Wildlife ecotourism elicits spatial and temporal shifts in grizzly bear activity in Kitasoo Xai'xais Territory on the Central Coast of British Columbia

by

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Abstract

Ecotourism offers a non-consumptive form of economic activity globally. Human activity, however, might negatively affect the ecology of areas and their biota, likely varying with type and intensity of ecotourism. Wildlife, for example, might perceive ecotourists as predators, and adjust behaviour accordingly (i.e., human avoidance). Alternatively, wildlife might actually seek human activity if it protects them from greater risks (Human Shield Hypothesis). The Anthropause, a period of decreased human activity due to COVID-19, provided unparalleled opportunity to examine wildlife behaviour when perceived risks from humans were removed. In partnership with the Kitasoo Xai'xais First Nation (KX), we assessed if and how ecotourism, in the form of bear-viewing, might influence spatial and temporal activity of grizzly bears. We deployed remote cameras in the Khutze watershed in 2020 in the absence of human use. To provide increased inference when tourism resumed in 2021, KX implemented alternating spatial closure experiments within the watershed. Additionally, in 2021 we implemented a tourist group size experiment in a second watershed, Green River. In Khutze, we found that a closure of 25 days was required for bear detection rate to return to the 2020 (non-ecotourism) level. We did not observe an influence of the alternating within-watershed north-south closures on activity. The data also revealed complex relationships among bear detections, ecotourism activity, and salmon availability, varying by age and sex of bears. Specifically, we found a human shield effect for females with young when salmon levels were moderate to high, but this effect diminished in times of low salmon. An activity pattern analysis in Khutze did not show an effect of ecotourism. In Green, where inference was likely constrained by our short-term experiment, we found a positive influence of the number of days since people were present on detection rate. We additionally found temporal avoidance of within 100m of the viewing site on days when people were present. These patterns from both watersheds show the complex ways in which wildlife can respond to even seemingly benign human presence. Inference from this research has application to wildlife, land, and ecotour management by the KX, who are reasserting authority in governance. More broadly, this study contributes to literature on the dynamic landscape of fear induced by spatiotemporal variation in human activity.

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Acknowledgements

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Chapter One: Introduction

When we examine ecological systems without including the potential influence of human presence, there is much that we might miss, owing to the complexity of these intertwining systems (Bennett & McGinnis, 2008). The frameworks used to study human-environment interactions have evolved over time as our understanding of these interactions, as well as our concerns as scientists and societies, have shifted. Human-environment interactions were first studied through the lens of environmental determinism, where humans and societal traits were thought to be determined by the environment within which they lived (Harden, 2012). Impacts of humans on the environment increased considerably after the second world war (Dearing et al., 2006), which sparked a reversal to studies commonly aimed at the human impact on the environment in which researchers sought a better understanding of humanity's role in shaping ecosystems (Harden, 2012). Recently, research has been more focused on sustainability, which accounts for the feedbacks and reciprocal relationships between human and natural systems (Harden, 2012).

This framework of reciprocal human – environment relationships, while relatively new to Western academics, is foundational to Indigenous nations, which have a deep understanding of the connectedness and reciprocity among humans and the environment (Berkes et al. 2000, Ban et al. 2019, Dick et al. 2022). Indigenous nations globally have been stewarding their lands for millennia. Settler colonization, however, acted to violently dispossess Indigenous peoples from their lands and ways of life, disrupting these reciprocal relationships and systems of governance (Claxton and Price 2020, Turner et al. 2013, Whyte 2018). As Indigenous nations continue to reassert governance authority over their territories, ecological research has become increasingly partnered between scholars and Indigenous communities, which has enriched both the quality and relevance of ecological research (Adams et al., 2014).

Indigenous nations, as well as other land stewards, wildlife ecologists and managers, seek information about the ways in which people can induce behavioural change in animals (and how these effects might be mitigated). Industrial and other development can displace animals, including large carnivores, and change the environment, creating novel contexts in which animals make behavioural decisions (Ripple et al., 2014; Watson et al., 2016; Wilson et al., 2020; Wolf & Ripple, 2017). These changes vary in intensity, from urban development or resource extraction, to trail networks for seemingly benign hikers (Fortin et al., 2016; Naidoo and Burton, 2020). Even simulated human presence has been shown to change animal activity (Smith et al., 2017; Suraci et al., 2019). Regardless of the actual mortality risk to wildlife, human activities on these landscapes may be perceived as risks and induce spatial or temporal activity shifts.

Much of the insight ecologists have on risk avoidance, or the 'ecology of fear', in large mammals comes from observational studies. While observational studies have provided valuable insight into predator prey relationships, experimental approaches can add immense value in their ability to specifically test for drivers of animal activity changes (Smith et al., 2020). Experimental approaches focussed on predator-prey dynamics can be effectively applied to human-animal relationships through simulating or eliminating risk cues associated with people (Smith et al., 2020; Suraci et al., 2017). For example, the effects of humans on wildlife have been experimentally simulated using audio recordings of people, showing the vast range of species influenced by humans (Suraci et al., 2019).

The ways in which humans impact animal activity can vary based on the context, type of activity, and degree to which animals perceive humans as a threat. This context dependence requires place-based studies that can guide local management, as well as contribute to literature on human-wildlife interactions. Our study contributes to both these objectives through the use of remote cameras and experimental manipulation of human activity to test how grizzly bears (*Ursus arctos*) may respond spatially and temporally to ecotourism pressure. This methodology allows us to answer specific, management-related questions and provides insight into the dynamic landscape of fear associated with ecotourism. Specifically, this study offers a novel experimental remote camera study of grizzly bear viewing along the Central Coast of British Columbia.

Chapter Two

Introduction

Wildlife commonly encounter contexts that require trade-offs between risks, such as predation, and benefits, such as access to resources. Avoiding risk requires allocation of time otherwise spent on foraging or other fitness-enhancing activities and can manifest via animals shifting their spatial and temporal use of habitat (Lima and Dill, 1990; Lima and Bednekoff, 1999; Palmer et al., 2022; Spitz et al., 2019; Zanette and Clinchy, 2019). Given an enduring and long history of predation by humans (Barnosky et al., 2004; Darimont et al., 2015; Ripple and Valkenburgh, 2010), even seemingly benign human activity can be perceived as a source of risk and can elicit avoidance (Gaynor et al., 2018; Spitz et al., 2019; Suraci et al., 2019).

Human avoidance can occur on various spatial and temporal scales. Spatial avoidance can range within a few meters to a few kilometers. For example, cougars (*Puma concolor*) avoided human voice recordings by ~150 meters (Suraci et al., 2019); and black bears (*Ursus americanus*) avoided roads by over 2000 meters (Stillfried et al., 2015). Temporal avoidance can occur on the scale of hours, through shifting diurnal patterns (Gaynor et al., 2018; Suraci et al., 2019), or occur through lagged avoidance effects that last days (e.g., Ordiz et al., 2013). Moreover, avoidance can also occur in a combination of spatial and temporal avoidance (Palmer et al 2022; Ordiz et al., 2013). The response and scales of avoidance are likely influenced by the perceptual range of species and the perceived magnitude of the threat; for example larger perceived threats like motorized vehicles can elicit broader scale avoidance compared with hikers (Naidoo and Burton, 2020; Procko et al., 2022). As predicted by the dynamic landscape of fear, responses may relate to predictability and magnitude of perceived risks. When predictable in space and time, animals can use fine-scale spatiotemporal risk avoidance; as risk becomes less predictable, animals may show larger spatial or temporal responses (Palmer et al., 2022).

Despite humans being perceived as risky by many species, in some cases wildlife may seek human activity if it protects them from predation or competitive risks, a phenomenon described by the human shield hypothesis (Berger 2007). Use of human shields has been observed in many animals, including moose (*Alces alces*; Berger, 2007), monkeys (*Cercopithecus mitis erythrarcus*; Nowak et al., 2014), goats, (*Oreamnos americanus;* Sarmento and Berger 2017), and mountain nyala (*Tragelaphus buxtoni*; Atickem et al., 2014). The human shield has also been observed in female grizzly bears (*Ursus arctos*) with cubs, who used human presence as protection from infanticide by male bears (Steyaert et al., 2016). In general, female grizzly bears with cubs alter their habitat selection to avoid male bears (Steyaert et al., 2016). Females who successfully avoid infanticide tend to select habitats closer to humans than those who suffered cub loss (Steyaert et al., 2016). In ecotourism settings, male grizzlies have been observed to avoid tourist areas during the day, providing a temporal refuge for female bears with cubs to feed in resource rich areas (Nevin and Gilbert, 2005*a, b*).

Studies on bear-viewing have occurred throughout British Columbia and Alaska (Nevin and Gilbert, 2005*a, b*; Elmeligi and Shultis, 2015). These studies have found that male and female bears respond to ecotourism differently (Nevin and Gilbert, 2005*a, b*), and that different types of ecotourism may induce responses at different distances (Elmeligi and Shultis, 2015; Jacobs and Schloeder 1992). However, multiple gaps remain in the literature. One of these gaps is the way that ecotourism group size may influence the magnitude of bear responses to people. Furthermore, it is unknown how long the influence of human presence may last after a tour ends.

Finally, this research also provides better resolution of temporal and spatial avoidance though using continuous data collection with remote cameras.

Guided by this theory, we regarded the Anthropause, a period of decreased human activity due to COVID-19, as an unparalleled opportunity to examine wildlife behaviour when perceived risks from humans were diminished or absent (Rutz et al. 2020). Given that studies of ecotourism are primarily observational, the Anthropause also provided an opportunity to employ a semi-experimental context to address hypotheses related to risk theories. Specifically, 2020 provided a 'before' condition, against which we could set up inference treatments 'after' in 2021 (Green, 1979). This size and duration of closure would not have been possible without the Anthropause, and provided a valuable setting to gain inference on bear viewing. In coastal British Columbia (BC), bear ecotourism, which typically occurs during peak resource (salmon; *Salmonidae spp*.) availability when bears congregate at prime fishing areas, was cancelled in 2020, and resumed in 2021, however at a lower level than pre-pandemic ecotourism.

As a partnership between the Kitasoo Xai'xais Stewardship Authority (KXSA) and applied scientists, we assessed how bear-viewing ecotourism influences spatial and temporal activity of grizzly bears within the Kitasoo Xai'xais (KX) Territory on the Central Coast of British Columbia. We worked at two sites, Khutze and Green. In Khutze we collected data throughout 2020 when ecotourism was fully closed, and 2021 when we implemented experimental spatial closures and closely monitored the timing and intensity (number of tours, group size) of ecotourism operations. We also collected data in Green in 2021 during an additional tour group size experiment. Given predictions from the dynamic ecology of fear, whereby animals shift their activity in space and time to avoid predation risk (Palmer et al., 2022), and previous bear viewing literature (Nevin and Gilbert 2005*a*; Elmeligi and Shultis, 2015; Penteriani et al., 2017), we developed three main hypotheses. First, we predicted that grizzly bear spatial activity would be negatively correlated with ecotourism pressure. Second, we predicted that adult male bears would be more negatively influenced by tourism pressure than females, creating a human shield for females with young from infanticidal males. Third, in areas with diurnal tourism, we predicted that male bears would be more nocturnally active in the presence of tourism, and females with young would show the opposite temporal response to males.

Methods

Study Area

We deployed remote cameras across portions of two watersheds, ~5km^2 of the ~340 km^2 Khutze and ~2km^2 of the ~190km^2 Green watershed (Figure 1). Khutze has an extensive estuary (~2 km^2), whereas Green is a river that drains into a large (~5.5km^2) lagoon. Both have a dominant river and riparian trails through temperate rainforest. Both host grizzly (*Ursus arctos*) and black bears (*Ursus americanus*). Salmon spawn throughout the camera array (Figure 1), as well as ~6km further up Khutze, and ~200m further up Green, however the camera arrays cover much of the habitat for pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*), which are the most important species to bears. The next nearest salmon bearing stream to both watersheds is ~7.5 km away. Ecotourism operators and the public can only visit these roadless areas via ocean-going boat (Figure 1A). Khutze has been subject to bear watching ecotourism by multiple operators for over 15 years, in addition to public access, whereas the harder-to-access Green watershed has primarily only hosted infrequent tours by the KX-run ecotour lodge in the last several years. Authorized viewing sites for both (Figure 1 B, C) are accessed by boat or on foot. The popularity of bear-viewing has been increasing, which has led to increased tours, and larger tour group sizes in Khutze. The use of these two watersheds may provide greater insight into the context-dependence of ecotourism influences, as well as allow us to make inference on how different forms of tourism (boat vs. land based) and different environments (estuary vs. river) may influence the responses of bears to people.

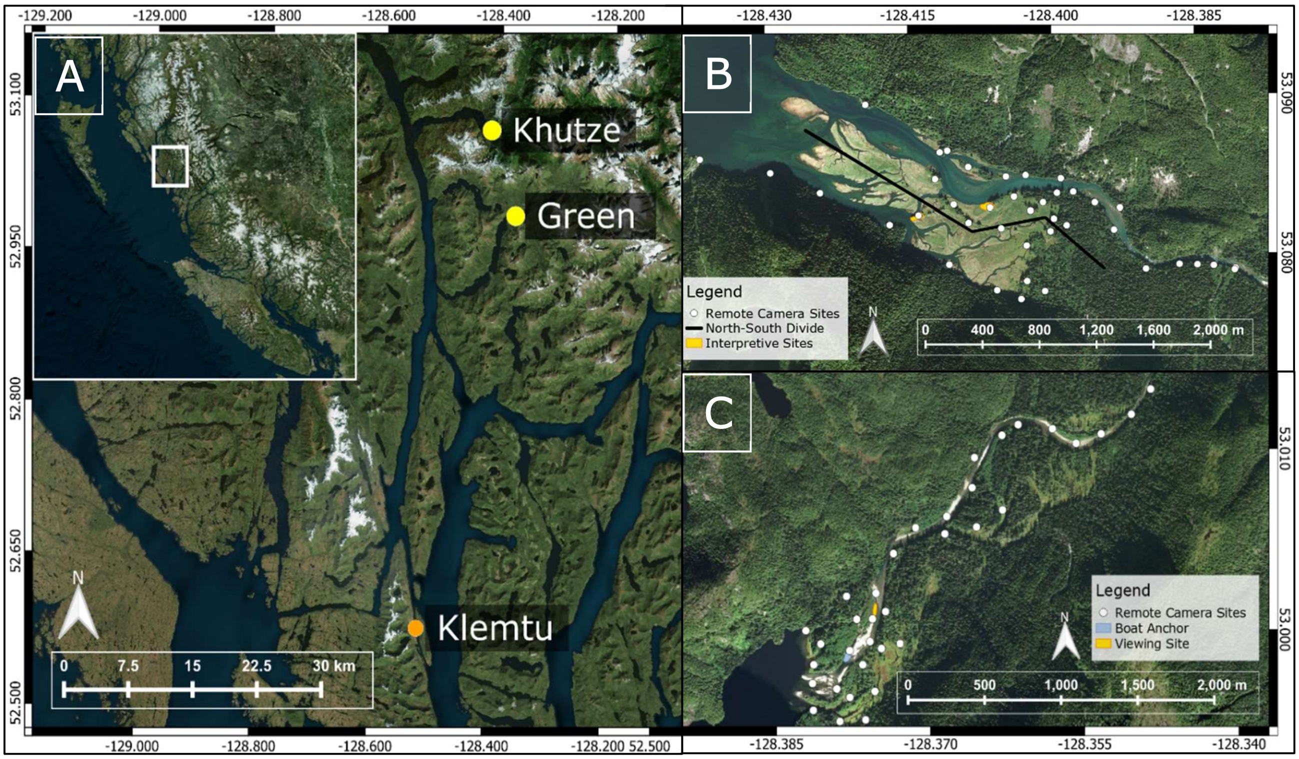

Figure 1. A) Study area within Kitasoo Xai'xais Territory on the Central Coast of British Columbia, Canada, showing the locations of Khutze, Green, and the village of Klemtu, the current village of the KX; B) Khutze remote camera array, north-south divide (black line) for the alternating weekly spatial closures, and land-based interpretive sites; C) Green remote camera array, land-based viewing site, and boat anchor site.

Observational and Experimental Design

We analyzed camera trap data (Appendix S1) from Khutze during periods when ecotourism and salmon co-occurred (July 20 – September 27, 2020, and July 26 – October 3, 2021). Owing to COVID-19, ecotourism was closed in Khutze in 2020. In 2021, KXSA applied alternating weekly closures of the north and south regions of the watershed (Figure 1B) to test how modified human presence might influence bear activity. This resulted in 5,008 camera trap days across 40 remote cameras, including 51 days with tours, and 89 days with no tours. Tour group sizes varied from 1 to 14 people (median = 8.5), with 1 to 5 tours each tour day (median = 1). Daily tour hours ranged from 0.6 to 13.4 hours (mean = 3.4). Bear-viewing in Khutze was primarily boat based, with one land based interpretive site on the north and south sides of the estuary. All ecotourist groups carried a Bad Elf ® GPS Pro in Khutze to record spatial and temporal data on human activity (Appendix S1).

In Green, we conducted an experiment to test for the influence of tourist group size on grizzly bear activity. We sampled August 23 – September 27, 2021, a period of peak salmon availability and assessed two levels of tourist group size - small groups (8 people) and large groups (14 people) – and compared these to no-tour-group control periods. Each treatment was implemented during alternating two-day periods, interspersed by two-day control periods with no tour groups (Appendix S1: Table S1). Treatments consisted of the group walking ~380 metres along the riverbank to a viewing site, where they set up small benches and a tent for shelter and then remained at this site. Duration ranged from 1.75 to 4.5 hours (average = 3.85). Due to weather issues restricting site access, we were unable to access the site on four large group days, leading to 4 total large group, 8 small group, and 12 control days.

Analyses

We modeled how ecotourism and environmental variables influenced grizzly bear activity. The response variable was the number of independent bear detections at a camera on a given day (‘detection rate’). Each ‘day’ (24-hour period) started at the earliest tour time in each sampling system (07:00:00 for Khutze and 10:00:00 for Green) because we would only expect bear activity to change during or after human presence. Each 'detection' was considered independent if bear images were separated by 30 minutes, or if it was clearly a different bear than the immediately previous detection, based on age and sex class or visible differences in scarring or coat colour (Burton et al., 2015; O'Brien, Kinnaird & Wibisono 2003). Occasionally, a single detection included two adult bears (~0.7% of detections in Khutze, ~0.5% in Green). These detections were separated into two individual detections for the age and sex class analysis (below) but were considered a single detection in the detection rate model. Females with young were scored as a single detection, given they comprise an age-sex class of interest, and served as a single unit.

Detection rate models

In Khutze we tested for the effects of ecotourism activity, including human presence, number of people per day, number of tours, tour hours, distance to tours, site ecotourism exposure (open or sheltered), spatial closures (north or south in 2021, fully closed in 2020), and temporal closures (closed in 2020 and open in 2021) in separate detection rate models (Appendix S1: Table S2). All models included an indicator variable for year or the spatial closures (capturing the full site closure in 2020), as well as variables for salmon biomass, and water level, which together determine salmon availability, a primary food source for bears. We accounted for camera site, and week as random effects.

Using these variables, we developed a candidate model set including interaction terms (Appendix S1: Table S4; Table S5; Burnham and Anderson, 2002). Briefly, we included interaction terms between water level and salmon biomass, as well as salmon biomass and each ecotourism metric. Additionally, we included interaction terms between ecotourism metrics and the spatial closures, the ecotourism metric and camera site exposure, and between days since people and year (Appendix S1). Ecotourism metrics were considered in separate models and competed to test which ecotourism metrics were more important in predicting bear activity.

In Green, we tested for the effects of human presence, group size, and inverse distance to people (Appendix S1: Table S3). All models in Green included salmon, water level, and their interaction, because flooding resulted in multiple days when cameras were submerged. We accounted for camera site as a random effect.

Given the interest in multiple ecotourism metrics (presence/absence, number of people, number of tours, and hours in the day with tours), we developed a separate candidate model set for each of these ecotourism metrics in Khutze (Appendix S1: Table S4). For Green, we followed the same procedure using the two available ecotourism metrics (human presence/absence, group size; Appendix S1: Table S5). We competed each set against the null and environmental models (Appendix S1: Table S4; Table S5), as well as against each other to determine which ecotourism metric is most important in predicting detection rate.

We ran generalized linear mixed effects models (GLMMs) using glmmTMB in R (Brooks et al., 2017; R Core Team, 2021). We used the family binom2, which is the quadratic parameterization of the negative binomial distribution, because it provided the best estimation of zeros (Brooks et al., 2017; Appendix S1: Figure S2). We checked the models for additional zero-inflation, using the DHARMa package in R and did not include a zero-inflation parameter (Hartig, 2022).

Age and sex class multinomial models

Given results from previous bear viewing studies, we would expect that bears respond differently to ecotourism based on their age and sex (Nevin and Gilbert, 2005*a, b*). To assess potential differences, we used a multinomial model to test the effect of ecotourism and environmental variables on the probability of a detection being an adult female, adult male, female with young, or subadult. Of 1934 bear detections in Khutze the age and sex class were successfully classified for 1348 (~70%). Of 887 detections in Green, the age and sex were classified for 562 (~63%) (Appendix S1). We included a nocturnality metric, calculated as the absolute value of the time between the darkest point in the night, averaged across the study period (00:12) and any given bear detection (Suraci et al., 2019), as a predictor variable, given that age and sex classes tend to be active during different times of the day (Nevin and Gilbert 2005a). Additional predictor variables for Khutze were the yearly closures, salmon biomass, number of people, inverse distance to tour, treatment, site ecotourism exposure, and days since people, (Appendix S1: Table S6; Table S7; Table S8; Table S9), and in Green we included salmon biomass, human presence, inverse distance to people, and days since people. Additionally, we included the camera site as a random effect. We used adult male as the base condition because we hypothesised that adult males would have the largest difference in activity compared with the other three age sex classes (Nevin and Gilbert, 2005*a, b*).

We evaluated the performance of the multinomial model by calculating the area under the receiver operator curve (ROC) for comparisons of each age-sex class to adult males (Appendix S1; Hosmer & Lemeshow, 2000; Wilmers et al., 2020). The multinomial model to predict whether a detection was an adult female, female with young, or sub-adult had areas under the ROC of 0.71, 0.65, and 0.59, respectively. The model showed acceptable discrimination between adult females and adult males (Hosmer & Lemeshow, 2000). The discrimination between female with young or subadults with adult males are below the acceptable range of 0.7, but above the 0.5 cut-off for no discrimination (Hosmer & Lemeshow, 2000).

Top model set identification and RVI estimation

For both the detection rate model and age-sex class multinomial model, we considered the model set with the ecotourism metric that produced the lowest AIC value as the final model set. For the final model set, we calculated the AIC values and weights, determining the top model set using the cumulative AIC weights to define a 95% confidence set of best ranking models (Symonds and Moussali, 2011). We additionally calculated the relative variable importance (RVI) for each variable in the detection rate model set, standardizing the RVI based on the number of models including each variable (Kittle et al., 2008).

Activity pattern analysis

To assess potential temporal displacement of bears by ecotourism, we compared activity patterns during days with and without tourism. We performed an activity pattern analysis (APA), using a nonparametric kernel density function to model activity as a continuous distribution over a wrapped 24-hour cycle (Frey et al., 2017; Ridout and Linkie 2009). To include a potential spatial influence on temporal activity, we ran our APA at multiple distances from human activity, based on recorded overt reaction distances for bears (Elmeligi and Shultis, 2015; Jacobs and Schloeder 1992). We binned the remote cameras into distances of 0-100m, 100-450m, and 450-1000m (and 1000-2000m in Green) from the tours (Khutze) or viewing site (Green). We used the Mardia-Watson-Wheeler (MWW) test to assess whether differences between activity patterns were statistically significant using the R packages, ‘Overlap’, and ‘Circular’ (Agostinelli and Lund, 2017; Ridout and Linkie, 2009).

Results

Detection rate models

We found multiple signals of ecotourism influence on bear detection rate. Comparing four model sets with alternative metrics for ecotourism revealed the models using number of people per day outperformed others (Appendix S2: Table S1; see Appendix S2 for alternate ecotourism metric results). In the top model (and similarly in other models within this set and others; Appendix S2: Table S1; Table S2), although we did not detect an effect of year alone, daily detections decreased with higher numbers of people visiting Khutze (Figure 2A). An interaction term revealed that as the number of people increased, detections were higher at sheltered camera sites with the opposite trend observed at open sites (Figure 2B). Specifically, we found an increase in detection rate at sheltered sites of ~2.2% for each additional person. Finally, we observe a positive association between overall detection rate and the number of days since people were present in the watershed in 2021 when ecotourism was open (Figure 2C; Appendix S2: Table S2). With each additional day since people, the detection rate increased by ~9.2%. The predicted detection rate in 2021 aligned with the 2020 mean at 25 days since people, suggesting a full watershed closure of 25 days would be required for activity to return to a 2020-like non-tourism level; although, there is considerable uncertainty around this estimate (Figure 2C).

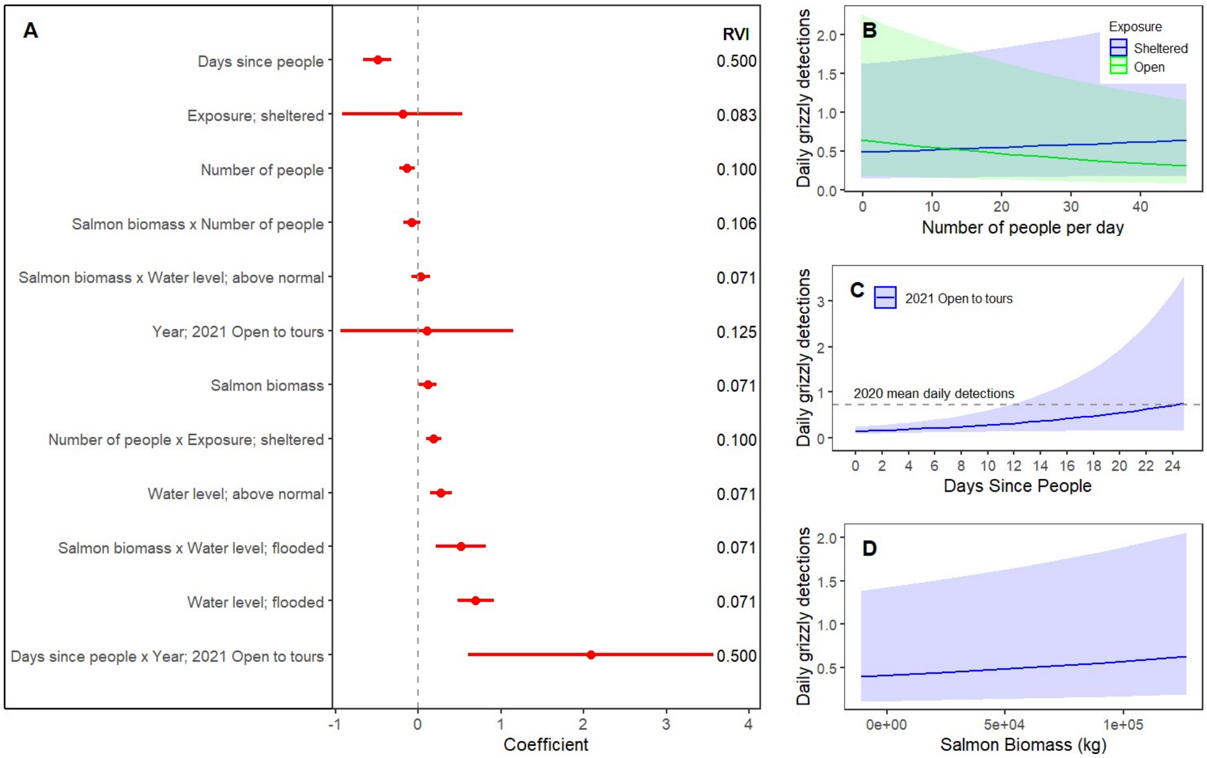

Figure 2. Top detection rate model for Khutze: A) parameter coefficient, centered and scaled by two standard deviations, and confidence intervals for model fixed effects. Red dots represent the parameter coefficients, or the magnitude of effect on the bear detection rate, and red lines span the 95% confidence intervals. Relative variable importance (RVI) is annotated for each fixed effect; B) site-level daily grizzly detection rate at sheltered and open sites as a function of the number of people per day. Shaded regions represent the 95% confidence interval for model estimates, and the curves represent the model predictions. The green shaded region represents detections at open sites, and the blue shaded region represents detections at exposed sites. There is a positive influence of number of people on detection rate at sheltered sites, and a negative influence of number of people at open sites; C) site-level daily grizzly detection rate as a function of days since people in 2021, across all remote camera sites. Blue shaded region represents the 95% confidence interval for model predicted detection rate, and the curve shows the model

predicted values. The grey dotted line represents the 2020 (non-ecotourism) mean detection rate. The confidence interval overlaps the 2020 mean at 12 days, and the model predicted detection rate is equal to the 2020 mean at 25 days; D) site-level daily grizzly detection rate as a function of salmon biomass. Salmon biomass has a positive influence on detection rate.

Additional and finer-scale temporal and spatial measures of variation of ecotourism activity were not influential on overall detection rate. Specifically, neither the treatment of alternative north/south closures, nor the inverse distance to tours, appeared in any top model.

Variation in salmon had a more modest effect than ecotourism metrics. However, salmon biomass, water level, and the interaction between salmon and water level had positive associations with daily detection rate (Figure 2D and Table 2). For an increase in salmon biomass by 10,000kg (mean = 57,777kg; SD = 34,431kg), we observed a ~3.4 % increase in daily detection rate. An interaction term indicated that when water level was flooded salmon biomass had a positive effect (Figure 2A; Table 2). Water level alone additionally had a positive influence on detection rate across Khutze.

Relative variable importance additionally showed that ecotourism had a greater influence than environmental covariates. Days since people and the interaction between days since people and year have the greatest influence (RVI = 0.5; 0.5; Figure 2) on grizzly bear detection rate. Days since people in 2021 was ~7 times as important as salmon biomass or the interaction between salmon biomass and water for predicting detection rate.

In Green we found that the human presence and group size metrics performed similarly to one another, but human presence performed slightly better (Appendix S2; Table S8). We found that days since people had a positive association with grizzly detection rate (Figure 3A, 3B).

Additionally, when the water level was flooded, we detected fewer bears. We did not detect any effects of human presence or salmon biomass (Figure 3A, Figure 4). Furthermore, the top 95% model set included the environmental only model, which consists of salmon, water level, and their interaction (Appendix S2; Table S8).

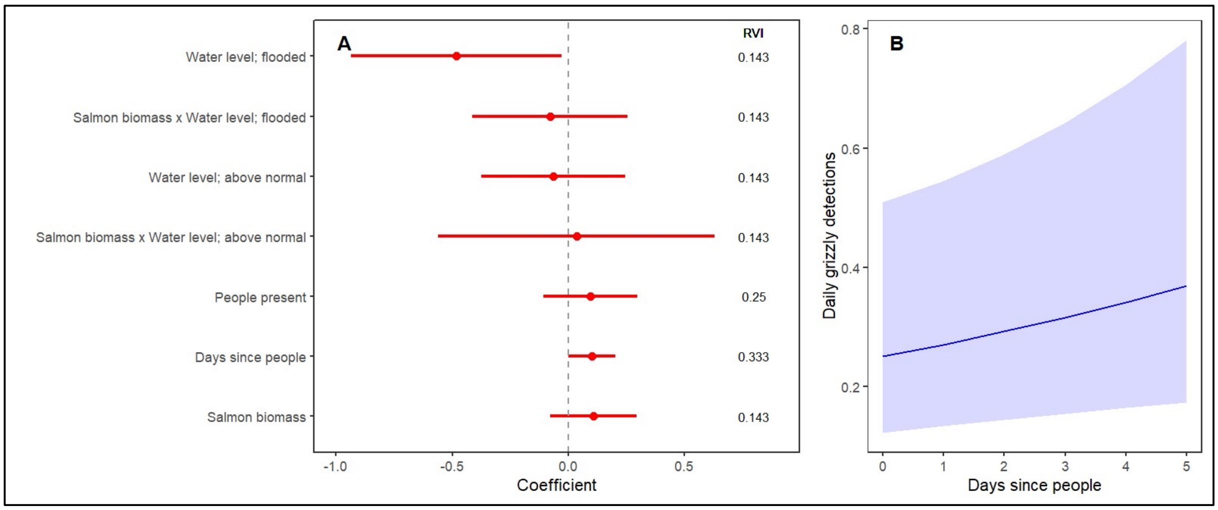

Figure 3. Top detection rate model for Green: A) parameter coefficients and confidence intervals for fixed effects. Red dots represent parameter coefficients and red lines span 95% confidence intervals. Relative variable importance (RVI) is annotated for each fixed effect; B) site level daily grizzly detection rate as a function of days since people. The blue shaded region represents the 95% confidence interval around the curve, which represents the model predicted values. Days since people has a positive influence on detection rate.

Age and sex class multinomial models

Age-sex classes responded differently to ecotourism activity in Khutze. It was more for a detection to be an adult female, female with young, or subadult, compared with adult males on days when the number of people were higher (Figure 4A). When people were closer to remote cameras, it was more likely for detections to be adult females or females with young than adult males (Figure 4A, D, Appendix S2: Table S12). Although we did not find effects of days since people or year individually, an interaction term revealed complex dynamics. Specifically, the 95% model set indicated that as the days since people were in the watershed in 2021increased, the likelihood that a detection was an adult male increased, but the likelihood of detections being adult females, females with young and subadults did not change (Appendix S2: Figure S8).

Salmon availability also influenced age-sex classes differently. It was more likely for a detection to be an adult female, female with young, or subadult than adult male as salmon biomass increased (Figure 4A). An interaction between salmon biomass and the number of people showed that when salmon were low, the number of people had little influence on the likelihood of a detection being an adult male, but when biomass was moderate to high, increasing numbers of people was associated with a lower likelihood of a detection being an adult male (Figure 4B). Specifically, the likelihood of a detection being male on days with mean salmon levels decreased significantly when 6 or more people were in Khutze. The interaction had an opposite influence on females with young. We observed a positive association between the number of people and the likelihood of a detection being a family group, but only when salmon biomass was moderate or high (Figure 4C).

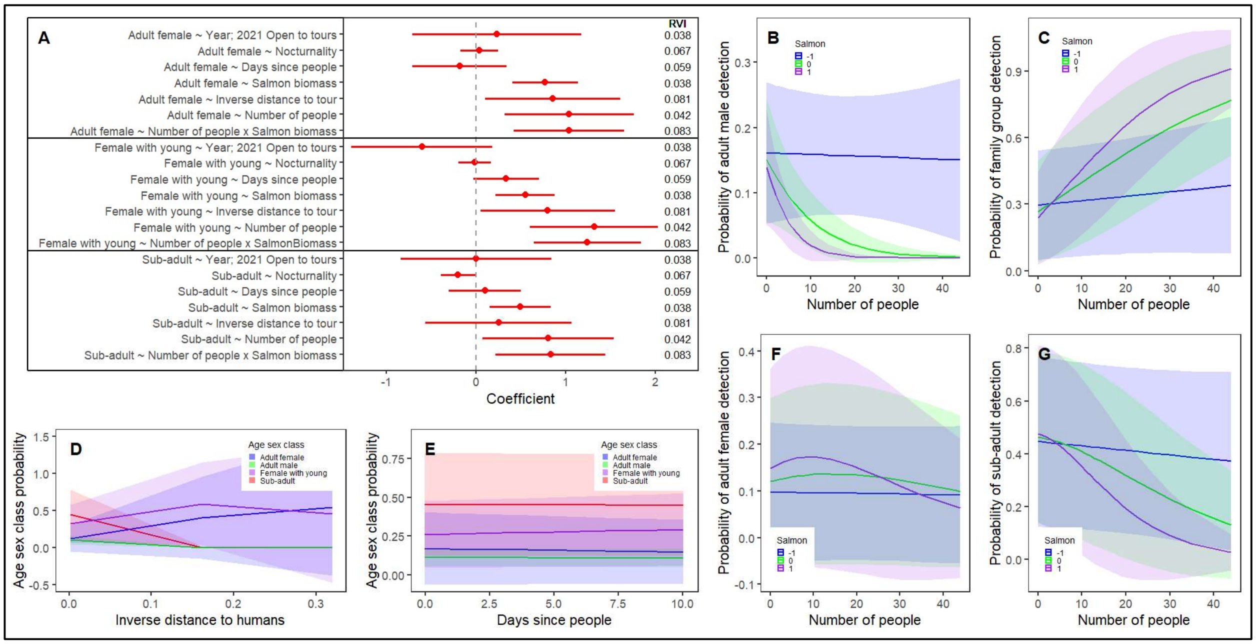

Figure 4. Age and sex class top multinomial model for Khutze. A) parameter coefficients, and confidence intervals for fixed effects. Red dots represent parameter coefficients and red lines span 95% confidence intervals. Relative variable importance (RVI) is annotated for all fixed effects; B) likelihood of a detection being adult male as a function of the number of people per day and salmon biomass. Salmon biomass levels are the mean, and one standard deviation above and below the mean. When salmon biomass is at its mean or high, number of people have a strong negative influence on the probability of a detection being adult male; C) likelihood of a detection being a family group (female with young) as a function of the number of people per day and salmon biomass. When salmon biomass is at its mean or high, number of people have a positive influence on the probability a detection being a family group; D) likelihood of a detection being any given age-sex classes as a function of the inverse distance to humans. When salmon biomass is at its mean or higher, inverse distance to people has a negative influence on the probability of a detection being an adult male or subadult, but a positive influence on the likelihood that a detection is an adult female or female with young; E) likelihood of a detection

being any given age-sex classes as a function of the number of days since people. The top model shows no influence of days since people on age-sex class; F) likelihood of a detection being an adult female as a function of the number of people per day and salmon biomass; G) likelihood of a detection being a sub-adult as a function of the number of people per day and salmon biomass. Shaded regions represent the 95% confidence interval for the model predictions, represented by the curve.

Relative variable importance additionally showed how ecotourism influence related to environmental covariates in Khutze for age-sex class. The interaction between number of people and salmon biomass had the highest influence (RVI = 0.083), which was ~2.2 times as important as salmon biomass alone. The inverse distance to people had the next highest influence (RVI = 0.0806), which was ~2 times as important as salmon biomass for predicting age-sex class.

In Green, we did not find any significant effect of the environmental or ecotourism variables on age-sex class (Figure 5, Appendix S2: Table S14)

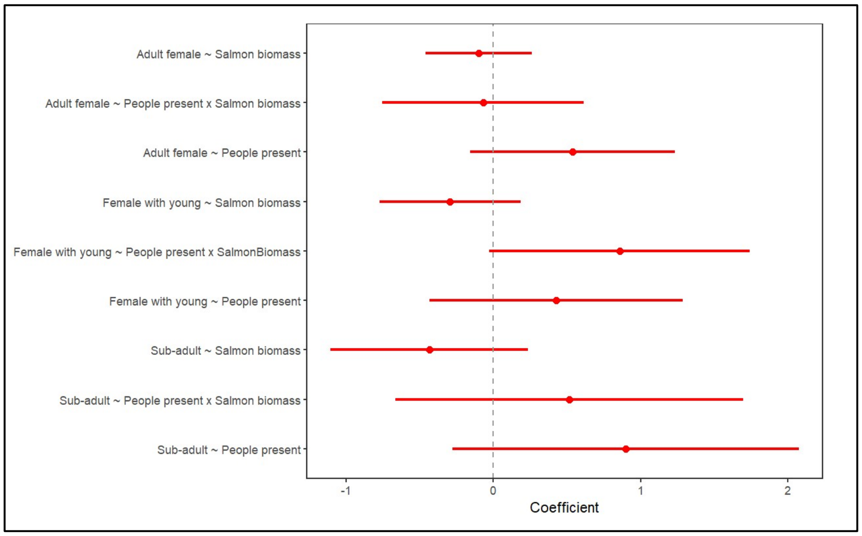

Figure 5. Age and sex class top multinomial model for Green: parameter coefficients and confidence intervals for fixed effects. Red dots represent parameter coefficients and red line span the 95% confidence intervals.

Activity pattern analysis

In Khutze we did not detect a shift in temporal activity at any of the distance levels (0-100m dhat4 = 0.84, p = 0.3; 100-450m dhat1 = 0.88, p = 0.6; 450-1000m dhat1=0.89, p = 0.6). Likewise, subset using the different age-sex classes also detected no changes (adult male dhat1 = 0.81, p = 0.6; female with young dhat1 = 0.83, p = 0.3; adult female dhat1 = 0.88, p = 0.55; sub-adult dhat1 = 0.87, p = 0.47).

In Green we found a shift in activity for cameras within 100m of the viewing site (dhat1 = 0.72, p = 0.002), and cameras beyond 1000m of the viewing site (dhat4 = 0.89, p = 0.035). We found no changes for cameras within 100-450m (dhat4 = 0.88, p = 0.34) or 450-1000m (dhat1 = 0.84, p = 0.64) of the viewing site. Within 100m of the viewing site, we see a decrease in activity during tour times, indicating temporal avoidance, and beyond 1000m we see an increase in activity during tour times (Figure 6). We tested whether different age sex classes showed any temporal shifts and detected no changes (Adult male dhat1 = 0.75, p = 0.54; Female with young dhat1 = 0.83, p = 0.3; adult female dhat1 = 0.90, p = 0.57).

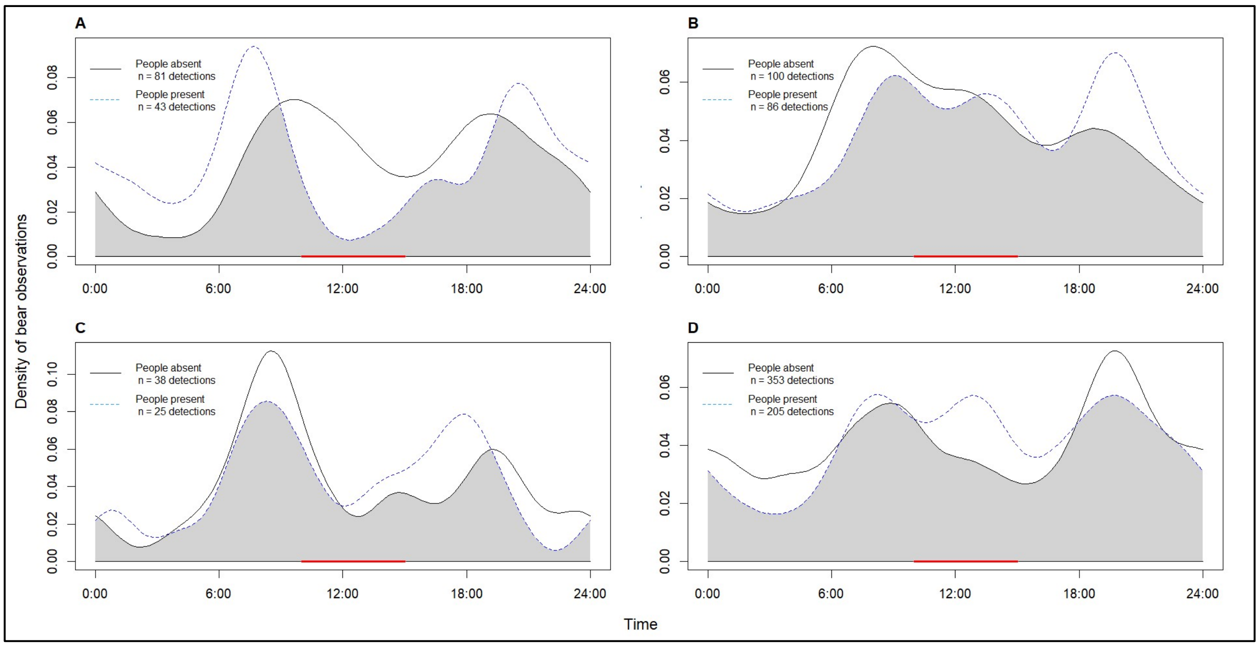

Figure 6. Activity pattern analysis for Green. A) Activity patterns for all bears at cameras 0 - 100m from tours (n = 2 cameras) on days with people present and absent. Temporal activity shifted away from tour times when people were present; B) Activity patterns for all bears at cameras 100-450m from tours (n = 9 cameras) on days with people present and absent. There is no shift in temporal activity; C) Activity patterns for all bears at cameras 450-1000m from tours (n = 10 cameras) on days with people present and absent. There is no shift in temporal activity; D) Activity patterns for all bears at cameras beyond 2500m (n = 8 cameras) on days with people present and absent. Temporal activity shifted towards tour times when people were present.

Discussion

Our results revealed complex relationships among grizzly bear activity, ecotourism, and salmon availability. We found multiple lines of support for our hypothesis that overall activity was negatively correlated in space and time with ecotourism. As the number of people visiting Khutze increased, we observed increased detections at sheltered sites and decreased detections at open sites, indicating a spatial shift towards safer habitat and away from the sightline of humans. Detection rate in 2021 across the watershed was higher as the days since humans were present increased, indicating that bears shifted their spatial activity beyond our camera array, and outside of the area exposed to humans. This suggests that ecotourism can also have lasting effects on time scales beyond the length of tours. We did not detect an effect of the alternating north/south closures, suggesting the partial watershed closure was not of sufficient size for bears to resume non-ecotourism levels of activity within the closed area. In Green we found a positive association between grizzly activity and days since humans were present. However, we did not detect a direct effect of human presence or group size.

We also found support for our hypothesis that adult male bears were more negatively influenced by ecotourism than other age-sex classes. In Khutze, it was least likely for a detection for be male during ecotours, and specifically, when there was moderate or high salmon levels. Salmon continue upstream of the camera array for ~6km in Khutze which likely offers alternate fishing opportunities without the perceived risks humans impose. However, the fishing opportunities upstream may not be comparable quality to those within the ecotour zone. When salmon levels were low, however, males may be more likely to remain because presumably similar low levels of salmon elsewhere might not meet their extensive requirements for meat-based protein (Robbins et al., 2004). Such an apparent trade-off between risk and reward aligns with literature on the landscape of fear, where animals navigate a heterogeneous landscape of predation risk and resources (Lima and Dill, 1990; Gaynor et al., 2019). When resources are concentrated at a site, animals may have no choice but to remain in an area they perceive as risky (Gaynor et al., 2019; Schmidt and Kuijper, 2015, Smith et al. 2019). Despite these strong patterns in Khutze, we did not detect any influence of ecotourism on activity levels of different age-sex classes in Green.

We also found support for the human shield hypothesis in Khutze, observing an increase in the likelihood of detections being females with young with increasing number of people when salmon levels were moderate to high. This pattern is opposite to that exhibited by adult male bears, suggesting that the displacement of adult males by human presence may provide a shield for females with young to access fishing areas, and aligns with observations at another bear-viewing system (Nevin and Gilbert 2005a, b).

Finally, our results did not support our third hypothesis, that adult males would become more nocturnally active during times of ecotourism. This differs from other ecotourism systems, where males and females with young temporally partition their activity in relation to ecotourism (Nevin and Gilbert 2005*a*). We found, however, that displacement of bears primarily occurred on a multi-day rather than hourly scale. In Khutze, the daily temporal patterns of ecotourism were highly varied, with tours running anytime between 7am and 10pm (Appendix S2: Figure S12). Spatially, however, the tours were confined to waterways within the ~5km^2 camera array and two discrete interpretive sites. The net result is that the spatial patterns of ecotourism were more predictable than the temporal patterns. Such a context would allow animals to modify spatial activities to avoid high risk areas (Palmer et al., 2022), but does not create a predictable schedule of risk. In Green, however, tours were predictable in both space and time and thus may have imposed fewer non-consumptive effects on bears (Palmer et al 2022; Penteriani et al., 2017). Specifically, we suspect that the conditions in Green allowed for more precise spatiotemporal avoidance of the single viewing site during the unvarying tour hours. Additionally, the results in Green were more similar to temporal displacement in other bear viewing areas in British Columbia, including Knight Inlet, where tours were also constrained to specific hours and static viewing site (Nevin and Gilbert, 2005a). Together, the results from Khutze and Green reinforce the theory that more predictable spatial and temporal ecotourism may result in smaller scale displacement (Penteriani et al., 2017).

Our results in Khutze and Green likely varied for multiple reasons. First, data collection in Khutze occurred over two seasons, providing greater statistical power to detect changes in bear activity compared with one month of data collection in Green. Second, the mode of ecotourism in the watersheds differed. In Khutze, ecotourists were mobile and visited the area at varied times of day, whereas in Green tour groups remained stationary at a viewing site during consistent hours. Consequently, the spatial and temporal footprint of ecotourism in Green was limited, and offered a predictable human presence. Additionally, the human presence in Khutze may be perceived at a greater distance than in Green, given the differences between an open estuary and a forested river. Finally, Khutze and Green have different histories of ecotourism, and thus the individual bears in these watersheds likely have different perceptions of people, based on their past experiences.

Avoidance of human activity can influence animal fitness through limiting an animal's access to food (e.g., salmon), as well as changing hunting and foraging efficiency, social behaviour, mating, and navigation (Gaynor et al., 2018; Suraci et al., 2016; Tucker et al., 2018; Wilson et al., 2020; Zanette and Clinchy, 2019). Such effects might be particularly pronounced in contexts when a perceived risk is present at a crucial feeding area or time, such as bear-viewing at fishing sites during hyperphagia. How the modest spatial and temporal patterns in avoidance scale up to seasonal access to salmon and population dynamics is unknown. In this ecosystem, however, hormonal data suggested increased levels of nutritional and social stress associated with lower salmon consumption (Bryan et al., 2013). Additionally, at least across ecosystems, salmon consumption is positively related to body mass, mean litter size and reproductive success (Hilderbrand et al., 1999). If avoidance of tour areas by adult males provides a refuge for females with young, this may provide benefits to the population through greater reproduction and cub survival. The cost of avoidance for bears such as adult males however is unknown.

These findings have several management implications. The closure of ecotourism in 2020 provided an unprecedented opportunity to assess bear activity in the absence of humans, directly measure the magnitude of ecotourism influence, and identify potential interventions. Given the lower bear activity up to 25 days after ecotours, multi-week closures would be required in Khutze for bears to return to non-ecotourism levels of activity. As indicated by the high RVI and large effect size of our ‘days since people’ metric, a multi-week closure would be the most effective intervention to manage for periods of bear activity levels that approximate those without human interference. However, our results show that closures on smaller temporal scales can also dampen the effects of human presence. For example, for each day of closure our model suggests a ~9.2% increase in bear detections.

This large-scale spatial avoidance may also be mitigated by other interventions. One management lever is to constrict tour times in Khutze to predictable and consistent hours. This may allow bears to develop a schedule of temporal avoidance to access important habitat during times without tours (Palmer et al., 2022). Such a presumed response was observed in Green, where even in the short period bears showed a small scale, but highly specific pattern of temporal avoidance of the viewing site during viewing hours. Another management tool is to limit the number of people on each tour in Khutze. During mean salmon levels, the likelihood of a detection being an adult male was significantly lower when there were greater than 6 people per day in Khutze. If the goal is to maintain bear activity and age-sex class dynamics at a non-ecotourism level, trips should remain below 6 people per day. Given that the number of people was highly correlated with the number of tours and the number of hours with tours, limiting Khutze to one tour per day or to specific viewing hours may have a similar influence. The number of people per day likely produced the best model given that it provided a finer scale resolution of ecotourism intensity than other metrics, such as human presence/absence or number of tours. Management goals, however, likely do not only seek to maintain bear activity at non-ecotourism levels, but instead to find an appropriate trade-off where ecotourism influences can be minimized, while still gaining the social and economic benefits of ecotourism.

Chapter Three: Conclusion

The experimental approaches employed in this study provided a powerful context to test risk avoidance hypotheses. The 2020 closure in particular provided important baseline data on bear activity in the absence of human presence. This provided a closure long enough to calculate the 25-day closure required to return to non-ecotourism levels of bear activity, which provides valuable information for management, as well as use in future experimental studies. Specifically, this finding can inform experimental treatment timeframes to ensure treatments are long enough to elicit and detect responses (at least in Khutze), as well as ensure independence in replications.

This finding also suggests that our 2-day treatment periods for our group size experiment in Green was likely not sufficient length for bears to adjust to each treatment.

This study additionally highlights challenges associated with field ecology experiments. One such challenge is replication (Filazzola and Cahill, 2021). In both systems, we employed within-study temporal replication. Within field ecology replications, however, there are often biotic or abiotic factors that we cannot control, and may act as confounding variables (Hustson, 1997). To account for variation among replications, we included covariates, such as salmon, water level, week of the year, and remote camera site. While there were likely additional variables we could not account for, this allowed us to distinguish among potential drivers of behavioural patterns (Smith et al., 2020). One such variable we were unable to account for was variation in timing and abundance of berries, another important food source for bears. An additional year of data would be able to reduce this uncertainty. Additional logistic challenges exist for experimental ecology, including social and economic factors of implementing closures, as well as unpredictable environmental conditions, such as flooding. These challenges are especially pronounced when working at a watershed scale with a highly mobile and low density animal. Despite these challenges, the experimental approach allowed us to answer specific questions and identify strong management tools.

Our findings also provide insight into the importance of place-based management in ecotourism. As seen in Khutze and Green as well as other bear-viewing systems along coastal British Columbia (Nevin and Gilbert 2005*a, b*; Elmeligi and Shultis, 2015), different systems, particularly when exposed to different forms of ecotourism, can show varied wildlife responses. This requires management tailored to the bear viewing context. In wildlife conservation and beyond, and as measured by large-scale measures of sustainability, Indigenous place-based management has proven more effective than settler-colonial structures (Artelle et al. 2019; Artelle et al. 2018; Lee et al. 2019; Peterson and Nelson 2017; Trosper 1998). Traditionally, stewardship of lands along the Central Coast of British Columbia consisted of decentralized managers, facilitating specific place-based knowledge and protocols (Lee et al. 2019; Trosper 1998). Despite the imposition of colonial structures, modern Indigenous governance is still localized, and many Indigenous nations are revitalising and continuing their longstanding systems of tribal governance (Ban et al. 2019). Through this revitalisation, Indigenous nations, often in partnership with conservation scientists, have been leading the way in wildlife conservation and policy (Artelle et al., 2021; Jessen et al. 2022; Frid et al. 2016, Ban et al. 2017; Service et al., 2020; Service et al., 2014). Our findings in Khutze and Green have demonstrated the utility of such partnership and have provided approaches and evidence for the KXSA to develop context-specific bear viewing guidelines within their territory.

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Appendices

Appendix S1: Methods

Camera trap sampling design

We installed 40 remote cameras ~150 - 200m apart throughout Khutze. Owing to displacement by bears or running out of batteries, 16 cameras had shortened active periods in 2020, and 4 cameras had shortened active periods in 2021. This resulted in 2,328 camera days in 2020 (~83% of potential camera days) and 2,680 camera days in 2021 (~96% of potential camera days). Because of the camera failures in 2020, we swapped cards and batteries on the cameras August 9, 10, and 13 in 2021. In Green, 35 cameras were set up ~100-200m apart throughout the watershed from August 23– September 27, 2021. Two cameras were lost to flooding, which resulted in 1,201 camera days.

Cameras were set up without lures at ~0.8m height on wildlife trails where possible, including those leading to and from estuaries, which could not be sampled directly (owing to tall sedges and limited trees to which we could affix cameras). Cameras were set to photo settings with the most sensitive trigger settings, shortest time between triggers, most photos per trigger. Given available resources, there were multiple camera models in 2020 (Bushnell Trophy Camera, n = 36; Bushnell E3, n = 1; Reconyx Hyperfire HT500, n = 3). Models were randomly assigned to sites to avoid bias from potential differences across models. In 2021, Reconyx Hyperfire 2 cameras were used across all camera sites at Khutze and Green.

Spatial-temporal data from ecotourists

In 2021, all ecotourist groups carried a Bad Elf ® GPS Pro to record spatial and temporal data on human activity. The Bad Elf ® GPS Pro has an accuracy of 2.5 m when stationary and has an update rate of 1-10 Hz. Ecotourist groups began tracking their location prior to beginning their tour, and recorded their positional data until the completion of the tour. From these data we calculated the closest distance tour groups approached each camera site on each day (Figure S1).

Age and sex classification

The age of bears was assigned though the body size, body and face shape of bears, the presence of cubs, of a mating pair (M Clapham University of Victoria pers. comm; Rode et al., 2006). Subadults have a narrower face than adults, as well as a less defined body shape (Clapham pers. comm). Subadults are also of smaller size and lankier (Jope, 1985). Sex class of bears was identified for bears who showed visible genitalia, direction of urination, lactating females, or presence of cubs. If the sex class could not be confidently identified, the bear was assigned 'unknown'.

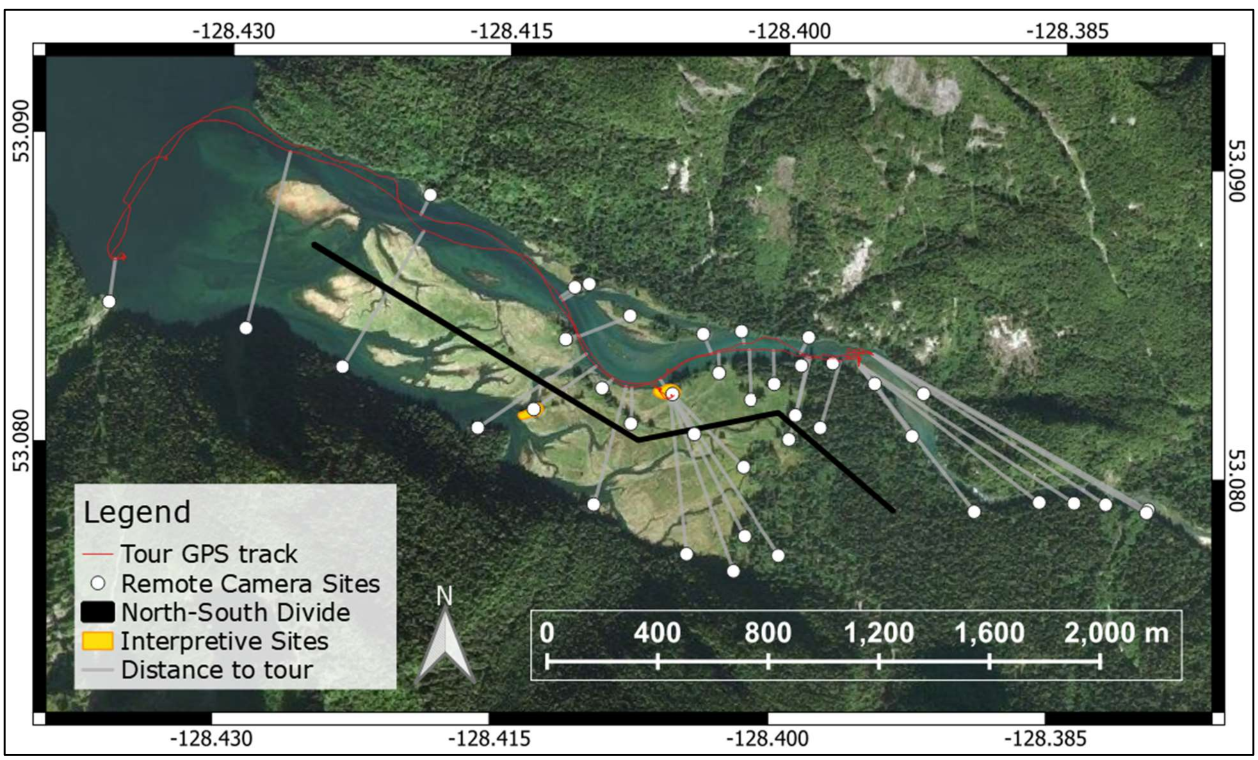

Figure S1. Closest distance to tour for an example GPS track line in Khutze.

Table S1: Green Experimental Schedule: green: small group, pink: large group, blank: no group

Sunday	Monday	Tuesday	Wednesday	Thursday	Friday	Saturday
	30 Eight people: 2 guides 6 guests	31 Eight people: 2 guides 6 guests	1	2	3 Fourteen people: 2 guides 12 guests	4 No access: FLOODING
5	6	7 Eight people: 2 guides 6 guests	8 Eight people: 2 guides 6 guests	9	10	11 Fourteen people: 2 guides 12 guests
12 Fourteen people: 2 guides 12 guests	13	14	15 Eight people: 2 guides 6 guests	16 Eight people: 2 guides 6 guests	17	18
19 Fourteen people: 2 guides 12 guests	20 No access: FLOODING	21	22	23 Eight people: 2 guides 6 guests	24 Eight people: 2 guides 6 guests	25
26	27 No access: FLOODING	28 Camera pick-up	29	30		

Table S2. Khutze ecotourism metrics and environmental variables for detection rate model

Variable name	Type of variable	Value	Variable description and rationale
Detection rate	Response	Continuous numeric	The number of independent grizzly detections on a given day. Day is defined as the 24 hr period form 7am-7am because we would expect bears to only respond during or after human presence, rather than before.
Year	Fixed effect	Categorical: 2020: Closed to tours 2021: Open to tours	This variable indicated the yearly closures in Khutze.
Human presence	Fixed effect	Categorical (yes, no)	Whether humans were present in Khutze on a given day.
Number of people	Fixed effect	Continuous numeric	Number of people to enter Khutze on a given day.
Number of tours	Fixed effect	Continuous numeric	Number of tours on a given day.
Tour length	Fixed effect	Continuous numeric	Hours of the day with tours present.
Distance to tour	Fixed effect	Continuous numeric	Inverse distance from each remote camera to the closest point on the GPS tour track for that

			day. On days with multiple tours, the tour that traveled the furthest into the watershed was used as the reference track. We calculated the inverse of these distances, to account for days with no people, which were assigned a value of 0.
Treatment	Fixed effect	Categorical (North open, south open, fully closed [2020])	The alternating weekly closures of Khutze in 2021 and the full closure in 2020.
Days since people	Fixed effect	Continuous numeric	Given that human presence likely has a lasting influence on bears beyond the time when they leave the watershed (Ordiz et al., 2013), we included a variable to indicate how many days it has been since humans have entered the watershed, to account for potential multi-day lag effects of human activity.
Salmon biomass	Fixed effect	Continuous numeric values of salmon biomass	Salmon data for Khutze were derived from the New Salmon Escapement Database System (NuSEDS) maintained by Fisheries and Oceans Canada. We interpolated daily salmon estimates using a natural spline curve-fitting

			procedure across the 9 stream inspection dates in 2020 and 7 dates in 2021. Following Bryan et al (2014), we converted all salmon count estimates to biomass with species-specific masses (Groot & Margolis, 1991), and assumed a 1:1 sex ratio. If the spline interpolation produced a negative count value, this day was assigned a value of 0.
Water level	Fixed effect	Categorical (normal, high, flooded)	We reasoned that water level would affect bear activity because high flow reduces salmon foraging opportunities. Data were derived from a daily image at noon from camera site KZ29. In 2020 cameras in Khutze were not set to take daily images, and thus the closest image to noon was used for each day. Water level was classified into normal, high, and flooded, which corresponded with specific features in the images (Table S10).
Site exposure	Fixed effect	Categorical (exposed, sheltered)	This variable indicated whether the remote camera site was secluded or open to ecotourism presence. Sheltered sites were those that were surrounded by trees on all sides of the camera and sites upriver of the canyon where people do

			not travel. Exposed sites were those that were partially or fully open.
Site	Random effect	Categorical, remote camera site ID	Remote camera site ID as a random effect to account for variation among camera sites not accounted for in other variables.
Week	Random effect	Integer (week of year 30-39)	We included the week of the year to account for temporal variations throughout the sampling period that were not captured in salmon abundance or water level. This includes environmental condition shifts, such as seasonal changes in vegetation resources such as berry availability, crab apples (*Malus* fusca) and sedge grasses (*Carex* spp.).

Table S3. Green ecotourism metrics and environmental variables for detection rate model

Variable name	**Type of variable**	**Value**	**Variable description and rationale**

Detections	Response	Continuous numeric	The number of independent grizzly detections on a given day. Day is defined as the 24 hr period from 10am- 10am because we would expect bears to only respond during or after human presence, rather than before.
Human presence	Fixed effect	Categorical (yes, no)	Whether humans were present in Green on a given day.
Group size	Fixed effect	Categorical (small, large, none)	Number of people to enter Khutze, or the group size treatment in Green on a given day.
Distance to tour	Fixed effect	Continuous numeric	Inverse distance from each remote camera to the closest point on the GPS tour track for that day. On days with multiple tours, the tour that traveled the furthest into the watershed was used as the reference track. We calculated the inverse of these distances, to account for days with no people, which were assigned a value of 0.
Days since people	Fixed effect	Continuous numeric	Given that human presence likely has a lasting influence on bears beyond the time when they leave the watershed (Ordiz et al., 2013), we included a variable to indicate how many days it has been since humans have entered the

			watershed, to account for potential multi-day lag effects of human activity.
Salmon biomass	Fixed effect	Continuous numeric	In Green, we counted live pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) within a reference pool adjacent to tour site, as well as salmon carcasses along the riverbank from boat tie-up to the viewing site (Figure 1) each day that a group entered the system. For days without tours, we interpolated count data using a natural spline.
Water level	Fixed effect	Categorical (normal, high, flooded)	We reasoned that water level would affect bear activity because high flow reduces salmon foraging opportunities. Data were derived from a daily image at noon from camera site GN08. Water level was classified into normal, high, and flooded, which corresponded with specific features in the images (Table S11).
Site	Random effect	Categorical, remote camera site ID	Remote camera site ID as a random effect to account for variation among camera sites not accounted for in other variables.

Candidate model set development: interaction terms

We included interaction terms between water level and salmon biomass, given that the availability of salmon to bears is influenced by water level, as well as salmon biomass and each ecotourism metric, reasoning that the ways bears respond to humans likely varies with salmon abundance, as related to the risk allocation hypothesis; when salmon levels are high, bears may respond to humans less strongly, predicting bears trade-off some security for access to abundant food. Alternatively, bear detections may decrease when salmon and ecotourist pressure are both high, traveling to alternative fishing sites without ecotourists. We included an interaction term between the ecotourism variables and the spatial closures in Khutze, with the understanding that the level of tourism will likely influence bears differently, predicting that the north channel (where salmon spawning occurs) may elicit a stronger response. Additionally, we included an interaction between the ecotourism variable and camera site exposure because we would expect open (i.e., 'exposed') areas to be more influenced by tourism than forested (i.e., 'sheltered') areas. Finally, we included an interaction term between days since people and year, given that we would expect days since people to be more important in 2021, when there were more human trips into the watershed than solely the camera set-up days in 2020.

Table S4. Khutze detection rate model candidate model set. This model structure is applied equally to each of the ecotourism variables. Corresponding models for the ecotourism variables are models A10 – A55 for human presence, B10 – B55 for number of humans, C10-C55 for number of tours, and D10-D55 for tour length.

Null model	
M1	Random effects only (site, week)
Environmental models	
M2	Salmon biomass + water level + salmon biomass x water level
M3	Salmon biomass + water level + site exposure + salmon biomass x water level
M4	Salmon biomass + yearly closure + water level + salmon biomass x water level
M5	Salmon biomass + yearly closure + water level + site exposure + salmon biomass x water level
Models with ecotourism metrics	
M6	Ecotourism metric + salmon biomass + water level + yearly closure + site exposure + salmon biomass x water level + site exposure x ecotourism metric
M7	Ecotourism metric + salmon biomass + water level + yearly closure + site exposure + salmon biomass x water level + ecotourism metric x salmon biomass + site exposure x ecotourism metric
M8	Ecotourism metric + inverse distance to tour + salmon biomass + water level + yearly closure + site exposure + salmon biomass x water level + site exposure x ecotourism metric

M9	Ecotourism metric + inverse distance to tour + salmon biomass + water level + yearly closure + site exposure + salmon biomass x water level + ecotourism metric x salmon biomass + site exposure x ecotourism metric
M10	Ecotourism metric + days since tours + salmon biomass + water level + yearly closure + salmon biomass x water level + site exposure + site exposure x ecotourism metric + days since tours x yearly closure
M11	Ecotourism metric + days since tours + salmon biomass + water level + yearly closure + site exposure + ecotourism metric x salmon biomass + salmon biomass x water level + site exposure x ecotourism metric + days since tours x yearly closure
M12	Ecotourism metric + treatment + salmon biomass + water level + site exposure + salmon biomass x water level + site exposure x ecotourism metric
M13	Ecotourism metric + treatment + salmon biomass + water level + site exposure + salmon biomass x water level + ecotourism metric x salmon biomass + site exposure x ecotourism metric
M14	Ecotourism metric + treatment + salmon biomass + water level + site exposure + salmon biomass x water level + treatment x ecotourism metric + site exposure x ecotourism metric
M15	Ecotourism metric + treatment + salmon biomass + water level + site exposure + salmon biomass x water level + ecotourism metric x salmon biomass + treatment x ecotourism metric + site exposure x ecotourism metric

Table S5. Green detection rate model candidate model set

Null model	
M1	Random effect only (site)
Environmental model	
M2	Salmon biomass + water level + salmon biomass x water level
Models with presence/absence data	
M3	Human presence + salmon biomass + water level + salmon biomass x water level
M4	Human presence + salmon biomass + water level + salmon biomass x water level + human presence x salmon biomass
M5	Inverse distance to humans + salmon biomass + water level + salmon biomass x water level
M6	Human presence + days since humans + salmon biomass + water level + salmon biomass x water level
M7	Human presence + days since humans + salmon biomass + water level + salmon biomass x water level + human presence x salmon biomass
M8	Days since humans + inverse distance to humans + salmon biomass + water level + salmon biomass x water level
Models with group size	
M9	Group size + salmon biomass + water level + salmon biomass x water level
M10	Group size + salmon biomass + water level + salmon biomass x water level + group size x salmon biomass

M11	Group size + inverse distance to humans + salmon biomass + water level + salmon biomass x water level
M12	Group size + inverse distance to humans + salmon biomass + water level + salmon biomass x water level + group size x salmon biomass
M13	Group size + days since humans + salmon biomass + water level + salmon biomass x water level
M14	Group size + days since humans + salmon biomass + water level + salmon biomass x water level + group size x salmon biomass
M15	Group size + days since humans + inverse distance to humans + salmon biomass + water level + salmon biomass x water level
M16	Group size + days since humans + inverse distance to humans + salmon biomass + water level + salmon biomass x water level + group size x salmon biomass

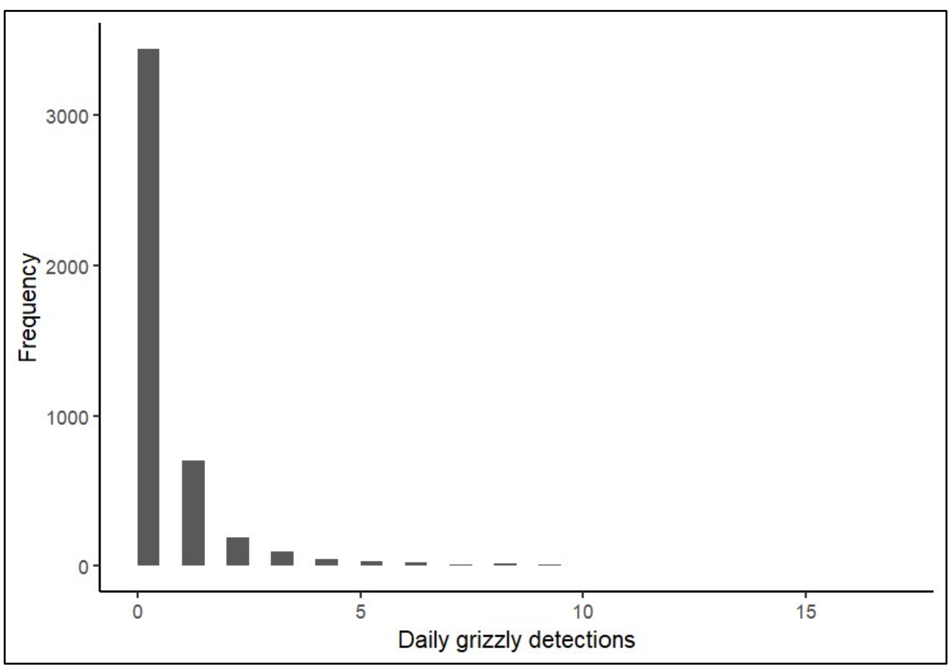

Figure S2. Histogram for camera-site level daily grizzly bear detections.

Table S6. Khutze ecotourism metrics and environmental covariate data for the age and sex class multinomial model

Variable	Type of variable	Value	Variable description and rationale
Age-sex class	Response variable	Categorical: Adult male Adult female Female with young Sub-adult	The age-sex class of the bear in the detection. Bears classified as 'unknown' were excluded from the analysis.
Year closure	Fixed effect	Categorical: 2020: Closed to tours 2021: Open to tours	See Table S4
Number of people	Fixed effect	Continuous numeric	See Table S4
Distance to tour	Fixed effect	Continuous numeric	See Table S4
Treatment	Fixed effect	Categorical (North open, south open, fully closed (2020))	See Table S4
Days since people	Fixed effect	Continuous numeric	See Table S4

Nocturnality	Fixed effect	Continuous numeric	The absolute value between the detection event and the darkest point in the night, averaged across the study time.
Salmon biomass	Fixed effect	Continuous numeric	See Table S4
Site	Random effect	Categorical, remote camera site ID	See Table S4

Table S7. Green ecotourism metrics and environmental covariate data for the age and sex class multinomial model

Variable	**Type of variable**	**Value**	**Variable description and rationale**
Age-sex class	Response variable	Categorical: Adult male, adult female, female with young, sub-adult	The age-sex class of the bear in the detection. Bears classified as 'unknown' were excluded from the analysis.
Human presence	Fixed effect	Categorical (yes, no)	See Table S5
Group size	Fixed effect	Categorical (small, large, none)	See Table S5
Distance to tour	Fixed effect	Continuous numeric	See Table S5
Days since people	Fixed effect	Continuous numeric	See Table S5
Nocturnality	Fixed effect	Continuous numeric	The absolute value between the detection event and the darkest point in the night, averaged across the study time.
Salmon biomass	Fixed effect	Continuous numeric	See Table S5
Site	Random effect	Categorical, remote camera site ID	See Table S5

Table S8. Khutze age and sex class multinomial model candidate model set. This model structure is applied equally to each of the ecotourism variables. Corresponding models for the ecotourism variables are models A8 – A39 for human presence, B8 – B39 for number of humans, C8-C39 for number of tours, and D8-D39 for tour length.

Null model	
M1	Random effects only (site)
Environmental models	
M2	Salmon biomass + year
M3	Salmon biomass + nocturnality + year
Models with ecotourism metrics	
M4	Ecotourism metric + salmon biomass + year
M5	Ecotourism metric + salmon biomass + year + ecotourism metric x salmon biomass
M6	Ecotourism metric + salmon biomass + nocturnality + year
M7	Ecotourism metric + salmon biomass + nocturnality + year + ecotourism metric x salmon biomass
M8	Ecotourism metric + inverse distance to humans + salmon biomass + year
M9	Ecotourism metric + inverse distance to humans + salmon biomass + year + ecotourism metric x salmon biomass
M10	Inverse distance to humans + ecotourism metric + salmon biomass + nocturnality + year
M11	Inverse distance to humans + ecotourism metric + salmon biomass + nocturnality + year + ecotourism metric x salmon biomass

M12	Ecotourism metric + days since people + salmon biomass + year
M13	Ecotourism metric + days since people + salmon biomass + year + ecotourism metric x salmon biomass
M14	Ecotourism metric + days since people + salmon biomass + nocturnality + year
M15	Ecotourism metric + days since people + salmon biomass + nocturnality + year + ecotourism metric x salmon biomass
M16	Ecotourism metric + inverse distance to humans + days since people + salmon biomass + year
M17	Ecotourism metric + inverse distance to humans + days since people + salmon biomass + year + ecotourism metric x salmon biomass
M18	Ecotourism metric + inverse distance to humans + days since people + salmon biomass + nocturnality + year
M19	Ecotourism metric + inverse distance to humans + days since people + salmon biomass + nocturnality + year + ecotourism metric x salmon biomass
M20	Ecotourism metric + days since people + salmon biomass + year + days since people x year
M21	Ecotourism metric + days since people + salmon biomass + year + ecotourism metric x salmon biomass + days since people x year
M22	Ecotourism metric + days since people + salmon biomass + nocturnality + year + days since people x year
M23	Ecotourism metric + days since people + salmon biomass + nocturnality + year + ecotourism metric x salmon biomass + days since people x year

M24	Ecotourism metric + inverse distance to humans + days since people + salmon biomass + year + days since people x year
M25	Ecotourism metric + inverse distance to humans + days since people + salmon biomass + year + ecotourism metric x salmon biomass + days since people x year
M26	Ecotourism metric + inverse distance to humans + days since people + salmon biomass + nocturnality + year + days since people x year
M27	Ecotourism metric + inverse distance to humans + days since people + salmon biomass + nocturnality + year + ecotourism metric x salmon biomass + days since people x year

Table S9. Green age and sex class multinomial model candidate models

Null model	
M1	Random effect only (site)
Environmental models	
M2	Salmon biomass
M3	Salmon biomass + nocturnality
Models with human presence/absence data	
M4	Human presence + salmon biomass
M5	Human presence + salmon biomass + human presence x salmon biomass
M6	Human presence + salmon biomass + nocturnality
M7	Human presence + salmon biomass + nocturnality + human presence x salmon biomass
M8	Inverse distance to humans + salmon biomass
M9	Inverse distance to humans + salmon biomass + nocturnality
M10	Human presence + days since humans + salmon biomass
M11	Human presence + days since humans + salmon biomass + human presence x salmon biomass
M12	Human presence + days since humans + salmon biomass + nocturnality
M13	Human presence + days since humans + salmon biomass + nocturnality + human presence x salmon biomass
M14	Inverse distance to humans + days since humans + salmon biomass
M15	Inverse distance to humans + days since humans + salmon biomass + nocturnality

Multinomial model assessment

Following the guidance of Wilmers et al., 2020 and Hosmer and Lemeshow (2000), we calculated the area under the receiver operator curve for each age-sex class in comparison to adult males to assess how well the model discerns the difference between age sex classes. We derived the parameters for the ROC estimations from the top multinomial model, as identified through AIC. Areas under the ROC range from 0 to 1, with values up to 0.5 indicating no distinction between classes, 0.7-0.8 indicating acceptable, and above 0.8 indicated excellent discrimination between classes (Wilmers et al., 2020). The ROC curves were calculated and assessed using the pROC package in R.

Table S10. Khutze water level classification from remote camera images

Water level	Description	Example images
Normal	Beach visible in ~1/3 of the image; small upward branch (circled) exposed	 
High	Beach visible in ~1/4 of the image, and small upward branch submerged	 
Flooded	Beach fully flooded; log submerged	 

Table S11. Green water level classification from remote camera images

Water level	Description	Example images
Normal	Gravel bar visible.	 
High	Gravel bar submerged.	 
Flooded	Remote camera partially or fully submerged.	 

Table S12. Remote camera image classification inter- and intra-observer variance for Khutze

Variance type	Observer	Number of detections (excluding 'unknown' age-sex)	Number of detections (including 'unknown' age-sex)	Species (% same, excluding 'unknown' age-sex)	Species (% same, excluding 'unknown' age-sex)	Age-sex class excluding 'unknown' (% same)	Age-sex class including 'unknown' (% same)
2020							
Intra-observer	01	44	115	100	98.3	90.9	84.3
Intra-observer	02	2	7	100	100	100	100
Intra-observer	03	1	14	100	64.3	0	92.9
Inter-observer	01, 02	2	7	100	100	100	100
Inter-observer	01, 03	2	15	100	86.7	100	86.7
2021							
Intra-observer	01	58	72	100	100	100	100
Intra-observer	02	1	3	100	100	100	100

Intra-observer	03	6	6	100	100	100	100
Inter-observer	01, 02	1	3	100	100	100	100
Inter-observer	01, 03	5	6	100	100	100	83.3

Table S13. Remote camera image classification inter- and intra-observer variance for Green

Variance type	Observer	Number of detections (excluding 'unknown' age-sex)	Number of detections (including 'unknown' age-sex)	Species (% same, excluding 'unknown' age-sex)	Species (% same, excluding 'unknown' age-sex)	Age-sex class excluding 'unknown' (% same)	Age-sex class including 'unknown' (% same)
Intra-observer	01	20	50	100	100	90	80

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Appendix S2: Results

Table S1. Khutze GLMM 99% model set including all four ecotourism metrics

Model	Fixed effects	Log-likelihood	Δ AIC	Weight
B11	Number of people + days since people + salmon biomass + water level + year + site exposure + number of people x salmon biomass + salmon biomass x water level + days since people x year + site exposure x number of people	-3272.38	0.00	0.2648
B10	Number of people + days since people + salmon biomass + water level + year + site exposure + salmon biomass x water level + days since people x year + site exposure x number of people	-3273.50	0.23	0.2360
A10	People present + days since people + salmon biomass + water level + year + site exposure + salmon biomass x water level + days since people x year + site exposure x people present	-3273.52	0.27	0.2319
C11	Number of tours + days since people + salmon biomass + water level + year + site exposure + number of tours x salmon biomass + salmon biomass x water level + days since people x year + site exposure x number of tours	-3273.20	1.63	0.1171

A11	People present + days since people + salmon biomass + water level + year + site exposure + people present x salmon biomass + salmon biomass x water level + days since people x year + site exposure x people present	-3273.42	2.08	0.0935
C10	Number of tours + days since people + salmon biomass + water level + year + site exposure + salmon biomass x water level + days since people x year + site exposure x number of tours	-3275.30	3.84	0.0388

Table S2. Khutze detection rate model set with rankings

Model	Fixed effects	Log-likelihood	Δ AIC	Weight	Marginal R^2	Conditional R^2
B11	Number of people + days since people + salmon biomass + water level + year + site exposure + number of people x salmon biomass + salmon biomass x water level + days since people x year + site exposure x number of people	-3272.38	0.00	0.5287	0.0707	0.5036
B10	Number of people + days since people + salmon biomass + water level + year + site exposure + salmon biomass x water level + days since people x year + site exposure x number of people	-3273.50	0.23	0.4713	0.0705	0.5082
B14	Number of people + treatment + salmon biomass + water level + salmon biomass x water level +	-3283.49	24.22	0.0000	0.0849	0.5245

	treatment x number of people + site exposure + site exposure x number of people					
B15	Number of people + treatment + salmon biomass + water level + salmon biomass x water level + number of people x salmon biomass + treatment x number of people + site exposure + site exposure x number of people	-3283.37	25.97	0.0000	0.0842	0.5224
B8	Number of people + inverse distance to tour + salmon biomass + water level + year + salmon biomass x water level + site exposure + site exposure x number of people	-3288.15	27.53	0.0000	0.0795	0.5173
B6	Number of people + salmon biomass + water level + year + salmon biomass x water level + site exposure + site exposure x number of people	-3289.43	28.08	0.0000	0.0786	0.5168

B9	Number of people + inverse distance to tour + salmon biomass + water level + year + salmon biomass x water level + number of people x salmon biomass + site exposure + site exposure x number of people	-3287.54	28.31	0.0000	0.0790	0.5134
B7	Number of people + salmon biomass + water level + year + salmon biomass x water level + number of people x salmon biomass + site exposure + site exposure x number of people	-3288.78	28.79	0.0000	0.0780	0.5127
B12	Number of people + treatment + salmon biomass + water level + salmon biomass x water level + site exposure + site exposure x number of people	-3289.39	30.01	0.0000	0.0786	0.5166
B13	Number of people + treatment + salmon biomass	-3288.64	30.50	0.0000	0.0780	0.5121

	+ water level + salmon biomass x water level + number of people x salmon biomass + site exposure + site exposure x number of people					
M4	Salmon biomass + year + water level + salmon biomass x water level	-3296.63	36.49	0.0000	0.0755	0.5221
M5	Salmon biomass + water level + salmon biomass x water level + site exposure	-3352.34	147.92	0.0000	0.0376	0.4933
M2	Salmon biomass + water level + salmon biomass x water level	-3352.44	146.11	0.0000	0.0357	0.4940
M3	Salmon biomass + water level + salmon biomass x water level + site exposure	-3352.34	147.92	0.0000	0.0376	0.4933
M1	Intercept only	-3396.46	224.15	0.0000	0.0000	0.4627

Table S3: Khutze detection rate model parameter estimates with confidence intervals for 95% model set. Bold estimates are those whose confidence interval does not overlap zero.

Model	B11	B10
Intercept	-0.60 (-1.25, 0.05)	-0.59 (-1.25, 0.07)
People	**-0.14** (-0.23, -0.04)	**-0.11** (-0.20, -0.02)
Days since people	**-0.49** (-0.67, -0.32)	**-0.48** (-0.66, -0.31)
Salmon biomass	**0.11** (0.01, 0.22)	**0.15** (0.06, 0.24)
Water level; flooded	**0.69** (0.47, 0.91)	**0.69** (0.47, 0.91)
Water level; above normal	**0.27** (0.14, 0.41)	**0.27** (0.14, 0.41)
Year; 2021 Open to tours	0.11 (-0.94, 1.15)	0.12 (-0.92, 1.16)
Site exposure; sheltered	-0.19 (-0.92, 0.53)	-0.19 (-0.92, 0.53)
Days since people x Year; 2021 Open to tours	**2.08** (0.61, 3.57)	**2.10** (0.62, 3.58)
Salmon biomass x Water level; flooded	**0.51** (0.21, 0.81)	**0.46** (0.16, 0.75)
Salmon biomass x Water level; above normal	0.03 (-0.08, 0.14)	0.03 (-0.08, 0.15)
People x Salmon biomass	-0.08 (-0.18, 0.02)	NA
People x Site exposure; sheltered	**0.19** (0.09, 0.28)	**0.19** (0.10, 0.29)

Khutze detection rate model fit

The fixed effects in our detection rate model explained approximately 7% of the variation in the data (Table S2), and our complete model including the random effect explained over half of the data variation ($R^2 = 0.527$). There are likely additional covariates influencing grizzly bear detections that we were unable to account for, including variation in resource availability or use, such as berries and sedges (Deacy et al., 2017), as well as inter and intra- species interactions, such as social hierarchies among grizzlies (Gende and Quinn, 2004), as well as the presence of other competitors such as wolves, and black bears, who may influence bear site use (Darimont et al., 2008; Mattson et al., 2005).

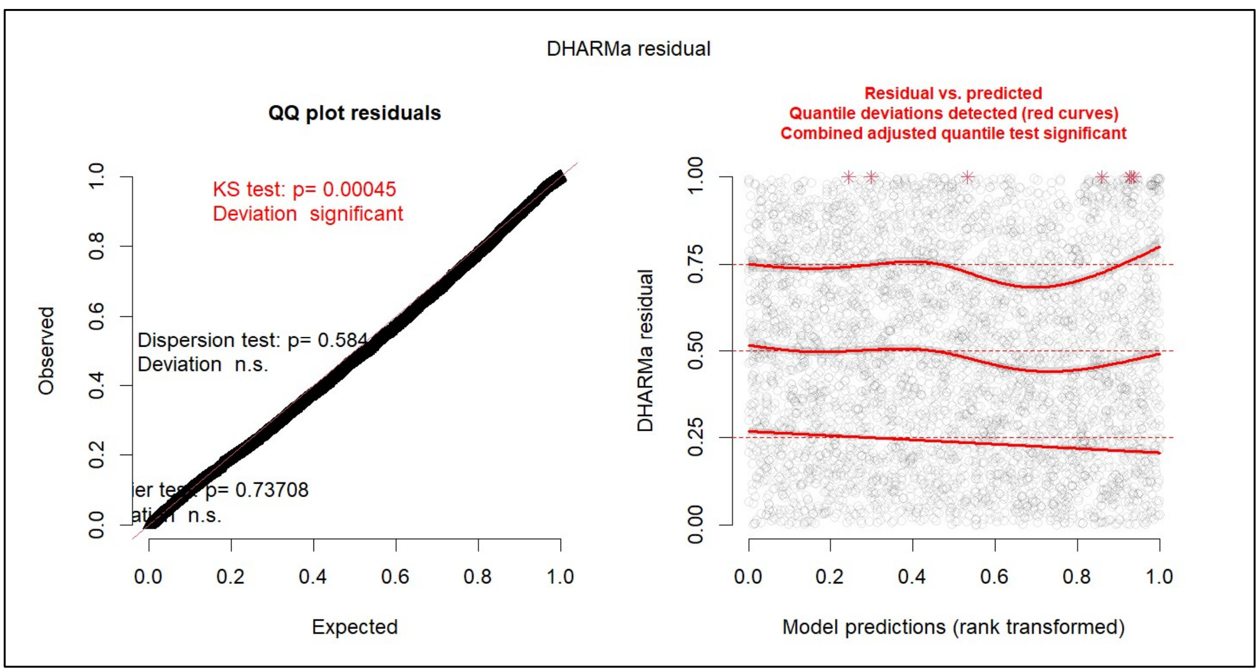

Figure S1. Khutze detection rate model checking. The QQ plot displays a statistically significant, but very small magnitude deviation from the expected values. The residuals vs predicted plot shows unsystematic small magnitude deviations.

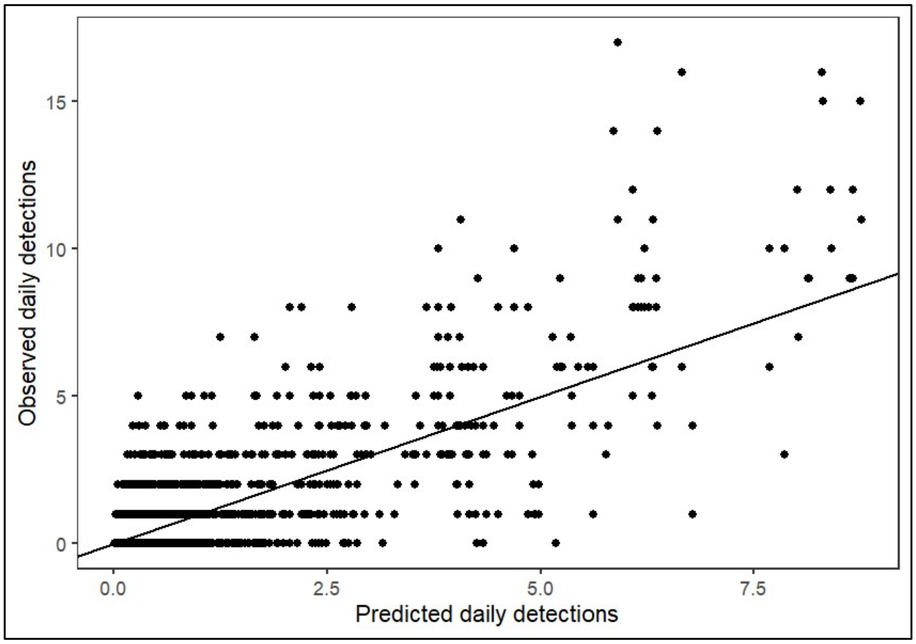

Figure S2. Khutze detection rate model predicted vs observed values for the top model

Table S4. Model predictrions for daily grizzly detections given days since people in 2021. The mean detection rate for 2020 was 0.7142. The predicted detections on 0-11 days since people have confidence intervals that do not overlap the 2020 mean.

Days since people	Predicted detections	Low confidence interval	High confidence interval
0	0.1427	0.0820	0.2482
1	0.1520	0.0878	0.2631
2	0.1620	0.935	0.2806

3	0.1754	0.1003	0.3068
4	0.1870	0.1054	0.3316
5	0.1992	0.1102	0.3603
6	0.2123	0.1146	0.3934
7	0.2299	0.1196	0.4418
10	0.2783	0.1299	0.5961
11	0.2965	0.1328	0.6621
12	0.3211	0.1362	0.7571
13	0.3422	0.1387	0.8442
14	0.3646	0.1410	0.9428
15	0.3886	0.1433	1.0540
16	0.4141	0.1454	1.1796
17	0.4484	0.1479	1.3595
18	0.4779	0.1498	1.5243
19	0.5092	0.1516	1.7102
20	0.5427	0.1534	1.9198
21	0.5876	0.1555	2.2198
22	0.6262	0.1572	2.4945
23	0.6673	0.1588	2.8043
24	0.7112	0.1604	3.1536
25	0.7579	0.1619	3.5475
26	0.8206	0.1638	4.1114
27	0.8745	0.1653	4.6276

28	0.9320	0.1667	5.2098
29	0.9932	0.1682	5.8664
30	1.0584	0.1696	6.6069

Alternate ecotourism metric model set results

Table S5. Khutze 95% top model set for 'human presence' ecotourism metric

Model	Fixed effects	Log-likelihood	Δ AIC	Weight
A10	Human presence + days since people + salmon biomass + water level + year + site exposure + salmon biomass x water level + days since people x year + site exposure x human presence	-3273.52	0.00	0.7127
A11	Human presence + days since people + salmon biomass + water level + year + site exposure + human presence x salmon biomass + salmon biomass x water level + days since people x year + site exposure x human presence	-3273.42	1.82	0.2873

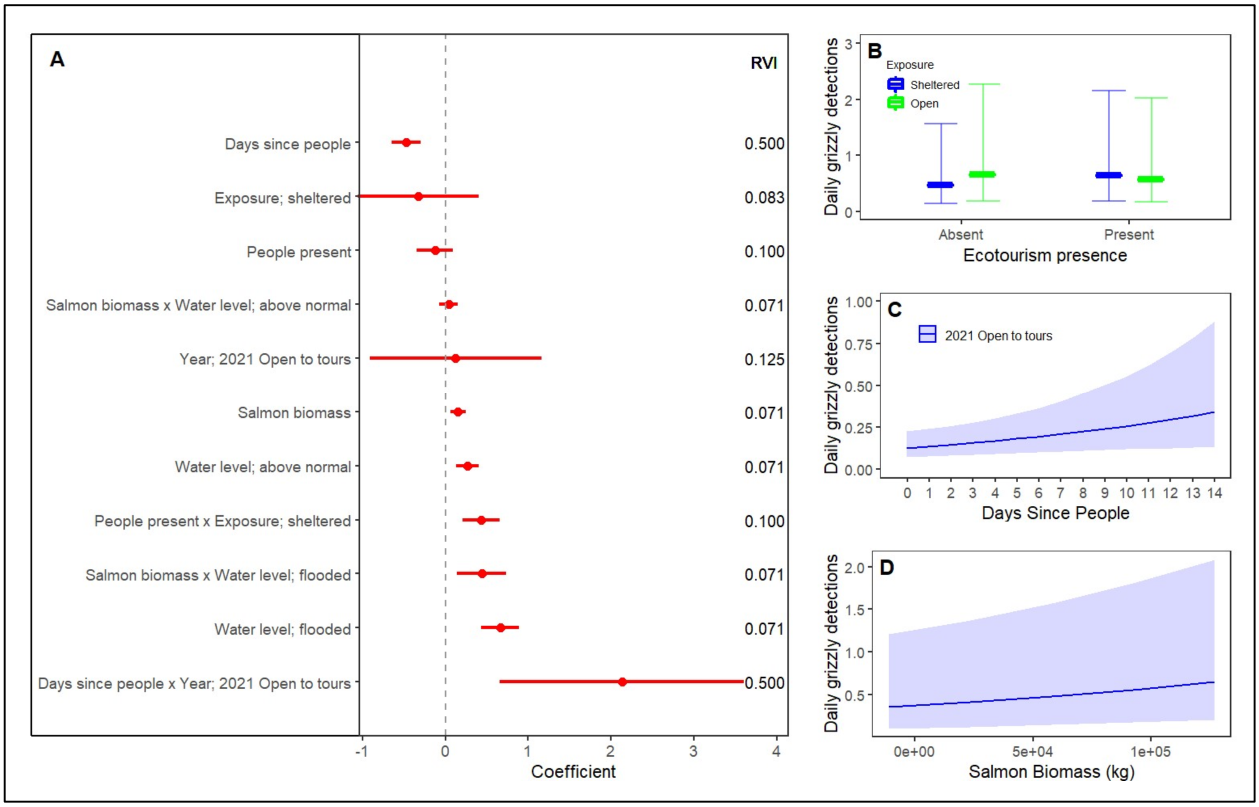

Figure S3. Top detection rate model for the human presence ecotourism metric in Khutze: A) parameter coefficients and confidence intervals for model fixed effects. Red dots represent parameter coefficients and red lines span the 95% confidence intervals. Relative variable importance (RVI) is annotated for each fixed effect; B) site-level daily grizzly detections at sheltered and open sites as a function of human presence, showing the mean and 95% confidence intervals for model estimates. The green lines represent detections at open sites, and the blue lines represent detections at exposed sites; C) site-level daily grizzly detections as a function of days since people in 2021, across all remote camera sites. Blue shaded region represents the 95% confidence interval for model predicted detection rate, and the curve shows the model predicted values. Days since people have a positive influence on site-level daily grizzly detections; D) site-level daily grizzly detections as a function of salmon biomass. Salmon biomass has a positive influence on detection rate.

Table S6. Khutze 95% top model set for 'number of tours' ecotourism metric

Model	Fixed effects	Log-likelihood	Δ AIC	Weight
C11	Number of tours + days since people + salmon biomass + water level + year + site exposure + number of tours x salmon biomass + salmon biomass x water level + days since people x year + site exposure x number of tours	-3273.20	0.00	0.7513
C10	Number of tours + days since people + salmon biomass + water level + year + site exposure + salmon biomass x water level + days since people x year + site exposure x number of tours	-3275.30	2.21	0.2487

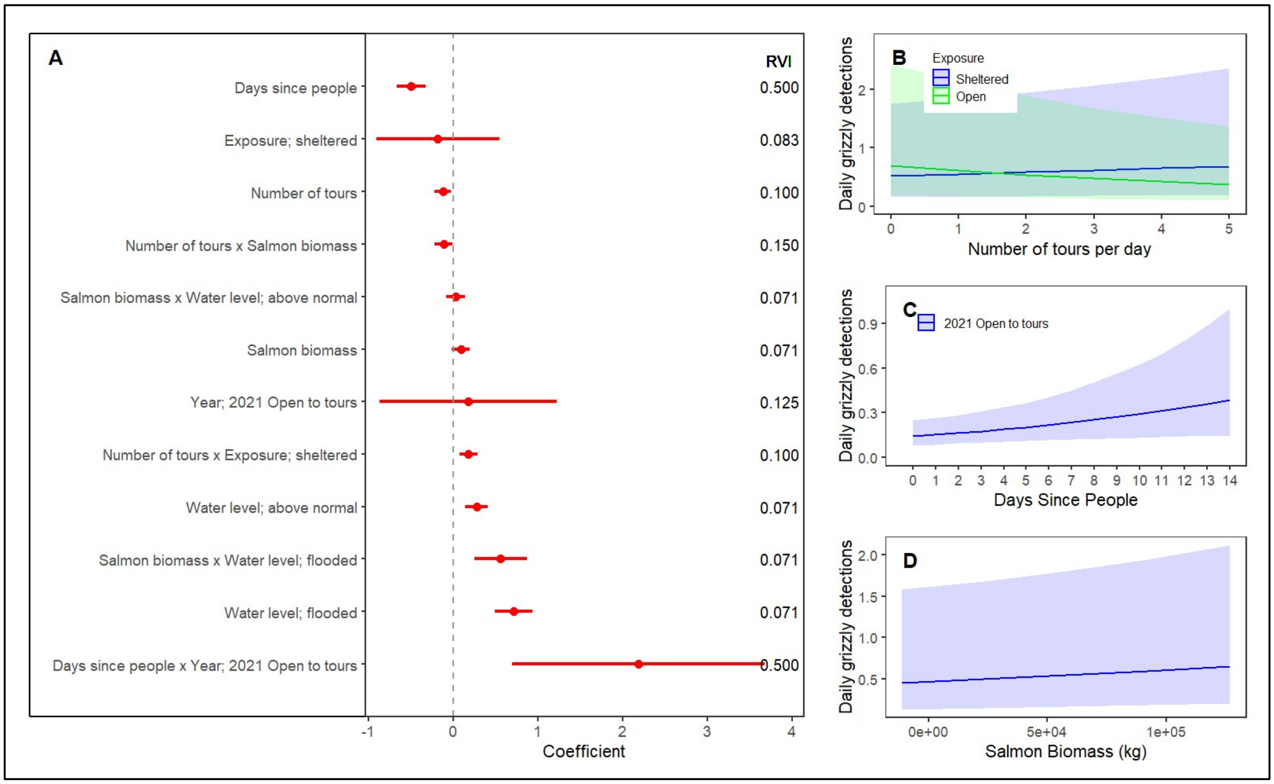

Figure S4. Top detection rate model for the number of tours ecotourism metric in Khutze: A) parameter coefficients and confidence intervals for model fixed effects. Red dots represent parameter coefficients and red lines span the 95% confidence intervals. Relative variable importance (RVI) is annotated for each fixed effect; B) site-level daily grizzly detections at sheltered and open sites as a function of number of tours, showing the mean and 95% confidence intervals for model estimates. The green shaded region represents detections at open sites, and the blue shaded region represents detections at exposed sites; C) site-level daily grizzly detections as a function of days since people in 2021, across all remote camera sites. Blue shaded region represents the 95% confidence interval for model predicted detection rate, and the curve shows the model predicted values. Days since people have a positive influence on site-level daily grizzly detections; D) site-level daily grizzly detections as a function of salmon biomass. Salmon biomass has a positive influence on detection rate.

Table S7. Khutze 95% top model set for 'tour length' ecotourism metric

Model	Fixed effects	Log-likelihood	Δ AIC	Weight
D11	Tour length + days since people + salmon biomass + water level + year + site exposure + tour length x salmon biomass + salmon biomass x water level + days since people x year + site exposure x tour length	-3275.47	0.00	0.6787
D10	Tour length + days since people + salmon biomass + water level + year + site exposure + salmon biomass x water level + days since people x year + site exposure x tour length	-3277.22	1.50	0.3213

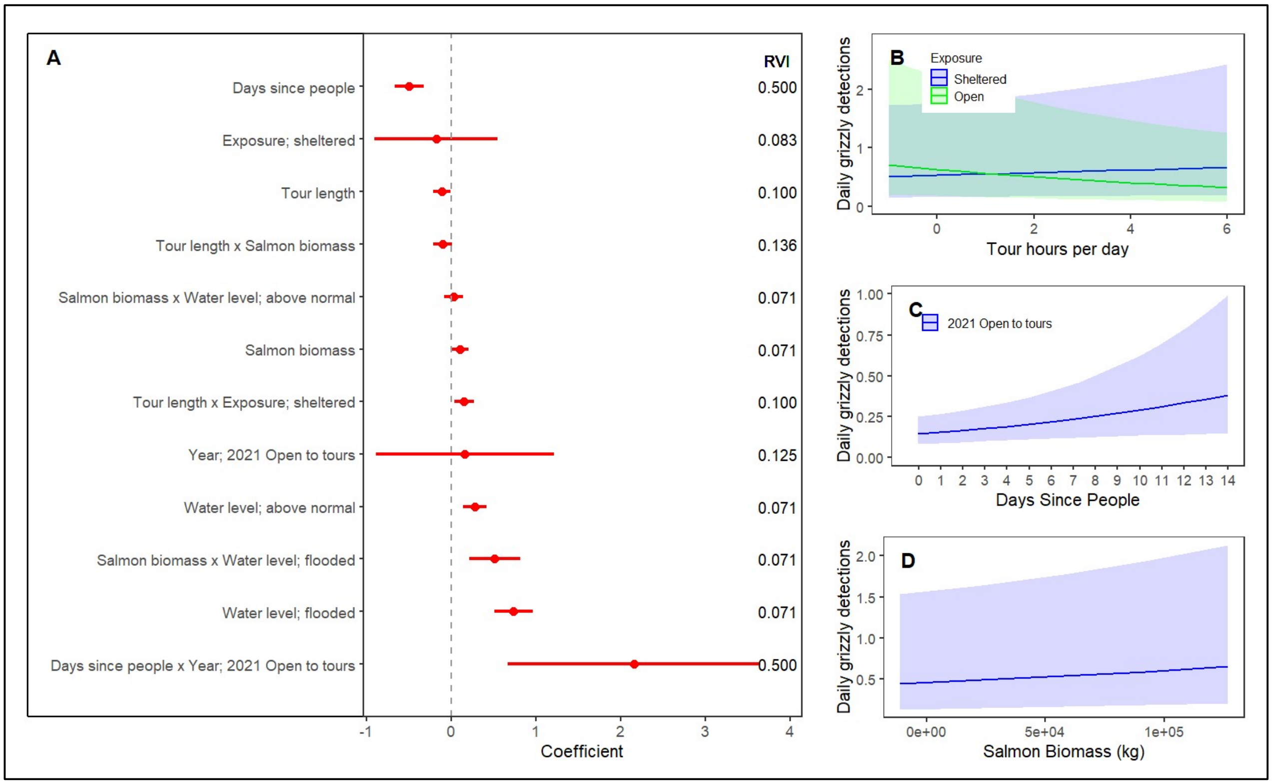

Figure S5. Top detection rate model for the length of tours ecotourism metric in Khutze: A) parameter coefficients and confidence intervals for model fixed effects. Red dots represent parameter coefficients and red lines span the 95% confidence intervals. Relative variable importance (RVI) is annotated for each fixed effect; B) site-level daily grizzly detections at sheltered and open sites as a function of tour length, showing the mean and 95% confidence intervals for model estimates. The green shaded region represents detections at open sites, and the blue shaded region represents detections at exposed sites; C) site-level daily grizzly detections as a function of days since people in 2021, across all remote camera sites. Blue shaded region represents the 95% confidence interval for model predicted detection rate, and the curve shows the model predicted values. Days since people have a positive influence on site-level daily grizzly detections; D) site-level daily grizzly detections as a function of salmon biomass. Salmon biomass has a positive influence on detection rate

Table S8. Green detection rate model 95% model set including both ecotourism metrics

Model	Fixed effects	Log-likelihood	Δ AIC	Weight
M6	Human presence + days since people + salmon biomass + water level + salmon biomass x water level	-823.55	0.00	0.1442
M13	Group size + days since humans + salmon biomass + water level + salmon biomass x water level	-822.61	0.11	0.1368
M8	Days since humans + inverse distance to humans + salmon biomass + water level + salmon biomass x water level	-823.84	0.58	0.1081
M14	Group size + days since humans + salmon biomass + water level + salmon biomass x water level + group size x salmon biomass	-821.09	1.08	0.0840
M9	Group size + salmon biomass + water level + salmon biomass x water level	-824.21	1.30	0.0751
M15	Group size + days since humans + inverse distance to humans + salmon biomass + water level + salmon biomass x water level	-822.25	1.39	0.0721
M2	Salmon biomass + water level + salmon biomass x water level	-826.34	1.56	0.0660
M3	Human presence + salmon biomass + water level + salmon biomass x water level	-825.47	1.84	0.0575

M7	Human presence + days since humans + salmon biomass + water level + salmon biomass x water level + human presence x salmon biomass	-823.51	1.91	0.0555
M16	Group size + days since humans + inverse distance to humans + salmon biomass + water level + salmon biomass x water level + group size x salmon biomass	-820.66	2.22	0.0475
M10	Group size + salmon biomass + water level + salmon biomass x water level + group size x salmon biomass	-822.77	2.44	0.0426
M11	Group size + inverse distance to humans + salmon biomass + water level + salmon biomass x water level	-823.89	2.67	0.0380
M5	Inverse distance to humans + salmon biomass + water level + salmon biomass x water level	-826.27	3.43	0.0259

Table S9. Green detection rate model set with rankings

Model	Fixed effects	Log-likelihood	Δ AIC	Weight	Marginal R^2	Conditional R^2
M6	Human presence + days since people + salmon biomass + water level + salmon biomass x water level	-823.55	0.00	0.3001	0.0161	0.6626
M8	Days since humans + inverse distance to humans + salmon biomass + water level + salmon biomass x water level	-823.84	0.58	0.2249	0.0153	0.6630
M2	Salmon biomass + water level + salmon biomass x water level	-826.34	1.56	0.1373	0.0130	0.6609
M3	Human presence + salmon biomass + water level + salmon biomass x water level	-825.47	1.84	0.1196	0.0141	0.6615
M7	Human presence + days since humans + salmon biomass + water level + salmon biomass x water level + human presence x salmon biomass	-823.51	1.91	0.1154	0.0163	0.6627

M5	Inverse distance to humans + salmon biomass + water level + salmon biomass x water level	-826.27	3.43	0.0539	0.0129	0.6613
M4	Human presence + salmon biomass + water level + salmon biomass x water level + human presence x salmon biomass	-825.38	3.66	0.0481	0.0145	0.6616
M1	Intercept only	-836.77	12.43	0.0006	0.0000	0.6548

Table S10. Green detection rate model parameter estimates with confidence intervals for the 95% model set. Bold estimates are those whose confidence interval does not overlap zero

Model	M6	M8	M2	M3	M7
Intercept	**-1.28** (-1.98, -0.58)	**-1.23** (-1.92, -0.54)	**-1.20** (-1.89, -0.51)	**-1.28** (-1.98, -0.58)	**-1.29** (-1.99, -0.58)
People present	0.10 (-0.11, 0.30)	NA	NA	0.13 (-0.07, 0.33)	0.10 (-0.10, 0.30)
Days since people	**0.10** (0.00, 0.20)	**0.11** (0.01, 0.21)	NA	NA	0.10 (-0.00, 0.20)
Salmon biomass	0.11 (-0.08, 0.30)	0.11 (-0.08, 0.29)	0.03 (-0.14, 0.21)	0.05 (-0.13, 0.23)	0.12 (-0.08, 0.33)
Water level; flooded	**-0.48** (-0.93, -0.03)	**-0.47** (-0.92, -0.01)	**-0.55** (-1.01, -0.10)	**-0.54** (-1.00, -0.09)	**-0.49** (-0.95, -0.04)
Water level; above normal	-0.06 (-0.37, 0.25)	-0.11 (-0.41, 0.19)	-0.04 (-0.34, 0.25)	0.01 (-0.29, 0.32)	-0.06 (-0.37, 0.25)
Salmon biomass x Water level; flooded	-0.08 (-0.41, 0.26)	-0.06 (-0.39, 0.27)	-0.02 (-0.36, 0.32)	-0.04 (-0.38, 0.29)	-0.09 (-0.43, 0.25)
Salmon biomass x Water level; above normal	0.04 (-0.56, 0.63)	0.05 (-0.55, 0.64)	-0.09 (-0.68, 0.50)	-0.09 (-0.68, 0.50)	0.02 (-0.58, 0.62)

People x Salmon biomass	NA	NA	NA	NA	-0.03 (-0.24, 0.18)
Distance to tour	NA	-0.02 (-0.10, 0.06)	NA	NA	NA

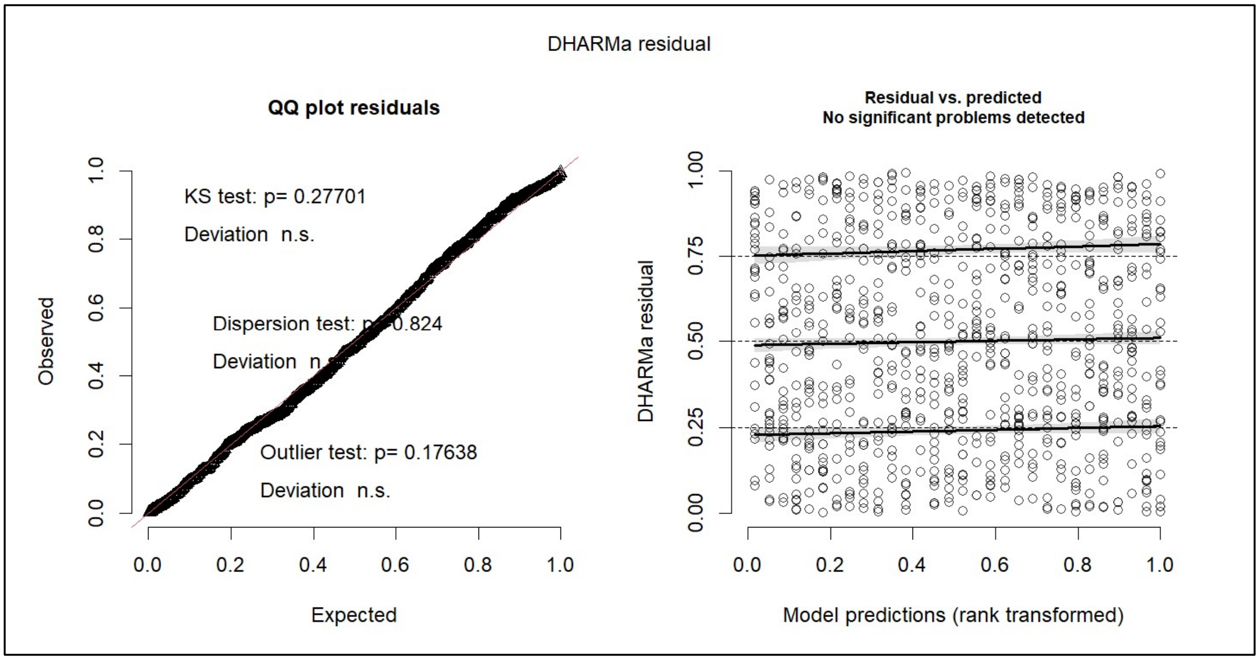

Figure S6. Green detection rate model checking. The QQ plot displays no deviations, dispersion or outliers. The residual vs predicted plot displays no deviations.

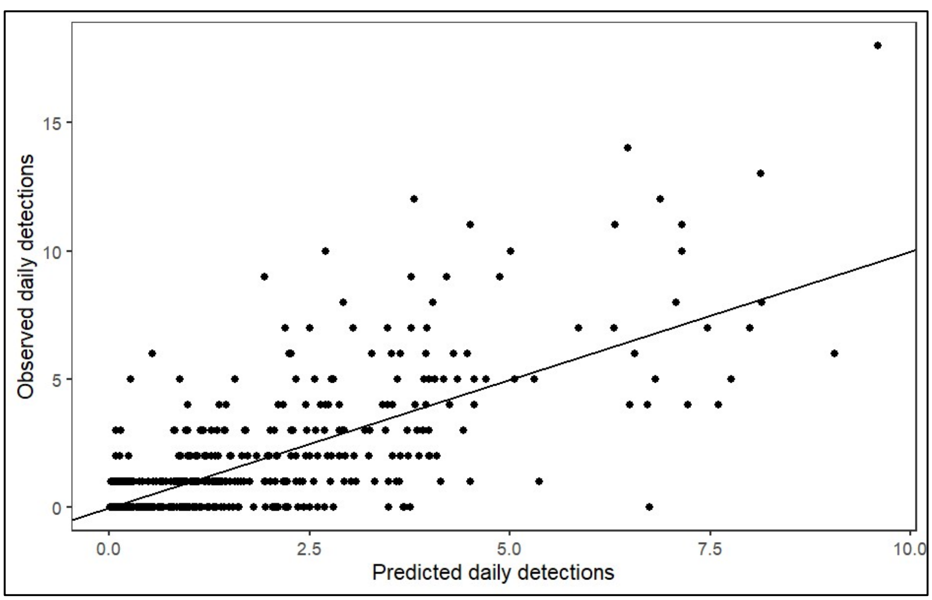

Figure S7. Green detection rate model predicted vs observed values for the top model.

Table S11. Khutze age and sex class multinomial model set with rankings

Model	Fixed effects	Δ AIC	Weight
B19	Number of people + inverse distance to humans + days since people + salmon biomass + nocturnality + number of people x salmon biomass + year	0.00	0.5184
B27	Number of people + inverse distance to humans + days since people + salmon biomass + nocturnality + year + number of people x salmon biomass + days since people x year	1.31	0.2697
B17	Number of people + inverse distance to humans + days since people + salmon biomass + number of people x salmon biomass + year	3.71	0.0813
B11	Number of people + inverse distance to humans + salmon biomass + nocturnality + number of people x salmon biomass + year	4.64	0.0510
B25	Number of people + inverse distance to humans + days since people + salmon biomass + year + number of people x salmon biomass + days since people x year	5.14	0.0397
B15	Number of people + days since people + salmon biomass + nocturnality + year + number of people x salmon biomass	6.37	0.0213
B9	Number of people + inverse distance to humans + salmon biomass + year + number of people x salmon biomass	8.60	0.0070
B23	Number of people + days since people + salmon biomass + nocturnality + year + number of people x salmon biomass + days since people x year	8.70	0.0067

B13	Number of people + days since people + salmon biomass + year + number of people x salmon biomass	10.90	0.0022
B7	Number of people + salmon biomass + nocturnality + year + number of people x salmon biomass	11.18	0.0019
B21	Number of people + days since people + salmon biomass + year + number of people x salmon biomass + days since people x year	13.48	0.0006
B5	Number of people + salmon biomass + year + number of people x salmon biomass	15.92	0.0002
B10	Number of people + inverse distance to humans + salmon biomass + nocturnality + year	30.98	0.0000
B16	Number of people + inverse distance to humans + days since people + salmon biomass + year	32.14	0.0000
M3	Salmon biomass + nocturnality + year	33.08	0.0000
B14	Number of people + days since people + salmon biomass + nocturnality + year	33.09	0.0000
B18	Number of people + inverse distance to humans + days since people + salmon biomass + nocturnality + year	33.21	0.0000
B26	Number of people + inverse distance to humans + days since people + salmon biomass + nocturnality + year + days since people x year	33.21	0.0000
B8	Number of people + inverse distance to humans + salmon biomass + year	35.01	0.0000

B6	Number of people + salmon biomass + nocturnality + year	36.00	0.0000
B24	Number of people + inverse distance to humans + days since people + salmon biomass + year + days since people x year	37.04	0.0000
B22	Number of people + days since people + salmon biomass + nocturnality + year + days since people x year	37.49	0.0000
B12	Number of people + days since people + salmon biomass + year	37.55	0.0000
M2	Salmon biomass + year	37.84	0.0000
B4	Number of people + salmon biomass + year	40.78	0.0000
B20	Number of people + days since people + salmon biomass + year + days since people x year	42.09	0.0000
M1	Intercept only	89.00	0.0000

Table S12. Khutze age and sex class multinomial model parameter estimates and confidence intervals for 95% model set. Estimates that are bold have confidence intervals that do not overlap zero.

Model	B19	B27	B17	B11
Adult female ~ Intercept	0.42 (-0.16, 1.01)	0.48 (-0.11, 1.07)	0.43 (-0.16, 1.01)	0.36 (-0.21, 0.92)
Adult female ~ People	**1.04** (0.32, 1.76)	**1.15** (0.39, 1.90)	**1.03** (0.31, 1.76)	**1.03** (0.32, 1.75)
Adult female ~ Distance to tour	**0.86** (0.11, 1.61)	**0.97** (0.19, 1.75)	**0.87** (0.11, 1.62)	**0.86** (0.11, 1.61)
Adult female ~ Days since people	-0.18 (-0.71, 0.34)	-0.15 (-0.68, 0.38)	-0.19 (-0.72, 0.34)	NA
Adult female ~ Salmon biomass	**0.77** (0.40, 1.14)	**0.82** (0.45, 1.19)	**0.77** (0.41, 1.14)	**0.72** (0.39, 1.06)
Adult female ~ Nocturnality	0.03 (-0.18, 0.24)	0.03 (-0.18, 0.24)	NA	0.04 (-0.17, 0.25)
Adult female ~ Year; 2021 Open to tours	0.23 (-0.71, 1.17)	-6.75 (-13.33, -0.17)	0.22 (-0.72, 1.16)	0.49 (-0.20, 1.17)
Adult female ~ People x salmon biomass	**1.04** (0.42, 1.65)	**1.17** (0.52, 1.81)	**1.03** (0.42, 1.65)	**1.05** (0.44, 1.66)

Adult female ~ Days since people x year; 2021 open to tours	NA	**-6.33** (-12.27, -0.40)	NA	NA
Female with young ~ Intercept	**1.90** (1.40, 2.39)	**1.95** (1.44, 2.46)	**1.89** (1.40, 2.38)	**2.02** (1.54, 2.49)
Female with young ~ People	**1.32** (0.60, 2.03)	**1.42** (0.67, 2.16)	**1.31** (0.60, 2.03)	**1.29** (0.58, 1.99)
Female with young ~ Distance to tour	**0.80** (0.05, 1.55)	**0.91** (0.13, 1.69)	**0.81** (0.06, 1.56)	**0.80** (0.05, 1.55)
Female with young ~ Days since people	0.34 (-0.03, 0.70)	0.36 (-0.01, 0.73)	0.34 (-0.03, 0.70)	NA
Female with young ~ Salmon biomass	**0.55** (0.22, 0.88)	**0.60** (0.26, 0.94)	**0.55** (0.22, 0.88)	**0.65** (0.34, 0.96)
Female with young ~ Nocturnality	-0.01 (-0.19, 0.17)	-0.02 (-0.20, 0.17)	NA	-0.01 (-0.19, 0.17)
Female with young ~ Year; 2021 Open to tours	-0.60 (-1.39, 0.18)	**-7.04** (-13.34, -0.74)	-0.60 (-1.39, 0.18)	-1.05 (-1.70, -0.41)
Female with young ~ People x salmon biomass	**1.24** (0.64, 1.84)	**1.36** (0.73, 1.99)	**1.24** (0.64, 1.84)	**1.19** (0.60, 1.79)
Female with young ~ Days since people x year; 2021 open to tours	NA	**-5.83** (-11.51, -0.15)	NA	NA

Sub-adult ~ Intercept	**1.18** (0.66, 1.70)	**1.23** (0.70, 1.77)	**1.17** (0.66, 1.68)	**1.20** (0.70, 1.71)
Sub-adult ~ People	**0.80** (0.07, 1.54)	**0.90** (0.14, 1.66)	**0.79** (0.06, 1.52)	**0.79** (0.06, 1.51)
Sub-adult ~ Distance to tour	0.25 (-0.56, 1.07)	0.36 (-0.48, 1.20)	0.26 (-0.55, 1.08)	0.25 (-0.56, 1.06)
Sub-adult ~ Days since people	0.34 (-0.03, 0.70)	0.36 (-0.01, 0.73)	0.34 (-0.03, 0.70)	NA
Sub-adult ~ Salmon biomass	**0.49** (0.15, 0.83)	**0.54** (0.19, 0.89)	**0.49** (0.15, 0.83)	**0.52** (0.20, 0.85)
Sub-adult ~ Nocturnality	-0.20 (-0.39, -0.01)	-0.20 (-0.40, -0.01)	NA	-0.20 (-0.39, -0.01)
Sub-adult ~ Year; 2021 open to tours	-0.001 (-0.84, 0.84)	-6.11 (-12.67, 0.44)	0.03 (-0.81, 0.87)	-0.12 (-0.79, 0.55)
Sub-adult ~ People x salmon biomass	**0.83** (0.22, 1.44)	**0.95** (0.30, 1.59)	**0.82** (0.20, 1.43)	**0.81** (0.20, 1.42)
Sub-adult ~ Days since people x year; 2021 open to tours	NA	-5.54 (-11.44, 0.37)	NA	NA

TableS13 . Model predictrions for likelihood of adult male detections given number of people and mean salmon level. When there are 6 people in Khutze, the 95% confidence interval does not overlap the mean detections when there were 0 people

Number of people	Likelihood of adult male	Low confidence interval	High confidence interval
0	0.1502	0.0560	0.2443
1	0.1378	0.0535	0.2222
2	0.1252	0.0500	0.2004
3	0.1145	0.0463	0.1828
5	0.0945	0.0372	0.1519
6	0.0861	0.0326	0.1396
8	0.0704	0.0229	0.1179
9	0.0639	0.0186	0.1091
10	0.0579	0.0146	0.1011
11	0.0518	0.0105	0.0931
12	0.0469	0.0073	0.0864
13	0.0423	0.0044	0.0802
14	0.0378	0.0018	0.0738
19	0.0220	-0.0057	0.0497
20	0.0195	-0.0064	0.0454
23	0.0139	-0.0074	0.0351
26	0.0098	-0.0072	0.0268

30	0.0061	-0.0062	0.0185
35	0.0033	-0.0046	0.0113
43	0.0012	-0.0024	0.0049
44	0.0011	-0.0022	0.0044

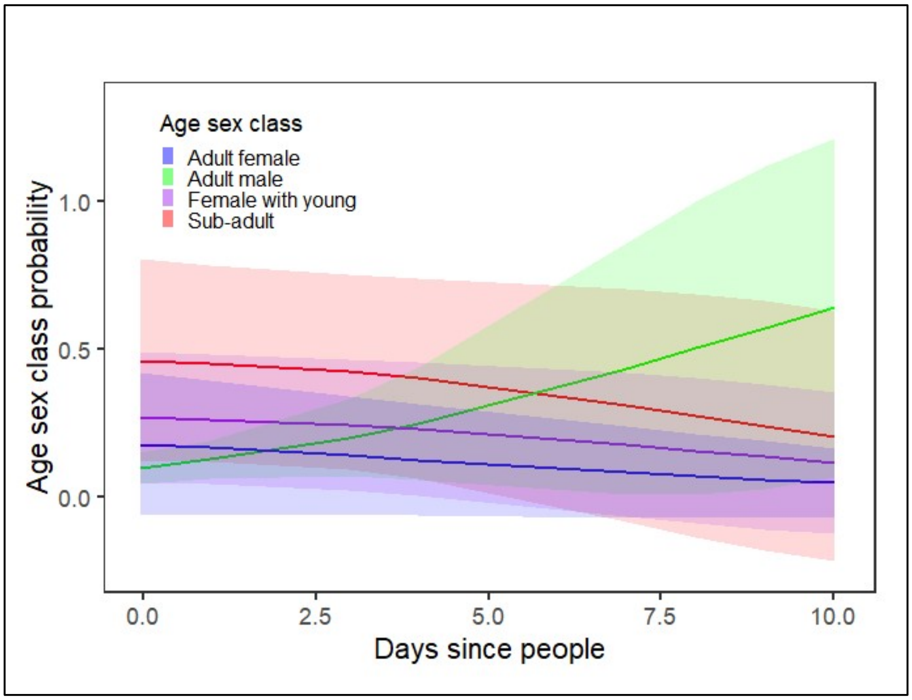

Figure S8. Likelihood of detecting any given age-sex classes as a function of the number of days since people, as predicted by the second-best age-sex multinomial model in Khutze. Days since people has a positive influence on the probability of detecting an adult male.

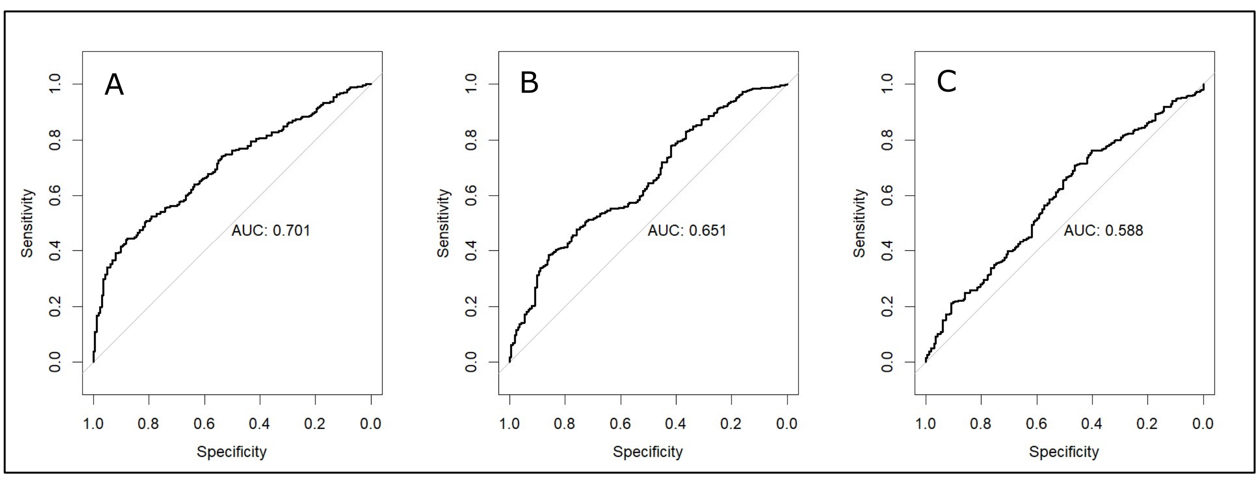

Figure S9. Receiver operator curves for Khutze age and sex class multinomial model A) adult females, AUC = 0.701; B) female with young, AUC = 0.651; and C) sub-adults in comparison to adult males, AUC = 0.588.

Table S14. Green age and sex class multinomial model set with rankings

Model	Fixed effects	Δ AIC	Weight
M1	Intercept only	0.00	0.5882
M5	Human presence + salmon biomass + human presence x salmon biomass	2.47	0.1711
M11	Human presence + days since people + salmon biomass + human presence x salmon biomass	3.45	0.1048
M2	Salmon biomass	4.39	0.0655
M7	Human presence + salmon biomass + nocturnality + human presence x salmon biomass	6.88	0.0188
M4	Human presence + salmon biomass	7.18	0.0162
M13	Human presence + days since people + salmon biomass + nocturnality + human presence x salmon biomass	7.90	0.0113
M3	Salmon biomass + nocturnality	8.21	0.0097
M10	Human presence + days since humans + salmon biomass	8.71	0.0076
M14	Inverse distance to people + days since humans + salmon biomass	10.69	0.0028
M6	Human presence + salmon biomass + nocturnality	11.30	0.0021
M12	Human presence + days since people + salmon biomass + nocturnality	12.78	0.0010
M9	Inverse distance to people + salmon biomass + nocturnality	13.18	0.0008

Table S15. Green age and sex class multinomial model parameter estimates for 95% model set. Estimates that are bold have confidence intervals that do not overlap zero.

Model	M1	M5	M11	M2	M7
Adult female ~ Intercept	**2.46** (1.27, 3.64)	**2.30** (1.07, 3.52)	**2.30** (1.07, 3.52)	**2.47** (1.29, 3.64)	**2.35** (0.96, 3.73)
Adult female ~ Salmon biomass	NA	-0.098 (-0.46, 0.26)	-0.09 (-0.49, 0.30)	-0.11 (-0.42, 0.19)	-0.10 (-0.46, 0.26)
Adult female ~ Nocturnality	NA	NA	NA	NA	-0.01 (-0.11, 0.09)
Adult female ~ People present	NA	0.54 (-0.16, 1.23)	0.54 (-0.17, 1.24)	NA	0.54 (-0.16, 1.23)
Adult female ~ People present x salmon biomass	NA	-0.07 (-0.75, 0.61)	-0.07 (-0.75, 0.61)	NA	-0.07 (-0.75, 0.61)
Adult female ~ Days since people	NA	NA	0.01 (-0.38, 0.39)	NA	NA
Female with young ~ Intercept	-0.35 (-2.51, 1.82)	-0.54 (-2.78, 1.70)	-0.55 (-2.78, 1.69)	-0.35 (-2.50, 1.81)	-0.62 (-3.01, 1.76)
Female with young ~ Salmon biomass	NA	-0.29 (-0.77, 0.19)	-0.36 (-0.87, 0.15)	0.03 (-0.37, 0.43)	-0.29 (-0.77, 0.19)
Female with young ~ Nocturnality	NA	NA	NA	NA	0.01 (-0.11, 0.14)

Female with young ~ People present	NA	0.43 (-0.43, 1.29)	0.44 (-0.43, 1.30)	NA	0.44 (-0.42, 1.30)
Female with young ~ People present x salmon biomass	NA	0.86 (-0.03, 1.74)	0.87 (-0.01, 1.75)	NA	0.85 (-0.04, 1.73)
Female with young ~ Days since people	NA	NA	-0.15 (-0.62, 0.32)	NA	NA
Sub-adult ~ Intercept	-1.07 (-2.72, 0.58)	-1.38 (-3.10, 0.33)	-1.46 (-3.16, 0.25)	-1.05 (-2.67, 0.57)	-0.91 (-2.94, 1.12)
Sub-adult ~ Salmon biomass	NA	-0.43 (-1.10, 0.24)	-0.31 (-1.08, 0.45)	-0.23 (-0.78, 0.32)	-0.44 (-1.12, 0.23)
Sub-adult ~ Nocturnality	NA	NA	NA	NA	-0.07 (-0.24, 0.09)
Sub-adult ~ People present	NA	0.90 (-0.28, 2.08)	0.82 (-0.38, 2.02)	NA	0.84 (-0.35, 2.03)
Sub-adult ~ People present x salmon biomass	NA	0.52 (-0.66, 1.70)	0.62 (-0.64, 1.87)	NA	0.53 (-0.65, 1.71)
Sub-adult ~ Days since people	NA	NA	0.47 (-0.14, 1.07)	NA	NA

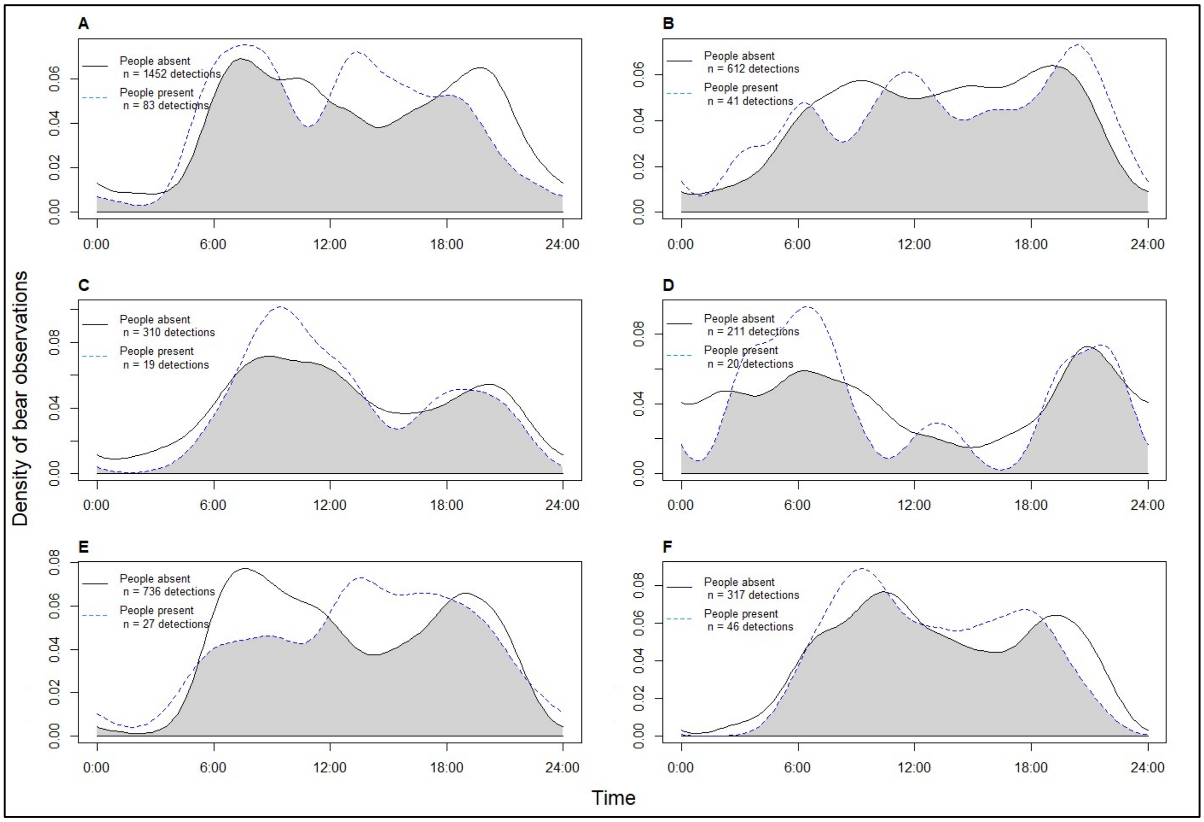

Figure S10. Activity pattern analysis curves for Khutze: A) Activity patterns for all bears for cameras at 0 -100m from tours (n = 26 cameras); B) Activity patterns for all bears for cameras at 100-450m from tours (n = 7 cameras); C) Activity patterns for all bears for cameras at 450-1000m from tours (n = 6 cameras); D) Activity patterns for adult males at all remote cameras; E) Activity patterns for family groups at all cameras; F) Activity patterns for adult solo females at all cameras. There are no significant shifts at any distance or for any age-sex class.

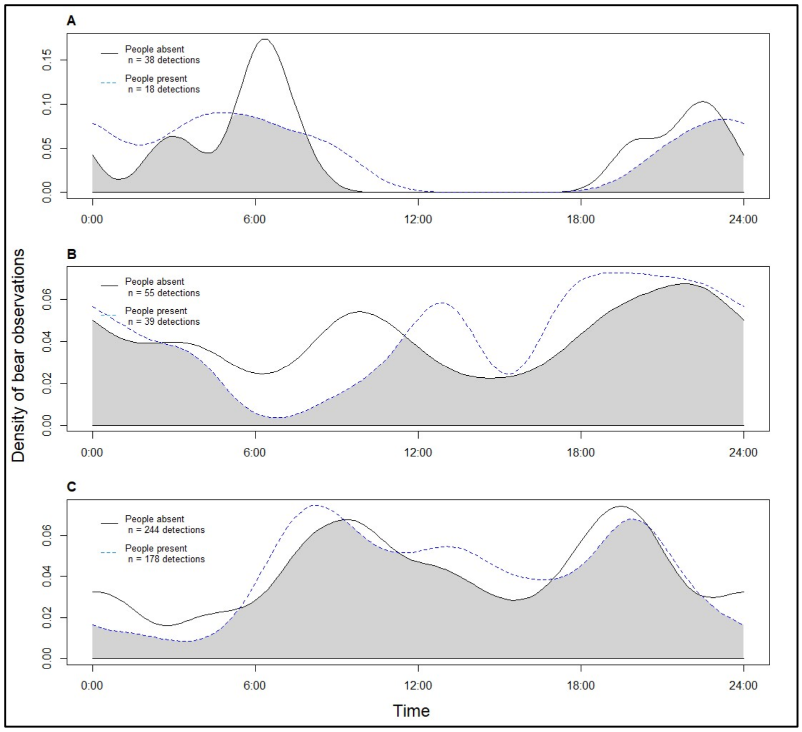

Figure S11. Activity pattern analysis curves for Green by age-sex class A) Activity patterns for adult males at all cameras; B) Activity patterns for family groups at all cameras; C) Activity patterns for adult solo females at all cameras. There are no significant shifts for any age-sex class.

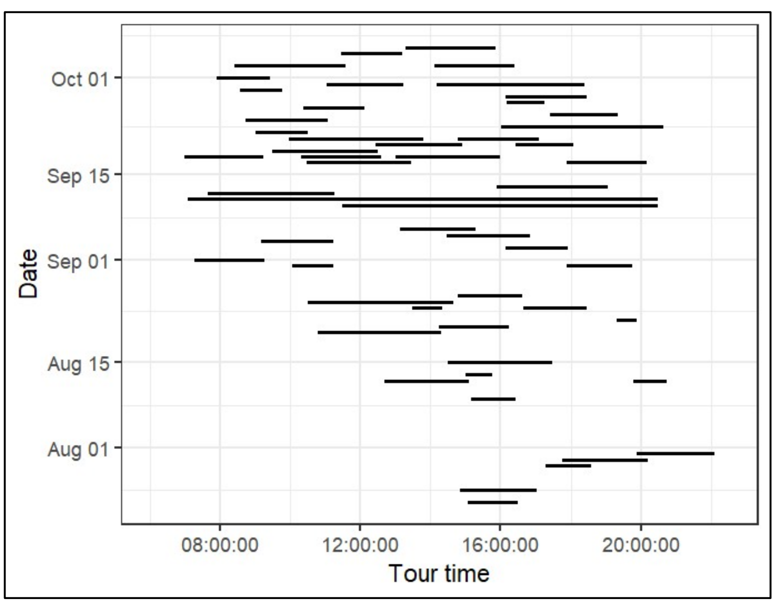

Figure S12. Khutze ecotour times for 2021

Figure S13. Influence of ecotourism metrics on bear detections and possible management levers

Variable	Influence on detection rate	Possible management levers
Days since people	9.2% increase in detections for each day closure	Multi-day closures, such as 3 consecutive days per week. 12 days required for activity levels to approximate those without human activity
North/south closures	No influence	Full watershed closures required for response (see above)
Number of people per day	1.6% decrease in detections for each additional person	Limit tour group sizes. A limit of 6 people per day required to avoid influencing age-sex class composition.
Number of tours	11.6% decrease in detections for each additional tour	Limit viewing to one tour per day
Number of hours with tours	5.3% decrease in detection rate for each additional hour with people in Khutze	Limit viewing time on any given day. For example, viewing only permitted in the mornings

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