruess, 2011), potentially compounding the trade-offs between reproductive asset protection (avoiding risk) or enhancement (accepting risks associated with foraging). For example, Jones and Rydell (1994) found that specialist bat (*Chiroptera*) species emerged early to forage during peaks in activity of their dipteran prey, thereby exposing themselves to increased risk of predation by avian predators. By contrast, generalist bat species adapted to feed on moths (*Lepidoptera*), flightless prey, or plants, emerged to forage later in the diel period, thus minimizing risk (Jones & Rydell 1994).

Finally, how prey balance asset protection and risk exposure trade-offs may also vary with characteristics of predators. For example, the 'dynamic landscape of fear' body of theory suggests that the predictability of predator activity in space, time, or both will influence the dynamics of prey responses (Palmer et al., 2022). If predation is predictable in space and time, the allocation of anti-predator response can be matched accordingly, thereby minimizing risk effects on prey. For example, the sensitivity of Yellowstone elk (*Cervus elaphus*) to spatially and temporally predictable risk from wolves (*Canis lupus*) resulted in negligible net effects on body condition and pregnancy rates (Kohl et al., 2018). On the other hand, such behavioural responses can bear costs with enduring effects, including reduced foraging time and neurobiological effects (Brown & Kotler, 2004; Zanette & Clinchy, 2020), which can exert non-consumptive effects on prey survival. As another example, although humans clearly induce antipredator responses (Frid

& Dill, 2002), their generally diurnal activity patterns and fidelity to their own built environments might be particularly predictable in time and space compared with other risks. Prey, however, evidently respond to such human-associated risk. Recent meta-analyzes have revealed how wildlife have shifted temporal patterns to avoid largely diurnal activity of humans (Gaynor et al., 2019) as well as spatial patterns to avoid human features of the landscape in which human activity is concentrated (Tucker et al., 2018).

At the intersection of prey and predator characteristics is the human shield hypothesis. When prey consider some predators riskier than humans, they can seek human activity in contexts in which the riskier predator is less likely to be present. In this way, humans can provide ‘shields’ that protect prey (Berger, 2007). Support for this hypothesis has been demonstrated in a range of predator-prey interactions (Atickem et al 2014), including moose (*Alces alces*) and grizzly bears (*Ursus arctos*; Berger 2007), elk (*Cervus elaphus*) and wolves (*Canis lupus*; Hebblewhite et al., 2005), and roe deer (*Capreolus capreolus*) and lynx (*Lynx lynx*; Basille et al., 2009). The process can also act within species. For example, Steyaert et al. (2016) found that humans acted as ‘shields’ for female grizzly bears against sexually selected infanticide by males; mothers that successfully reared cubs strongly selected for areas near human habitation and unsuccessful mothers avoided such areas, suggesting the use of human shields can increase offspring survival. This process was similarly suggested when humans temporally displaced adult males at important foraging locations, creating a temporal refuge for females with cubs (Nevin & Gilbert, 2005).

Here we test hypotheses related to the Asset Protection Principle and Human Shield Hypotheses in a system comprising grizzly bear-ecotourism interactions along the Atnarko river in the unceded territory of the Nuxalk First Nation. Insight regarding ecotourism-associated effects on individual- and population-level fitness in other systems vary from positive to negative (Penteriani et al., 2017). For example, bears constrained to foraging opportunities close to viewing sites may increase vigilance behaviour and divert time away from fitness-enhancing behaviours. Nevin and Gilbert (2005), however, suggested positive population-level effects of viewing, whereby temporal avoidance of human activity by males created a temporal refuge for subordinate age/sex classes that might have increased their survival. Wildlife ecotourism on the Atnarko river co-occurs with grizzly bear pre-denning, and provides a system in which non-lethal human stimuli occurs in predictable ways over space and time. Each year, wildlife ecotourism occurs in the same places and weeks, with varied numbers of humans and methods for viewing (see Methods), providing a relatively predictable pattern of human activity for bears, especially pronounced in certain times (daylight, during peak visitor periods) and places (ecotourism sites). The Atnarko river provides bears access to aggregations of spawning salmon (*Oncorhynchus* spp.) during hyperphagia—a critical period to amass large amounts of energy before denning. Foraging is directly and strongly related to reproductive asset enhancement; pre-denning fat reserves from salmon and other meats are positively correlated with over-winter survival and reproduction in the following year (Hilderbrand et al., 2000). Grizzly bears with access to salmon have higher population density, body size and litter size (Hilderbrand et al., 1999). Accordingly, salmon acquisition strongly links to reproductive asset in the context of APP.

Guided by APP and HSH theory outlined above, our hypotheses consider grizzlies as ‘prey’ and humans as ‘predators,’ in the context of non-consumptive risk effects that humans can impose on wildlife, as others have done in ecotourism scenarios (Frid & Dill, 2002). Specifically, we focus on a key prediction from Clark (1994): foragers with lower energy reserves will accept greater predation risk than foragers having adequate energy reserves. In this context, we interpret predation risk as analogous to nonlethal disturbance stimuli caused by humans (Frid & Dill, 2002). Additionally, given infanticidal and competitive behaviour, we consider adult male grizzlies an additional risk (Steyaert et al., 2013), predicting that other age-sex classes would seek humans as shields to limit exposure (Berger 2007). We predict that males perceive humans as risky because they show much stronger avoidance behaviour than females across a number of studies (Graham et al., 2010; Kite et al., 2016; Nevin & Gilbert, 2005; Steyaert et al., 2016). We also predict that perceived risk by females with young from humans is less than that from males, given data from similar systems in which evidence for human shielding was presented (e.g., Nevin & Gilbert, 2005; Steyaert et al., 2016)

Theory and characteristics of predators, prey and foods in this system allowed us to make several predictions. Generally, we predicted that grizzlies would allocate anti-predator behaviour in times and places with high human activity, as indicated by reducing their own activity. Given their specialization on salmon during the fall (Adams et al., 2017) and aligning with APP predictions, we predicted that allocation to anti-predator behaviour (i.e., avoidance of greater human numbers) would be especially pronounced when spawning salmon were abundant (and thereby widely available beyond the ecotourism area). Finally, we predicted that male bears would avoid human activity, thereby creating shields for females with young, which would be more likely than males to occur in ecotourism areas during daylight when visitors are present. To quantify responses by bears across a spatial gradient and daily activity periods of humans, we used camera traps to measure activity along the river. We reasoned that higher bear activity (weekly detections) related to increased allocation to foraging, whereas decreased activity signalled allocation towards risk avoidance behaviour.

2.2 Methods

2.2.1 Study area

The study occurred in the Atnarko River Corridor (herein 'Atnarko'; Figure 2.1). Located on what is now gazetted by colonial settlers as the central coast of British Columbia, Canada, in Tweedsmuir Provincial Park (9,896 km^2), the Atnarko spans the transition between Coastal Western Hemlock and Interior Douglas Fir biogeoclimatic zones. Grizzly bears congregate each summer and fall (~July-November) on the Atnarko and its tributaries to forage on spawning salmon. Resident spawning salmon species include Chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), sockeye (*O. nerka*) and pink (*O. gorbuscha*).

Human presence and activities in the corridor vary during the spawning season (Appendix A1; Figure A1 and S2), with most forms having the potential to interact with grizzly bear foraging. Visitors to the Atnarko seek commercial and self-guided recreational activities. Examples include angling, paddling, hiking, camping, swimming, picnicking, and several modes of bear viewing. We defined 'spatial treatments' according to where bear viewing occurred: a 'no tour' reference area; a 'land-based tour' area; and a 'land- and boat-based tour' area. These are management-based categories in which specific activities occur or not. Human visitation in the 'no tour' area was mostly limited to backcountry hikers and crews monitoring fish and wildlife via a rough 4x4-only access road. The 'land-based tour' area has some trail access to the river and light but consistent use by professionally-guided ecotours. The 'land- and boat-based tour' area hosted ~2 orders of magnitude more visitors than the 'no tour' area (average weekly visitors to 'land- and boat-based tour' area was 1363 across years, compared with 11 in the 'no-tour' area); it contained a privately regulated platform on the grounds of a commercial ecotourism lodge, and two areas where bear viewing is self-pursued by visitors. One site a purpose-built platform managed by BC Parks and the Nuxalk Nation with an electric fence and a regulated entry and exit system. The second is a BC Parks ‘recreation site’ that is actively used by the public for bear viewing, but was neither managed for bear viewing nor formally designated as such at the time of the study. This latter site also includes a campground and picnic area. Along this ‘land- and boat-based tour’ stretch, up to 11 commercially operated and professionally guided ‘drifts’ (slow-pace rafting-base viewing) were permitted per day between August 15 and October 15. There were currently no limits on the number of boat launches permitted for public recreation (e.g., self-guided boating) at the time of the study.

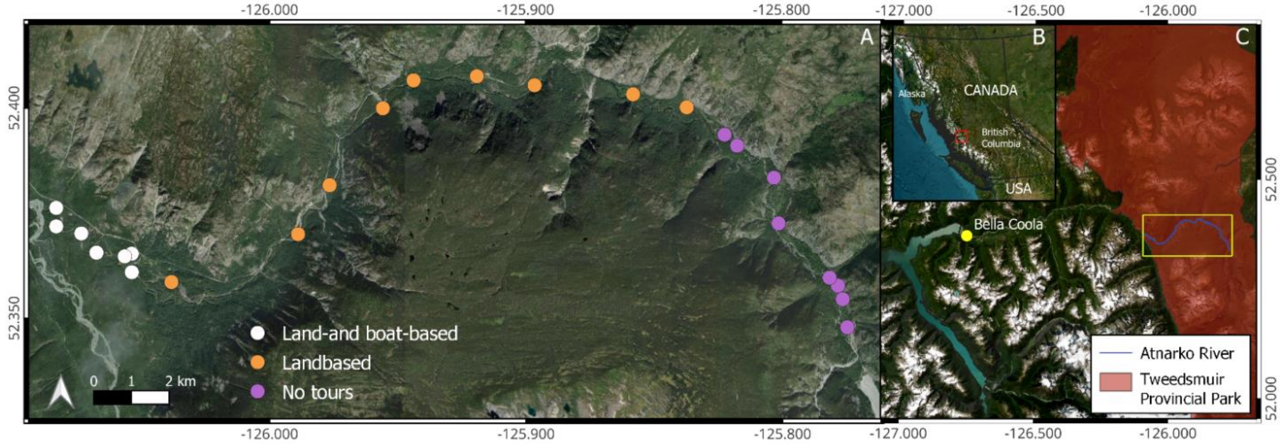

Figure 2.1. Study area: A) Atnarko River Corridor camera trap array by spatial treatment; land- and boat-based tours, land-based tours, and no tours. B) British Columbia, Canada, with red frame denoting panel C; C) Atnarko River and surrounding area, which is located in the unceded Territory of Nuxalk First Nation, with yellow frame denoting panel A.

2.2.2 Camera trap sampling design

We used a camera trap array to estimate weekly patterns of bear activity. We defined our study period as August 15 to October 15 over three years (2019-2021). We deployed cameras along the riverbank and adjacent forest, aiming them at bear trails near key fishing locations, such as pools, log jams, and where spawning substrate occurs, as well as at fishing locations (*i.e.,* in-stream locations). We positioned Browning Strike Force HD PRO (Model: BTC-5HDP) and Browning Strike Force Extreme (Model: BTC-5HDX) cameras every ~0.5-2 km along the river. We set cameras to record two-minute videos when motion-activated, with cameras operating 24 hours a day (see camera trap settings in Appendix A2; Table A1). We checked cameras and downloaded images weekly or bi-weekly, depending on site activity (Wheat & Wilmers, 2016). Cameras were affixed to trees at approximately 1-1.5m height to maximize detection probability of grizzly bears (Meek et al., 2016), with expected area of bear passage within 20 meters.

The camera array consisted of 21, 24, and 24 camera stations in 2019, 2020, and 2021, respectively (Appendix A2, Table A2). Most camera-weeks collected data on all seven days (85%, n = 573 out of 673; Appendix A1, Figure A3), however, some cameras experienced periods of inactivity because of malfunctions and theft. Cameras were active for seven days for more than 80% of camera weeks for each spatial treatment area (Appendix A1; Figures S4, S5, S6). The lead author and research assistants manually scored all video footage initially before data exploration. We determined sex by observing genitals, whether urine was excreted from between the legs (males) or from below the tail (females), or whether it was a family unit (female with young). Subadults were differentiated from adults via relative size and behaviour (Rode, Farley & Robbins, 2006). We omitted unknown bear species (n = 29 of 2,035 total bear detections; 1.4%) from the analysis (e.g., if it was too dark to determine if the detection was a grizzly bear or a black bear, which are much less common in the area in the autumn salmon runs).

2.2.3 Analyses

Our modelling approach tested predictions under APP by measuring bear response to visitors and food resource abundance (i.e., salmon) while accounting for other environmental variables (e.g., water levels). We conducted two analyzes. We first modeled how grizzly bear activity varied as a function of risk, food and environmental variables. This allowed us to confront the Asset Protection Principle. Specifically, this model structure allowed us to test how anti-predator behaviour varied across scenarios of different risk (spatial treatment area, number of visitors) and limitation of a resource that is tightly coupled to reproduction (salmon), while accounting for other environmental variables (water levels, berry ripeness). Additionally, to confront the human shield hypothesis and using detection event data only, we modeled how variation in a key resource (salmon), visitors, and time of day (diurnality) predicted the age-sex class of detections.

Weekly detection models

Because human- and resource-related (i.e., salmon, berries) variables changed throughout the season, we estimated weekly detections (n = 10 weeks in each year). We defined a detection as independent if two images of bears at the same station were separated by 30 minutes (Burton et al., 2015) or if a second detection within 30 minutes was of a noticeably different bear, as identified by colour, size, age, sex, or unique markings (Prop et al., 2020). Females with young were scored as a single detection, because they comprise an age-sex class of interest and single biological unit in analyzes.

We used *a priori* hypotheses to construct a suite of candidate models (Appendix A2; Table A3) and ran generalized linear mixed models using lme4 in R (Bates et al., 2015; R Core Team 2021) using a Poisson distribution, including site and year as random effects. We centred all predictors and scaled (divided by 2 SDs), backtransforming to raw data in figures, so as to most clearly inform managers of patterns. Given management interest in the potential influence of human activity (metrics of which vary in space and time with ecotourism), we developed candidate model sets that incorporated human and environmental metrics. We included salmon biomass in each model, reasoning that detections will always be influenced by salmon abundance, as related to risk-foraging trade-offs. In some models, we included interaction terms between water level and salmon biomass (because if there is a flood event, we would expect decreased accessibility of salmon to bears (Quinn et al., 2017). We also included phenological status of fruit-bearing shrubs in some models, given potential attenuation of grizzly bear-salmon interactions when berries are available (*i.e.,* bears may depart salmon-spawning streams to forage on berries on nearby hillsides) (Deacy et al., 2017). In other models, we included visitors and/or spatial treatment, reasoning that one or both of these measures of human influence may affect detections, as related to risk perception. Finally, we included interaction terms between salmon biomass and human influence metrics in some models, reasoning that bears with lower energy reserves will accept greater risk, as predicted by APP. We compared each model set against null and environmental-only models.

Age and sex class models

Reasoning that detections of different age-sex classes might vary by human and resource-related conditions, we modeled the probability that a detection was a given age-sex class (*i.e.,* female with cubs or yearlings [herein ‘female with young’], sub-adults, adult females, and adult males) as a function of the same variables used for our weekly detection models. We excluded water level, assuming responses to changing levels would vary little among age-sex class. We additionally included, however, a measure of diurnality, reasoning that differences among age-sex classes would vary by diurnal period (Nevin & Gilbert, 2005). We defined this as the number of hours since the average darkest point in the night throughout the study period (Suraci et al., 2019). We defined the darkest point in the night as the midpoint between sunset and sunrise. We identified the darkest point in each night throughout the study area, and used the average darkest point from which to calculate the number of hours since a detection occurred. We ran a multinomial model using mblogit in R and included site and year as random effects.

Model selection and multimodel inference

We compared models based on differences in AICc values. For both modeling approaches, we gained inference from the top model from each analysis. Top model sets were identified from cumulative AICc weights to define a 95% confidence set (Symonds & Moussali 2011). We also calculated relative variable importance (RVI) for each variable by summing Akaike weights of all models containing a common variable for each analysis, standardized by the number of models including each variable (Kittle et al. 2008). Relative Variable Importance is a multi-model measure of how important in terms of explanatory utility each variable is relative to other variables considered (Burnham & Anderson 2004). For example, a variable with an RVI of 3 is three times more important that one with an RVI of 1.

2.2.4 Explanatory variables

Salmon biomass

We estimated salmon biomass as an index for salmon availability to bears along four river segments during each week of the study. The river segments were defined by whether salmon counts occurred, as dictated by boat-launch accessibility. Salmon biomass estimates for each of the four segments were attributed to each camera site according to the river segment in which it occurred (Appendix A3). We quantified salmon biomass by conducting weekly counts from a non-motorized raft and by drawing from the New Salmon Escapement Database System (NuSEDS; Pacific Region's central database, maintained by Fisheries and Oceans Canada, which stores individual spawner survey data records and spawner abundance estimates). Counts were converted to biomass estimates for each salmon species and sex, assuming a 1:1 sex ratio (Bryan et al., 2014). We included Chinook, pink, and sockeye in our estimates because those were the only species assessed by Fisheries and Oceans Canada during our study period and constituted most of the salmon biomass during that time. Salmon biomass was calculated by multiplying raw counts (or estimates thereof; below) with average species-specific weights. Biomass values per fish used, in kilograms, were: Chinook: 13.6, Pink, odd years: 2.4, Pink, even years: 1.7, Sockeye: 2.7 (Groot & Margolis, 1991). Given missing count data for some river segments and weeks, we used a spatially and temporally explicit approach to impute within- and across-year salmon biomass availability (e.g., Bryan et al., 2014; Ruggerone et al., 2010; Appendix A3).

Berry availability

We assessed shrub phenology approximately every two weeks to estimate berry availability to bears. We counted the number of berry-producing species (from a pre-determined list of 16 on which the area's bears feed; Himmer & Gallagher, 1995; Appendix A2; Table A5) that had ripe berries in each survey. We used this species count as a coarse proxy for berry availability in the valley. Each survey, repeated every two weeks, consisted of 16 plots of approximately 5m^2, spaced at four elevations (Appendix A1; Figure A7) along a ~1300m elevational gradient. We assumed that bears were able to access any region of the valley for berries, so we applied the same two-week estimate for each pair of camera site-weeks over our time series (Appendix A1; Figure A8).

Visitors

We used two measures of human influence. First, we recognized three distinct zones of the river as ‘spatial treatments’ (Figure 2.1). We defined treatments according to where commercial bear viewing occurred: a ‘no tour’ reference area; a ‘land-based tour’ area; and a ‘land- and boat-based tour’ area (as described above).

Within these three zones, we also derived an index of human foot traffic (i.e., visitors on land; herein ‘visitors’). Specifically, we sampled index sites using ©TRAFx (https://www.trafx.net/) infrared trail counters and camera traps (Reconyx Hyperfire 2 Model: HP2X Professional) placed at one representative spot within each of the three spatial treatments that British Columbia Parks Rangers and Nuxalk Fisheries and Wildlife crew members, both with extensive knowledge of the study system, considered representative of human activity within each spatial treatment (Appendix A3). Camera traps set to index human foot traffic were set to motion activated videos of 30 second durations (see full settings in Appendix A2; Table A1). People were informed of camera trap research in the park through a public notice on the BC Parks website, communication with bear viewing operators, and research signs. We assumed a consistent level of human activity within each treatment, attributing a given week’s estimate to all camera trap sites within the same treatment area where we measured bear activity.

Water level

We estimated water levels along the Atnarko using hydrometric data obtained from the Government of Canada water office, station “ATNARKO RIVER NEAR MOUTH (08FB006)” (https://wateroffice.ec.gc.ca/report/real_time_e.html?stn=08FB006). We summarized the data by year and week, and used the weekly mean as our unit of measure (Appendix A1; Figure A9).

2.3 Results

2.3.1 Weekly detection models

We found evidence for associations between human activity and grizzly bear activity. Accounting for all other terms, weekly detections were higher in the land- and boat-based area compared with other areas (Figure 2.2A). As we predicted, the number of visitors had a negative association with bear weekly detections within any spatial treatment (Figure 2.2A and B). Holding all other variables at their mean values, an additional 100 visitors/week (i.e., ~7% of mean visitors/week in the land- and boat-based treatment) was associated with a 3% decrease in weekly detections.

The strongest patterns linking human activity to bear activity, however, depended on measures of salmon abundance. An interaction term between spatial treatment and salmon biomass was more than twice as important (RVI = 0.140) as the number of visitors (RVI = 0.062). Contrary to our predictions, when salmon biomass was high (+1 SD), weekly detections were higher in the land- and boat-based treatment; but lower in the other two treatments (Figure 2.2C). Additionally, an interaction term between visitor numbers and salmon biomass was of similarly high importance (RVI = 0.124), revealing that when salmon abundance was high (+1 SD), weekly detections decreased when more visitors were present, aligning with our predictions. Under this high salmon scenario, weekly detections decreased by 13% with every 100 visitor/week increase (7% of weekly visitor mean [n = 1363] in the land- and boat-based treatment). As we predicted, under a low salmon scenario (-1SD), we observed the opposite pattern: an increase in detections with increased visitors (Figure 2.2D).

Environmental variables also influenced bear weekly detections. Water level and the number of fruit-bearing plant species with ripe berries were negatively associated with grizzly bear detections (RVI = 0.071; 0.071; Figure 2.2A), whereas salmon biomass was positively associated with detections (RVI = 0.036). These variables were between ~1.2 and ~2.5 times less important than the human-related variables highlighted above.

We assessed the performance of our top GLMM using both marginal and conditional R^2 values. We obtained marginal R^2 values of 0.197 for our top model, with a corresponding conditional R^2 value of 0.653. We performed a Moran's I test to assess potential spatial autocorrelation in log-transformed residuals. The Moran's I statistic standard deviate was 1.23 (p = 0.11), suggesting no significant spatial autocorrelation in the log-transformed residuals.

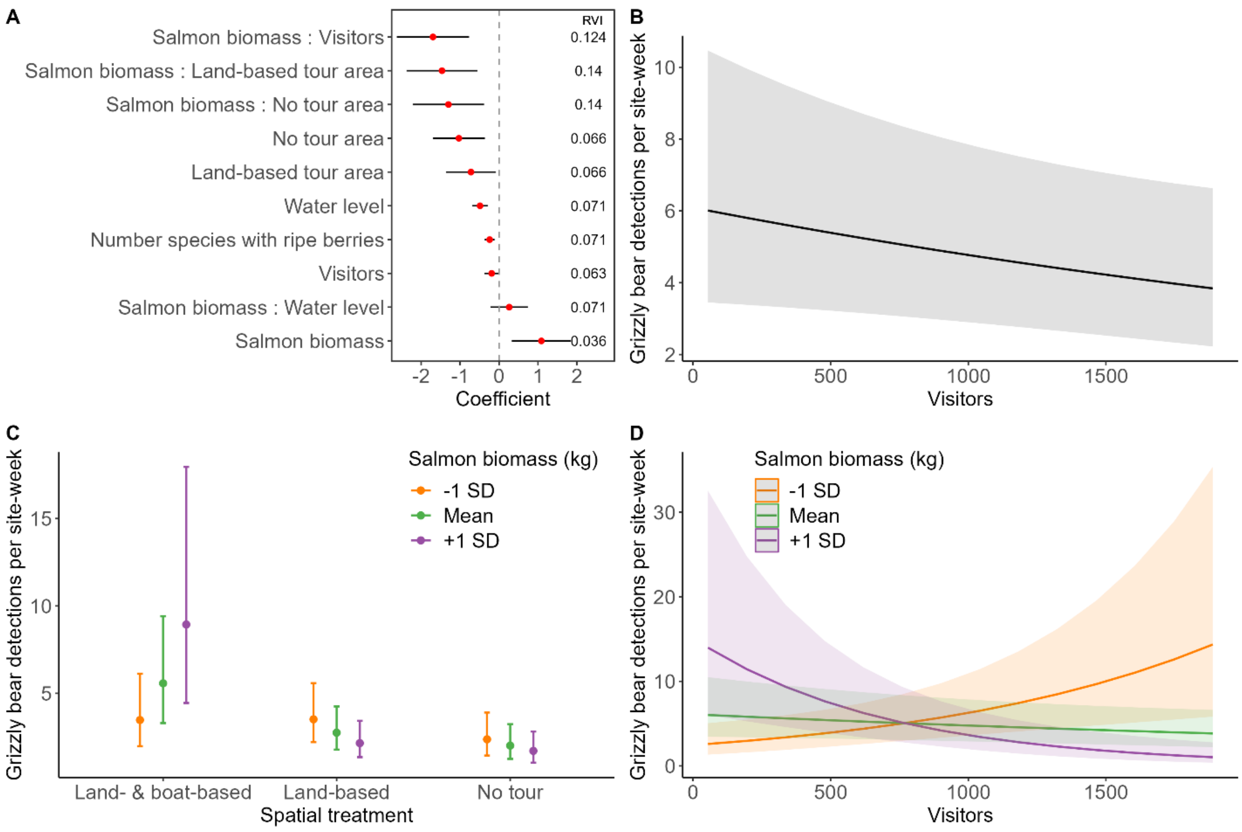

Figure 2.2. Top weekly detection model. A) parameter coefficients and CIs for fixed effects, centred and scaled by 2 standard deviations. Red dots represent parameter coefficients and black lines span 95% CIs. RVI shown for all fixed effects. B) Weekly detections as a function of the number of visitors; C) weekly detections by salmon biomass as a function of spatial treatment; D) weekly detections by salmon biomass as a function of number of visitors. Colors for panels C and D indicate model predictions for mean salmon biomass (green), one standard deviation below the mean (orange), and one standard deviation above the mean (purple). Atnarko River, Nuxalk Territory, British Columbia (2019-2021).

2.3.2 Age-sex class models

The probability of detections being of certain age-sex classes varied primarily with measures related to human influence, specifically visitor numbers and diurnality. In line with our predictions, with higher visitor numbers, there was increased likelihood of detections being female with young and sub-adults compared to adult males and females (Figure 2.3; Figure 2.4A). Similarly, with increased diurnality, the likelihood of a detection being all other age-sex classes increased compared with males, which were strongly nocturnal in their detections (Figure 2.3; Figure 2.4B).

Among environmental variables, only berry availability influenced age-sex class detection probabilities. Specifically, compared with males, detections were less likely to be sub-adults when berries were ripe (Figure 2.3). Salmon biomass did not affect the probability of a detection being a given age-sex class (Figure 2.3).

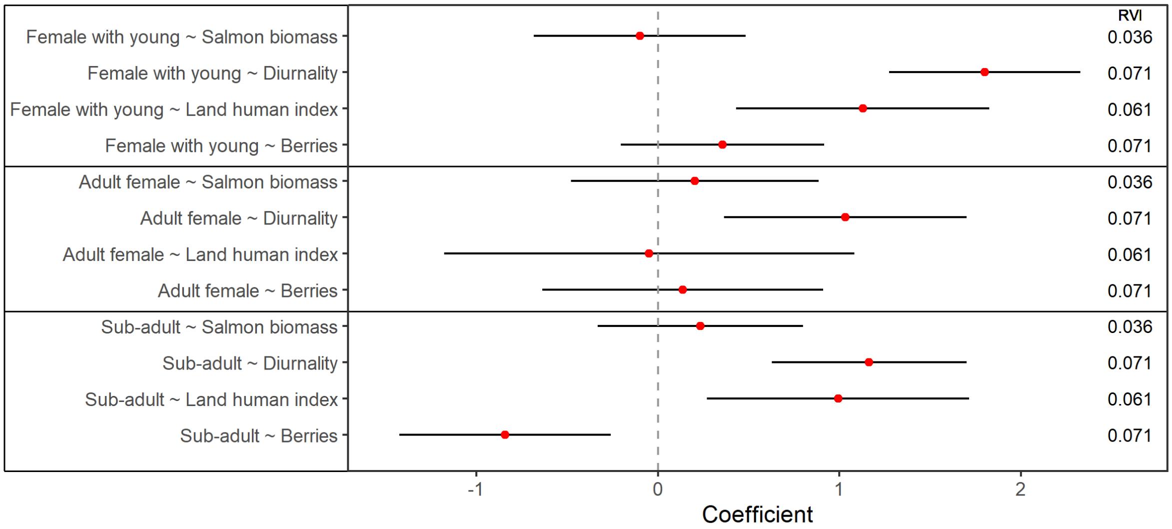

Figure 2.3. Age and sex class top multinomial model. Parameter coefficients and CIs for fixed effects, centered and scaled by 2 standard deviations. Red dots represent parameter coefficients and black lines span 95% CIs. Atnarko River, Nuxalk Territory, British Columbia (2019-2021).

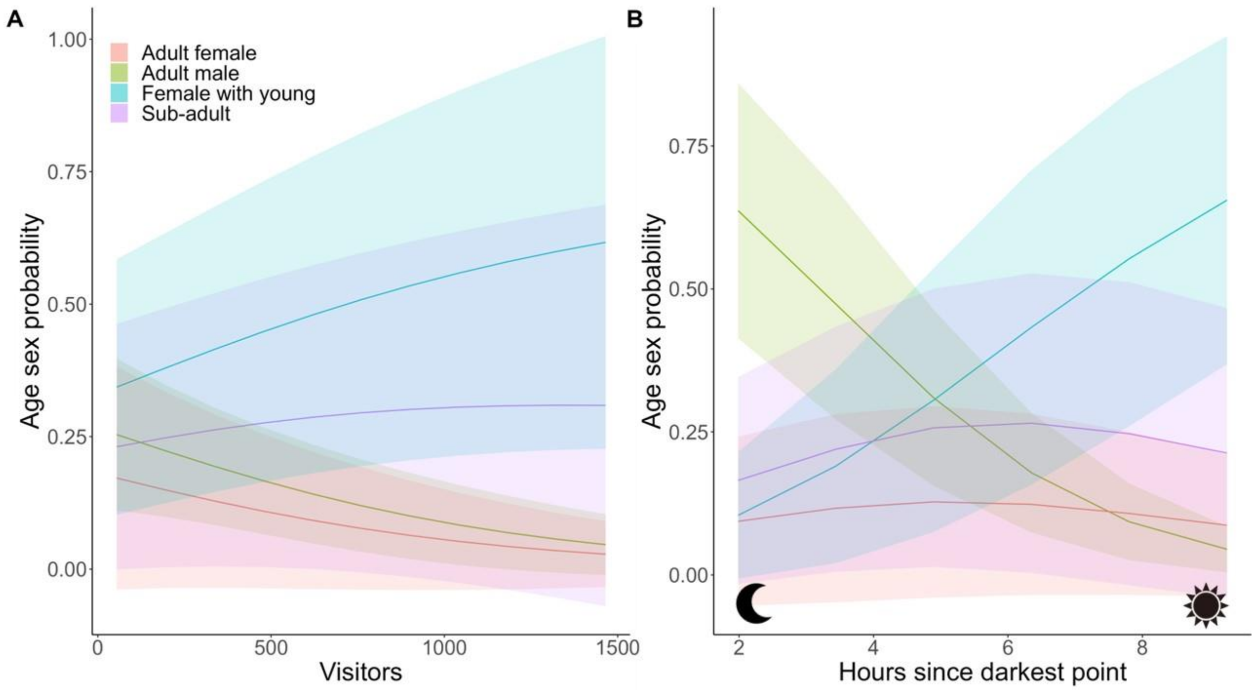

Figure 2.4. Age and sex class top multinomial model. A) Age-sex probability as a function of number of visitors; B) Age-sex probability as a function of number hours since the darkest point in the night. Shaded regions represent 95% CIs for model predictions. Atnarko River, Nuxalk Territory, British Columbia (2019-2021).

2.4 Discussion

Our findings revealed varied spatial and temporal relationships among humans, food resources, and grizzly bear activity. We found several lines of support for the asset protection principle and human shield hypotheses. Specifically, how bears allocated their spatial-temporal activity varied and interacted across human and environmental contexts, as well as age-sex classes. Generally, bear activity was lower during weeks in which the number of visitors present was higher. Detections during those scenarios (especially during daylight, when humans are active) were more likely to be females with young, adult females, and sub-adults. Salmon abundance was especially influential in its interaction with the number of visitors, leading to opposite patterns during periods of low and high salmon. Collectively these patterns of bear activity align with, and can be explained in the context of, risk perception.

The ways weekly detections varied with human activity differed between our two primary measures (number of visitors and spatial treatment). In the spatial treatment with the highest ecotourism activity, bear activity was higher compared with upstream areas where human activity was lower (Figure 2.2A). This pattern also emerged when salmon abundance was high (Figure 2.2C). We suspect this result in part occurred because the ecotourism sites occur near the mouth of the Atnarko river, where salmon congregations are dense and highly available to fishing bears. After accounting for the effect of spatial treatment, however, bear activity along the Atnarko declined during weeks with higher visitor numbers (Figure 2.2D). Owing to varied spatial and temporal human behaviour among the types of bear viewing (i.e., professionally-guided tours and tightly managed bear stand versus a comparably unregulated recreation area not designated for bear viewing), we infer that bears generally reduced their activity when and where visitor numbers are high because perceived risk was higher with variable and largely unregulated behaviour among visitors, especially in areas with high visitation; namely, the BC Parks recreation site that was actively used by the public for bear viewing, but not formally designated as a bear viewing area. Given that predictable patterns enable wildlife to anticipate risk (Palmer et al., 2021; Laundre et al., 2001; Gaynor et al, 2019), we suspect bears at this site modulate non-consumptive risk-effects of visitor numbers and behaviour accordingly, as prey do with varied characteristics of predators.

More detailed and important inference emerged when we further considered salmon biomass, a key environmental variable. Specifically, an interaction term (with the highest RVI among variables in the top GLMM) revealed that when salmon levels were high, bear activity decreased when the number of visitors were high, but increased when salmon abundance was low. Aligning with our prediction under asset protection principle, this pattern supported our hypothesis that grizzlies would be more likely to tolerate risk (i.e., remain at sites) when food resources were low, but re-allocate their time away from such sites when resources were abundant. Indeed, when salmon are abundant at ecotour sites, they are also available in tributaries beyond our sampled portion. Variation in non-consumptive risk effects become evident across contexts in the Atnarko where bears specialize on Pacific salmon that are sometimes (i.e., when abundance is generally low) constrained to areas that co-occur with pulses of human activity. The pattern of evidently accepting risk in times and places of low salmon biomass is especially important for female grizzly bears because foraging is directly related to reproductive assets; pre-denning fat reserves are positively correlated reproduction and females with access to salmon have higher litter size (Hilderbrand et al., 2000; Hilderbrand et al., 1999). Accordingly, neglecting context-dependent decision-making, such as resource availability, limits the practical utility of measuring non-consumptive risk effects (Beale, 2007).

We also found strong support for the human shield hypothesis. Whereas the probability that a detection was a given age-sex class did not vary by spatial treatment, when visitors increased, the probability of detections being adult male decreased and the probability that a detection was female with young or subadult increased. Whereas, as noted above, activity across detections of all age-sex classes decreased when visitor numbers where high, we infer that the underlying mechanism of this decrease is avoidance of humans by adult males. Indeed, lower weekly bear detections are comprised of a lower proportion of adult males (Appendix A1; Figure A10). Additionally, females with young, adult females, and subadults were more likely to be detected during daylight hours than adult males, which were more likely to occur during darker periods of the day (Figure 2.4B). This pattern was consistent with previous research findings. In Sweden, mother grizzly bears selected human-dominated sites, which were avoided by males (Steyaert et al., 2016). In an ecotourism context elsewhere in coastal British Columbia, males and females with young similarly partitioned their temporal activity in relation to ecotourism periods (Nevin & Gilbert, 2005).

Our approach had several limitations. Logistical constraints (e.g., segments of the river that were inaccessible by boat to count salmon) required us to impute missing spatial and temporal dimensions of salmon data. More broadly, data on spawner abundances of wild salmon are not always consistently collected through space and time for each species, requiring similar estimation via imputation (Bryan et al., 2014; Ruggerone et al., 2010). Nonetheless, that we detected qualitatively similar patterns in datasets with and without imputed data (Appendix A1; Figure A11) suggested our results were not sensitive to our imputation approach. Moreover, we note that we used only two relatively coarse metrics of grizzly bear activity, assessed with a suite of covariates for which variation was expressed over a weekly period. Whereas broad patterns emerged, only a finer-scale ethological approach could evaluate how more specific behaviours (i.e., activity budgets) might be influenced by ecotourism. Such an approach could also assess if fitness-related behaviours (e.g.., salmon consumption; Hilderbrand et al., 1999) were influenced by human activity. Finally, and relevant to many ecotourism contexts, genetic sampling over a broader area could identify whether there are risk-adverse and -tolerant individuals in the population of mobile wildlife that avoid or tolerate high-density human presence. Similarly, more comprehensive genetic approaches could assess whether exposure to ecotourism might predispose individuals to subsequent conflict (e.g., Cui et al., 2021). We note that bear culture, personality, and individual capacity for logic and thought (Paquet & Alexander, 2018; Whiten, 2021) might be important individual trait contexts, which are not captured via camera trap weekly detections, a measure that pools the detections of unknown individuals. Whereas this work confronts only one of three lines of inquiry (i.e., broad activity patterns via analysis of camera trap data) associated with our research project and its objectives, subsequent analyzes of behavioural and genetics data (as described above) will aim to confront these limitations and yield more detailed inference.

Several specific management implications of this work span both conservation and social domains. If activity levels of bears are important targets for management consideration, the interactive influences of salmon abundance and number of visitors requires special consideration. Specifically, when salmon runs are low, management might consider limiting the number of visitors more than during high salmon weeks. This is because grizzly bears with few alternatives for foraging opportunities during low salmon scenarios may be more vulnerable to non-consumptive risk effects of increased humans (Gill et al., 2001). Indeed, if an animal's riskier behavioural options are also those that result in a higher rate of energy intake, then relatively food-deprived animals would be expected to accept a greater risk while feeding (Lima, 1998, p. 5). Predictions from our top model's output provides insight into how many visitors present under different salmon scenarios would align with several candidate targets of bear activity (Table 2.1). These options of management interventions allow managers to consider varying visitor numbers under different salmon scenarios to manage for a level of predicted responses in bear activity they consider acceptable. How the human-induced effects and any interventions by managers might scale to measurable changes to population fitness is unknown, but offers an important avenue for future research to address

Table 2.1. Visitor numbers associated with grizzly bear weekly detection scenarios under high, mean, and low salmon conditions as predicted by the top model. Visitor numbers are rounded to the nearest 50. Note that under low salmon and high visitor scenarios, bear detections increase. In low salmon scenarios, managers might consider limiting visitor numbers to no greater than those associated with mean bear detections to mitigate disturbance when bears have little alternatives for foraging opportunities.

Salmon biomass (kg)	**Grizzly bear activity (detections/week)**	**Detections/ week**	**Lower confidence interval bound (95%)**	**Upper confidence interval bound (95%)**	**Visitors/ week**
+1 SD	50% of mean	2.6	1.3	5.1	1250
	Mean	5.2	2.8	9.5	750
	200% of mean	10.3	4.9	21.5	250
Mean	50% of mean	2.4	1.0	5.7	3800
	Mean	4.9	2.9	8.1	900
	200% of mean	9.7	3.9	23.7	0
-1 SD	50% of mean	3.5	1.9	6.5	400
	Mean	7	3.7	13.3	1100
	200% of mean	14	6.0	32.6	1850

Human safety might also be considered by managers. A proactive approach would favour the regulation of times, places and permitted human behaviour (e.g., constraining humans to within-site spaces if bears viewing is permitted at multi-use recreation areas), so as to make interactions more predictable for bears and humans alike. Such scenarios not only reduce apparent risk perception (Palmer et al., 2021) but also avoid unanticipated encounters, which can underlie cases of human injury by bears (Herrero, 1985). As we suggest, low salmon conditions might present few foraging options for bears, thereby creating congregations at available feeding sites where human activity is high. At the larger British Columbia and yearly scales, Artelle et al.

(2016) found that grizzly-human conflict rises in years with poorer salmon returns. Such context presents not only a bear conservation challenge for managers (i.e., managing for disturbance during a critical time for bears to amass large amount of energy to support themselves and offspring during dormancy; Farley & Robbins, 1995; Hilderbrand et al., 1999) but also a safety consideration for managing visitors who are actively pursuing grizzly bear encounters at recreation sites that are not designated for bear viewing.

Although our bear ecotourism system has a unique constellation of properties (i.e., discrete foraging patches [some of which also easily accessible to visitors], high carnivore densities, hyperphagia, potential for human safety issues), our work offers broader implications for conservation science and practise. First, we designed our work to confront and contribute to two bodies of theory (the Asset Protection Principle and the Human Shield hypothesis) that are relevant to the conservation of any predator-prey system, including the many in which wildlife show prey-like antipredator behaviour in the presence of humans. Second, we showcase with rich detail how data from animal behaviour can be harnessed to directly inform specific and context-dependent management actions (Table 2.1).

Evidence-based management that considers the data and inference this work provides can serve multiple purposes. Attending to questions related to bears and humans can contribute to effective management by Nuxalk Stewardship, while also relevant for other partnering levels of government (e.g., British Columbia). More broadly, the management of wildlife ecotourism can draw on not only theory relating to non-consumptive risk but also site- and case-specific empirical data. Risk effects can manifest with innocuous recreation activities (Anderson et al., 2023; Sytsma et al., 2022), including grizzly bear ecotourism, which can have positive and negative effects on bear populations (Penteriani et al., 2017). Specialized feeders, such as grizzly bears that rely on spatially and temporally constrained Pacific salmon, have limited scope to respond to disturbance when salmon availability is low without incurring potential costs (e.g., lost foraging opportunity). This insight, informed by our results, offers additional context to the APP prediction that foragers with lower energy reserves will accept greater risk. Specifically, foragers with lower energy reserves that are also constrained to foraging windows in space and time may be especially sensitive to risk effects. Our engagement of these theories and multiple analytical approaches addressed whether and how non-consumptive risk of purpose-driven grizzly bear encounters during wildlife ecotourism manifests in the Atnarko Corridor. We emerged with management implications that are not only relevant for Nuxalk and BC Parks, but also broadly applicable to conservation science and practice.

Chapter 3. Intrapopulation variation in space-use and behavioural states in a grizzly bear-ecotourism system: a multi-dimensional approach reveals spatial filtering of tolerance

3.1 Introduction

Intrapopulation variation in wildlife behaviour is common and can be examined on several dimensions. In the context of risk, individuals and the demographic classes (i.e., age, sex) they comprise can vary in tolerance (i.e. the degree of reaction by an individual to a stimulus that signals a potentially risky situation [Čapkun-Huot et al., 2023]). Variation in tolerance can manifest in different ways. For example, some individuals may spatially avoid risk, while others may tolerate the presence of risky stimuli by responding behaviourally by, for example, investing in vigilance.

A multi-lens perspective can provide a comprehensive vantage to increase inference about age-sex class and individual variation in tolerance. Specifically, whether individuals observed to invest in anti-predator behaviours (e.g., vigilance) in response to risk represent the only individuals affected by disturbance and associated risk is unknown without examining whether there was prior spatial segregation of the population according to variation in their tolerance to accept such risk in the first place (Bejder et al., 2009). Similarly, whether animals avoid disturbance spatially or not may not provide an accurate indication of the population's range of vulnerability to disturbance without additional measures of behaviour (Gill et al., 2001). A comprehensive assessment that simultaneously draws on both spatial and behavioural dimensions can therefore provide more insight than either lens alone. Indeed, antipredator behaviours are not always expected to respond the same way, which justifies an approach for considering more than one behavioural response (Uchida & Blumstein, 2021). Finally, practical utility might emerge when human activity comprises the risk stimuli (Frid & Dill, 2002), and managers seek to understand and potentially minimize any behavioural change such perceived risk might elicit.

Tolerance related to human-dominated spaces can vary, owing to different drivers. On one hand, differences in risk-perception among age-sex classes and individuals may elicit spatial segregation in a heterogenous environment according to the level of risk animals perceive (Čapkun-Huot et al., 2023). Abundant data from wildlife show considerable intrapopulation variation in the use of risky areas (Brown et al., 1999; Gaynor et al., 2019), including those in which humans pose risks (e.g., Dingemanse et al., 2010; Ducros et al., 2020; Hahn et al., 2022). Such patterns can be mediated by personality traits (e.g., shy or bold individuals [Toms et al., 2010]), whereby shyer individuals tend to occupy areas with less disturbance (Miranda et al., 2013). On the other hand, individuals might not sort spatially based on perceived risk from humans but instead based on perceived protection. Specifically, some individuals or groups they comprise within populations might perceive humans as 'shields' that protect them from greater perceived risk from conspecifics or other species (Berger, 2007; Steyaert et al., 2016). Consequently, an understanding of the extent to which human activity might influence variation in space-use within populations may increase our understanding of the variation in tolerance within populations and the processes underlying it.

Individuals that tolerate space where human activity is pronounced can modify other dimensions of behaviour, especially if valuable resources are present. Predation risk theory predicts that these individuals can invest in anti-predator behaviour (e.g., vigilance, fleeing) to reduce the potential costs of spatially tolerating an area perceived as risky (Lima and Dill, 1990). If food resources are constrained to, or concentrated in, human-occupied areas, individuals there might perceive the risk of lost opportunity in the form of foregone resource acquisition (opportunity cost) a greater cost than the risk the area poses (Blumstein, 2016; Field et al., 2024; Gill et al., 2001).

Beyond the consideration of resources, animals may also show increased tolerance to human activity in disturbed areas, especially if the activity is benign. Such a scenario can arise when individuals consistently exposed to people display reduced responsiveness. Such an outcome depends on the specificity, novelty, predictability, and level of risk; specifically, contexts that are specific, not novel, highly predictable and pose low risk should promote tolerance (Čapkun-Huot et al., 2023). Moreover, the extent to which animals tolerate human activity varies with life history traits; species that invest more in their offspring tend to be more tolerant of non-threatening encounters because the cost of avoidance is particularly costly for those with greater parental investment (Samia et al., 2015). Collectively, these scenarios suggest that individuals that tolerate sharing space with humans will either allocate anti-predator behaviour to reduce perceived risk or assess the risk of benign human activity as nonconsequential and associated anti-predator behaviour too costly.

Systems in which human disturbance and potential risk vary spatially, and associated behavioural trade-offs are present, lend themselves to applying a multi-dimensional approach for examining tolerance. Commonly, wildlife ecotourism creates such scenarios, with its myriad influences studied across a range of taxa globally (Blumstein et al., 2017; Buchholz & Hanlon, 2012; Steven et al., 2011) . Specifically, some animals can perceive even non-consumptive human activities like ecotourism as a lethal risk (Frid & Dill, 2002), whereby repeated tourist visitation can act as a stressor with consequences for reproduction and survival (Geffroy et al., 2017). Moreover, ecotourism tends to occur in finite locations across a landscape in which such pronounced perceived risk can be elevated, and potentially avoided. For example, tourist presence predicted avoidance by large-bodied animals as measured by field sign (i.e., direct sightings, sounds, tracks, faeces, diggings and tree scraping) in a protected area in China (Zhou et al., 2013). Ecotour sites also tend to be resource rich, offering abundant natural foods (e.g., Field et al., 2024), or even provisioned of foods by ecotour operators (e.g., Maréchal et al., 2016). Accordingly, some individuals within species targeted for ecotourism may be unwilling to avoid people at the cost of forgoing resources (Gill et al., 2001), and therefore reduce perceived risks behaviourally. Despite the valuable inference provided from this body of work, how wildlife individuals, especially of species that are highly mobile, might vary both in their presence -- and for those present, their behaviour -- at ecotourism sites that are embedded within their larger home ranges is less understood. Such insight requires knowledge of space-use by individuals both within and beyond areas of ecotourism, as well as detailed behavioural data at ecotourism sites.

Here, we examine whether grizzly bears show intrapopulation variation in spatial and behavioural tolerance to ecotourism along the Atnarko River Corridor in coastal British Columbia. Several case studies have demonstrated that grizzly bears show varied anti-predator responses towards humans (see Mattson, 2024 for review), including varied responses to ecotourism (see Penteriani et al., 2017 for review). For example, several studies have shown that recreational activity by people can displace bears from preferred habitat, increase energetic costs, and reduce nutritional intake (Fortin et al., 2016, Dyck and Baydack, 2004). In other cases, bears may habituate to people over time to reduce the detrimental effects of a stress response (Wheat and Wilmers, 2016). Whereas ecotourism is a non-consumptive activity, grizzly hunting was common in British Columbia (Artelle et al., 2013) and has only recently ceased (Darimont et al., 2017). Moreover, the region immediately adjacent to the study area (Bella Coola Valley, British Columbia) has been a hot spot of bear-human conflict, as measured in human-caused grizzly bear mortality (Artelle et al., 2016). By contrast, ecotourists can also be perceived as shields from dangerous adult males by sub-dominant grizzly bears (i.e. sub-adults, females with young; Nevin & Gilbert, 2005; Steyaert et al., 2016; Field et al., 2024;). Accordingly, guided by the theory outlined above, our hypotheses consider how the population might vary in how individuals or the age-sex classes they comprise perceive humans (as risky or benign), and modulate their spatial and behavioural tolerance accordingly.

Our sampling approach capitalized on the characteristics of our study area. The Atnarko River provides bears access to aggregations of spawning salmon (*Oncorhynchus* spp.) during hyperphagia—a critical period to amass large amounts of energy before denning. The ecotour areas in particular ('land- and boat-based' area, below) host readily-accessible spawning aggregations throughout the study area (Field et al., 2024). Wildlife ecotourism thus provides a system in which non-lethal human stimuli are present, trade-offs related to foraging under the perceived risk of predation (by humans and male bears) are relevant, and potential grizzly bear responses in the form of space-use and anti-predator behaviour are measurable.

We sampled grizzly bears both within and beyond the ecotour area during summer and autumn over three years. Specifically, we measured space-use of genetically identified grizzly bears (sex and individual identity) both within and upstream from the ecotourism area to assess the possibility of spatial segregation across a gradient of ecotourism exposure. Additionally, among bears that occurred at ecotour sites in daytime and crepuscular hours, our scan sampling approach to observe bear behaviour allowed us to record measures of behavioural tolerance, assigning three broad categories of behaviour (fishing, alertness, and other). We reasoned that alertness represented investment in anti-predator behaviour and comprised an indicator of reduced tolerance. We also collected covariate data to measure the intensity of ecotourism activity (i.e., ‘ecotourism metrics’: visitor numbers and presence of tour boats), resource availability (i.e., salmon biomass) and the presence of conspecifics (i.e. other bears).

We made several predictions about intrapopulation variation in behaviour based on theory relating to tolerance, predation risk, and human shielding. Within a tolerance framework and considering the possibility of varied tolerance to risk among individuals, we predicted that there would be variation in space-use (as measured by spatial detection histories) among genetically-identified individuals. Specifically, and aligning with the human shield hypothesis, we predicted those detected in the area with highest human activity would be primarily female. Moreover, among those individuals using the ecotour area, we also made predictions about variation in behavioural tolerance and their correlates. Specifically, owing to risk-foraging trade-offs under predation risk theory, we considered multiple hypotheses. We hypothesized that grizzly bears tolerant enough to spatially co-occur with humans where salmon is plentiful could offset such potential risk by investing in anti-predator behaviour. Accordingly, we predicted a positive association between alertness and ecotour metrics. On the other hand, the relatively predictable tourist activity could be perceived as benign, eliciting little responses. Specifically, aligning with the human shield hypotheses, female with young would be less likely to be alert with greater ecotour intensity. Additionally, because our behavioural state data are comprised of females, females with young, and subadults (see Methods), we also considered the presence of other bears as risky stimuli, predicting a positive association between alertness and other bear presence. Finally, aligning with asset protection principle, we predicted a positive association between salmon biomass and alertness, reasoning that when food resources are limited, allocating energy away from fishing would be perceived as more costly than allocating energy to anti-predator behaviours because foragers with lower energy reserves will accept greater risk than foragers that have adequate energy reserves (Clark, 1994). Our results may help identify individuals and contexts that are potentially more sensitive to the potential influences of ecotourism and thereby provide evidence-based guidance for consideration by ecotour management.

3.2 Methods

3.2.1 Study area

The study occurred in the Atnarko River corridor (hereafter ‘Atnarko’; Figure 3.1A) in Tweedsmuir Provincial Park, British Columbia, which is located in unceded Nuxalk Territory. Genetic sampling and behavioural observations occurred simultaneously with a companion study using an array of camera traps in the same area described recently (see Field et al., 2024 for details).

The abundance and activity of people in the park vary spatially during the salmon spawning season. We defined ‘spatial treatments’ according to where bear viewing occurred: a ‘no tour’ reference area furthest upstream, a ‘land-based tour’ area in the middle, and a ‘land- and boat-based tour’ area furthest downstream (Field et al., 2024). Activities in the ‘land- and boat-based tour’ area, which have the potential to elicit perceived risk by bears are varied but include camping, swimming, angling, hiking, paddling, picnicking, mushroom picking, and bear viewing (on land and aboard drift boats). Owing to a well-established industry of bear-viewing infrastructure and drift boat tours, the ‘land- and boat-based tour area’ (Figure 3.1A) hosts on average ~2 orders of magnitude more people compared with the ‘no tour’ area of the corridor

~35 km upstream (average weekly visitors to ‘land- and boat-based tour’ area was 1,363 across years, compared with 11 in the ‘no-tour’ area and 14 in the ‘land-based tour’ area, which represented the lower end of middle in terms of human activity; Field et al., 2024).

We collected behavioural state data from two sites within the ‘land- and boat-based’ area, which varied in their management of human behaviour and activity (Figure 3.1A). One site was the Belarko bear viewing platform (‘Belarko’), a purpose-built bear viewing platform staffed by BC Parks and the Nuxalk Nation that included an electric fence and a regulated entry and exit system. The second site was BC Parks Fisheries Pool campground (‘Fisheries Pool’), an area designed for camping and recreation, including swimming, picnicking, and angling. Although signage to regulate the behaviour of campers and day-users is posted in prominent locations at Fisheries Pool, bear viewing is self-pursued by the public at their own risk. Ecotourism boats were also present in the river at and between these two ‘land- and boat-based’ sites. Up to 11 commercially operated and professionally guided ‘drifts’ (slow-pace rafting-base bear viewing with up to 6 guests each) were permitted per day. Drift boats launched ~200m upstream from Belarko and hauled out at Fisheries Pool.

3.2.2 Field methods

Space-use data collection using genetic re-captures

We non-invasively sampled bears to identify how individuals used the Atnarko corridor. Specifically, as approved by University of Victoria Animal Use Permit 2019-004, we deployed passive, non-baited hair snags (Proctor et al., 2010; Woods et al., 1999) to genetically identify individuals using microsatellite data (Paetkau, 2004; Field et al., *in press*). Snags were set of barbed wire at ~0.5 m height (Quinn, Wirsing, & Proctor, 2022) every ~0.5 - 2km along the

Atnarko river across bear trails or riverside banks where bears were commonly observed. We monitored hair snag sites for 317 days over three years during the late summer and autumn salmon runs (late July to early November; n = 28 sites in 2019 for 113 days; n = 29 sites in 2020 for 101 days; and n = 28 sites in 2021 for 103 days). In 2021, there were 7 snags in the 'land- and boat-based' area (~4 km river network distance), 13 snags in the 'land-based' area (~22 km river network distance), and 8 in the 'no tour' (~9 km river network distance) (Figure 3.1A). Across years, crews sampled hair on average every 9 days ($\bar{x}$ = 8.6 days in 2019, $\bar{x}$ = 9.0 days in 2020, and $\bar{x}$ = 8.8 days in 2021), collecting 1,806 samples. We subsampled high-quality samples (with abundant guard hair; n = 713), identifying 118 bears (73 female and 45 male) over the three years.

Behavioural state data collection using observational approach

Sampling methods

We collected behavioural state data from early August to late October, 2019-2021. The first sampling sessions (i.e., time blocks awaiting bears to be present, and if bears were present, observation periods of collecting behaviour data; defined below) of the season occurred after all hair snags had been installed. Sampling sessions occurred ~2 weeks before, during, and ~2 weeks after bear viewing season, and during diurnal and crepuscular periods. We defined an 'observation period' as the period during which a focal bear was present during a sampling session, and 'focal bear' as the bear from which behaviour data were collected. All observation periods occurred between 0600 and 2100. The two sites were sampled on a rotating schedule of ~4-hour blocks to capture different photic regimes and periods of human activity. In total, we recorded 35 hours and 58 minutes of bear behaviour during observation periods; 18 hours and 46 minutes at Belarko and 17 hours and 12 minutes at Fisheries Pool.

We collected behavioural state data by video-recording the full duration of the observation period. We recorded behaviour with a Nikon® camera (Z6 body, 200-500mm lens). The camera was tripod-mounted, with leg angle and height adjustments, and a video head that allowed panning, tilting and swiveling to permit viewing of entire visible sequences . Behaviours were coded from the video recordings (see ‘Coding behavioural states’) and behavioural states of ‘fishing’, ‘alertness’, or ‘other’ (Table 3.1) were then attributed to each case, along with their associated co-variate data. We herein refer to these as ‘scan samples’ (Altmann, 1974) and each served as a case in our analysis (below). The mean number of scans per observation period was 9.0, with a range of 2 to 33 and a median of 7.

Selecting a focal bear

The observation period (and video recording) began when a focal bear entered our view. If a focal bear went out of view but returned within ten minutes, we considered the two portions a single observation period. If we were observing a family group, we considered the mother the focal bear. We determined bear sex by direct observation of genitals, including vulva hair, urination patterns, or presence of young, or by opportunistically consulting local ecotour guides in the field if they were present, based on their knowledge of the individual. Additionally, given that grizzly bears are sexually dimorphic (McDonough & Christ, 2012), age-class and sex may be identified from size and body shape, provided a clear view of the bear in side profile and prior to extreme weight gain in the mid to late fall. We used features in Timelapse Image Analyzer (https://timelapse.ucalgary.ca/) to aid in identifying bear sex (e.g., playback speed, magnification tool).

We could discern most but not all individual bears, enabling a minimum estimate of numbers. We used of physiognomic features, such as patterns of scars or wounds, hair coverage on outer ear, and hair pattern on muzzle (Prop, Staverløkk, & Moe, 2020). Despite this approach and extensive variation within the population, we could not confidently identify all bears visually. Nonetheless, after subsampling described in section 3.3.2, we could estimate individual identifications for 81% of observation periods in 2019 (10 individuals [4 adult female, 4 female with young, and 2 subadult] across 27 of 33 observation periods), 65% of observation periods in 2020 (9 individuals [4 adult female, 1 female with young, and 4 subadult] across 21 of 32 observation periods), and 82% of observation periods in 2021 (18 individuals [8 adult female, 10 female with young] across 37 of 45 observation periods). Owing to changes that can occur across years (Hilderbrand et al., 1999; Kingsley et al., 1983; Clapham et al., 2020), separated by 9 months of no observations, we did not attempt to match individuals among years. Accordingly, we could not consider individual identification (i.e. as a random factor) in our analyses.

Coding behavioural states

We collected data for three coarse behaviours: 'alertness', 'fishing', and 'other' (Table 3.1; Appendix B, Figure B1). Because detection of a stimulus is the outcome of vigilance (Beauchamp, 2015), we identified alertness as more appropriate than vigilance to examine bears that appeared to be monitoring stimuli from people and other bears. That is, people seldom go undetected by bears in an ecotourism context; therefore, vigilance may not accurately describe monitoring of stimuli in every case. We note, however, that subtle and overt alertness can include routine and induced vigilance, respectively (Tabel 3.1) (Blanchard & Fritz, 2007). Behavioural states were then attributed to the scan sample by timestamp. We tested for inter- and intra-observer agreement between the two behaviour coders. Inter- and intra-observer precision test results were 88.6% and 93.6% agreement, respectively.

Table 3.1 Operational definitions for grizzly bear behaviour and associated sub-components

Behavioural State	**Operational definition and associated sub-components**
Alertness	Subtle alertness (apprehension); overt alertness. Subtle alertness: low intensity monitoring of external stimuli. Includes glancing (direct look lasting <3 seconds), looking around (direct gaze in one area and then another, not focused on an object for >3 seconds), and routine vigilance (Beauchamp, 2015). Can be during locomotion or not. Overt alertness: high intensity response to, and monitoring of, external stimuli upon detection, as detectable by observer. Includes ceasing other behaviour, with or without staring (directed gaze) for >3 seconds, and/or induced vigilance (Beauchamp, 2015). May be accompanied by high or low intensity non-aggressive vocalisations (including chuffing, subtle teeth clacking/jaw popping, chomping) yawning, scratching (combination of both), salivation while locomoting or not.
Fishing	Search; pursuit; handle; consume. Search: head pointed at an angle less than 90 degrees from the horizontal towards the water for >3 sec, ears forward. Bear locomoting or stationary. ‘Snorkeling’, swimming with dorsum exposed, eyes and nose under water, and only the ears above the waterline, for any amount of time. Pursuit: River-directed charge (rapid and directed locomotion) where focal point is water surface; dive Handle: In contact with and/or having captured fish. Carrying, grasping, sniffing, or flipping parts of live fish, carcass, or fish eggs. Consume: Ingesting parts of a live fish, carcass, or fish eggs, or biting, tearing off pieces, licking.
Other	Any behaviour other than alertness and fishing (e.g., locomotion)

3.3 Analysis

3.3.1 Individual space-use

We created a visualization to illustrate how individuals showed different spatial detection histories. Limited detection data precluded any detailed spatial statistical approach. Instead, we examined detection histories of each individual bear by constructing a clustered heatmap with R package ‘pheatmap’ (version 1.0.12; R Core Team, 2018). Specifically, we used a hierarchical clustering algorithm to categorize individuals based on the similarity of their spatial detection histories. To determine the optimal number of clusters, we employed the ‘elbow’ method to identify the point at which the total intra-cluster variation, or total within-cluster sum of squares (WSS), was minimized (Appendix B; Figure B2). We used the ‘fviz_nbclust’ function from the ‘factoextra’ package (version 1.0.7) to plot WSS against different numbers of clusters, and selected the ‘elbow point’ as the optimal number.

3.3.2 Behavioural states

We used a multinomial model to examine the potential effects of ecotourism and environmental variables on the probability of a behavioural state (Table 3.1) being ‘fishing’ or ‘alertness’, with ‘other’ behaviour as the reference category. Due to small sample sizes at upstream sites (230 hours at upstream sites across years, yielding only 9 observation periods), we analyzed behavioural state data exclusively from individuals that visited ecotour sites in the ‘land-and-boat-based’ area. Our case was a scan sample, defined by a behavioural state (Altmann, 1974). After subsampling, described below, scan samples totalled 936 across years; 233 in 2019; 374 in 2020; and 329 in 2021) across 107 observation periods, which summed to 35 hours and 58 minutes of time observing bear behaviour.

Scans recorded the behavioural state of the focal bear as well as co-variate data. Although we aimed to collect covariate data on two-minute intervals, sometimes there were observation periods when doing so was more challenging within this period. This resulted in longer times between scans. We thus excluded observation periods if scans were on average more than 5 minutes apart (n = 9). We also excluded observation periods where only one scan occurred (n = 2) because we were interested in examining lead effects (see below), which require more than one scan per observation period. These steps resulted in a mean of 2.52 minutes between scans across 107 observation periods.

We excluded limited data on males. Although we initially included all age-sex classes (adult males, adult females, subadults, and females with young), we encountered convergence problems with all models that included age-sex class when males were included. As such, we excluded males (n = 87 scans across 4 hours and 7 minutes) from our analysis.

We constructed a set of *a priori* candidate models that considered combinations of multiple environmental- and ecotourism-related variables (i.e., 'environmental metric models', 'ecotour metric models', and 'lead ecotour metric models'; Table 3.2). We compared each model set against null and environmental-only models. Models included weekly salmon biomass, presence of other bears, number of people viewing bears from the shore, number of boats, and bear age-sex class (i.e., female with young, adult female, and subadult). We included salmon biomass and other bear presence in each model (all 'environmental' and 'ecotour' models, and excluding the null model), reasoning that behavioural states would always be influenced by food availability and presence of conspecifics, as related to predation risk (Lima and Dill, 1990). In 'ecotour metrics' models (Table 3.2), we considered people visiting Fisheries Pool and Belarko who were viewing bears from shore (herein 'visitors') and/or the number of boats, reasoning that one or both measures of human activity may affect behavioural states, also related to risk perception (Frid and Dill, 2002, Field et al 2024). Additionally, in 'lead ecotour metrics' models, we considered lead effects of boats and visitors (i.e., boats t+1 and boats t+2, which represent the counts of these measures in the following 1 and 2 scans, respectively), reasoning that bear behaviour might not only be influenced by human activity in 'real time' but before a boat is visible to observers, potentially heard or smelled by bears in the minutes prior. Finally, in 'ecotour metrics' models we considered an interaction between boats and visitors, reasoning that the number of boats might be important, but only when visitors were also high in numbers. We nested observation periods (i.e., multiple scans covering the duration over which a focal bear was present) within site and year, and included observation periods as a random effect in all models. As noted, owing to uncertainty in visually identifying individuals, we did not include individual as a random effect.

Table 3.2. Candidate model set

Null model	
M1	Random effect only (observation period)
Environmental models	
M2	Salmon biomass + other bears
M3	Salmon biomass + other bears + age-sex
Models with ecotourism metrics	
M4	Salmon biomass + other bears + visitors
M5	Salmon biomass + other bears + visitors + age-sex
M6	Salmon biomass + other bears + boats
M7	Salmon biomass + other bears + boats + age-sex
M8	Salmon biomass + other bears + boats + visitors
M9	Salmon biomass + other bears + boats + visitors + age-sex
M10	Salmon biomass + other bears + boats + visitors + boats * visitors
M11	Salmon biomass + other bears + boats + visitors + boats * visitors + age-sex
Models with lead ecotourism metrics	
M12	Salmon biomass + other bears + visitors [t+1]
M13	Salmon biomass + other bears + visitors [t+1] + age-sex
M14	Salmon biomass + other bears + boats [t+1]
M15	Salmon biomass + other bears + boats [t+1] + age-sex
M16	Salmon biomass + other bears + boats [t+1] + visitors [t+1]
M17	Salmon biomass + other bears + boats [t+1] + visitors [t+1] + age-sex
M18	Salmon biomass + other bears + boats [t+1] + visitors [t+1] + boats [t+1] * visitors [t+1]
M19	Salmon biomass + other bears + boats [t+1] + visitors [t+1] + boats [t+1] * visitors [t+1] + age-sex
M20	Salmon biomass + other bears + visitors [t+2]
M21	Salmon biomass + other bears + visitors [t+2] + age-sex
M22	Salmon biomass + other bears + boats [t+2]
M23	Salmon biomass + other bears + boats [t+2] + age-sex
M24	Salmon biomass + other bears + boats [t+2] + visitors [t+2]
M25	Salmon biomass + other bears + boats [t+2] + visitors [t+2] + age-sex
M26	Salmon biomass + other bears + boats [t+2] + visitors [t+2] + boats [t+2] * visitors [t+2]
M27	Salmon biomass + other bears + boats [t+2] + visitors [t+2] + boats [t+2] * visitors [t+2] + age-sex

We evaluated the performance of our models. We evaluated over-dispersion, only considering models with an over-dispersion parameter below 1.15 (McCullagh & Nelder, 1994). We centered continuous predictors and scaled (divided by 2 SDs), back-transforming to raw data in figures. We calculated a variance inflation factor for each covariate in all models to test for collinearity; all values were below 2, other than the multiple variables related to boat presence (t, t + 1, t +2), which were highly collinear. Accordingly, we only considered one time period's measure of boats and visitors in a single model. We assessed the relative performance of models by comparing AIC values, focusing inference on top performing models (i.e., those with Δ AIC < 2).

3.4 Results

3.4.1 Individual space-use

We identified 118 grizzly bears (73 female and 45 male) along the Atnarko river. Of those 118 bears, 80 (68%) were detected at least twice. We subset those individuals with multiple detections, which resulted in a dataset of 53 females and 27 males. Across years, individuals were detected on average 4.3 times (range = 2 - 22; SD = 4). Forty-four of these 80 (55%; 31 female and 13 male) were detected in more than one year, and thirteen (16%; 9 females and 4 males) were detected in all three years. We pooled data across years to assess any patterns of space-use among the three spatial treatments by these multiple-detected individuals.

Hierarchical clustering identified three clusters of bears based on their similarities in spatial detection histories (Figure 3.1B; with clusters delineated as B1, B2, and B3). Each cluster was comprised of individuals that were most similar to each other in their space-use. Cluster B1 was comprised of 11 individuals, all of which were detected within the 'land- and boat-based' area at high proportions of detections (9 female and 2 male). Cluster B2 was comprised of 32 individuals, all of which were detected in high proportions within the ‘land-based’ area (20 female and 12 male). Cluster B3 was comprised of 37 individuals, all of which were detected in high proportions within the ‘no-tour’ area (24 female and 13 male). Cluster B1 was comprised of individuals that were the most spatially constrained (i.e., contained the highest within-cluster proportion of individuals (82%) that were detected exclusively in one spatial treatment; those two that occurred in the land-based area did so at low frequencies, though see limitations related to detection frequencies below).The second most spatially constrained cluster was B3 (67% of individuals were detected exclusively in the ‘no tour’ area), and the least spatially constrained cluster was B2 (43% of individuals were detected exclusively in the ‘land-based’ area). In these B2 and B3 clusters, a higher proportion of individuals crossed boundaries (at a higher frequency), but mostly did so only into the adjacent land-based or reference, and not the ecotourism-dominated ‘land- and boat-based’ area.

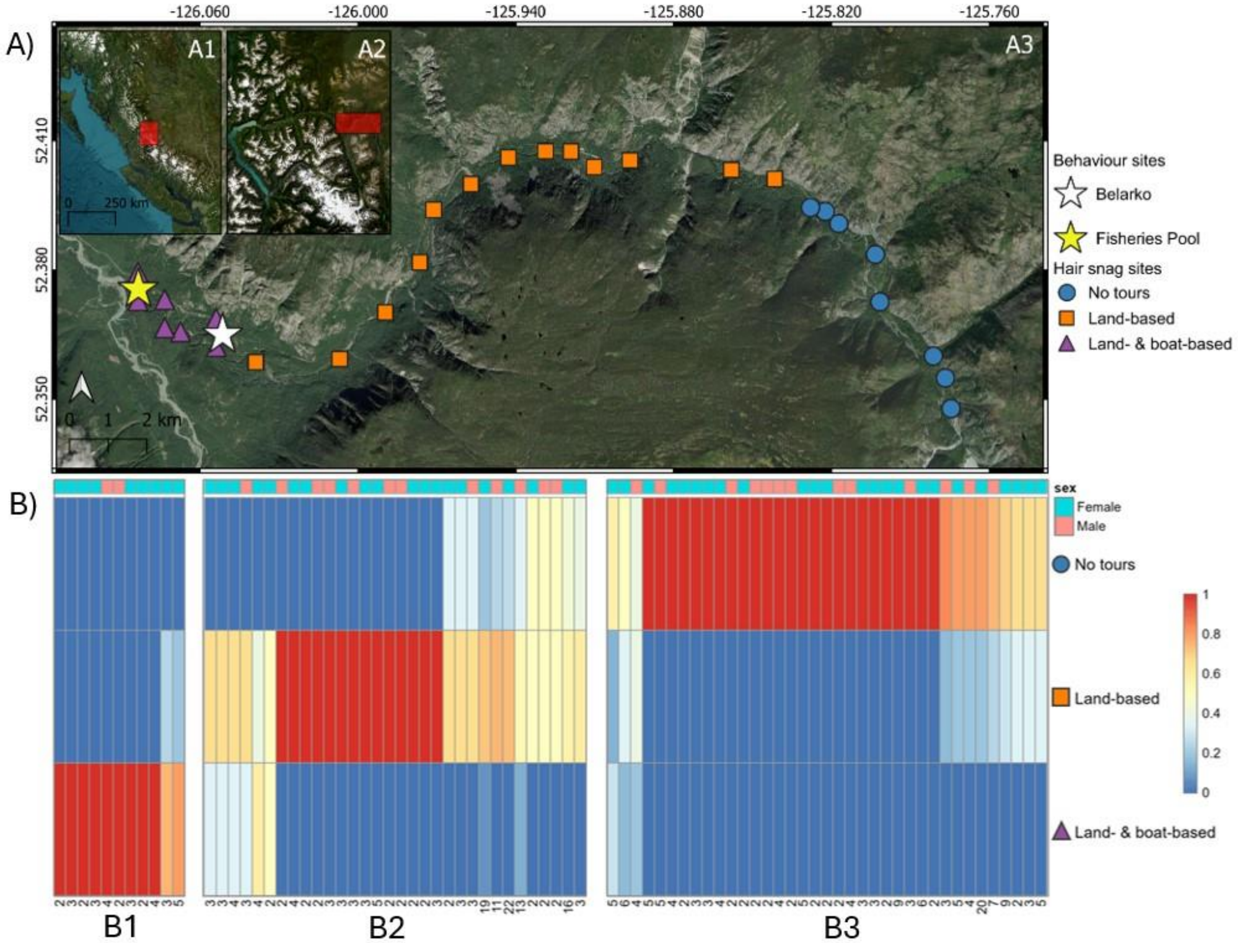

Figure 3.1 A) Atnarko River Corridor hair snag and behaviour sites. Inset A1: Pacific Coast of British Columbia, Canada, with red frame denoting Inset A2; Inset B: Bella Coola Valley and surrounding tributaries, with red frame denoting Map A3; Map A3: Atnarko River Corridor study area, including behaviour sites and hair snag sites, where hair snag sites are categorized by spatial treatment. B) Heatmap illustrates the detection histories of each individual grizzly bear. Each column represents an individual, with annotated values below each column representing detection frequencies (data were subset to include individuals that were detected at least twice; n = 80 individuals out of original 118). The colour ramp represents the proportion of detections per individual that occurred in each spatial treatment. The heatmap identifies three clusters (three

identified as optimal number of clusters via elbow method in k-means clustering), which clusters individuals with similar spatial detection histories (B1, B2, and B3).

3.4.2 Behavioural states

Multi-model inference suggested that only salmon biomass influenced behavioural states (Figure 2A). Specifically, the only evident pattern was a strong negative association (P = 0.002) between salmon biomass and the probability of alertness (Figure 2B); the top model also included whether other bears and boats (t + 2) were present but neither influenced the probability of alertness. A similar and similarly ranked model (Δ AIC = 0.002) likewise identified only a strong negative association between salmon biomass and the probability of alertness (Appendix B; Figure B3). There were no associations between any covariate in the top models and the probability that a behavioural state was fishing (Appendix B; Figure B3).

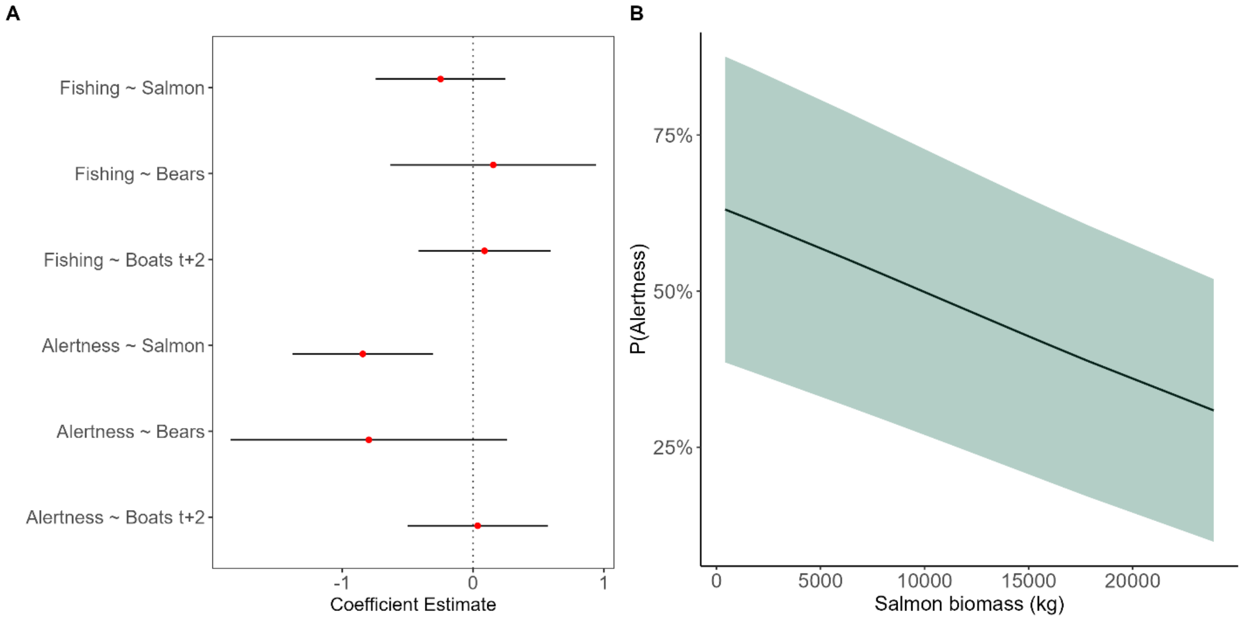

Figure 3.2 Top multinomial model (Δ AIC = 0.0) predicting ‘fishing’, ‘alertness’, and ‘other’ behavioural states among grizzly bears subject to ecotourism in the Atnarko River Corridor, Nuxalk Territory, British Columbia (2019–2021). (A) Parameter coefficients and CIs for fixed effects, centered and scaled by two standard deviations. Red dots represent parameter coefficients and black lines span 95% CIs. (B) Probability that a bear was alert as a function of salmon biomass

3.5 Discussion

We assessed whether and how a grizzly bear population might show intrapopulation variation in tolerance to ecotourism activity using both spatial and behavioural lenses. Despite the high mobility of grizzlies and the abundant salmon resources present at ecotour sites, we found that only a small subset of individuals detected at least twice (n = 11 of 80) showed spatial histories that favoured the area of pronounced human activity. Most of these individuals (n = 9 of 11) were female (Figure 3.1B). This pattern suggests that the population may include distinct subgroups that vary in their spatial tolerance of ecotourism (though, see limitations below). Our companion behavioural observations that occurred exclusively in the ‘land- and boat-based’ area considered how ecotourism intensity (number of visitors, number of boats) and environmental variables (presence of other bears, salmon biomass) might affect fishing and alertness behaviour. Our findings revealed no evidence for an effect of ecotour metrics on grizzly behaviour. Instead, we found a negative association between salmon biomass and alertness, a pattern opposite to predictions based on predation risk theory. As we explain below, such a pattern might be explained by hyperphagia, a relatively rare feeding strategy exhibited by grizzlies. Collectively, our multi-lens approach illustrates how comprehensive insight into wildlife tolerance of human activity can emerge.

We differentiated the spatial behaviour of genetically marked individuals by examining their space-use, finding three distinct subgroups that were comprised of individuals with minimal intra-cluster variation in their spatial detection histories (Figure 3.1B; with clusters delineated as B1, B2, and B3). Individuals that comprised cluster B1 were the most spatially constrained; 82% of these individual were never detected outside of the ‘land- and boat-based’ area, which represents the smallest portion of the study area (~4 km river network distance). By contrast, the least spatially constrained individuals comprised cluster B2, whereby only 43% of individuals were detected exclusively in the ‘land-based’ area (~22 km river network distance), and the remaining 57% traversed spatial treatments, with most individuals entering the adjacent reference area upstream that hosts very limited human activity. Sixty seven percent of individuals that comprised cluster B3 were never detected downstream from the ‘no-tour’ area, which hosts ~2 orders of magnitude less people than the ‘land- and boat-based area’ (Field et al., 2024). These findings suggest fine spatial scale variation.

Other case studies have suggested that human recreation can elicit individual-level variation in fine-scale space-use. For example, Huveneers et al. (2013) found individual variation in fine-scale spatial distribution among white sharks (*Carcharodon carcharias*) in response to cage-diving tourism; some individuals spent more than 60% of their time within 60m of cage-diving tourists, while others were mostly detected further than 120m away. As another example, Martin & Réale (2008b) found evidence for non-random spatial distribution of home ranges among individual Eastern chipmunks (*Tamias striatus*) of different temperaments in a protected area with high human use.

A similar pattern emerged in our system. Given the high mobility of grizzly bears, and considering the relatively small study area in the context of their home ranges (i.e., river network distance of ~35 km, which falls well within potential travel distances inside the home range of both male and female grizzly bears [MacHutchon et al. 1993]), our findings suggest the possibility of spatial segregation among individuals aligning with the spatial heterogeneity of risk. Specifically, some individuals were seldom or never detected in the areas with highest human activity, and others were more flexible in their space-use.

Sex ratios also differed among spatial treatments, likely related to human shielding. The proportion of male detections increased with distance from the area with highest human activity, suggesting a human shield effect. In this same study area, Field et al. (2024) found that camera trap detections were more likely to be male at night and when visitor numbers were low. This suggests a possibility that males detected by our hair snags in the 'land- and boat-based' were captured at night, a possibility that aligns with our infrequent observations of males in our behavioural data set (details in Methods). Although data limitations prevent detailed consideration, we also consider the possibility that individual variation in space-use is mediated by personality type, whereby bold individuals use areas with higher human disturbance and shy individuals use areas with reduced disturbance (Samia et al., 2015).

Among those individual bears that use the land- and boat-based area, human activity did not influence the behavioural metrics we recorded. Contrary to our prediction that emerged from predation risk theory, whereby bears that were tolerant enough to spatially co-occur with humans would offset risk by investing more in alertness behaviour when human activity was higher, we found no such evidence. Instead, the bears we observed in the 'land- and boat-based' area during daylight and crepuscular hours demonstrated two dimensions of tolerance: they were present, and they did not respond behaviourally to ecotourism. Nisbet (2000) defined tolerance as “the intensity of disturbance that an individual tolerates without responding in a defined way” (p. 315), and tolerance can be attributed to animals when they permit close proximity by humans without overtly responding or fleeing (Blumstein, 2016). Our ‘non-response’ (no relationship between alertness and either ecotourism metric) result suggests behavioural tolerance among those individuals that do not avoid the ecotour area. We infer that the stimuli at ecotourism sites were perceived as non-novel, predictable, specific, and low risk. However, we note that bears responded in their activity rates to the number of visitors at a weekly scale; specifically, bear activity decreased with higher visitor numbers/week (Field et al., 2024). Responses of bears to ecotour visitor numbers appear to be measurement- and scale-dependent.

Alertness behaviour varied solely as a function of salmon biomass, whereby contrary to our prediction, grizzlies were less likely to be alert when salmon availability was high. Should this be representative of patterns elsewhere in grizzly bears, this result suggests that the fitness benefits that result from increased food intake are greater than gains that result from increased alertness. We speculate that such a pattern could arise in a species that undergoes hyperphagia. This is a life history strategy marked by periods of extraordinarily intense food consumption made possible by the ability to store readily the body reserves extra calories provide (Hilderbrand et al., 2000). Notably, among females (most individuals in our observational dataset), the consumption of salmon positively correlates with multiple measures of over-winter survival and reproductive success (Hilderbrand et al., 2000) Thus, we speculate that investing in anti-predator behaviour could reduce time spent foraging at times when food is appropriately hyper-abundant and easily-acquired, thus imposing potential fitness costs (Lima, 1987). This interpretation, however, is tempered by the reality that we observed no variation in the presence of the fishing behavioural state over the range of salmon biomass. Data and theory from other contexts, however, provide insight. Notably, Repasky (1996) found support for a negative relationship between vigilance and food patch profitability in Sage Sparrows (*Amphispiza belli*) and Black-throated Sparrows (*A. bilineata*), suggesting that wintering birds near starvation are confronted with starvation versus predation trade-offs. Moreover, McNamara and Houston (1987) considered a model in which an animal can control both its probability of starvation and its probability of predation, whereby increases in food requirements will cause an animal to increase their predation risk to avoid starvation. Although as large-bodied omnivores grizzlies are at low risk of starvation, we suspect a similar trade-off might be relevant to another fitness measure (reproduction). Finally, we note that the shield-seeking subordinate age-sex classes, which comprise our behaviour data, are seemingly tolerant to real-time measures of human activity (number of visitors and boats) perhaps predispose them to allocate only modest time to alertness when salmon are abundant at the key opportunities for hyperphagia.

Learned experiences of animals through repeated exposure to a stimulus can shape tolerance to human activity, such as we observed, and has mixed implications for the management of wildlife ecotourism. On one hand, tolerance that is shaped by habituation-like processes can allow animals to better tolerate ecotour activities (Blumstein et al., 2017). On the other hand, exposure to benign human activity and associated tolerance has potential to create ecological traps if tolerant individuals later encounter humans that present a real threat (Geffory, 2015; Darimont & Shukla, 2023). Following this logic, reduced reaction to stimuli perceived as neither aversive nor beneficial (i.e., habituation [Blumstein, 2016]) could presumably cause individuals to become ensnared in conflict with humans. Not all human individuals pose the same risk to wildlife, posing a cognitive challenge in risk-perception. However, in this same population of bears, Field et al. (*in press; chapter 4*) found that grizzly bears that were exposed to ecotourism were less likely than predicted by chance to encounter subsequent conflict in communities downstream of ecotour sites. Although this result might arise from well-fed ecotour bears not needing to acquire human foods (predisposing them to conflict), its also possible that grizzlies might be as equipped to recognize different sources and levels of risk. African elephants (*Loxodonta africana*) can reliably make functionally relevant distinctions between human subcategories that differ in the level of threat they pose (McComb et al., 2014). Levey et al. (2009) similarly found behavioural flexibility and a keen awareness in Northern Mockingbirds (*Mimus polyglottos*) of different levels of threat posed at the finer scale of individual people.

Managers might also consider our results, while also acknowledging the limitations to inference. Specifically, in the apparent absence of behavioural responses, there may be concealed physiological responses. Ditmer et al. (2015) observed physiological responses (elevated heart rates) of American black bears (*Ursus americanus*) to unmanned aerial vehicles, despite a lack of observed behavioural changes. Charuvi et al. (2020) simultaneously measured behavioural and physiological responses during human approaches to incubating Masked Lapwings (*Vanellus miles*), finding that reduced flight initiation distance (generally interpreted as a sign of tolerance) was associated with greater physiological costs through longer durations of elevated heart rate. Future studies might therefore add another dimension of inquiry by incorporating physiological measures of stress as indicators of tolerance in addition to spatial and behavioural measures. More broadly, how such variation in response to disturbance affects demographic parameters such as survival and reproduction would also broaden the scope of conclusions that can be drawn from impact case studies (Gill et al., 2002). In our system, given the spatial filtering we observed, managers might now also consider limiting the number of new ecotourism sites in the future to complement considerations identified for the existing two sites based on variation in activity levels associated with human visitation, salmon biomass, and their interaction (Field et al 2024).

There are several limitations to our approach. For example, the strength of inferences related to space-use by bears with lower detection frequencies is weaker than those we detected more often. To address this, we assessed whether the optimal number of clusters changed as we subsampled our data to include only those individuals that were detected using higher thresholds for 'minimum detection number' (3 and 4), finding the optimal number and general spatial characteristics of clusters was unchanged (Figures B4-B7). Additionally, an unequal number of hair snags per treatment might bias the number of individuals detected, whereby more snags might detect more individuals. We note, however, that across years, more individuals were detected in the 'no tour' area (n = 62 out of 118) than in the 'land- and boat-based' area (n = 59 out of 118), despite there being less snags in the 'no tour' area (13 snags in the 'land-based' area [~22 km river network distance], and 8 in the 'no tour' [~9 km river network distance] in 2021). Moreover, the lack of additional information about other ecological factors (e.g., conspecific competition for optimal fishing locations; home range centers) compromises the inferences we can make about whether space-use is directly linked to individual tolerance. Spatial data may include samples that are biased to those individuals with home ranges that include or are centered on the river valley bottom, where probability of detection is a decreasing function of distance from home range center (Efford and Mowat 2014). However, the river network distance of our study area falls well within potential travel distances inside the home range of both male and female grizzly bears in coastal temperate rainforests (MacHutchon et al. 1993), especially considering the relatively easy movement along riparian routes. An additional limitation is our lack of behavioural state data from sites without ecotourism. We suspect that we were able to collect such few data in the area related to the fact that researcher presence was novel, unpredictable and potentially perceived as risky for bears in the land-based and especially reference areas with lower human activity. Despite the lack of behavioural state data, we know bears were present, as evidenced by our genetically-informed spatial data described above, as well as camera trap data (Field et al., 2024). Nonetheless, given these limitations, we note that we could not attribute measures of tolerance to individuals based on their space-use alone. Instead, we drew on our spatial data to create a visualization tool to illustrate a possibility that not all bears in the corridor are using the ecotour area. Doing so, however, illuminates a key point: behavioural studies may be collecting data solely from individuals that tolerate human presence.

Our work has broader implications for management and wildlife conservation. Investigating more than one modality of wildlife response to disturbance broadens the scope of conclusions that can be drawn because different antipredator responses reflect different aspects of predation risk management (Uchida & Blumstein, 2021). Such an approach can provide richer insight for managers. When our behavioural and spatial data were considered in tandem, our work suggests a ‘filtering of tolerance’ that might not otherwise be detected if we examined only the behavioural states of those individuals that were present. Put another way, considering only the absence of association between behavioural states and ecotourism metrics in isolation from spatial data could suggest a grizzly bear population tolerant of ecotourism. This was not the case. Indeed, important insight can emerge when behavioural data under risky contexts are interpreted in tandem with information about intrapopulation variation in space-use within and beyond such areas. More broadly, research does not often distinguish between whether individuals decrease behavioural response towards humans because they are tolerant, or because shyer individuals move away from disturbed areas (Martin & Réale, 2008a). Our conclusions support Bedjer et al.'s (2009) argument that placing emphasis on only one modality of response effectively limits the conclusions that can be drawn from the investigation. Specifically, our work contributes to this concept by highlighting that in addition to behavioural data, concurrent spatial inquiry can provide richer insight into the extent to which animals might be disturbed.

Chapter 4. Grizzly bears detected at ecotourism sites are less likely than predicted by chance to encounter conflict

Adapted from: Field, K. A., Moody, J. E., Levi, T., Darimont, C. T. *In-press.* Grizzly bears detected at ecotourism sites are less likely than predicted by chance to encounter conflict. *Canadian Journal of Zoology.*

4.1 Introduction

Multiple ecological and social processes can predispose wildlife to conflict with humans. Among them, temporal and spatial dynamics of wild and human-associated food availability are important across a range of taxa and geographic contexts (Nyhus, 2016). For example, high proportions of pasture combined with low proportions of cropland largely explained spatial patterns in wolf (*Canis lupus*) depredation on livestock across wildland-farm landscapes in Wisconsin (Treves et al. 2004). Moreover, human-wildlife conflict in the form of crop raiding by mountain gorillas (*Gorilla beringei beringei*) in Uganda was influenced by human-associated food availability outside a protected area (Seiler and Robbins 2016). In Alberta, Canada, anthropogenic food sources such as bird feeders, compost, and cultivated fruit trees may contribute disproportionately to encounters between people and coyotes (*Canis latrans*) (Murray et al. 2015). Food provisioning of great white sharks (*Carcharodon carcharias*) during cage dives has been associated with increased chance of divers, beachgoers, and swimmers being attacked (Shannon et al. 2017). Lion (*Panthera leo*) attacks on people and livestock in Africa were higher in areas of lower prey abundance or when native prey populations were more difficult to find (Patterson et al. 2004; Inskip and Zimmermann 2009;). Moreover, among grizzly bears (*Ursus arctos horribilis*) that feed on salmon (*Oncorhynchus* spp.) in British Columbia, Canada, conflict kills of grizzlies were 20% higher for each 50% decrease in annual salmon biomass (Artelle et al. 2016).

In addition to association with foods, wildlife ecotourism could theoretically be associated with conflict if it increases tolerance of humans by wildlife. Although wildlife can avoid people in space or time as a risk reduction strategy (Palmer et al., 2022; Tucker et al., 2018), thereby also likely minimizing conflict, some populations or individuals that comprise them can tolerate benign human activity like wildlife viewing. Some species or reproductive classes within species might in fact use humans as protective ('human shields'; Berger, 2007; Field et al., 2024; Nevin & Gilbert, 2005). Any associated tolerance of humans among these individuals might thus predispose them to engage in risky behaviour and subsequently encounter conflict with humans. Indeed, behavioural changes associated with habituation to tourists have been linked with increased boldness (Geffroy et al. 2015), suggesting that increased tolerance to benign human activity makes wildlife more vulnerable to negative interactions with people. In considering a global review of animals subject to ecotourism, Kc et al. (2022) suggested that communities adjacent to ecotourism in protected areas may face frequent, novel, and severe conflict in the form of livestock predation or attacks on people, a proposition not widely subject to empirical testing.

Here, we examine a case study in which the distribution and abundance of foods, as well as tolerance of humans, might underlie a pattern of conflict. In the unceded Territory of Nuxalk First Nation, located in what is now also known as the central coast of British Columbia, Canada, well-established and popular grizzly bear ecotourism occurs along the salmon-bearing Atnarko river in Tweedsmuir Provincial Park; approximately 41-58 km downstream, conflict occurs in the lower Bella Coola Valley (i.e., in or between the communities of Bella Coola and Hagensborg), an area with human-associated food attractants and a hotspot for grizzly-human conflict within British Columbia (Artelle et al., 2016). Given the high mobility of grizzlies, and responding to questions within communities as to whether bears subject to ecotourism might be commonly involved in conflict, local managers sought an assessment of the available evidence. We thus addressed the hypothesis that grizzly bear presence at ecotourism sites increases the probability it subsequently encounters conflict with humans at downstream sites due to higher tolerance of humans. Specifically, we screened data sets comprised of bears genetically identified via non-invasive hair-snagging at ecotour sites (and beyond) and those that were captured after encountering conflict with humans in adjacent areas within the Bella Coola Valley (Figure 4.1). We then considered two alternative scenarios, which relied on mutually-exclusive assumptions, to assess the evidence, each with associated analyses. Our first assumption ('Scenario 1', below) considered that all bears in the area are free to mix; that is, ecotour bears and non-ecotour bears comprise part of a larger, mobile population capable of occurring at ecotour sites, in and around sites of human occupation and activity (i.e. 'downstream sites' of conflict on rural properties or townships) and the larger surrounding areas (Figure 4.1). Our associated probability approach likewise considered individual bears as freely-mixing constituents of the entire population. The second scenario ('Scenario 2', below) considered the 'upstream' and 'downstream' populations as spatially-segregated. That is, ecotour and non-ecotour bears comprise an 'upstream' population in a region approximately 41-58 kms upstream from the downstream area where conflict occurs (Figure 4.1). This assumption enabled us to use a Fisher's exact test to examine whether there was a relationship between conflict occurrence and whether individual bears were detected in the ‘ecotour’ area or the ‘upstream’ area prior to conflict.

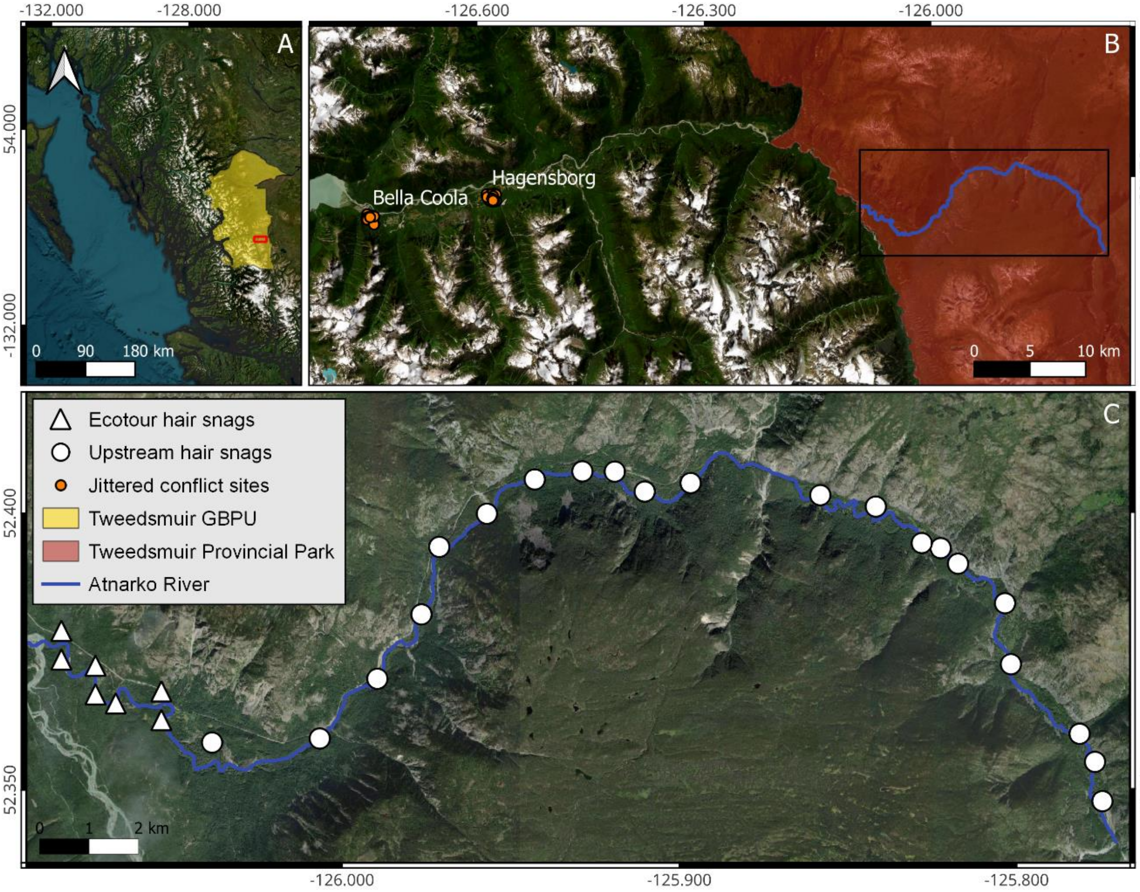

Figure 4.1. Bella Coola and Atnarko Valleys and surrounding areas, Nuxalk Territory. Map A displays the central coast of British Columbia, Canada, and the boundary encompassing the British Columbia Provincial Tweedsmuir Grizzly Bear Population Unit (GBPU), as well as the red rectangular ‘area of interest’ denoting Map B (referred to in Results calculations). The black rectangle in Map B denotes the hair snag sampling array, which is displayed in Map C. We genetically identified grizzly bears that encountered conflict in the Bella Coola Valley (‘downstream’ conflict area; n = 30; orange circles denote jittered locations of sampling areas, all

of which had unknown geographical coordinates but occurred in Hagensborg, Bella Coola, or in between) and via our hair snags upstream in the nearby Atnarko Valley (n = 118; white triangles and circles represent 'ecotour' and 'upstream' sites, respectively). Map attribution: © Esri — Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community. Spatial Reference System EPSG:3005 - NAD83/BC Albers. Tweedsmuir GBPU and park shapefiles were retrieved from British Columbia Data Catalogue.

4.2 Methods

4.2.1 Field Methods

Our hair snag sampling was originally designed to test hypotheses related to the potential effects of ecotourism on grizzly bear activity (see Field et al. 2024), and before community-driven questions about conflict catalyzed this research. Specifically, we had deployed passive, non-baited hair snag (Woods et al. 1999; Proctor et al. 2010) to genetically identify individuals as approved by University of Victoria Animal Use Permit 2019-004 and following guidance from the 'Canadian Council of Animal Care: Wildlife' (https://ccac.ca/Documents/Standards/Guidelines/CCAC_Guidelines-Wildlife.pdf). Areas hosting abundant natural attractant such as salmon provide an appropriate and efficacious context for non-baited, non-invasive hair collection because the snags likely do not affect the distribution and movement of bears (Wold et al., 2020). Snags (n = 28 in 2019; n = 29 in 2020; and n = 28 in 2021) were set of barbed wire at ~0.5 m height (Quinn et al., 2022) every ~0.5 - 2 km along the Atnarko river across well-worn bear trails or riverside banks where bears or their sign (i.e., tracks, scat) were commonly observed by local wildlife managers and technicians from the

Nuxalk Fisheries and Wildlife Department, who survey the river and its banks each week or more, over many years prior to this work. The distance along the river from the most downstream hair snag to the most upstream hair snag was ~36 km. Sites occurred in riparian habitat where bears commonly travel, which is bounded to the east by the Interior Douglas-Fir biogeoclimatic zone of the Fraser Plateau-Western Chilcotin Ranges, and to the west by the Coastal Western Hemlock biogeoclimatic zone of the Northern Pacific Ranges. The valley is steep-sided, bounded by cliffs and talus slopes with a pronounced floodplain along the Atnarko River. We actively monitored 'ecotour' and 'upstream' hair snag sites (Figure 4.1) over three years during the late summer and autumn salmon runs (113 days in 2019 from July 15 to November 5; 101 days in 2020 from July 25 to November 3; and 103 days in 2021 from July 21 to November 1). Across years, crews sampled hair on average every 9 days ($\bar{x}$ = 8.6 days in 2019, $\bar{x}$ = 9.0 days in 2020, and $\bar{x}$ = 8.8 days in 2021), collecting 1,806 samples. We subsampled high-quality samples (with abundant guard hair; n = 713) to identify individuals using genetic data (see below). Our sampling window (~14 weeks each year) represented a considerable portion (approximately two thirds) of the estimated active, non-denning period of grizzlies in this area (Blood 2003), and conflict samples were collected during the same summer and autumn months during which we conducted field sampling.

We defined conflict samples as those hair samples collected by British Columbia Conservation Officer Service (BCCOS) from captured (i.e., relocated or sent to rehabilitation) or euthanized bears. Specifically, BCCOS trapped or killed bears when there was perceived risk to safety and property, and often related to unsecured food attractants. We obtained these samples under a research agreement with the British Columbia Ministry of Forests, Lands and Natural Resource Operations Fish and Wildlife Branch, and genotyped them for potential matches with hair samples collected in upstream and ecotour areas. Specific spatial coordinates related to conflict samples from this 'downstream' area were not available. Conflict samples were known to be attributed to (or in between) the communities of Bella Coola and Hagensborg, approximately 58 and 41 km downstream from the ecotour zone, respectively, and also occurring at the valley bottom (Figure 4.1). We analyzed 15, 13, and two conflict samples that were collected from July to November in 2019, 2020, and 2021, respectively. These windows of conflict samples aligned with our hair-snagging deployment (above).

4.2.2 Genetic identification of bears detected via field sampling and conflict sampling

We screened for genetic matches between individual bears that encountered conflict in the Bella Coola Valley and grizzly bears we detected previously (in same or previous years) via hair snags further upriver. All samples from the field and among the conflict sampling set were sent to Wildlife Genetics International (Nelson, BC), where information from seven microsatellite loci plus a sex marker revealed individual identity, sex, and species from hair samples. The laboratory procedures and methods used to minimize genotyping errors are detailed in Paetkau (2003). Specimens collected via hair snags are vouchered at the Applied Conservation Science Lab, University of Victoria.

Among hair snag samples, we identified 118 grizzly bears (73 female and 45 male) along the Atnarko river. Of these 118 individuals, 34 (28%; 24 female, 10 male) were detected in the ecotour zone at least once. Thirteen ecotour bears (11%; 10 female, 3 male) were detected in the snags upstream of the ecotour sites, and another 84 (71%; 49 female, 35 male) exclusively upstream (Figures 1 and 2). Of hair-snagged ecotour bears, 1 (female) of 34 (3%) encountered conflict in the Bella Coola Valley over our three season sampling period. The other 29 individuals that encountered conflict (18 female, 11 male) had been detected at neither ecotour nor upstream hair snags in the Atnarko Valley (Figure 4.2). Such a pattern suggests that ecotour bears are not commonly encountering conflict, but alone this approach does not consider the reality that the non-ecotour bear population is much larger, and that its relative size compared to the ecotour bear population could underlie the difference in proportions involved in conflict.

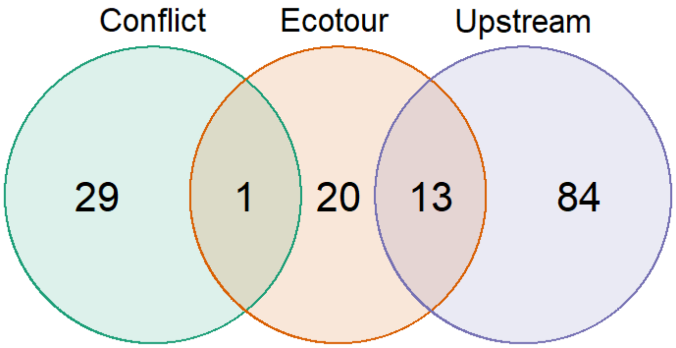

Figure 4.2. Genetic matches between grizzly bears detected via hair snags (at ‘ecotour’ and ‘upstream’ sites) and conflict sampling (from ‘downstream’ areas comprised of human communities downstream of ecotour area).

Given the distance between ecotour and downstream conflict areas, and to inform analytical considerations, we assessed the potential mobility of grizzlies in the region by drawing on our modest recapture data from genetically-tagged individuals (n = 81 recaptured individuals; Appendix C; Figure C1). Specifically, we calculated the distance between the two furthest sites at which each recaptured individual was detected across years. To do this, we calculated the river network distance (i.e., distance along the linear river feature) to account for preferred travel routes by bears during the salmon spawning season. Our bear movement data suggest that the distances bears travel varies (Appendix C; Figure C2), with some individuals detected across considerable distances (including the one individual that traveled the 47.8 km distance from the ecotour area to the downstream area of conflict), as well as individuals redetected within the 'ecotour' and 'upstream' areas (Figures 1 & S2). Such a varied pattern among individuals supports our consideration of both assumptions: a freely-mixing population and a spatially-segregated population, comprised of 'upstream'/'ecotour' population and 'downstream' sub-population.

4.3 Analysis

4.3.1 Accounting for uncertainty in raw detection data

Estimation of total 'ecotour' population of grizzly bears

Recognizing that we might not have detected all individuals using the ecotour sites with hair snags, we used jackknife and bootstrap methods to estimate the total 'population' of individuals using the ecotourism area. Specifically, whereas we assumed bears using ecotourism sites are well sampled by our hair-snagging approach and likely provide a representative account of individuals (see Wold et al. 2020), we nonetheless used the 'vegan' Community Ecology R package version 2.6-4 to estimate the total extrapolated number of individuals using a species accumulation curve (applied to individuals, in our case). The curve illustrates how the number of unique individuals detected accumulates as additional sampling events are included. This method provides an estimate of the ecotour bear population by extrapolating the observed accumulation trend. Whereas this approach is commonly used to estimate the number of unobserved species and adding them to an observed species richness in a community (Palmer 1990), we applied this concept to re-sampling of individuals. Using this approach, the total number of ecotour bears as estimated by bootstrapping and jackknife ranged from 41.3 (SE = 1.9) to 49.8 (SE = 3.9), respectively, as estimated using the ‘specpool’ function in the ‘vegan’ Community Ecology R package. These estimation approaches suggested that the 34 ecotourism individuals identified comprised a large proportion (68-82%) of the total number of bears subject to ecotourism, but there were likely individuals not detected for which we needed to account in subsequent analytical steps.

Some of the undetected individuals might arise from potential sources of biases in the form of possible differences in avoidance of hair snags among individuals. For example, Sawaya et al. (2012) reported that lure-scented hair traps under-sampled male brown bears but were unbiased for female brown bears and black bears (*Ursus americanus*) of both sexes. Beyond sex, detectability via non-invasive genetic sampling can also vary based on ‘trap-happy’ and ‘trap-shy’ responses following first capture (Zarnoch, 1979), capture heterogeneity due to individual differences (Boulanger et al., 2008), and seasonal effects (Boulanger et al., 2004). In the absence of bait and with the use of a non-invasive sampling technique, however, we considered detection heterogeneity minimal, and unlikely that the detection of an individual would influence the likelihood of subsequent detections (Wirsing et al., 2018). Moreover, using paired camera and hair traps, Wold et al. (2020) found a high proportion of bear approaches to wires that led to contact with the wire, suggesting the hair sampling method is generally unbiased. Spatial effects may include samples that are biased to those individuals with home ranges that include or are centreed on the river valley bottom, where probability of detection is a decreasing function of distance from home range center (Efford & Mowat, 2014). However, the Atnarko river features predictable patterns in salmon spawning timing during our sampling window and we suspect few individuals of this highly mobile species would forgo this resource during hyperphagia (Connors and Atnarko Sockeye Recovery Planning Committee 2016).

Using Bayes' theorem to account for imperfect detection of ecotour bears

Whereas only one detected ecotour bear encountered conflict, our ability to identify bears that encountered conflict as ecotour bears is limited by our imperfect ability to detect all bears that used the ecotour zone (*Estimation of 'ecotour' population of grizzly bears*; above). To estimate how many of the 30 bears that encountered conflict could have used the ecotour zone, and reflecting our uncertainty in the true number of bears that used the zone, we used Bayes' theorem to estimate the probability that a bear is an ecotour bear, *given that it engaged in conflict*:

$$\Pr(ecotour\ bear \mid conflict\ bear) = \frac{\Pr(conflict\ bear \mid ecotour\ bear)\ \cdot\ \Pr(ecotour\ bear)}{\Pr(conflict\ bear)}$$

The probability of conflict given that a bear engaged in ecotourism, $\Pr(conflict\ bear \mid ecotour\ bear)$, is 1/34. This statement is based on our observation that 1 out of 34 detected ecotourism bears engaged in conflict. $\Pr(ecotour\ bear)$ is approximated by the number of bears that visited ecotourism relative to the unknown total population of bears. We detected 34 bears using ecotourism, but we drew upon the observation that there may have been up to 16 undetected ecotour bears (i.e., the difference between ~50 individuals, as estimated by the higher jackknife estimation, minus the 34 individuals detected at ecotour sites). Finally, we estimated $P(conflict\ bear)$ as the number of bears that engaged in conflict (i.e., 30), relative to the total number of bears in the population. If E is the number of ecotour bears from 34 (observed value of detected bears at ecotour sites) to 50 (highest estimate calculated via resampling) and N is the total number of bears in the population, the calculation becomes equation 1:

Equation 1

$$P(ecotour\ bear \mid conflict\ bear) = \frac{\frac{1}{34} \cdot \frac{E}{N}}{\frac{30}{N}}$$

$$= \frac{E}{34 \cdot 30} = \frac{E}{1020}$$

If the true number of ecotour bears (E) was 34, as observed, the probability that a bear had used the ecotourism site given that it engaged in conflict is 3.3%. At the upper level of the jackknife estimate of ecotour bears (E; i.e,50), this probability increases to 5%. We repeated this calculation for all potential round numbers of ecotour bears between 34 and 50 (Figure 4.3A).

At a value of $E = 50$, we estimated that 1.47 of the 30 bears involved in conflict were ecotour bears (Figure 4.3B). Thus, even if 16 bears went undetected by our snags in the ecotour zone, the best estimate is that between 1 and 2 bears that encountered conflict were ecotourism bears. To correct for the possibility of falsely attributing all 29 non-ecotour conflict bears to the non-ecotour group, we repeated the probability approach based on the possibility that two (rounded from 1.47) of the 30 bears that encountered conflict could have been bears that used the ecotour zone but were not detected doing so (see Results).

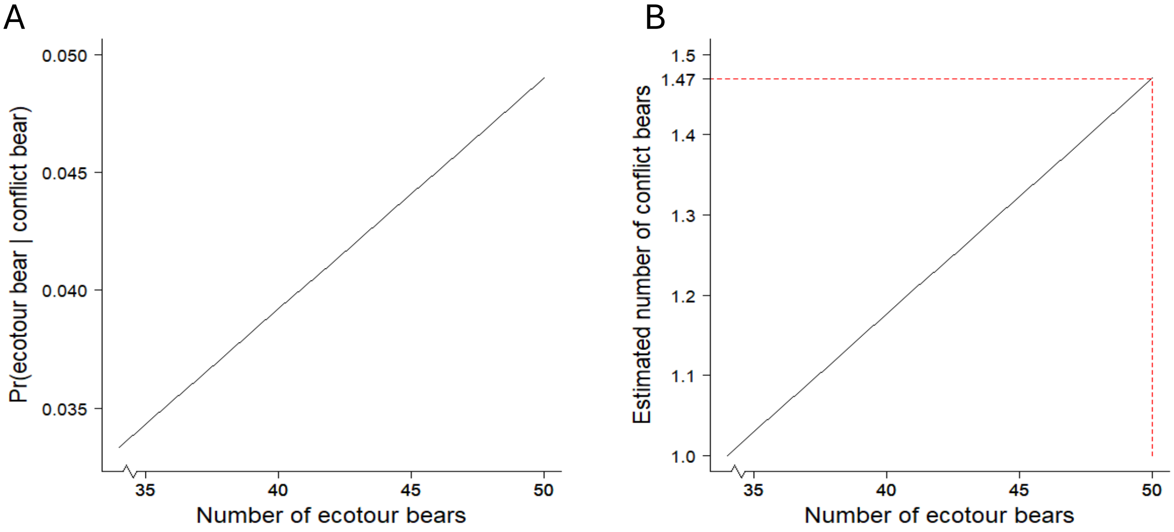

Figure 4.3. Output from Bayes' theorem calculations to account for up to 16 undetected ecotour grizzly bears to estimate the probability that a grizzly bear is an ecotour grizzly bear, given that it engaged in conflict (Panel A); and the outcome of equation 1 (see Methods) over the 34 to 50 range of possible undetected ecotour grizzly bears, required to estimate the expected number of grizzly bears that encountered conflict are also ecotour grizzly bears. At value of 50, we estimated that 1.47 ecotour grizzly bears were involved in conflict (Panel B), which we rounded to 2 in the subsequent probability analysis (below).

4.3.2 Probability approach to estimate whether ecotour individuals occurred more by chance among conflict samples (Scenario 1)

We used a probability approach to ask whether ecotour bears were more or less represented among conflict samples than predicted by chance. We define 'by chance' as the probability of ecotour bears encountering conflict being the same as the probability of those bears not detected in the ecotour area. Although our spatial data are limited, this approach assumes that ecotour bears and non-ecotour bears (detected genetically or not) collectively comprise a much larger, mobile population capable of occurring in towns, at ecotour sites, and the surrounding areas. We constructed a probabilistic argument by asking how large the unknown *non-ecotour* bear population would have to be to have observed *at least* 28 conflicts (the difference between 30 conflict samples minus an estimate of 2 ecotour individuals among these conflict samples) if the probability of conflict were equal to that observed with ecotourism bears (1 of 34).

To assess whether 28 non-ecotour bears could have been observed in conflict by chance given the observed rate of conflict among ecotour bears (1/34), we modeled the number of non-ecotour bears that encountered conflict, X, as a binomial random variable. The probability of conflict is given by the observed proportion of conflict among ecotour bears (1/34), and the true non-ecotour bear abundance, N, which is unknown.

$X \sim \text{Binomial}(N, 1/34)$

The cumulative distribution function (CDF) of X, $F_x(x)$, describes the probability that random variable X takes a value less than or equal to x:

$F_x(x) = P(X \leq x)$

Accordingly, we computed $1 - F_x(27)$ to determine the probability that at least 28 non-ecotour bears engaged in conflict while varying the unknown non-ecotour bear abundance, N.

Drawing on population density estimates for reference points

To provide reference points for comparing bear abundance along the cumulative distribution function, we drew on available density estimates for grizzly bears in the region. How many additional and unsampled individuals occurred in sampled and unsampled regions in the ‘area of interest' and the much larger Tweedsmuir Grizzly Bear Population Unit was key to interpretation. Specifically, we considered the possibility that so few ecotour individuals encountered conflict because the total population of bears, comprised of individuals equally likely to encounter conflict, was sufficiently large so that the relatively small number of ecotour bears could have occurred by chance given the potentially larger number of bears not detected at ecotour sites. That is, with high bear abundance beyond the ecotour sites, more conflicts would be expected in this group, but this does not necessarily indicate a higher frequency of conflict among non-ecotour bears.

We drew on density estimates from the grey literature and in a manuscript undergoing peer review. The former reported a point estimate, based on provincial government expert model (22 bears/1000 km^2; Environmental Reporting British Columbia). We applied this density estimate to an area within the Tweedsmuir Grizzly Bear Population Unit (GBPU) that is attributed by the province as 'area of usable habitat' (Environmental Reporting British Columbia; ~16,663 km^2), which excludes 'fresh water', 'salt water', 'glaciers and snow' as delineated by the province's *Baseline Thematic Mapping Present Land Use Version 1 Spatial Layer*. We also applied this density estimate to a smaller region (~2,460 km^2), which we refer to as our immediate 'area of interest' (rectangle in Figure 4.1), which roughly centred our samples and was bounded by topographic features that define the greater Bella Coola and Atnarko river valleys and some of their tributaries. Across these same two scales, we also considered a lower but empirically-derived mean estimate of density (10.2/1000 km^2; 95% CI: 9.6-11.1) from an 28,500 km^2 area of the central coast of British Columbia, which included our area of interest, some of the Tweedsmuir GBPU, and adjacent areas to the northwest (Artelle et al.[1]).

4.3.3 Fisher's exact test (Scenario 2)

We used Fisher's exact test to examine whether there was an association between conflict occurrence and bear type (i.e., ecotour and non-ecotour bears). This approach relied on the assumption that ecotour and non-ecotour bears comprised a population in a region distinct from the area where conflict occurs. This test was appropriate for our data given small sample size and low occurrences of conflict events among ecotour (1 of 34) and non-ecotour bears (0 of 84). We created a 2x2 contingency table to categorize the data according to bear type and conflict occurrence, and tested the null hypothesis that there was no association between bear type and conflict occurrence.

4.4 Results

Our approach considered the premise that so few ecotour individuals occurred as conflict bears because the total population, comprised of individuals equally likely to encounter conflict, was sufficiently large so that the relatively small number of ecotour bears could have occurred randomly and at no greater proportion than among bears not detected at ecotour sites. If non-ecotour bears encounter conflict at the observed rate of 1/34 for ecotour bears, our results suggested that the probability of observing at least 28 non-ecotour bears that engaged in conflict is nearly zero when true bear abundance is low; the probability increases to 5% as bear

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[1] Artelle K., Sun, C., Bourbonnais, M., Reynolds, J., Darimont, C. Unpublished manuscript. Combining Spatial Capture-Recapture and Network Analyses to inform land-use planning: insights from grizzly bears in the Great Bear Rainforest.

abundance reaches 674 bears (Figure 4.4). That is, the unknown non-ecotour bear population would have to be 674 to have observed at least 28 conflicts if the probability of conflict were equal to that observed with ecotourism bears (1 of 34).

We assessed how this 674 bear scenario (the estimate under which we would expect the pattern we observed to have occurred by chance) compared to a range of plausible estimates for population size calculated at two scales and using two information sources on density (Methods). Drawing on these estimates, the number of bears in a total population across this variation in density and scale potentially subject to conflict varied from 25 to 368 bears. Even the highest estimate, derived from calculating over an enormous area over 16,000 km^2 (far beyond the spatial capability of lifetime movements by males) was only approximately half the 674 bear scenario under which we would expect the pattern of ecotour bears involved in conflict to have occurred by chance (Figure 4.4).

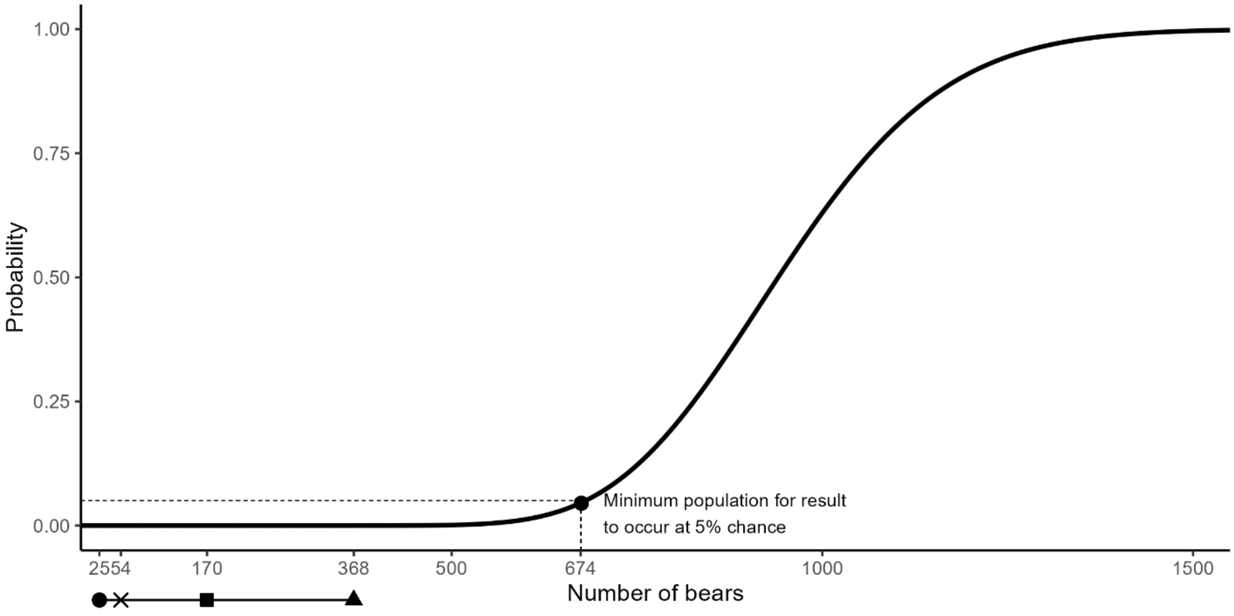

Figure 4.4. Cumulative distribution function used to compute the hypothetical number of non-ecotour grizzly bears that would need to comprise the population in order for 28 of 30 conflict

grizzly bears to have not been associated with ecotourism, given the observed proportion of 1 of 34 ecotourism grizzly bears engaged in conflict (i.e., the 'result' annotated above). For this probability to exceed 5% (dashed reference line), the non-ecotour grizzly bear population would have to be greater than 674, which greatly exceeds the plausible range of grizzly bear abundance. Solid reference line below the X-axis represents a range of population estimates among grizzly bears potentially encountering conflict: circle and square = derived from empirical density estimate from the central coast of British Columbia (Artelle et al.[2]), applied to our area of interest (~2,460 km^2) and Tweedsmuir GBPU (16,663 km^2) (Province of British Columbia Data Catalogue); x and triangle = derived from point density estimates by provincial government (Environmental Reporting BC), applied to our area of interest and Tweedsmuir GBPU.

In analysis scenario 2, we used Fisher's exact test to determine if the observed differences in conflict rates between ecotour and upstream bears were statistically significant. This complementary approach, which considered the sampled bears only and simply assessed the relationship between bear type (ecotour and non-ecotour) and the occurrence of conflict revealed no evidence of association (Fisher's exact test; $p = 0.288$). The 95% confidence interval for the odds ratio ranged from 0 to 15.79 with an estimated odds ratio of 0. Simply put, this tells us that there are similar conflict rates across both ecotour and upstream groups of bears.

4.5 Discussion

Our findings revealed no support for the hypothesis that bears that experienced ecotourism were later likely to encounter conflict. Our genetic screening approach identified only a single bear

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[2] Artelle K., Sun, C., Bourbonnais, M., Reynolds, J., Darimont, C. Unpublished manuscript. Combining Spatial Capture-Recapture and Network Analyses to inform land-use planning: insights from grizzly bears in the Great Bear Rainforest.

that encountered conflict among the 34 samples that were associated with ecotourism. Likewise, our probability approach, which considered the larger area's population (Scenario 1) as well as the uncertainty in the number of total bears exposed to ecotourism, offered no evidence of ecotourism predisposing bears to subsequent conflict. In fact, owing to the large difference between the range of population estimates and a calculated population at which it is possible that the pattern we observed arose by chance, ecotourism bears in fact appear as conflict individuals less than that predicted by chance. Finally, the Fisher's exact test applied to Scenario 2 suggested no association between bears exposed to ecotourism and those later detected among conflict samples.

There are several explanations for these results. First, those individuals involved in conflict might simply have home ranges that include a higher proportion of human-dominated areas (and far downstream of ecotourism areas). In other words, its unsurprising that individuals present at ecotourism sites in the Atnarko Valley did not frequent areas in the downstream Bella Coola Valley, and thus be subject to conflict. We recognize, however, the large movement ability of grizzlies, especially of males, and that rural properties and townships (sites of conflict) exist in, and all along, the valley bottoms, making long-distance travel less energetically-expensive. Moreover, the distance from the ecotour area to Hagensborg and Bella Coola (~41 and 58 km, respectively) falls well within potential travel distances inside the home range of both male and female grizzly bears in coastal temperate rainforests (MacHutchon et al. 1993), especially considering the relatively easy movement along riparian routes. Accordingly, we find this simple spatial explanation plausible but not entirely comprehensive in that by itself it cannot exhaustively discount the hypothesis that ecotour bears are more likely to encounter conflict. Accordingly, we also took a conservative approach, which incorporated uncertainty, by rounding up the number of ecotour bears potentially involved in conflict, and considered even the very highest estimates of the entire bear population in our probability framework. Despite these steps, which increase the likelihood of detecting evidence for an association between ecotourism and conflict, no such evidence emerged. In fact, our results suggested bears that used the ecotour zone were in fact less likely to encounter subsequent conflict.

Although our data can neither support nor refute the following interpretation, we also consider an explanation related to the relationship between food acquisition and risk-taking. Specifically, ecotourism and upstream sites occur at particularly dense aggregations of spawning salmon in the Atnarko River (Atlas et al. 2021). Accordingly, we speculate that bears that access the area can acquire the foods they require during the energetically-demanding season, and need not search for human-associated resources in the downstream communities, which are a considerable distance away. We speculate that this may provide an explanation for not detecting upstream bears in conflict. Such an explanation aligns with theory in that conflict patterns are driven be regional food supply (Gunther et al. 2004; Baruch-Mordo et al. 2014; Artelle et al. 2016).

There are several limitations to our approach. One, it is possible that those individuals more likely to be detected via hair snags might be somehow less likely to engage in conflict. We find this unlikely, given that hair snags themselves might be perceived by bears as human-associated items. On the other hand, hair-snagging can miss cubs with heights less than their 0.5 m arrangement, and these cubs – that mature around ecotourists – might be later prone to encounter conflict. We also find this explanation unlikely, given the typical three-year association between mothers and cubs combined with the three-year duration of this study. An additional limitation is the possibility that not all bears that encountered conflict were reported to BCCOS. We acknowledge that the conflict samples originated from a subset of all bears that encountered conflict with humans. We have no reason to believe, however, that this subset could have been skewed to include disproportionately more or less individuals subject to ecotourism. Future studies may consider conducting interviews to estimate the proportion of individuals that are reported within the total population of bears that encounter conflict. We also acknowledge the possibility that we did not detect all ecotour bears, and that an underestimate of ecotour bears could reflect an underestimate of the number of ecotour bears involved in conflict. To account for this uncertainty, our probability approach was based on the possibility that two (rounded from 1.47; see *Using Bayes' theorem to account for imperfect detection of ecotour bears*) of the bears that encountered conflict could have been unobserved ecotour bears. Finally, heterogenous distributions of wild and human-associated foods across the landscape may drive movement and thus differentially predispose grizzly bears to conflict. Although we recognize that movement patterns by individual bears may predispose some individuals to encountering conflict, our presence-only data, gathered from hair snags exclusively deployed in the ecotour areas and those further upstream (i.e, further from downstream conflict areas; Figure 4.1) provide only limited inference into bear movement. Future studies may therefore consider incorporating resource availability data in analyses, and sample bears across a broader extent of the landscape (i.e., including in areas immediately adjacent to areas of conflict, as well as in ecotour and upstream areas). Such a study design, which would aim to yield insight into the spatial origin of bears that encounter conflict, might use a grid hair snag array throughout the area of interest, rather than a linear hair snag array along the valley bottom.

Our probability approach relied on a central assumption. Namely, we assumed that all individuals within the 'area of interest' (Figure 4.1) could encounter both areas with ecotourism and where conflict occurred. Our result was conservative in that we considered an area as large as the Tweedsmuir Grizzly Bear Population Unit (16,663 km^2, compared with our area of interest of 2,460 km^2), which estimates about half the grizzly bear abundance as the minimum population required in order for our result to have occurred by chance, as derived from our probabilistic approach. We acknowledge that our approach is constrained by a lack of behavioural data on genetically-identified individuals. For example, we do not have information on the personality traits, measures of potential tolerance, or past experiences of the bears in our study. This limitation means that we cannot directly assess the extent to which individual behavioural tendencies contributed to the likelihood of conflict.

Our finding that ecotourism does not appear to contribute to conflict in this region might not be the case in other contexts. Human behaviour and characteristics of ecotourism management, for example, could influence outcomes. For example, ecotourism that provisions food to wildlife has been shown to increase habituation and aggression, exacerbating human-wildlife conflict in communities (Cui et al., 2021b). Although food provisioning is prohibited by law in our study area, supplemental feeding of bears at ecotourism sites occurs in Europe with unclear implications for 'nuisance-bear' behaviour (Penteriani et al., 2017). Broadly, climate's role in habitat suitability, as well as resource abundance, distribution, and phenology can propagate climate change as a contributing factor in human-wildlife conflict. Examples include severe drought eliciting crop-raiding by elephants (*Loxodonta africana*), and delayed sea ice freeze-up driving human-polar bear (*Ursus maritimus*) conflict (see review in Abrahms et al., 2023).

We speculate that social dimensions beyond our data underlie conflict dynamics in our case study. Specifically, the abundance and dispersion of human-associated food attractants is likely important in the Bella Coola Valley bottom. Indeed, grizzly-human conflict in other areas is associated with persistent anthropogenic attractants (Wilson et al. 2006). Responding to this challenge, the Nuxalk Nation Bear Safe Program and other community organizations (for example, WildSafe BC, Bella Coola Valley Tourism) have delivered education as well as non-lethal and preventative approaches, for example installing electric fences around high-reward attractants like salmon-cleaning stations and fruit trees (Artelle et al. 2021). More broadly, sociopolitical context is also likely influential. Conflict between humans and wildlife often involves human–human conflicts among different groups and includes dynamics related to perceived threats to lifestyles, values and world views (Nyhus 2016). Moreover, wildlife ecotourism has been shown to mitigate human-wildlife conflict through improved attitudes towards wildlife, particularly if the benefits it accrues are equitably distributed in communities adjacent to the protected areas within which ecotourism occurs (Maheshwari & Sathyakumar, 2019). Mitigation of conflict may thus be more complex in regions like the Bella Coola Valley where historical or cultural complexities related to settler colonization, dispossession, and commercialization predispose communities to conflict in varying ways.

More broadly, the methodological and conceptual approaches we used engaged multiple aspects of previous human-wildlife conflict research. Specifically, whereas much of the previous human-wildlife conflict work has used genetic analyses to identify which species were involved in conflict (e.g., Caniglia et al. 2013; Plumer et al. 2018, though see Morehouse et al. 2016), our analysis genetically identified individuals to focus on *within-species*, individual variation in conflict and ecotourism encounters. An examination of individual body condition, age, and life experiences of individuals would further enrich our understanding of conflict drivers. Conceptually, human-wildlife conflict research conducted in or adjacent to protected areas sometimes reflect human-human conflict (human disagreements over wildlife management decisions) (Peterson et al. 2010). This work may thus be informative during community dialogue about conflict drivers and mitigation. Specifically, our results suggest wildlife ecotourism does not appear to contribute to conflict in this area.

Chapter 5. Conclusion

Considering intrapopulation variation in wildlife behaviour in response to human disturbance at multiple spatial and temporal scales can help managers identify aspects of human activity that might require special consideration. My dissertation aimed to identify the different scales at which, and different contexts in which, grizzly bears may be affected by wildlife viewing. Guided by theory and community-driven research questions, this work generated contributions to scholarship, as well as insight to inform system-specific management application.

In Chapter 2, we revealed details of how broad activity patterns of grizzly bears were affected by wildlife viewing at spawning salmon sites (foraging under a presumably risky context). Specifically, we revealed context dependency in which the influence of ecotourists influenced the spatial–temporal activity of bears in different directions, depending on salmon biomass and age-sex classes. Generally, bear activity was lower during weeks in which the number of visitors present was higher. Detections during those scenarios were more likely to be females with young and sub-adults. Salmon abundance was especially influential in its interaction with the number of visitors, leading to opposite patterns during periods of low and high salmon. Collectively these patterns of bear activity align with, and can be explained in the context of, responses to risk while foraging. More broadly, this chapter offers implications for conservation science and practise. Specifically, we designed our work to confront and contribute to two bodies of theory (the asset protection principle and the human shield hypothesis) that are relevant to the conservation of any predator-prey system, including the many in which wildlife show prey-like antipredator behaviour in the presence of humans.

In Chapter 3, we examined among- and across-individual variation in space-use and behavioural states, respectively. Despite the high mobility of grizzlies and the abundant salmon resources present at ecotour sites, we found that only a small subset of individuals detected at least twice (n = 11 of 80) showed spatial histories that favoured the area of pronounced human activity. Our companion behavioural observations that occurred exclusively in the 'land- and boat-based' area during daylight and crepuscular periods considered how ecotourism intensity (number of visitors, number of boats) and environmental variables (presence of other bears, salmon biomass) might affect fishing and alertness behaviour. Our findings revealed no evidence for an effect of ecotour metrics on grizzly behaviour. When our behavioural and spatial data were considered collectively, our work suggests a 'filtering of tolerance' that might not otherwise be detected if we examined only those individuals that were present at ecotour sites and seemingly unaffected by variation in ecotour intensity. We suggest investigating more than one dimension of wildlife response to disturbance broadens the scope of inference, which in our context can provide richer insight for managers.

Finally, in Chapter 4, we asked whether grizzly bears that used the ecotour area, and were seemingly tolerant of intense human activity, were more or less likely to encounter conflict in downstream communities than predicted by chance. We considered the premise that so few ecotour individuals occurred as conflict bears because the total population, comprised of individuals equally likely to encounter conflict, was sufficiently large so that the relatively small number of ecotour bears could have occurred randomly and at no greater proportion than among bears not detected at ecotour sites. Our findings revealed no support for the hypothesis that bears that experienced ecotourism were later likely to encounter conflict, suggesting other drivers of conflict. This work may be informative during community dialogue about conflict drivers and mitigation. Specifically, our results suggest wildlife ecotourism does not appear to contribute to conflict in this area. More broadly, this chapter illuminates avenues for future investigation of predictors of tolerance, which I discuss in section 5.1.

5.1 Insights from drawing linkages among chapters

The structure of my dissertation capitalized on our study design to draw linkages among the findings from each chapter. Each chapter from this work drew on different datasets for which data were collected from the same study area in the same time period. Such an approach , which provided in-depth and diverse vantages of different measures and scales of system-specific grizzly bear behaviour. This framework also afforded me the opportunity to draw connections among results. Accordingly, I conclude my dissertation by sharing insights that emerged by considering this work as a whole.

There are several notable comparisons that can be draw from Chapters 2 and 3. Camera trap detection rates increased with increased salmon biomass (Figure 2.2A), while probability of alertness decreased as a function of salmon biomass (Figure 3.2). Collectively, these results can be explained by hyperphagic states of grizzly bears, which likely drive the increased detections of bear activity on the salmon-bearing river during times when abundance is high (Chapter 2 results) in conjunction with decreased alertness (Chapter 3). I speculate that gains in reproductive capacity that result from increased food intake when food is especially abundant for primarily female bears present are greater than gains that result from antipredator behaviours of avoidance or alertness. This might be especially likely considering that these subordinate age-sex classes are apparently shielded from dangerous male bears in the presence of generally non-novel and predictable (at least to those bears that are tolerant of people) human behaviour.

Additional insight emerged when reflecting in hindsight on Chapter 2's results after visualizing the relatively newer space-use data summary in Chapter 3. Specifically, our top age-sex class model in Chapter 2 revealed that detections were more likely to be sub-ordinate age-sex classes during the day and when visitor numbers were high. Our cluster analysis in Chapter 3 (Figure 3.1B) revealed that those individuals clustered as favouring the 'land- and boat-based' ecotourism area were mostly female, which is consistent with conclusions drawn in Chapter 2; that is, there is likely a human shield effect in the area with highest human activity. While it is not known at which time of day genetically identified bears encountered our hair snags, our camera trap data suggest evidence for nocturnality of males, suggesting the possibility that the males we genetically identified in the high-human area encountered our hair snags (and visited these sites primarily) at night.

Results from Chapters 3 and 4 are also complementary. Our study comprises a case in which human-wildlife conflict and ecotourism in a nearby protected area occur in concurrent time and adjacent space, thus carrying implications for wildlife management within and outside of the park. Chapter 3 suggests a possibility that individuals in the ecotour area are more tolerant of people than those detected upstream of the ecotour area. Following this logic, we might therefore also expect tolerant individuals to be more likely to become ensnared in ecological traps by becoming taking risks, encountering conflict with humans, and paying a lethal cost (Darimont & Shukla, 2023; Geffroy et al., 2015). However, Chapter 4 revealed that individuals exposed to ecotourism were in fact less likely than predicted by chance to encounter subsequent conflict. This raises a question as to whether grizzly bears can distinguish between individual humans or characteristics of human activity that vary in the level of risk they present. Indeed, not all human individuals pose the same risk to prey species, creating a major cognitive challenge. African elephants can reliably make functionally relevant distinctions between human subcategories that differ in the level of threat they pose (McComb et al., 2014). Accordingly, future research might address cognitive abilities of grizzly bears and other wildlife under tolerance and risk-perception frameworks to discern between individual humans (or groups thereof) and the level of risk they pose. Tying together the findings from Chapters 3 and 4, future research might therefore ask whether grizzly bears modulate their space-use and behavioural states according to varying characteristics of individuals humans. The cognitive ability of bears to distinguish among human individuals or groups thereof as a mechanism of co-existence is one avenue for future research to explore how variable human behaviour and characteristics might underlie variability in tolerance.

I note for clarity for managers and ecotour operators that there is a difference between the number of genotyped bears reported in Chapters 3 and 4. In Chapter 3, we subsampled grizzles that were detected at least twice (n = 80), resulting in 22 individuals detected in the 'land- and boat-based' area. In Chapter 4, we examined all bears regardless of detection frequency (n = 118), resulting in 34 individuals detected at least once in the 'land- and boat-based' area. Moreover, we acknowledged that we might not have detected all individuals using the 'land- and boat-based' sites with hair snags. Accordingly, we used jackknife and bootstrap methods to account for imperfect detection. Using this approach, the total number of 'land- and boat-based' bears as estimated by bootstrapping and jackknife ranged from 41.3 (SE = 1.9) to 49.8 (SE = 3.9), respectively. The difference in approaches between Chapters 3 and 4 reflect the different objectives for each chapter, whereby Chapter 3 examined bears solely in the Atnarko Corridor, and Chapter 4 sought to estimate the total (i.e., sampled and unsampled) population size, so this estimate could be used in our probability approach.

5.2 Applied conservation science: insights for managers

There are several management considerations that emerged from this work. Chapter 2 revealed evidence for high bear activity, as measured by camera traps, during high human and low salmon conditions. A proactive approach would favour the regulation of times, places and permitted human behaviour (e.g., constraining humans to within-site spaces if bear viewing is permitted at multi-use recreation areas, such as Fisheries Pool) to make interactions more predictable for bears and humans alike. Such scenarios not only reduce apparent risk perception (Palmer et al., 2021) but also avoid unanticipated encounters, which can underlie cases of human injury by bears (Herrero, 1985). As we suggest, low salmon conditions might present few foraging options for bears, thereby limiting alternatives to feed without people. More broadly, this result highlights that behavioural responses of wildlife to human disturbance ought not be divorced from context (e.g., resource availability).

Additional management-relevant insight emerged from Chapter 3. Specifically, our spatial data suggest a possibility that bears in the ‘land- and boat-based’ area are tolerant enough to be present in the area of highest human activity. Additionally, ecotour metrics did not affect behavioural states of bears we measured, suggesting drift boats and number of visitors viewing bears from land had no detectable impact on foraging or alertness behaviour. I note, however, that visitors viewing bears from land had effects on bear activity as measured by our camera traps at a weekly scale, as described in Chapter 2. This suggests there may be measurement- and scale-dependent responses by bears. Specifically, camera traps measured how active bears were (i.e., we did not identify individuals from the camera traps), whereas genetic data tracked individuals across space, and behavioural sampling measured behavioural states (Table 5.1). Each approach provided a different vantage point from which to measure bear behaviour at different scales and with associated management implications (Table 5.2). When behavioural state data were examined alongside our spatial data, it was suggestive of a possibility of a filtering of tolerance, whereby some individuals were never detected in the areas of highest human activity. Accordingly, we caution managers to take this information into account if there is consideration for future expansion of ecotourism (i.e., more sites) considered for the park. Specifically, ecotourism expansion into areas that are occupied by less tolerant individuals could cause displacement or otherwise disturbance to those bears that avoid people.

Table 5.1 Overview of the units of measure for each dataset.

Dataset	**Associated Chapter(s)**	**Case**	**Temporal resolution**
Camera traps	Chapter 2	Detection rate	Weekly
Behavioural states	Chapter 3	Scan sample	On average every 2.5 minutes
Genotyped individuals	Chapters 3 and 4	Presence only	On average every 9 days

Table 5.2 Management implications for each chapter

Chapter	**Management implications**
Chapter 2	Ecotour metrics (specifically visitors viewing bears from land) affected bear activity (as measured by camera trap detections) at a weekly scale. Detection rates increased when salmon were low and – concurrently– people were high. When salmon abundance was high, the opposite pattern emerged: bear activity decreased when more visitors were present. This second pattern suggests that bears used alternative foraging sites (where salmon were also abundant). The highest visitor numbers occurred at Fisheries Pool, which is a site that is not formally managed as a bear viewing area. To mitigate the occurrence of ‘high-visitor, high-bear activity, low-salmon’ scenarios, managers could consider limiting land-based visitors to a maximum of 1100 per week, per site during low salmon scenarios. This translates to 157 land-based visitors per day, per site (e.g., 157 visitors/day to Fisheries Pool). See Table 2.1 for detail.

Chapter 3	When our behavioural and spatial data were considered collectively, our work suggests a ‘filtering of tolerance’ that might not otherwise be detected if we examined only those individuals that were present (there were no detectable effects of ecotourism on behavioural states of bears that were present). Given the spatial filtering we observed, managers might consider limiting the number of ecotourism sites in the future to complement considerations identified for the existing two sites based on variation in activity levels associated with human visitation, salmon biomass, and their interaction (Chapter 2).
Chapters 4	We found no support for the hypothesis that bears that experienced ecotourism were later likely to encounter conflict, which suggests current ecotour activities in the park do not predispose grizzly bears to conflict in downstream communities. Accordingly, our results suggest that managers responsible for areas outside the park consider other drivers of conflict and appropriate intervention.

Finally, results from Chapter 4 suggest wildlife ecotourism does not appear to contribute to conflict in our case study. We conclude this chapter with a speculation that social dimensions beyond our data underlie conflict dynamics in our case study. Specifically, the abundance and dispersion of human-associated food attractants is likely important in the Bella Coola Valley bottom. Mitigation of conflict may be more complex in regions like the Bella Coola Valley where historical or cultural complexities related to settler colonization, dispossession, and commercialization predispose communities to conflict in varying ways. This work may thus be informative during community dialogue about conflict drivers and mitigation. Specifically, our results suggest wildlife ecotourism does not appear to contribute to conflict in this area.

5.3 Concluding Remarks

In conclusion, my dissertation integrates ecological theory, community-driven research, and diverse methodological approaches to understand wildlife behaviour in response to non-consumptive human activity. By examining how grizzly bears perceive and navigate potential risk associated with ecotourism at multiple scales, this work provides comprehensive insight into the nuanced interplay of environmental, behavioural, and spatial factors that shape wildlife responses to human activity. These findings have practical implications for management, which have been shared formally and informally throughout the project, and will continue.. More broadly, this research contributes to the growing body of literature examining how wildlife perceives and adapts to human-mediated risk. By addressing both theoretical and applied dimensions, this work contributes to our understanding of wildlife tolerance and risk perception, highlighting the critical role of collaborative, system-specific studies in informing evidence-based conservation efforts.

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Appendix A – Supplementary Information for Chapter 2

Appendix A1: Figures

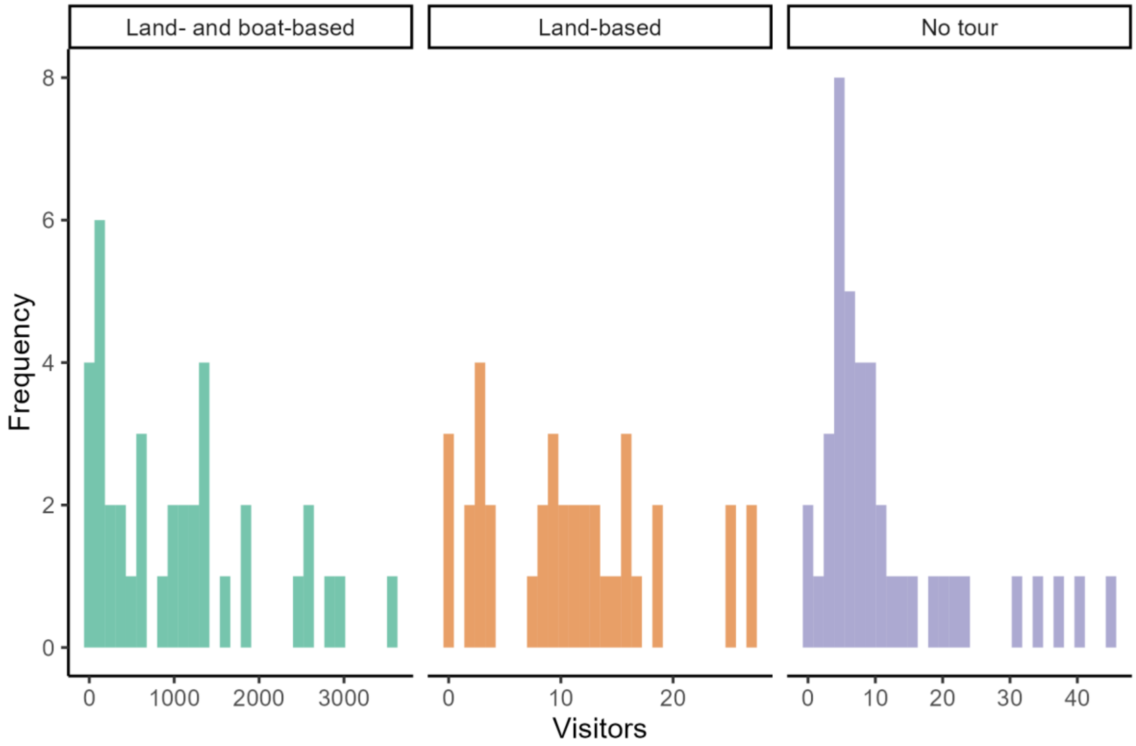

Figure A1. Frequency of weekly visitor counts, grouped by spatial treatment. Note difference among X-axis scales.

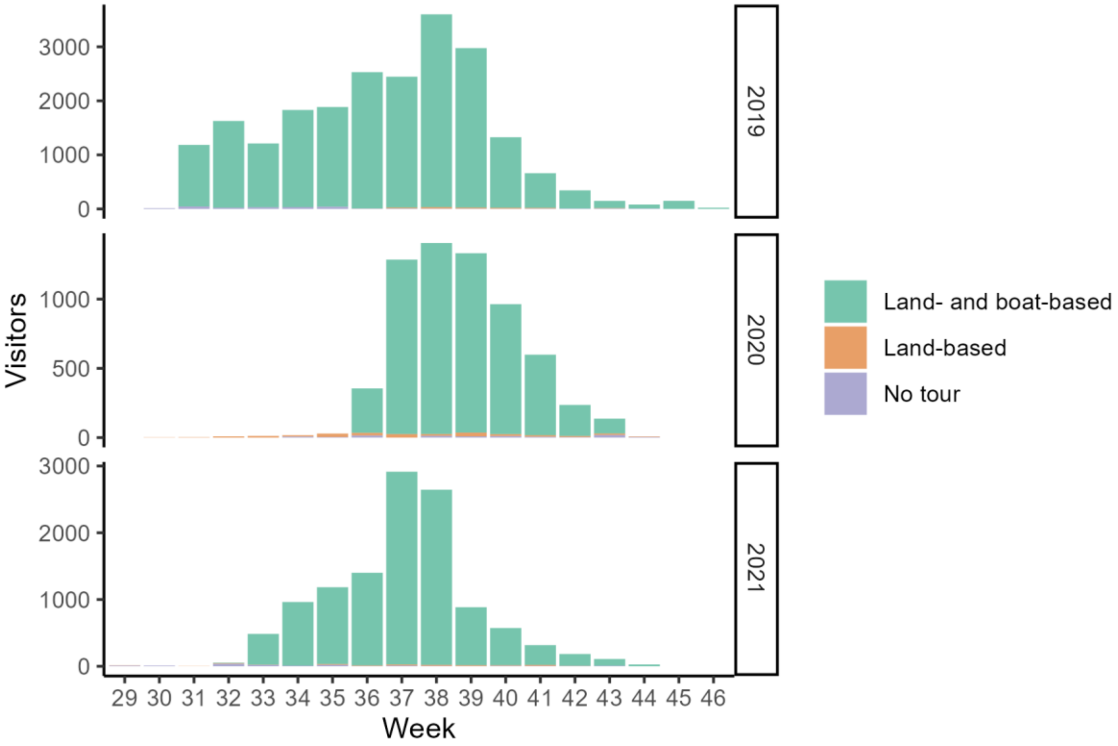

Figure A2. Visitor numbers by week and spatial treatment.

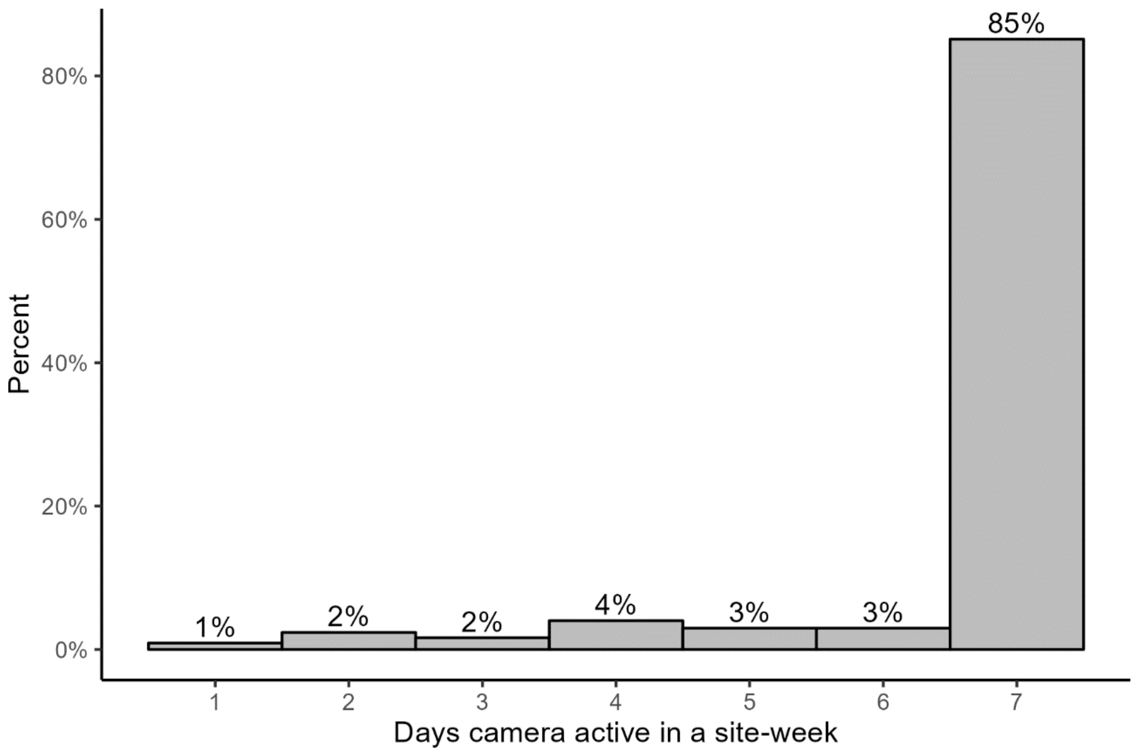

Figure A3. Number of days over which cameras were active across all site-weeks. Most (85%, n = 563 of 673) camera-weeks collected data on all 7 days.

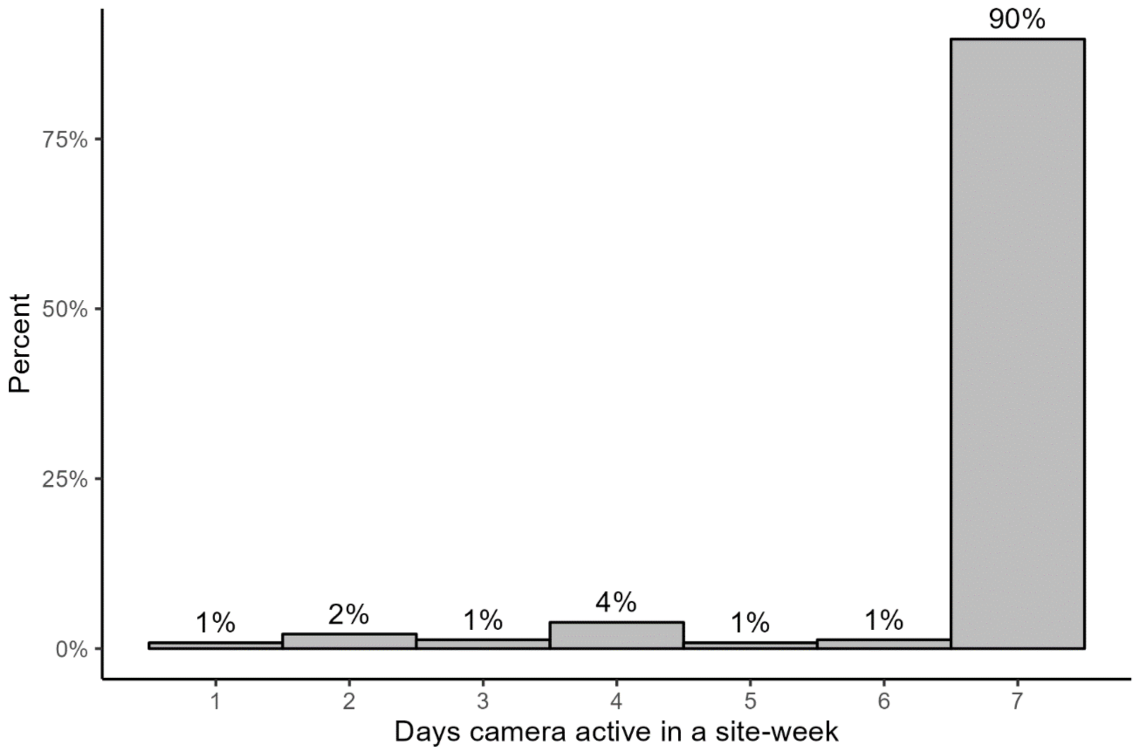

Figure A4. Number of days over which cameras were active across site-weeks in the 'no tour' spatial treatment. Most (90%) camera-weeks collected data on all 7 days.

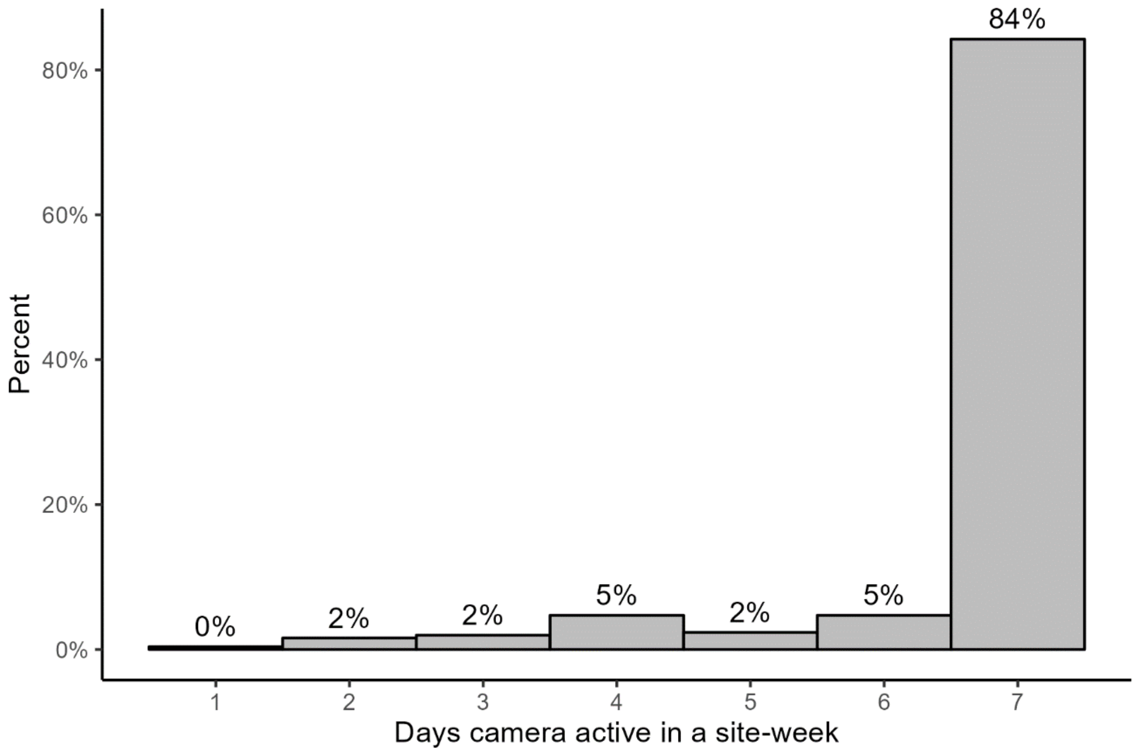

Figure A5. Number of days over which cameras were active across site-weeks in the ‘land-based’ spatial treatment. Most (84%) camera-weeks collected data on all 7 days.

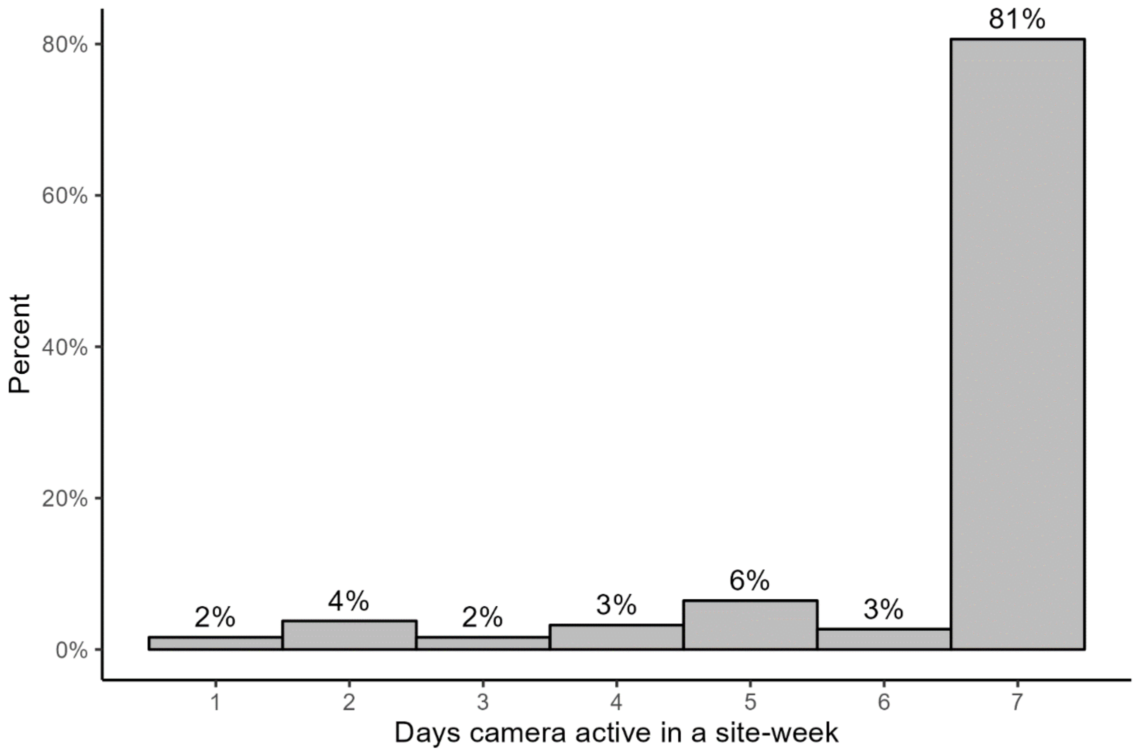

Figure A6. Number of days over which cameras were active across site-weeks in the 'land- and boat-based' spatial treatment. Most (81%) camera-weeks collected data on all 7 days.

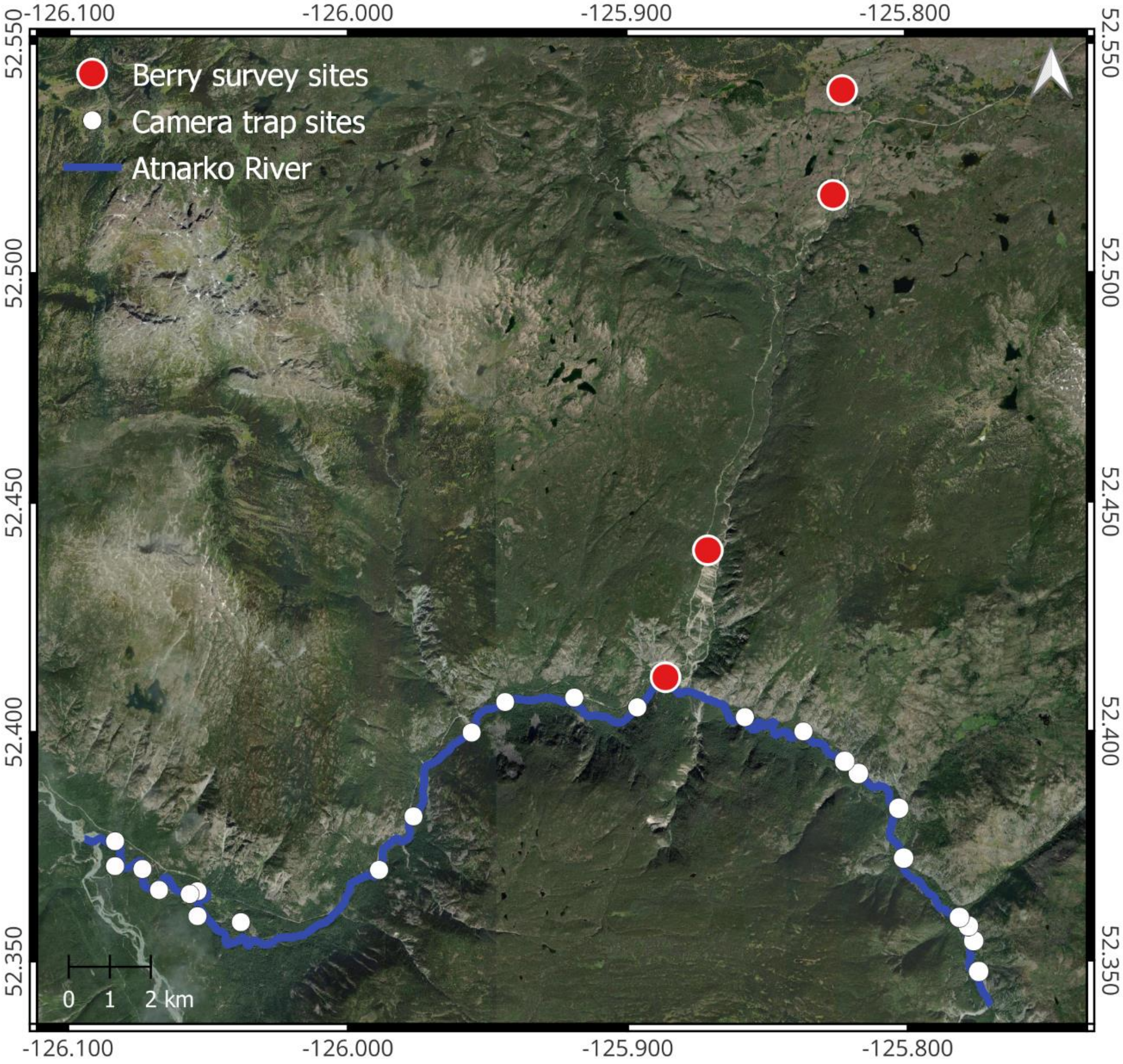

Figure A7. Berry survey sites spaced at four elevations along a ~1300m elevational gradient.

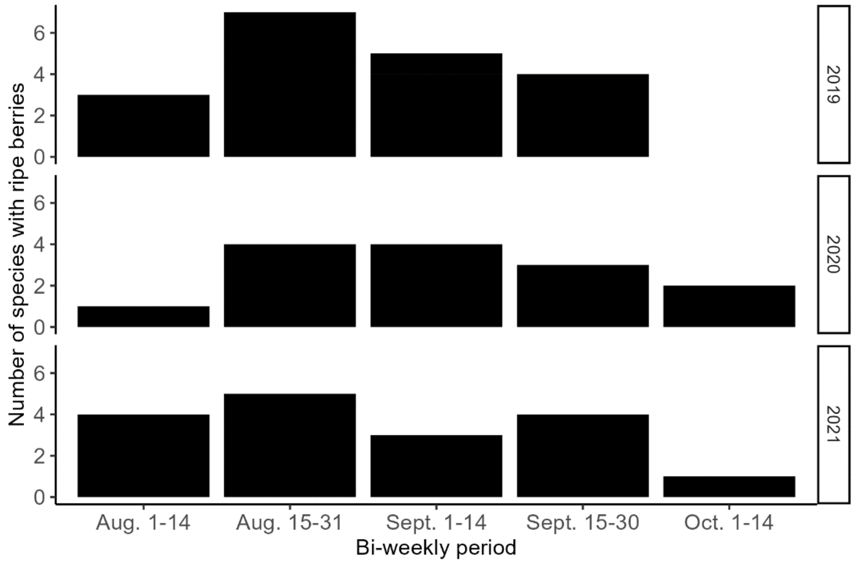

Figure A8. Number of species with ripe berries by bi-weekly period and year.

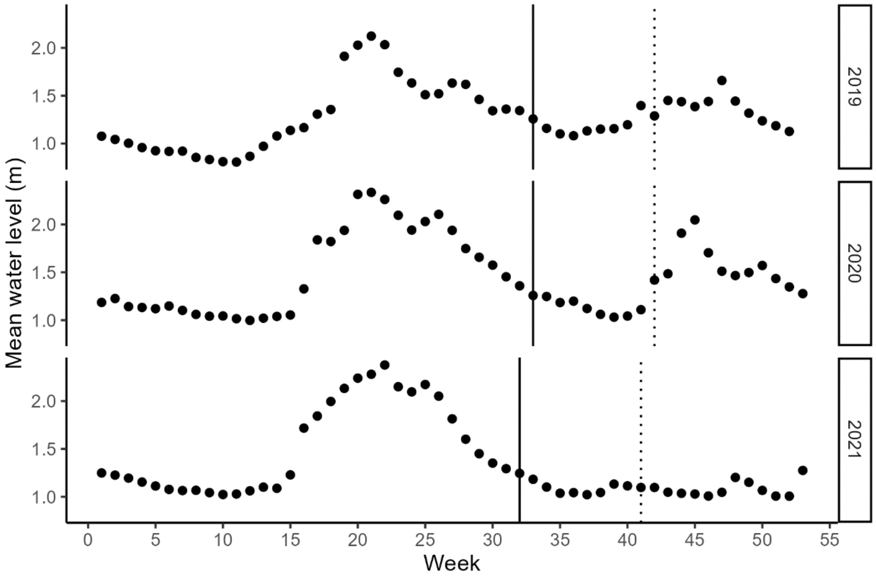

Figure A9. Weekly mean water level for the Atnarko River. Solid and dotted lines represent the beginning and the end of our study period, respectively. Real-time hydrometric data retrieved from Government of Canada, station number 08FB006 (https://wateroffice.ec.gc.ca/report/real_time_e.html?stn=08FB006).

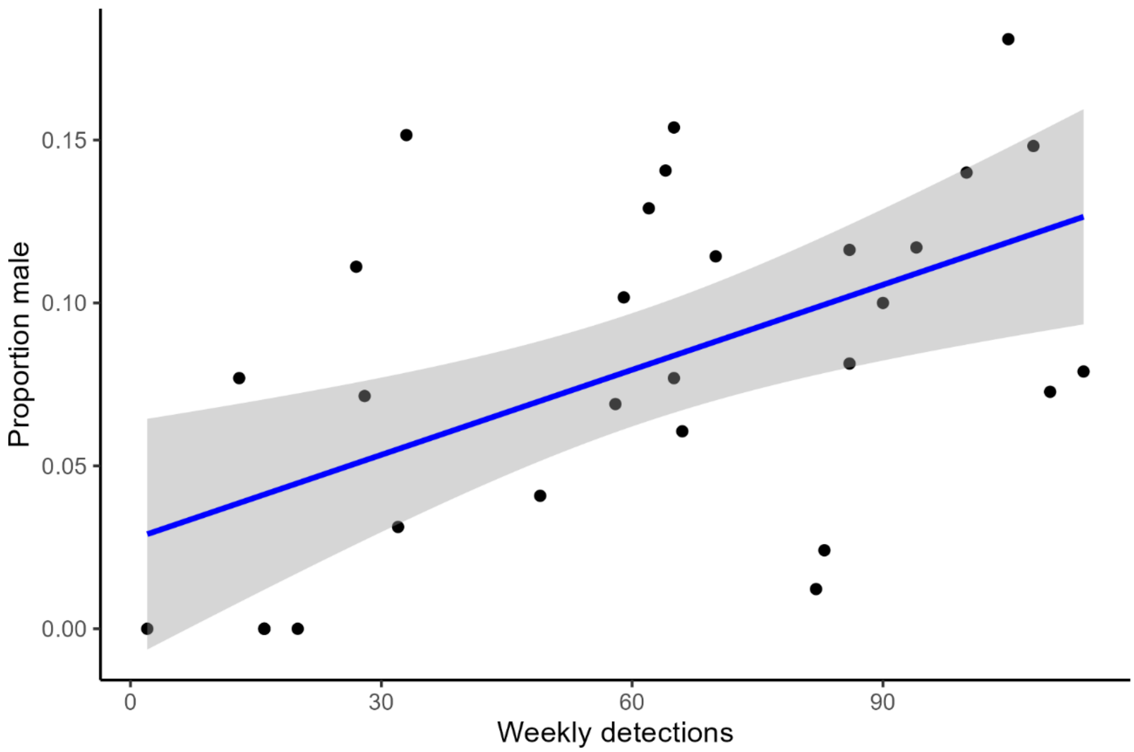

Figure A10. Relationship between weekly detections and proportion of males among detections.

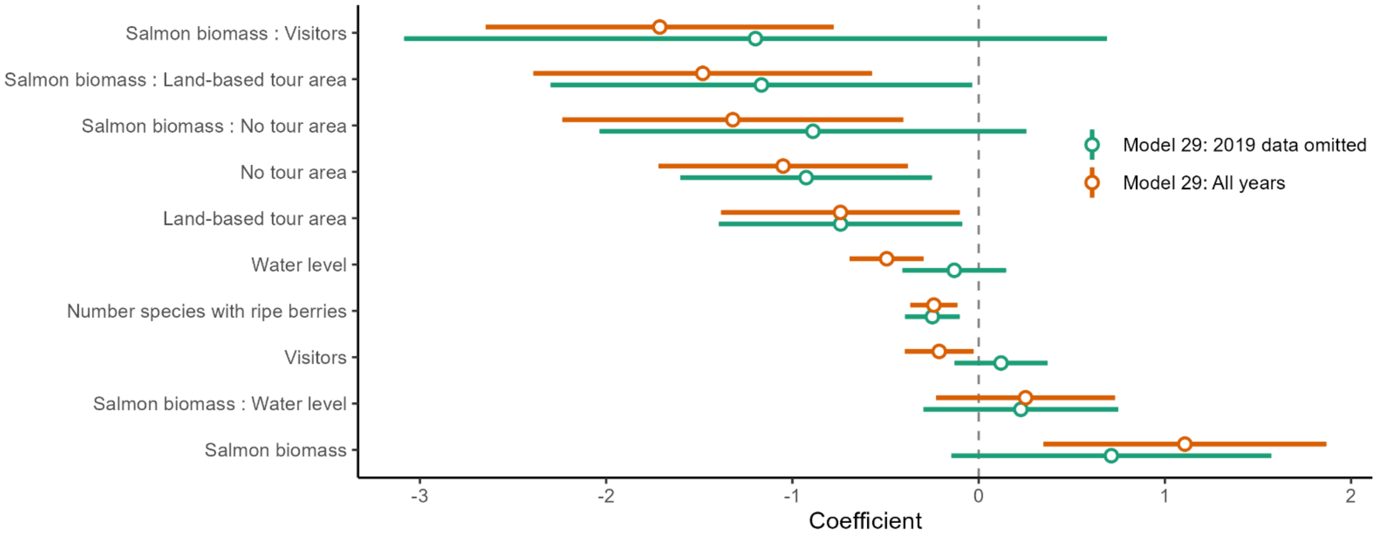

Figure A11. Detection rate analyses performed with and without 2019 data. Shown are outputs from top models from each analysis.

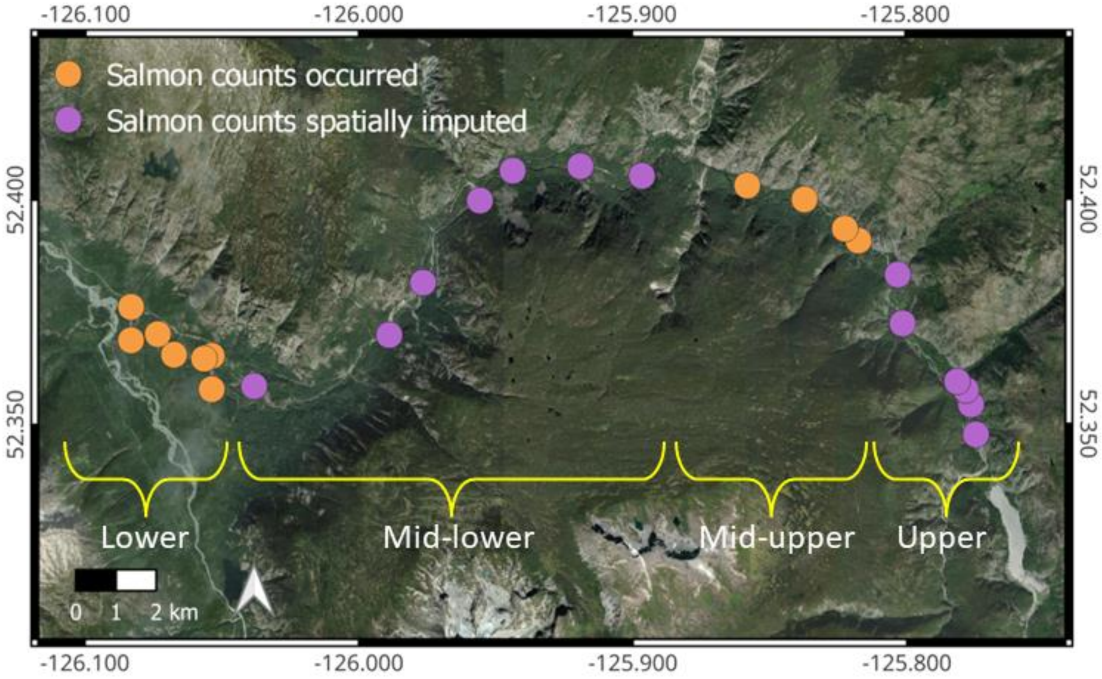

Figure A12. Camera sites coded by whether they were located in a river segment along which salmon counts occurred. River segments are defined as ‘lower’, ‘mid-lower’, ‘mid-upper’, and ‘upper.’ Camera sites within each river segment were attributed the same value for each week’s salmon count estimates.

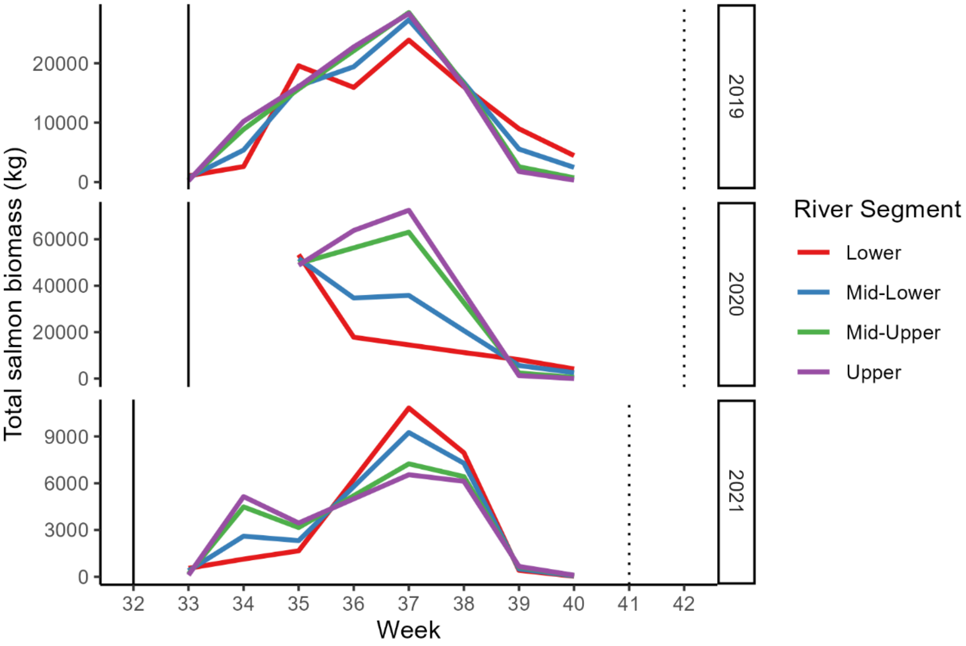

Figure A13. Weekly and yearly variation in salmon biomass along the four river segments of the Atnarko river study area. Solid and dotted reference lines represent the weeks in which August 15th and October 15th occur, respectively. Note difference among Y-axis scales.

Appendix A2: Tables

Table A1. Camera trap settings. We include settings relevant to videos only because we did not set cameras to capture photos.

Setting	**Set to**	**Camera**
Capture delay	1 sec	Browning Strike Force HD PRO (Model: BTC-5HDP)
Video quality	High	Browning Strike Force HD PRO (Model: BTC-5HDP)
Video length	2 min	Browning Strike Force HD PRO (Model: BTC-5HDP)
Smart IR video	Off	Browning Strike Force HD PRO (Model: BTC-5HDP)
SD card management	Off	Browning Strike Force HD PRO (Model: BTC-5HDP)
Adjustable IR Flash	Long range	Browning Strike Force HD PRO (Model: BTC-5HDP)
Video mode	On	Browning Strike Force Extreme (Model: BTC-5HDX)
Video resolution	High	Browning Strike Force Extreme (Model: BTC-5HDX)
Video length	2 min	Browning Strike Force Extreme (Model: BTC-5HDX)
Photo delay	1 sec	Browning Strike Force Extreme (Model: BTC-5HDX)
Smart IR video	Off	Browning Strike Force Extreme (Model: BTC-5HDX)
SD card management	Off	Browning Strike Force Extreme (Model: BTC-5HDX)
Video	On	Reconyx Hyperfire 2 (Model: HP2X Professional)
Video length	30 sec	Reconyx Hyperfire 2 (Model: HP2X Professional)
Dynamic video	Off	Reconyx Hyperfire 2 (Model: HP2X Professional)
Quiet Period	No delay	Reconyx Hyperfire 2 (Model: HP2X Professional)
Sensitivity	High	Reconyx Hyperfire 2 (Model: HP2X Professional)
Motion schedules	25 hours	Reconyx Hyperfire 2 (Model: HP2X Professional)

Lapse video	Off	Reconyx Hyperfire 2 (Model: HP2X Professional)
Take videos	Day & Night	Reconyx Hyperfire 2 (Model: HP2X Professional)
Flash output	Medium	Reconyx Hyperfire 2 (Model: HP2X Professional)
Resolution	4:3 Standard	Reconyx Hyperfire 2 (Model: HP2X Professional)
PIR type	Long range	Reconyx Hyperfire 2 (Model: HP2X Professional)
Loop recording	Off	Reconyx Hyperfire 2 (Model: HP2X Professional)
Record audio	Yes	Reconyx Hyperfire 2 (Model: HP2X Professional)
Ext trigger vids	Off	Reconyx Hyperfire 2 (Model: HP2X Professional)

Table A2. Number of camera stations in each year and treatment

Year	**Treatment**	**Number of Stations**
2019	Reference	8
2019	Land-based	8
2019	Land- and boat-based	5
2020	Reference	8
2020	Land-based	9
2020	Land- and boat-based	7
2021	Reference	8
2021	Land-based	9
2021	Land- and boat-based	7

Table A3. GLMM model set and rankings. Top models with ΔAICc less than 4 are bolded.

		Log-likelihood	Δ AICc	Weight
M1	Random effects only (site and year)	-1676.64	943.67	0.12
M2	Salmon biomass	-1300.61	193.65	0.86
M3	Salmon biomass + berry	-1290.90	176.27	0.51
M4	Salmon biomass + water level + (salmon biomass x water level)	-1278.02	152.55	0.73
M5	Salmon biomass + water level + (salmon biomass x water level) + berry	-1271.83	142.22	0.13
M6	Salmon biomass + visitors	-1226.39	47.25	0.53
M7	Salmon biomass + treatment	-1297.68	191.87	0.21
M8	Salmon biomass + visitors + treatment	-1224.17	46.93	0.62
M9	Salmon biomass + berry + visitors	-1218.13	32.79	0.74
M10	Salmon biomass + berry + treatment	-1287.89	174.35	0.13
M11	Salmon biomass + berry + treatment + visitors	-1215.72	32.10	0.10
M12	Salmon biomass + visitors + (salmon biomass x visitors)	-1223.37	43.26	0.39
M13	Salmon biomass + treatment + (salmon biomass x treatment)	-1296.38	193.39	0.98

M14	Salmon biomass + visitors + (salmon biomass x visitors) + treatment + (salmon biomass x treatment)	-1216.93	38.68	0.39
M15	Salmon biomass + berry + visitors + (salmon biomass x visitors)	-1215.07	28.72	0.56
M16	Salmon biomass + berry + treatment + (salmon biomass x treatment)	-1286.95	176.61	0.43
M17	Salmon biomass + berry + visitors + (salmon biomass x visitors) + treatment + (salmon biomass x treatment)	-1215.07	28.72	0.56
M18	Salmon biomass + water level + (salmon biomass x water level) + visitors	-1211.17	20.93	0.28
M19	Salmon biomass + water level + (salmon biomass x water level) + treatment	-1275.03	150.69	0.18
M20	Salmon biomass + water level + (salmon biomass x water level) + visitors + treatment	-1207.87	18.48	0.94
M21	Salmon biomass + water level + (salmon biomass x water level) + berry + visitors	-1205.79	12.23	0.21
M22	Salmon biomass + water level + (salmon biomass x water level) + berry + treatment	-1268.80	140.30	0.33

M23	Salmon biomass + water level + (salmon biomass x water level) + berry + visitors + treatment	-1202.33	9.49	0.84
M24	Salmon biomass + water level + (salmon biomass x water level) + visitors + (salmon biomass x visitors)	-1208.40	17.45	0.16
M25	Salmon biomass + water level + (salmon biomass x water level) + treatment + (salmon biomass x treatment)	-1273.81	152.41	0.78
M26	Salmon biomass + water level + (salmon biomass x water level) + treatment + (salmon biomass x treatment) + visitors + (salmon biomass x visitors)	-1201.50	12.019	0.24
M27	Salmon biomass + water level + (salmon biomass x water level) + berry + visitors + (salmon biomass x visitors)	-1202.67	8.08	0.18
M28	Salmon biomass + water level + (salmon biomass x water level) + berry + treatment + (salmon biomass x treatment)	-1267.65	142.18	0.13
M29	**Salmon biomass + water level + (salmon biomass x water level) + berry + visitors + (salmon biomass x visitors) +**	**-1194.43**	**0.000**	**0.97**

	treatment + (salmon biomass x treatment)			

Table A4. Age and sex class multinomial model set with rankings. Top models with ΔAICc less than 4 are bolded.

		Log-likelihood	Δ AICc	Weight
M1	Random effects only (site and year)	1191.07	48.09	0.33
M2	Salmon biomass	1906.92	56.39	0.51
M3	Salmon biomass + berry	1912.53	45.17	0.14
M4	Salmon biomass + diurnality	1926.57	17.09	0.18
M5	Salmon biomass + diurnality + berry	1932.69	4.85	0.80
M6	Salmon biomass + visitors	1908.57	53.09	0.27
M7	Salmon biomass + treatment	1901.26	67.71	0.18
M8	Salmon biomass + visitors + treatment	1899.54	71.15	0.32
M9	Salmon biomass + berry + visitors	1914.29	41.64	0.82
M10	Salmon biomass + berry + treatment	1906.71	56.80	0.42
M11	Salmon biomass + berry + treatment + visitors	1905.30	59.63	0.10
M12	Salmon biomass + visitors + (salmon biomass x visitors)	1903.71	62.79	0.21
M13	Salmon biomass + treatment + (salmon biomass x treatment)	1897.398	75.42	0.38

M14	Salmon biomass + visitors + (salmon biomass x visitors) + treatment + (salmon biomass x treatment)	1894.13	81.97	0.14
M15	Salmon biomass + berry + visitors + (salmon biomass x visitors)	1910.35	49.52	0.16
M16	Salmon biomass + berry + treatment + (salmon biomass x treatment)	1902.27	65.69	0.49
M17	Salmon biomass + berry + visitors + (salmon biomass x visitors) + treatment + (salmon biomass x treatment)	1901.73	66.77	0.29
M18	Salmon biomass + diurnality + visitors	1928.67	12.89	0.14
M19	Salmon biomass + diurnality + treatment	1923.12	23.99	0.56
M20	Salmon biomass + diurnality + visitors + treatment	1920.56	29.05	0.44
M21	Salmon biomass + diurnality + berry + treatment	1929.15	11.93	0.23
M22	**Salmon biomass + diurnality + berry + visitors**	**1935.11**	**0.00**	**0.90**
M23	Salmon biomass + diurnality + berry + visitors + treatment	1926.77	16.69	0.21
M24	Salmon biomass + diurnality + visitors + (salmon biomass x visitors)	1923.69	22.84	0.99

M25	Salmon biomass + diurnality + treatment + (salmon biomass x treatment)	1918.98	32.27	0.89
M26	Salmon biomass + diurnality + treatment + (salmon biomass x treatment) + visitors + (salmon biomass x visitors)	1915.17	39.90	0.20
M27	Salmon biomass + diurnality + berry + visitors + (salmon biomass x visitors)	1930.80	8.61	0.12
M28	Salmon biomass + diurnality + berry + treatment + (salmon biomass x treatment)	1924.37	21.47	0.20
M29	Salmon biomass + diurnality + berry + visitors + (salmon biomass x visitors) + treatment + (salmon biomass x treatment)	1923.51	23.20	0.83

Table A5. Shrub species for which phenological data were collected across years. We counted the number of berry-producing species every two weeks in sampled years.

Species	**Year**
Black-capped raspberry (*Rubus occidentalis*)	2019; 2020; 2021
Black gooseberry (*Ribes lacustre*)	2019; 2020; 2021
Black huckleberry (*Gaylussacia baccata*)	2019; 2020; 2021
Bog huckleberry (*Gaylussacia bigeloviana*)	2019
Dwarf blueberry (*Vaccinium cespitosum*)	2019; 2020; 2021
False solomon's seal (*Maianthemum racemosum*)	2019; 2020; 2021
Oval-leaf blueberry (*Vaccinium ovalifolium*)	2019
Kinnikinnick (*Arctostaphylos uva-ursi*)	2019; 2020
Rosehip (*Rosa gymnocarpa*)	2019; 2020; 2021
Red huckleberry (*Vaccinium parvifolium*)	2020; 2021
Red-osier dogwood (*Cornus sericea*)	2019
Saskatoon berry (*Amelanchier alnifolia*)	2019; 2020
Soap berry (*Sapindus*)	2019; 2020
Wild strawberry (*Fragaria vesca*)	2019; 2020; 2021
Thimble berry (*Rubus parviflorus*)	2019; 2020; 2021
Trailing blackberry (*Rubus ursinus*)	2021

Table A6: Comparisons between top models for datasets with and without 2019 imputed salmon biomass data.

Model	Fixed effects	Log-likelihood	Δ AICc	Weight
M29: 2020 and 2021 only	Salmon biomass + water level + (salmon biomass x water level) + berry + visitors + (salmon biomass x visitors) + treatment + (salmon biomass x treatment)	-835.55	0.00	0.26
M29: All years	Salmon biomass + water level + (salmon biomass x water level) + berry + visitors + (salmon biomass x visitors) + treatment + (salmon biomass x treatment)	-1194.43	0.00	0.97

Appendix A3: Supporting text

Methods

Explanatory variables

Salmon

Given missing count data for some river segments and weeks, we used a spatially and temporally explicit approach to impute within- and across-year salmon biomass availability, following methods from other studies (e.g., Bryan et al., 2014; Ruggerone et al., 2010). We identified four river segments, defined by whether they were accessible by boat, and thus whether salmon counts occurred (Appendix A1; Figure A12). Weekly species-specific counts of salmon were few in 2019, and missing from two of four segments of the river in all years. We therefore imputed data by drawing from adjacent counts in space and time in years 2020 and 2021. We used a different approach to impute a larger set of missing salmon data in 2019. Specifically, we drew on the relationship between New Salmon Escapement Database System (NuSEDS) annual escapement estimates and our field counts to derive an index for relative abundance. We describe these methods in detail below.

We imputed for temporal data gaps when there was one river segment-week (our unit of measure, herein ‘segment-week’) of missing data between two segment-weeks with salmon data. This resulted in temporal imputation for six segment-weeks across 2020 (n = 4) and 2021 (n = 2). After employing these imputation methods, 85% of weeks (n = 17 of 20 weeks in 2020 and 2021) had salmon data for river segments that were accessible to conduct salmon counts. The remaining three weeks lacked data because they occurred at the beginning or end of the field season. We treated one segment-week (‘mid-upper’ river segment, year 2020, week 36) as missing data, given poor visibility from river sediment during that week's estimation (Nuxalk Fisheries and Wildlife staff pers. comm.) and imputed accordingly.

Two river segments ('mid-lower' and 'upper', Appendix A1; Figure A12) always lacked salmon count data because of boat access limitations. We employed different imputation methods for each of these two river segments because, whereas the 'mid-lower' river segment had two adjacent river segments from which to impute, the 'upper' river segment had only one adjacent river segment.

We imputed salmon estimates for the 'mid-lower' river segment using the following steps. First, we identified the camera site closest to the center of each river segment (herein, 'mid-point location). We identified the mid-point location in the 'mid-lower' river segment as the spatial location at which to calculate an imputed salmon estimate. We identified the mid-point locations in adjacent river segments (where salmon estimates were known) as the spatial locations from which to calculate the imputed salmon estimate for the mid-point location in the 'mid-lower' river segment. We identified these mid-point locations along river segment center lines, which were derived from a river polygon using the Collapse Dual Lines to Centerline tool in ArcGIS. Next, we measured the meandering length of each river segment. Finally, we imputed for the 'mid-lower' river segment by calculating the weighted average of adjacent river segments, inversely weighted by the distance between mid-point locations (Equation 1). Each camera site was then attributed the salmon estimate at a mid-point location for its respective river segment.

$$x = \frac{\left(a \cdot \frac{1}{b}\right) + \left(c \cdot \frac{1}{d}\right)}{\left(\frac{1}{b} + \frac{1}{d}\right)}$$

Equation 1, where:

a = known salmon count in lower river segment;

b = river distance between a and x

c = known salmon count in mid-upper river segment; and

d = river distance between c and x

We imputed salmon estimates for the 'upper' river segment, where only one adjacent river segment had a known salmon estimate (i.e., 'mid-upper'), using the following steps. We calculated the mean rate of salmon change per kilometer between mid-point locations with known salmon estimates, and multiplied this rate by the distance in kilometers between the mid-point location in the 'mid-upper' river segment and the mid-point location in the 'upper' river segment. This calculated value (x in Equation 2 below) was then either added to or subtracted from the 'mid-upper' river segment salmon estimate, depending on when sampling occurred relative to the seasonal dynamics of the runs. Specifically, salmon estimates for a given segment were either added or subtracted, depending on their location in the river (upstream or downstream) and whether salmon were first entering the system or later in the run. For example, during the early pulse of the year when salmon were entering the system, we observed that there were more salmon in the 'lower' river segment than in the 'mid-upper' river segment. At a later point in time, if counts in the 'lower' segment were lower than the 'mid-upper' segment, we assumed that the salmon had moved upriver in their migration, and therefore would add, rather than subtract, to the salmon estimate for the ‘mid-upper’ river segment, reasoning that the salmon pulse had moved beyond the ‘mid-upper’ river segment.

$$x = a - \left(\left(\frac{\left(\left(\frac{b-c}{d}\right)+\left(\frac{c-a}{e}\right)\right)}{2}\right)\cdot f\right)$$

Equation 2, where:

a = known salmon count in mid-upper river segment

b = known salmon count in lower river segment

c = known salmon count in mid-lower river segment

d = river distance between b and c

e = river distance between a and c; and

f = river distance between a and upper river segment

We used a different approach to impute a larger set of missing salmon data in 2019. Specifically, we drew on the relationship between New Salmon Escapement Database System (NuSEDS; Pacific Region’s central database, maintained by Fisheries and Oceans Canada, which stores individual spawner survey data records and spawner abundance estimates) annual escapement estimates and our field counts (herein, ‘counts’) to derive a ratio that could be applied to index relative abundance. We assumed similar spatial and temporal salmon abundance dynamics between 2019 and other years. Accordingly, we calculated the relationship between our segment-week salmon count data in 2020 and 2020 NuSEDS escapement estimates to derive an annual:site-week ratio for each site-week (Box A1). We then used those relationships to estimate missing segment-week salmon counts in 2019.

For each species, we divided total counts in 2020 by 2020 NuSEDS escapement estimates for a proportion of total counts to NuSEDS estimates. We then multiplied this proportion by 2019 NuSEDS estimates for each species. We then calculated the proportion of total, within-year counts that occurred for each species at each segment-week for both 2020 and 2021 (herein 'segment-week proportions'). We averaged each segment-week proportion between years. Finally, we estimated salmon counts for each segment-week in 2019 by multiplying 2019 counts by average segment-week proportions (Box A1). We then calculated biomass for a final salmon biomass dataset (Appendix A1; Figure A13).

Box A1. Step-by-step 2019 salmon data imputation

Step 1: Divide 2020 total field counts by 2020 NuSEDS estimates for each species for a proportion of total field counts to NuSEDS estimate.

Step 2: Multiply 2019 NuSEDS estimates by the result from Step 1.

Step 3: Calculate the proportion of total, within year field counts at each segment-week. The following is a hypothetical example of an outcome for two weeks of data only.

Year	week	segment	pink.field.counts	pink.seg-week.prop
2020	35	lower	30000	0.75
2020	35	mid-lower	28901	0.61
2020	35	mid-upper	27500	0.48
2020	35	upper	27012	0.44
2020	36	lower	10000	0.25
2020	36	mid-lower	18784	0.39
2020	36	mid-upper	30000	0.52
2020	36	upper	33896	0.56

Step 4. Average the 2020 and 2021 segment-week proportions for each species (herein, ‘mean segment-week proportion’).

Step 5. Multiply the mean segment-week proportion by the product of Step 2 for 2019 segment-week salmon estimates.

We assessed how our methods affected the general patterns in our bear activity data by running models with and without imputed 2019 values. The interaction between salmon biomass and visitors revealed the same direction in grizzly bear detection rates, however confidence intervals overlapped 0 for this same salmon biomass and visitor interaction in the model that excluded imputed 2019 data. Additionally, the model that excluded imputed 2019 data suggested an opposite effect of visitors on grizzly bear detections, but overlapped zero.

Visitors

We used several datasets to derive an index of human foot traffic (herein 'visitors'). Counts in the 'land- and boat-based tour' treatment were derived from one-way vehicle counts at the BC Parks recreation site collected by ©TRAFx infrared trail counters in 2019 and camera traps in 2020 and 2021, as well as from count data collected by staff employed at the bear viewing platform. Vehicle counts were multiplied by 3, assuming an average occupancy in 'drive-in' parks in the region (Todd Windle; Parks Canada; personal communication). One-way counts in the 'no tour' and 'land-based tour' treatments were collected from camera traps in all years.

We estimated human index data when they were missing. Across years, there were 5 weeks (n = 3 in 2020 and n = 2 in 2021) when data were missing from the camera trap in the 'land- and boat-based tour' treatment due to theft and camera failure. Reasoning that peaks in human activity at the bear-viewing platform and the recreation site (both in the 'land- and boat-based tour' treatment) occurred during the same weeks, we estimated human counts for weeks with missing data at the recreation site by calculating the average ratio of visits to each site across weeks when data for both sites existed (data used from bear-viewing platform were collected by BC Parks and Nuxalk First Nation bear-viewing platform staff). For weeks with missing data from the recreation site when the bear-viewing platform was closed (n = 2 consecutive weeks), we used a similar approach as our salmon imputation methods, whereby we imputed for temporal data gaps between two weeks where data existed.

References

Bryan, H. M., Darimont, C. T., Paquet, P. C., Wynne-Edwards, K. E., & Smits, J. E. G. (2014). Stress and reproductive hormones reflect inter-specific social and nutritional conditions mediated by resource availability in a bear-salmon system. Conservation Physiology, 2(1), cou010–cou010. https://doi.org/10.1093/conphys/cou010

Haggerty, B.P., & Mazer, S.J. (2008). *The Phenology Handbook.* UCSB Phenology Stewardship Program

Ruggerone, G. T., Peterman, R. M., Dorner, B., & Myers, K. W. (2010). Magnitude and Trends in Abundance of Hatchery and Wild Pink Salmon, Chum Salmon, and Sockeye Salmon in the North Pacific Ocean. Marine and Coastal Fisheries, 2(1), 306–328. https://doi.org/10.1577/C09-054.1

Appendix B – Supplementary Information for Chapter 3

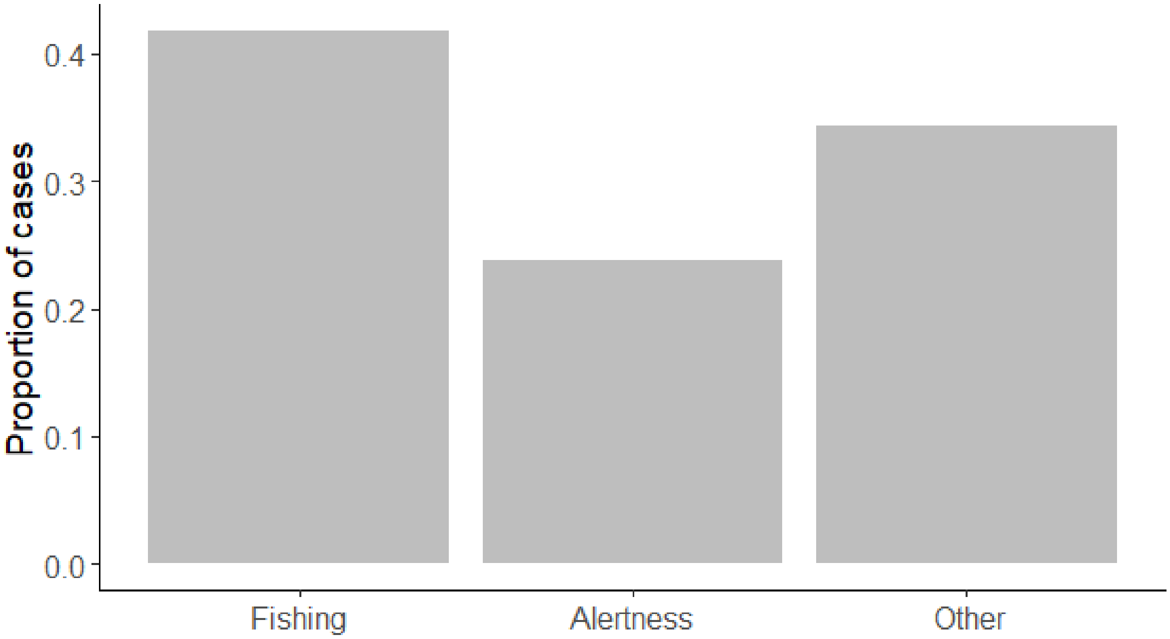

Figure B1. Proportion of cases that comprised fishing, alertness, and other behaviours.

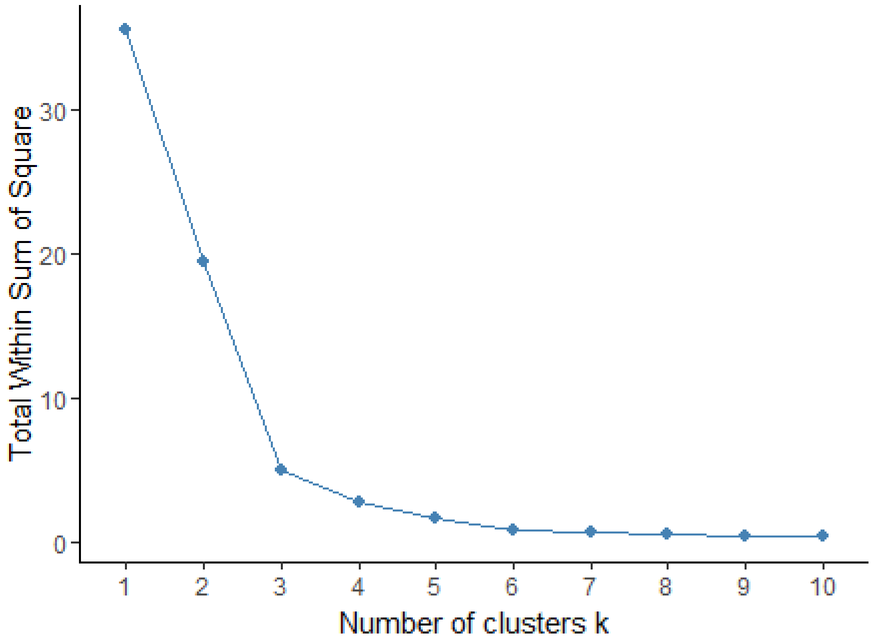

Figure B2. We identified three (the ‘elbow point’) as the optimal number of clusters. Figure plots within sum of square for different numbers of clusters, with the ‘elbow point’ indicating the number of clusters at which any further increasein clusters results in diminished improvement to model fit. Data were subset to include individuals that were detected at least twice (n = 80 individuals out of original 118).

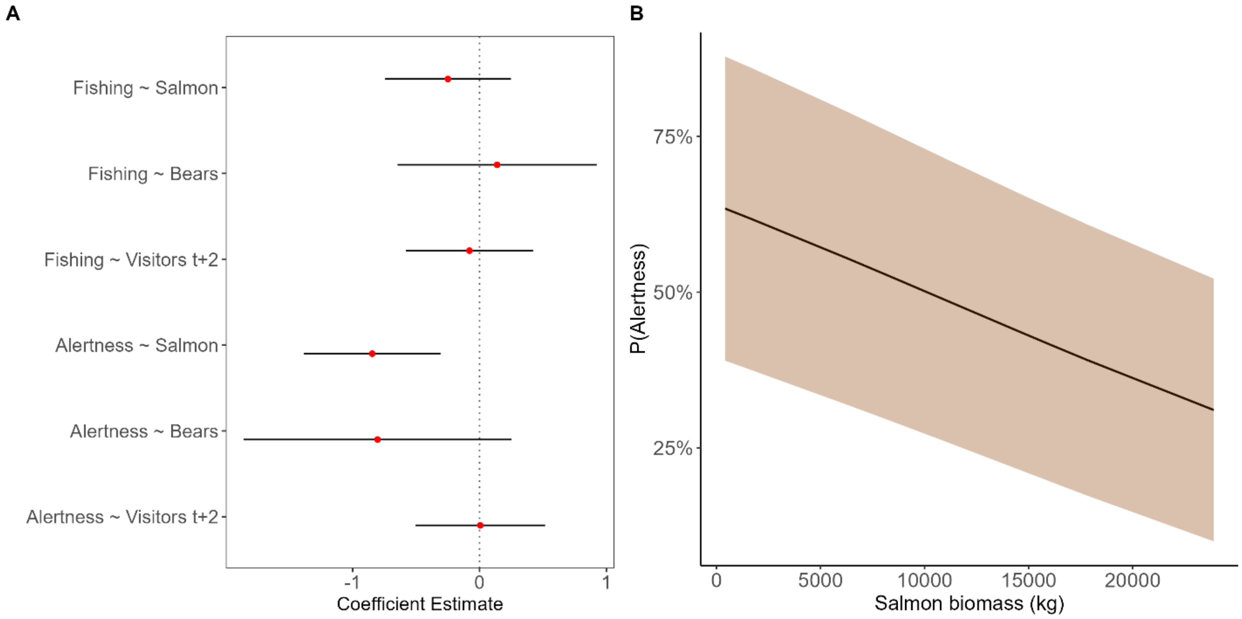

Figure B3. Second top multinomial model (Δ AIC = 0.002) predicting fishing, alertness, and 'other' behavioural states among grizzly bears subject to ecotourism on the Atnarko river, Nuxalk Territory, British Columbia (2019–2021). (A) Probability that a bear was alert as a function of salmon biomass (B) Parameter coefficients and CIs for fixed effects, centered and scaled by two standard deviations. Red dots represent parameter coefficients and black lines span 95% CIs.

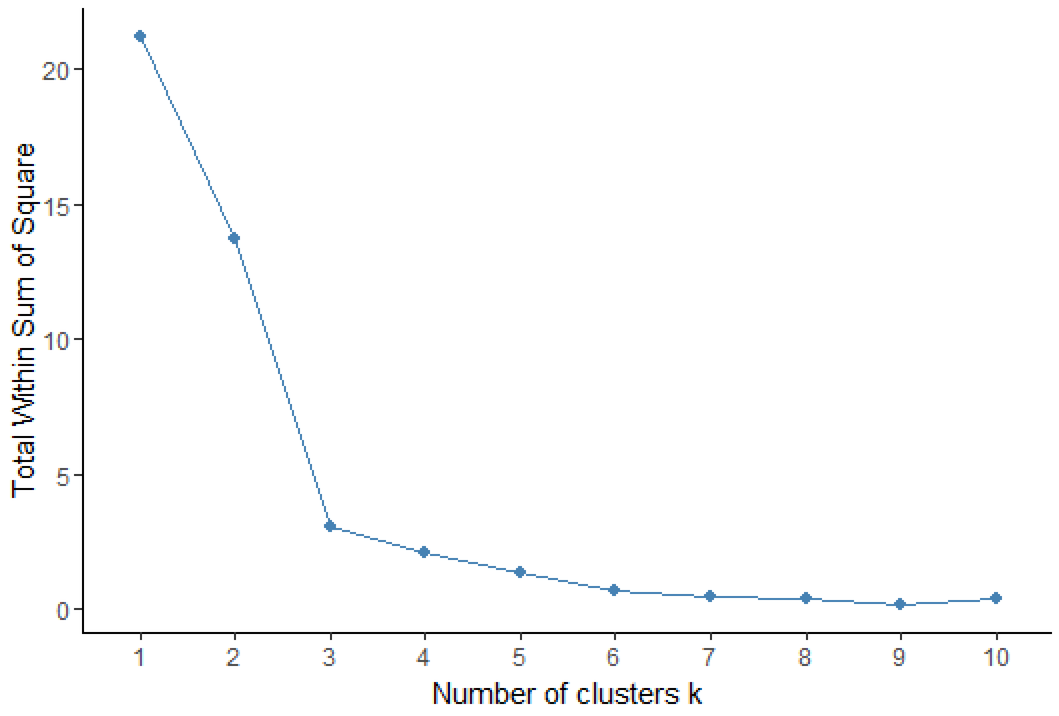

Figure B4. We identified three (the 'elbow point') as the optimal number of clusters. Figure plots within sum of square for different numbers of clusters, with the 'elbow point' indicating the number of clusters at which any further increasein clusters results in diminished improvement to model fit. Data were subset to include individuals that were detected at least three times (n = 52 individuals out of original 118).

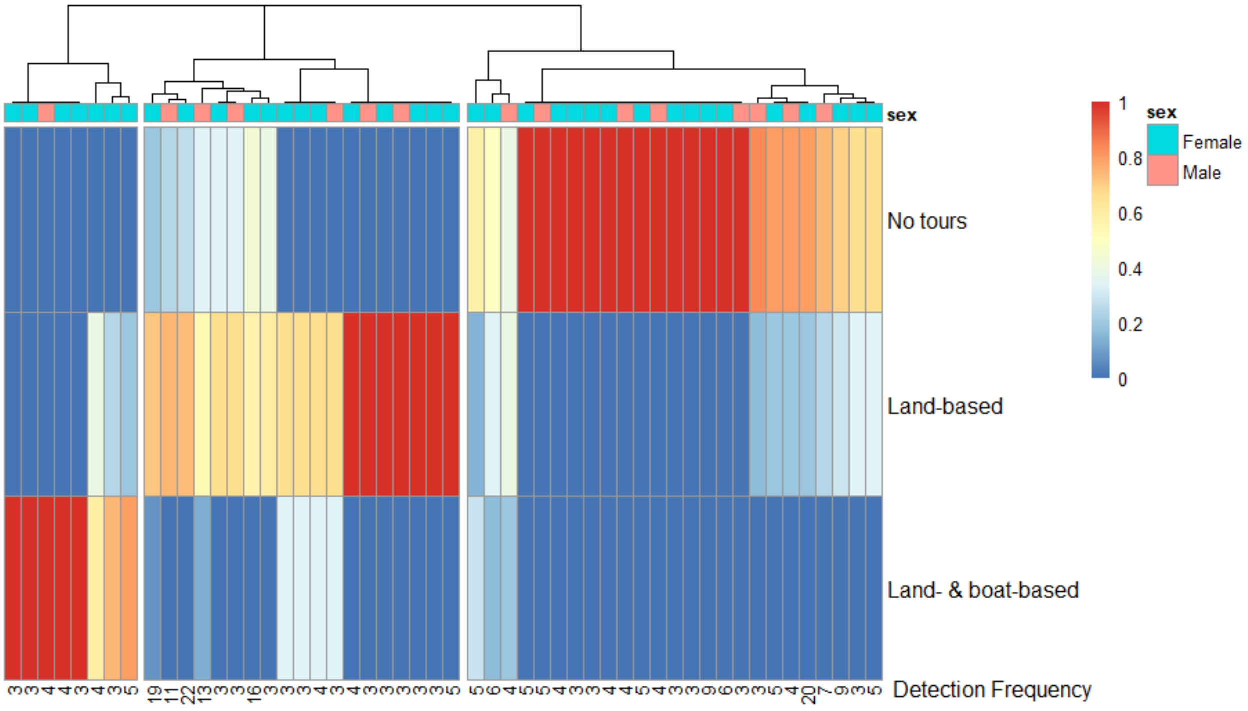

Figure B5. Three distinct clusters of individuals based on similarities in their detection histories. Heatmap and dendrogram illustrate the detection histories of each individual grizzly bear (with each column representing an individual). The colour ramp represents the proportion of detections per individual that occurred in each spatial treatment. The dendrogram tree identifies three clusters (three identified as optimal number of clusters via elbow method in k-means clustering), which clusters individuals with similar detection histories. Data were subset to include individuals that were detected at least three times (n = 52 individuals out of original 118).

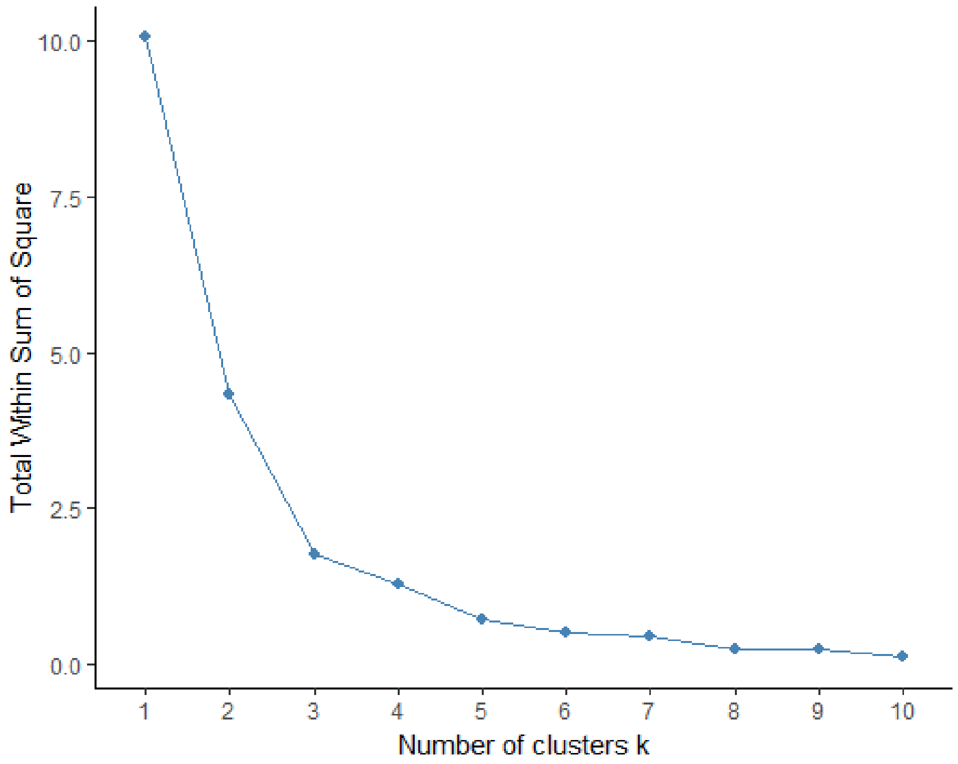

Figure B6. We identified three (the ‘elbow point’) as the optimal number of clusters. Figure plots within sum of square for different numbers of clusters, with the ‘elbow point’ indicating the number of clusters at which any further increasein clusters results in diminished improvement to model fit. Data were subset to include individuals that were detected at least four times (n = 30 individuals out of original 118).

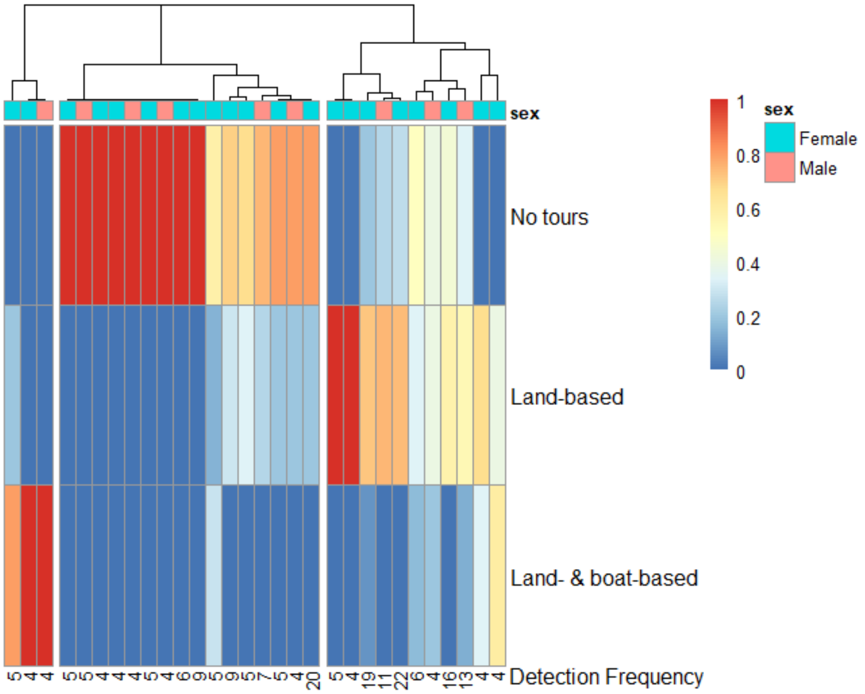

Figure B7. Three distinct clusters of individuals based on similarities in their detection histories. Heatmap and dendrogram illustrate the detection histories of each individual grizzly bear (with each column representing an individual). The colour ramp represents the proportion of detections per individual that occurred in each spatial treatment. The dendrogram tree identifies three clusters (three identified as optimal number of clusters via elbow method in k-means clustering), which clusters individuals with similar detection histories. Data were subset to include individuals that were detected at least four times (n = 30 individuals out of original 118).

Appendix C – Supplementary Information for Chapter 4

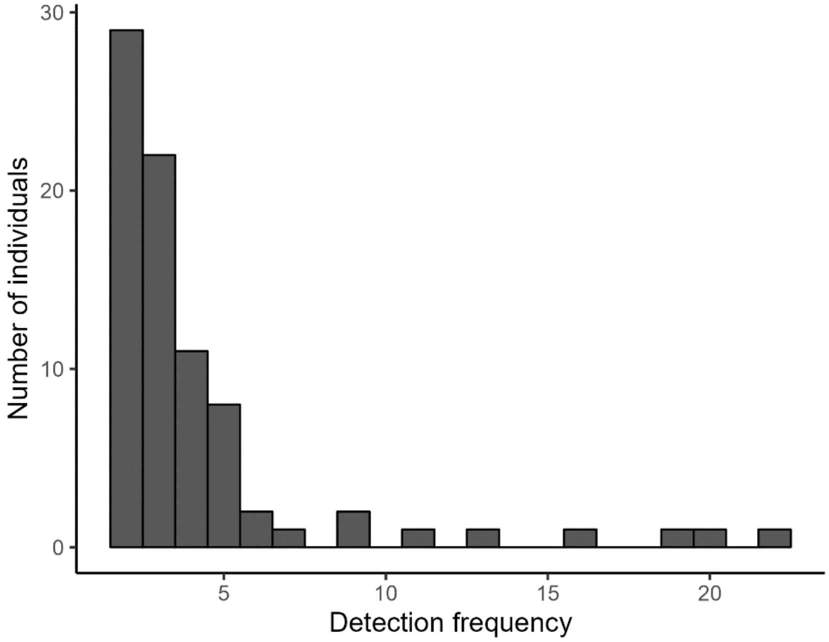

Figure C1. Detection frequency of individuals captured more than once (n = 81) across years.

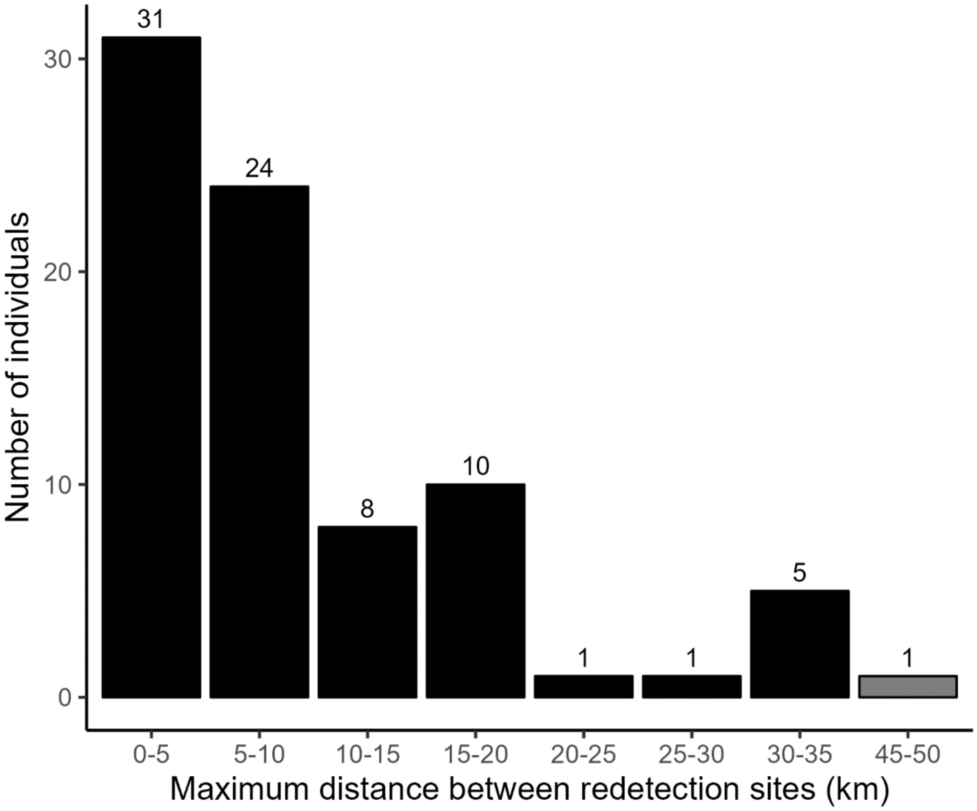

Figure C2. Maximum river network distance between hair snags at which each individual was detected. Although limited in sampling timespan, we consider these as a coarse measure for the ability of bears to move throughout and beyond the Atnarko river corridor (i.e. among upstream, ecotour, and downstream conflict areas; Figure 4.1). Data represent individuals that were detected more than once (n = 81) with detection frequency ranging from 2-22. The grey bar represents the single individual that travelled the furthest, traveling 47.8km from the ecotour area to encounter subsequent conflict downstream.