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Ecology of fear alters behavior of grizzly bears exposed to bear-viewing ecotourism

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Abstract

Humans are perceived as predators by many species and may generate landscapes of fear, influencing spatiotemporal activity of wildlife. Additionally, wildlife might seek out human activity when faced with predation risks (human shield hypothesis). We used the anthropause, a decrease in human activity resulting from the COVID-19 pandemic, to test ecology of fear and human shield hypotheses and quantify the effects of bear-viewing ecotourism on grizzly bear (*Ursus arctos*) activity. We deployed camera traps in the Khutze watershed in Kitasoo Xai'xais Territory in the absence of humans in 2020 and with experimental treatments of variable human activity when ecotourism resumed in 2021. Daily bear detection rates decreased with more people present and increased with days since people were present. Human activity was also associated with more bear detections at forested sheltered sites and less at exposed sites, likely due to the influence of habitat on bear perception of safety. The number of people negatively influenced adult male detection rates, but we found no influence on female with young detections, providing no evidence that females responded behaviorally to a human shield effect from reduced male activity. We also observed apparent trade-offs of risk avoidance and foraging. When salmon levels were moderate to high, detected bears were more likely to be females with young than adult males on days with more people present. Should managers want to minimize human impacts on bear activity and maintain baseline age–sex class composition at ecotourism sites, multiday closures and daily occupancy limits may be effective. More broadly, this work revealed that antipredator responses can vary with intensity of risk cues, habitat structure, and forage trade-offs and manifest as altered age–sex class composition of individuals using human-influenced areas, highlighting that wildlife avoid people across multiple spatiotemporal scales.

KEYWORDS
anthropause, antipredator behavior, camera traps, COVID-19, dynamic landscape of fear, ecology of fear, human shield, remote cameras, wildlife conservation

PANDEMIC PIVOT

This project seized the opportunity presented by COVID-19 closures of ecotourism in 2020 to experimentally test the potential effects of human presence on wildlife activity in an area that typically experiences ecotourism throughout key foraging times for grizzly bears. Our Indigenous Nation–academic partnership rapidly designed an approach that made use of both the "natural" experiment provided by the anthropause in 2020, as well as a structured spatiotemporal experiment in 2021. The Kitasoo Xai'xais (KX) Nation-led context, a part of resurgent stewardship activities, allowed for a rapid pivot to gain inference from an unprecedented natural experiment.

INTRODUCTION

Wildlife commonly encounter situations that require trade-offs between risks and benefits. Avoiding risk may come at the cost of other fitness-enhancing activities, like foraging, and can manifest via spatial or temporal shifts in activity (Lima & Dill, 1990; Palmer et al., 2022; Spitz et al., 2019; Zanette & Clinchy, 2019). Given a long history and high intensity of predation by humans (Darimont et al., 2015; Ripple & Van Valkenburgh, 2010), wildlife often perceive humans as risky. Even seemingly benign human activity can elicit avoidance (Gaynor et al., 2018; Spitz et al., 2019; Suraci et al., 2019). The "ecology of fear" concept allows an understanding of such avoidance and considers how fear, or an animal's perception of risk, may influence its behavior and spatiotemporal use of habitat (Brown et al., 1999). As a first step to mitigating the impacts of human-induced fear on wildlife, it is necessary to quantify the intensity of avoidance elicited by varying levels of human activity to inform management options.

Wildlife avoid humans on multiple spatiotemporal scales. Spatial avoidance can range from meters to kilometers. For example, in one study, cougars (*Puma concolor*) avoided human voice recordings by ~150 m (Suraci et al., 2019), whereas black bears (*Ursus americanus*) avoided roads by over 2000 m (Stillfried et al., 2015). Temporal avoidance can also vary, occurring on a scale of hours, via shifting diel activity patterns (Gaynor et al., 2018; Suraci et al., 2019), or as prolonged avoidance lasting days (e.g., Ordiz et al., 2013). The spatiotemporal extent of avoidance may depend on the characteristics of the risk cues, habitat variation, and behavioral differences among reproductive classes (Gaynor et al., 2020; Ruiz-Mar et al., 2022).

Characteristics of human-related risks are important in influencing responses. The "dynamic landscape of fear" predicts that avoidance behavior may relate to the predictability and intensity of perceived risks. When risk is predictable in space and time, animals can use fine-scale spatiotemporal risk avoidance; as risk becomes less predictable, animals may show more reactive risk avoidance responses (Palmer et al., 2022). Intensity of risk cues is also important. For example, Naidoo and Burton (2020) found that wildlife more strongly avoided mountain bikers and motorized vehicles compared with hikers, likely related to the more intense risk cues associated with faster moving and noisier stimuli.

Avoidance can also vary with features of the landscape, such as habitat structure. We might expect that wildlife may show more avoidance in more exposed areas compared with more secluded habitat. For example, Suraci et al. (2020) found that puma spatial activity in human-dominated landscapes was mediated by the amount of protective vegetative cover, which provided shelter from human-related risk, as well as access to better hunting opportunities. Moreover, an animal's response to a perceived risk can also be mediated by the variation in foraging opportunities across the landscape; access to foods in areas with less risk, for example, influences the potential cost of forgoing foraging opportunities in risky areas (Lima & Dill, 1990).

Although wildlife commonly perceive humans as risky, some age–sex classes might preferentially use areas of higher human activity if it protects them from predation from members of their own or other species. This phenomenon, described by the human shield hypothesis (Berger, 2007), has been observed in many taxa. In the canonical case, moose (*Alces alces*) selected areas closer to roads in areas of high grizzly bear (*Ursus arctos*) density (Berger, 2007). In the contexts of risk avoidance behavior by grizzly bears, females with young have been observed selecting areas of high human activity, presumably to avoid infanticide by adult males, which tend to avoid humans (Steyaert et al., 2016).

Here we confront these general hypotheses from the ecology of fear and human shield literatures in a grizzly bear–ecotourism system and offer specific predictions. Given the perceived risk of humans and the aggregation of ecotourists at a time and place of valuable foods for bears (during and situated amidst the spawning aggregations of Pacific salmon; *Oncorhynchus* spp.), we considered mechanisms of the ecology of fear, including trade-offs, intensity of risk cues, and landscape variation, as well as the potential for human shielding, to examine grizzly bear activity in response to perceived risk from ecotourists. The spatiotemporal overlap of ecotourism at

sites with dense aggregations of spawning salmon creates a context in which foraging trade-offs might be particularly acute for grizzly bears. Specifically, given the temporal alignment of salmon availability with hyperphagia (increased feeding prior to winter denning) in bears, the costs of avoiding areas with dense food aggregations may be high.

We regarded the anthropause, a period of decreased human activity due to COVID-19, as an opportunity to examine wildlife behavior when humans were absent (Rutz et al., 2020). In the Khutze watershed in KX Territory (Figure 1), bear-viewing ecotourism was canceled in 2020 and resumed in 2021. Our team, led by the Kitasoo Xai'xais Stewardship Authority (KXSA) sought inference from experimental methods regarding potential spatiotemporal effects of ecotourism. We collected data in 2020 when ecotourism was closed and 2021 during which experimental half-watershed spatial closures were implemented (Appendix S1: Table S1). This design consisted of alternating closures of the north and south channels of Khutze to test whether such a scale of spatial refugia would elicit behavioral changes. Additionally, we assessed how the habitat structure (i.e., sheltered vs. exposed camera trap sites), the intensity of risk cues (i.e., number of people), and foraging trade-offs, in the form of salmon availability, may influence how bears respond to ecotourism. We predicted that (1) bears would exhibit spatial avoidance of ecotourism at multiple scales (i.e., sheltered vs. exposed sites; half estuary or full estuary), with more intense risk cues, such as larger groups of ecotourists, eliciting greater avoidance; (2) age–sex class distribution of bears in times and places with more ecotourism would be different from those with less ecotourism; specifically, there would be a greater proportion of females with young, relative to males due to greater avoidance by males; (3) males would exhibit temporal avoidance during ecotourism by shifting their activity to times of the day when tours are absent and females with young would show the opposite response; and (4) bears would show greater avoidance of humans when they were satiated or when food sources are abundant, as indexed by high levels of salmon.

METHODS

Study area

We deployed camera traps ($n = 40$) across ~5 km^2 of the ~340-km^2 Khutze watershed in KX Territory (Figure 1). Khutze has an extensive estuary (~2 km^2), a salmon bearing river, and riparian bear trails through temperate rainforest. Salmon spawn throughout the study area (Figure 1) and ~6 km upstream, with the next nearest salmon bearing stream ~7 km away. Ecotourism operators and the public can view bears from boats or two land-based viewing sites (Figure 1A,B). Members of the public were accompanied by a KX Guardian Watchmen during their trip into Khutze to ensure the safety of both people and bears. Given that the public were guided by watchmen, any visitors to Khutze in 2021 were referred to as "tours." Bear viewing has occurred in Khutze for over 15 years, which may have resulted in bears in the area becoming more tolerant toward human activity

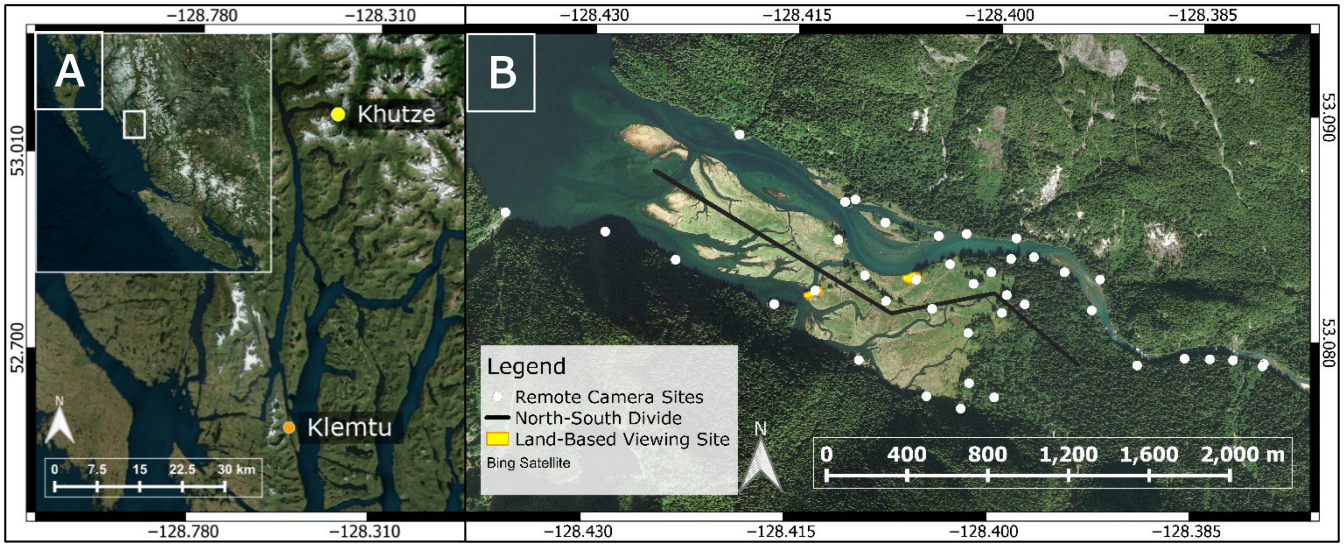

FIGURE 1 (A) Study area within Kitasoo Xai'xais (KX) Territory on central coast of British Columbia, Canada, showing Khutze and Klemtu, the current village of the KX; (B) Khutze camera trap array, north–south divide for alternating weekly closures, and land-based interpretive sites.

compared with bears elsewhere. We note, however, that any habituation in Khutze might have been reduced by the 2020 season in which people were absent.

Observational and experimental design

We analyzed camera trap data (Appendix S1) during times of the year when ecotourism and salmon typically co-occur (20 July–27 September 2020, and 26 July–3 October 2021). Ecotourism was closed in 2020, and in 2021 KXSA applied alternating weekly closures of north and south regions to test whether partial watershed closures could provide sufficient refuge to bears (Figure 1B). This resulted in 5008 camera trap days: 51 days with tours, 89 days without tours. The longest period with no tour in 2021 was 8 days. Group sizes varied from one to 14 people (median = 8.5), with one to five tours each tour day (median = 1). Daily tour durations ranged from 0.6 to 13.4 h (mean = 3.4). All groups carried a Bad Elf GPS Pro to record spatiotemporal data on human activity, which was used to calculate the distance between tour groups and the camera traps (Table 1; Appendix S1: Figure S1).

Detection rate models

We modeled how ecotourism and environmental variables influenced bear activity. The response variable was the number of total bear detections per camera day ("detection rate"; Table 1; Appendix S1). Each "day" (24-h period) started at the earliest tour time (07:00:00) because we would only expect bear activity to respond to a given day's presence of humans while or after it occurred. Additionally, this time aligned with dawn for much of the study period. We tested for the effects of multiple ecotourism metrics: human presence, number of people per day, number of tours, tour hours, distance to tours, camera site ecotourism exposure (open, i.e., estuary/riverbank or sheltered, i.e., forest), spatial north/south closures, and temporal closures (closed 2020; open 2021) in separate models (Table 1). All models included spatial or temporal closures and salmon biomass and water level (i.e., normal, high, or flooded), which together determine salmon availability, as predictors. We included camera site and week as random effects.

Using these variables, we developed a candidate model set (Appendix S1: Table S1). 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 vary with salmon abundance, as related to foraging trade-offs. When salmon levels are high, bears may respond to humans less strongly, which would indicate that bears trade off some security for access to abundant food. Alternatively, bear detections may decrease when salmon abundance and ecotourist numbers are both high, with bears potentially traveling to alternative fishing sites without ecotourists. We included an interaction term between the ecotourism variable and the spatial closures in Khutze, with the understanding that the level of ecotourism would likely influence bears differently depending on where in the watershed ecotourism occurred. We predicted that the north channel (where salmon spawning occurs) might elicit a stronger response given the potential for movement directly upstream to additional salmon foraging sites. 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 ecotourism than forested (i.e., "sheltered") areas. Finally, we included an interaction 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 in 2020, when the only visits were by researchers setting up cameras.

Given interest in multiple ecotourism metrics (and corresponding management options), we developed candidate model sets for each metric. We placed each set against null and environment-only models (Appendix S1: Table S2), as well as against each other, to determine which ecotourism metric best predicted the bear detection rate. We ran generalized linear mixed models using glmmTMB in R (Brooks et al., 2017; R Core Team, 2021), using the quadratic parameterization of the negative binomial distribution (binom2), as it best estimated the zero inflation in our data set (Brooks et al., 2017). We checked for additional zero inflation using the DHARMa package (Hartig, 2022).

Age and sex class models

We expected bears to respond differently to ecotourism based on their age and sex. Accordingly, we also ran the top detection rate model on subsets of detections for females with young and adult males. We also used a multinomial model to test the effects of ecotourism and environmental variables on the probability of a detection being an adult female, adult male, female with young, or subadult (Appendix S1). In the multinomial model, we included a nocturnality metric to indicate the relative

TABLE 1 Khutze ecotourism metrics and environmental variables for detection rate model.

Type of variable	Variable name	Value	Variable description and rationale
Response	Detection rate	Continuous numeric	Number of independent (see *Methods* for definition) grizzly detections at a camera on a given day. Day is defined as the 24-h period form 7 a.m. to 7 a.m. because we would expect bears to only respond during or after human presence, rather than before
Fixed effect	Year	Categorical: 2020: Closed to tours 2021: Open to tours	Year. This was included to directly test differences between years, as well as account for other interannual variability
	Human presence	Categorical (yes, no)	Whether humans were present in Khutze on a given day. This variable is assigned to all cameras
	Number of people	Continuous numeric	Number of people to enter Khutze on a given day. The same value was assigned to all cameras
	Number of tours	Continuous numeric	Number of tours on a given day. The same value was assigned to all cameras
	Tour length	Continuous numeric	Hours of day with tours present. The same value was assigned to all cameras
	Distance to tour	Continuous numeric	Inverse distance from each remote camera to closest point on 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 as this one approached remote cameras closer than tours that remained further out in the estuary. We calculated the inverse of these distances to account for days with no people, which were assigned a value of 0. This variable was assigned to each individual camera for each day
	Treatment	Categorical (north open, south open, fully closed [2020])	The alternating weekly closures of Khutze in 2021 and the full closure in 2020. This variable is a temporal variable, rather than a spatial variable, and thus applied to all camera trap locations
	Days since people	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 had passed since humans had entered the watershed to account for potential multiday lag effects of human activity. In 2020, this variable indicated the days since researchers were in the watershed setting up and checking the camera traps. The same value was assigned to all cameras on a given day
	Salmon biomass	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 nine stream inspection dates in 2020 and seven 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. The same value was assigned to all cameras
	Water level	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, and the same value was attributed to all cameras for a given day. There were no days with low water level, so the variable only varies from normal to flooded. In 2020, cameras in Khutze were not set to take daily images, so the closest image to noon was used for each day. Water level was classified into normal, high, and flooded, which corresponded to specific features in images (Appendix S1: Table S5)

(Continues)

TABLE 1 (Continued)

Type of variable	Variable name	Value	Variable description and rationale
	Site exposure	Categorical (exposed, sheltered)	This variable indicates 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. This was assigned to each camera trap and did not vary throughout the study period
Random effect	Site	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	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 included environmental condition shifts, such as seasonal changes in vegetation resources such as berry, crab apple (*Malus fusca*), and sedge (*Carex* spp.) availability. The same value was assigned to all cameras

time of day of detections (Appendix S1: Table S2), the 2020 closure, salmon biomass, number of people, inverse distance to tour, spatial closures, site ecotourism exposure, and days since people as predictor variables, and we further included camera site as a random effect (Appendix S1: Tables S2 and S3).

Top model set identification and relative variable importance estimation

For both modeling approaches, we assessed which model set produced the lowest AIC values. From that model set we used cumulative AIC weights to define a 95% confidence set of models (Symonds & Moussalli, 2011). We also calculated relative variable importance (RVI) for each variable, standardized by the number of models including each variable (Kittle et al., 2008). The RVI indicates which variables have the strongest influence on model performance.

Activity pattern analysis

To assess temporal avoidance, we compared activity patterns on days with and without ecotourism. We performed an activity pattern analysis using a nonparametric kernel density function to model activity over a 24-h cycle (Frey et al., 2017; Ridout & Linkie, 2009). To include a potential spatial influence, we ran our activity pattern analysis at multiple distances from human activity, based on observed overt reaction distances from other systems (Elmeligi & Shultis, 2015; Jacobs & Schloeder, 1992). We binned cameras by distances of 0–100 m, 100–450 m, and 450–1000 m from tours. We used the Mardia–Watson–Wheeler test to assess whether differences were significant using R packages Overlap and Circular (Agostinelli & Lund, 2017; Ridout & Linkie, 2009).

RESULTS

Detection rate models

We found multiple signals of ecotourism influence on detection rate of grizzly bears. Overall, our top detection rate model accounted for ~50% of the variation in the data, with the fixed effects alone accounting for ~7% of the variation. Comparison of model sets with alternative ecotourism metrics revealed that models with number of people per day outperformed others (human presence, number of tours, or tour length; Appendix S2: Table S1). Although we did not detect an effect of year, detection rate decreased by ~1.6% (95% CI: 0.4%–2.7%) for each additional person (Figure 2A). An interaction term revealed that as the number of people increased, detections increased at sheltered camera sites by ~2.2% (CI: 1.1%–3.4%) for each additional person with the opposite pattern at open sites (Figure 2B). Finally, we observed a positive association between overall detection rate and days since people were present in 2021 (Figure 2C; ~9.2% per day; CI: 2.6%–16.2% per day). The predicted mean detection rate in 2021 aligned with the 2020 mean (0.71 detections per camera day) at 25 days since people, suggesting a full watershed closure of 25 days would be required for activity to return to a 2020-like nontourism

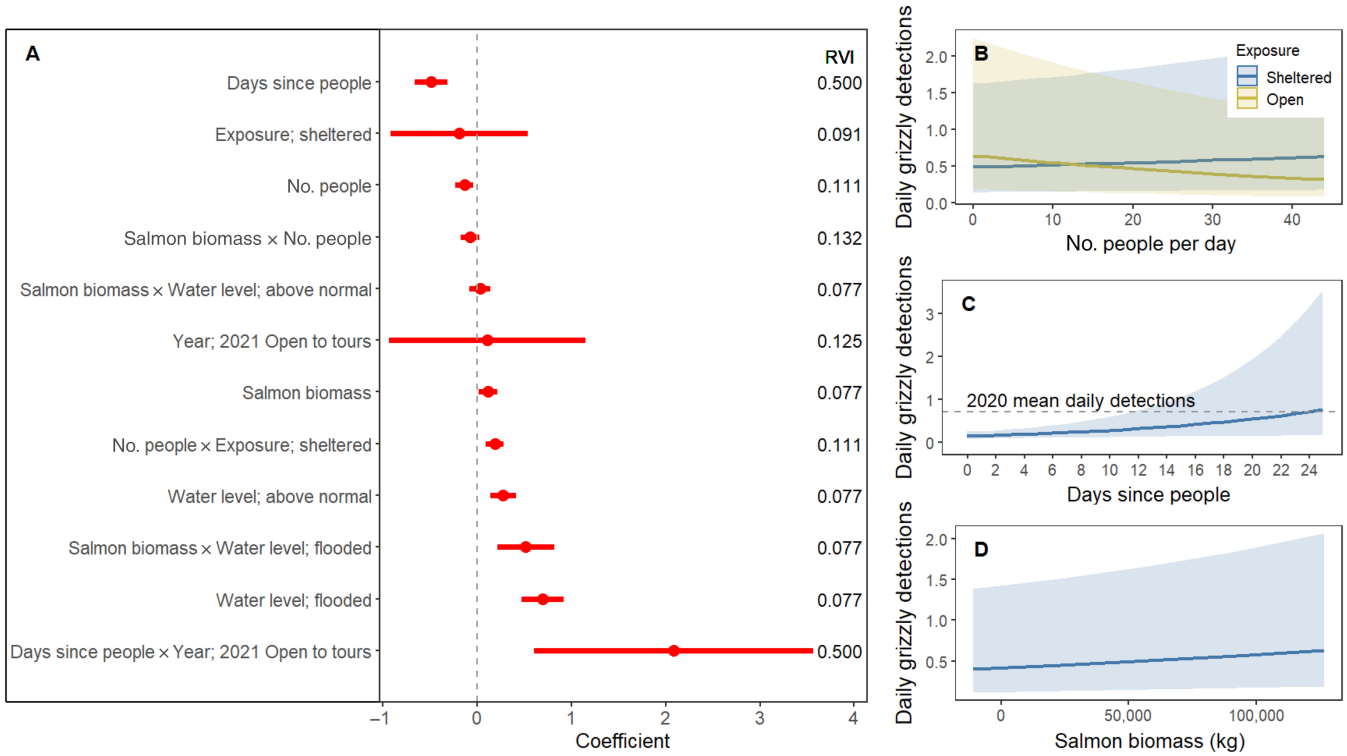

FIGURE 2 Top detection rate model: (A) parameter coefficients, centered and scaled by two SDs (Gelman, 2008), and CIs for fixed effects. Red dots represent magnitude of effect on detection rate, and red lines span 95% CI. RVI shown for each fixed effect; (B) site-level daily detection rate at sheltered and open sites as a function of the number of people per day. Shaded regions represent 95% CI for model estimates, and curves represent model predictions; (C) site-level daily detection rate as a function of days since people in 2021. Blue shaded region represents the 95% CI for model predicted detection rate, and the curve shows the model predicted values. The gray dotted line represents the 2020 (non-ecotourism) mean detection rate. The CI overlaps the 2020 mean at 12 days, and 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.

level, although there is considerable uncertainty around this estimate (Figure 2C). Finer-scale spatial variation of ecotourism activity (north–south closures, distance to tours) did not appear in top models.

Variation in salmon biomass had a more modest effect on bear detections. Days since people and its interaction with year (i.e., days since people in 2021) had the greatest influence (RVI = 0.5; Figure 2) and was ~7 times as important as salmon biomass (RVI = 0.07) or the interaction between salmon biomass and water (RVI = 0.07). However, salmon biomass, water level, and their interaction had positive associations with daily bear detection rate (Figure 2D and Table 2). For each increase in salmon biomass of 10,000 kg (mean = 57,777 kg; SD = 34,431 kg; Table 2), we observed an ~3.4% (CI: 0.3%–6.5%) increase in the bear detection rate. An interaction term indicated that when the water level was flooded, salmon biomass also had a positive effect (Figure 2A; Table 2). Flooding alone also had a positive influence on detection rate, as bears likely used the onshore trails more frequently when they could not travel along the river.

Age and sex class models

Age–sex classes of grizzly bears responded differently to ecotourism activity. In the detection rate models for adult males and females with young, number of people had a negative influence on adult male detection rate, but no influence on detection rates of females with young (Figure 3). In the multinomial model, detected bears were more likely to be adult females, females with young, or subadults, compared with adult males, on days with more people (Figure 4A). When people were closer to camera traps, detections were more likely to be adult females and females with young than adult males (Figure 4A,D, Appendix S2: Table S9). Although we did not find effects of days since people or year individually, an interaction term in the 95% model set indicated that as days since people in 2021 increased, the likelihood that a detection was an adult male increased, but the likelihood of detections being other age–sex classes did not change (Appendix S2: Table S9).

Salmon availability also influenced age–sex classes differently. As salmon biomass increased, detections were more likely to be adult females, females with young, or

subadults than adult males (Figure 4A). When salmon were low, the number of people had little influence on the likelihood that a detection was an adult male, but when biomass was moderate to high, increasing numbers of people were associated with a lower likelihood that a detection was an adult male (Figure 4B). Specifically, the likelihood that a detection was male (on days with mean salmon levels) decreased significantly (beyond 2 SDs of days with 0 people) when six or more people were in Khutze. The interaction had an opposite influence on females with young. We observed a positive association between number of people and the likelihood a detection was a family group, but only when salmon biomass was moderate or high (Figure 4C).

RVI additionally showed how ecotourism related to environmental covariates for age–sex class in the multinomial model. 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 alone. Distance to people (RVI = 0.076) was next most important, at approximately twice as important as salmon in predicting age–sex class.

TABLE 2 Influence of ecotourism metrics on bear detections and possible management levers.

Variable	Influence on detection rate	Possible management levers
Days since people	9.2% (95% CI: 2.6%–16.2%) increase in detections for each day closure	Implement multiday closures, such as three consecutive days per week (25 days were required for activity levels to approximate those without human activity)
North/south closures	No influence	Forgo north/south closures in favor of full watershed closures (see above)
Number of people per day	1.6% (95% CI: 0.4%–2.7%) decrease in detections for each additional person	Limit tour group sizes. A limit of six people per day required to avoid influencing age–sex class composition
Number of tours	11.6% (95% CI: 2.7%–19.6%) decrease in detections for each additional tour	Limit viewing to one tour per day
Number of hours with tours	5.3% (95% CI 0.6%–9.7%) decrease in detection rate for each additional hour with people in Khutze	Limit viewing time on any given day, for example, viewing permitted only in the morning

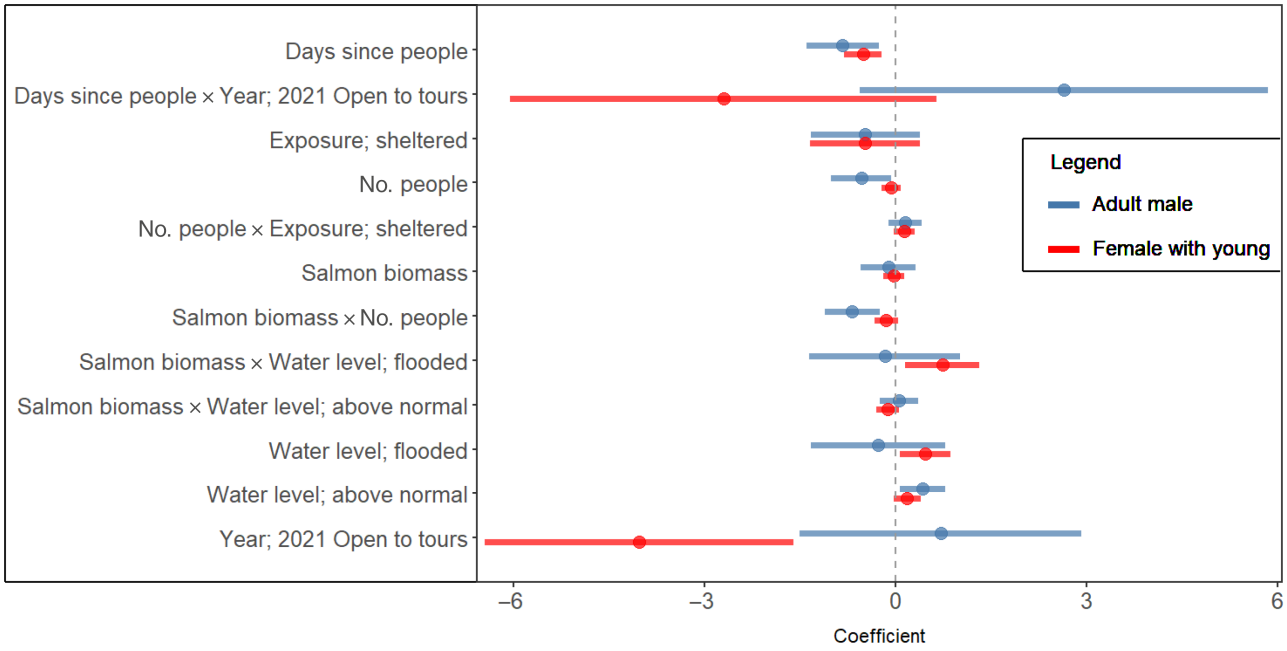

FIGURE 3 Detection rate model for female with young and adult male subsets of detections. For both subsets, the plot shows parameter coefficients, centered and scaled by two SDs (Gelman, 2008), and CIs for fixed effects for detection rates. Dots represent parameter coefficients and lines span 95% CIs.

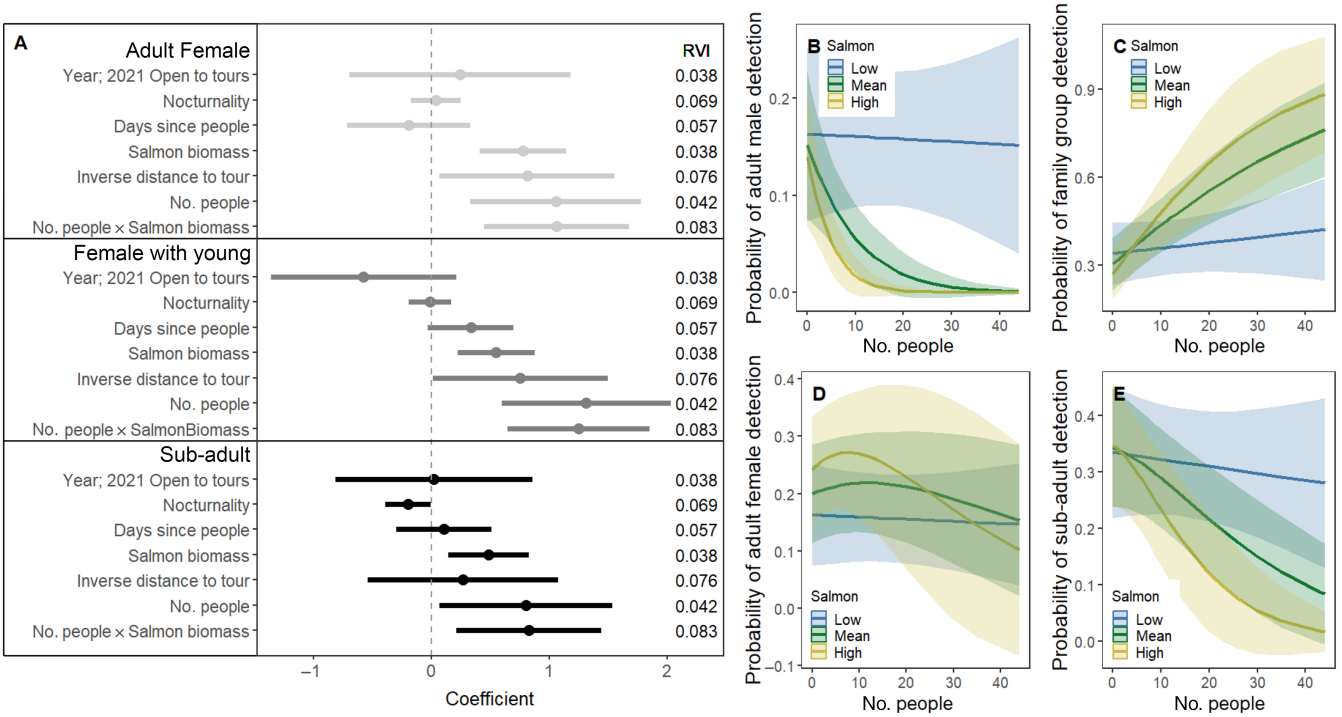

FIGURE 4 Age and sex class top multinomial model. (A) Parameter coefficients and CIs for fixed effects. Dots represent parameter coefficients and lines span 95% CIs. Relative variable importance shown for all fixed effects; (B) likelihood of a detection being adult male as a function of number of people per day and salmon biomass. Salmon levels are the mean and one SD above and below. When salmon biomass is at its mean or above, number of people has a negative influence on the probability a detection is male; (C) likelihood of a detection being a female with young as a function of number of people per day and salmon biomass. When salmon biomass is at its mean or above, number of people has a positive influence on the probability a detection is a family group; (D) likelihood of a detection being adult female as a function of number of people per day and salmon biomass; (E) likelihood of a detection being a subadult as a function of number of people per day and salmon biomass. Shaded regions represent 95% CIs for model predictions, represented by the curve.

Activity pattern analysis

We did not detect any shifts in temporal activity in response to human presence. This was the case for all bears at any distance and for all age–sex classes (Appendix S2: Figure S11).

DISCUSSION

Our results revealed complex relationships among grizzly bear activity, ecotourism, and salmon availability. In alignment with the ecology of fear, we found that grizzly bear activity in Khutze was influenced by intensity of risk cues (amount of people), habitat structure (sheltered vs. exposed sites), and foraging trade-offs (salmon availability). We found multiple lines of support for our hypothesis that overall bear activity decreased in space and time with ecotourism. With greater numbers of people visiting Khutze, grizzly bear detections across the watershed decreased. Additionally, with greater numbers of people, detections increased at sheltered sites and decreased at open sites, indicating both large- and fine-scale spatial shifts toward more secluded habitat. We did not, however, detect an effect of alternating north/south closures, suggesting that this fine-scale management approach may not be sufficient to offset the effects of ecotourism on bear behavior. This may be related to the acute aural and olfactory sensitivity of bears; they can likely often detect human activity (signaled by human scent, outboard engine noise) across the open estuary, deeming a partial closure insufficient to eliminate the perception of risk. We also detected a strong temporal lag in terms of time required for bear behavior to return to baseline following exposure to humans; in 2021, detection rates were higher as the days since people were present increased, indicating that bears shifted their spatial activity from human activity and returned on a gradual schedule. This suggests that bears responded on extended time scales beyond tour lengths.

We also found support for our hypothesis that adult males were more strongly influenced by ecotourism than other age–sex classes. It was least likely for a detection to be male during ecotours and, specifically, when there

was moderate or high salmon levels. Salmon continue upstream of the camera array for ~6 km, which likely offers alternate fishing opportunities without the perceived risks of humans. It is not fully understood why adult males are most strongly influenced by perceived risk. Unlike other age–sex classes, which may experience benefits such as a potential decrease in infanticide from being near humans, adult males have no clear benefit of remaining near people when alternate habitat is available. Also, a recently closed trophy hunt that targeted larger males (Darimont et al., 2017) might have shaped behavioral responses to human cues by this sex. When salmon levels were low, males may have been more likely to remain in areas exposed to ecotourism because presumably similarly low levels of salmon elsewhere might not meet their extensive requirements for meat-based protein (Robbins et al., 2004). Indeed, when resources are concentrated or low, animals may incur costs of exposing themselves to risk to access limited food (Gaynor et al., 2019; Schmidt & Kuijper, 2015; Smith et al., 2019). This finding is consistent with our hypothesis that avoiding risk from humans is traded off against access to foraging opportunities and that this trade-off is diminished when salmon abundance is high.

We did not find substantial support for the human shield hypothesis, despite observing an increase in the likelihood a detection was a female with young with increasing numbers of people (when salmon levels were moderate to high). Given that the detection rates for females with young remained unchanged across variation in ecotourism, this might simply suggest that females with young may be the component of the population least influenced by ecotourism. Insight from the multinomial model suggests that the increase in the likelihood of a detection being a female with young may not signal an increase in activity by this age–sex class (i.e., human shield effect) but simply a decrease in activity of other age–sex classes. Additional research would be needed to determine whether the displacement of adult males may allow females with young in our study system greater access to fishing areas without risk of infanticide as observed elsewhere (Nevin & Gilbert, 2005).

Finally, our results did not support the hypothesis that adult males would become more nocturnally active in response to ecotourism. This result differs from Knight Inlet, British Columbia (BC), where males and females with young differentially partitioned their temporal activity in relation to ecotourism (Nevin & Gilbert, 2005). Instead, we found that the displacement of all bears primarily occurred on a multiday scale, as indicated by the days since people variable, which might relate to the scale of predictability of human activity. In Khutze, daily temporal patterns of ecotourism were varied, with tours running anytime between 7 a.m. and 10 p.m. (Appendix S2: Figure S12). Spatially, however, the tours were confined to waterways within the ~5-km^2 camera array and two discrete interpretive sites. In contrast, Knight Inlet tours were constrained to specific hours at a static viewing site (Nevin & Gilbert, 2005). Accordingly, the watershed-level spatial patterns of ecotourism (~5 km^2 of ~340 km^2) in Khutze may be more predictable than 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. Such unpredictable temporal patterns of ecotourism may result in broader scale spatial avoidance (Penteriani et al., 2017), as we observed. Within the ~5-km^2 ecotourism zone, however, both spatial and temporal patterns of ecotourism are relatively unpredictable, which may induce a more reactive response to human presence on a smaller scale.

How the local-scale spatiotemporal patterns in avoidance scale up to seasonal access to salmon and population dynamics is unknown. Although ecotourism explained a modest proportion of variation in the detection rate models, the patterns can inform efforts to minimize influences on bears during this energetically important season in which small changes in activity might carry significant costs in food acquisition. Energetic costs of displacement from foraging are particularly acute when access to food is limited in space or time (Schmidt & Kuijper, 2015), such as bear viewing at important fishing sites during hyperphagia. In coastal BC, hormonal data suggested increased levels of nutritional and social stress associated with lower salmon consumption (Bryan et al., 2013). Additionally, across ecosystems, salmon consumption is positively related to body mass, mean litter size, and reproductive success (Hilderbrand et al., 1999). However, if humans provide females with young a shield from infanticidal males, ecotourism may provide benefits to the population through greater cub survival.

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. Given the lower bear activity up to 25 days after ecotours, multiweek closures would be required if management objectives were to return detection rates to nonecotourism levels. Although our model may underestimate higher detection rates (Appendix S2: Figure S2), and thus may overestimate recovery time, managers might adopt a precautionary approach under such uncertainty. As indicated by the high RVI and large effect size of our "days since people" metric, a multiweek closure might be the most effective intervention to manage for periods of bear activity levels that approximate those without human presence and provide the greatest opportunity to bears to access salmon without the

perceived risks of humans. However, our results show that closures on smaller temporal scales may also lessen the effects of human presence. For example, for each day of closure our model suggests an ~9.2% increase in bear detections. Another evidence-based management option is to limit tours to consistent hours (Appendix S1: Table S2). This may allow bears to develop a schedule of temporal avoidance (Palmer et al., 2022) to access resource-rich habitat during times without tours, which was not possible under the current context of unpredictable tour times. Another tool is to limit the number of people each day. When there were mean salmon levels, more than six people per day was associated with a decreased likelihood that a detection was an adult male. If the goal is to maintain bear activity across age–sex classes at a nonecotourism level, trips could remain below six people per day. Finally, flexible management may also be important and be connected to salmon returns. For example, given that male bears do not avoid ecotour areas when salmon are low, managers might implement an early season closure of ecotourism in years with low salmon returns. Management considerations from this work are also system-specific, as bear viewing in BC varies across multiple dimensions: the tolerance of individual bears, human behavior, and management objectives. As predicted by ecology of fear theory, we found that avoidance of people by bears depended on the habitat structure (i.e., sheltered vs. exposed sites), the intensity of risk cues (i.e., number of people), as well as forage trade-offs, in the form of salmon availability. This avoidance lasted for multiple days after the risk was removed, showing a prolonged recovery time for bears once the human disturbance was removed from the landscape.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Short, 2024a) are available in Dryad at https://doi.org/10.5061/dryad.brv15dvcq. Code (Short, 2024b) is available in Zenodo at https://doi.org/10.5281/zenodo.7995511.

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REFERENCES

Agostinelli, C., and U. Lund. 2017. "R Package 'Circular': Circular Statistics." R Package Version 0.4-93. https://CRAN.R-project.org/package=circular.

Berger, J. 2007. "Fear, Human Shields and the Redistribution of Prey and Predators in Protected Areas." *Biology Letters* 3(6): 620–23.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. "GlmmTMB Balances Speed and Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *The R Journal* 9(2): 378–400.

Brown, J. S., J. W. Laundré, and M. Gurung. 1999. "The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions." *Journal of Mammalogy* 80(2): 385–399.

Bryan, H. M., C. T. Darimont, P. C. Paquet, K. E. Wynne-Edwards, and J. E. G. Smits. 2013. "Stress and Reproductive Hormones in Grizzly Bears Reflect Nutritional Benefits and Social Consequences of a Salmon Foraging Niche." *PLoS One* 8(11): e80537.

Bryan, H. M., C. T. Darimont, P. C. Paquet, K. E. Wynne-Edwards, and J. E. G. Smits. 2014. "Stress and Reproductive Hormones Reflect Inter-Specific Social and Nutritional Conditions Mediated by Resource Availability in a Bear–Salmon System." *Conservation Physiology* 2: cou010.

Darimont, C. T., K. A. Artelle, F. Moola, and P. Paquet. 2017. "Trophy Hunting: Science on its Own Can't Dictate Policy." *Nature* 551: 565.

Darimont, C. T., C. H. Fox, H. M. Bryan, and T. E. Reimchen. 2015. "The Unique Ecology of Human Predators." *Science* 349(6250): 858–860.

Elmeligi, S., and J. Shultis. 2015. "Impacts of Boat-Based Wildlife Viewing in the K'tzim-a-Deen Inlet on Grizzly Bear (*Ursus arctos*) Behavior." *Natural Areas Journal* 35(3): 404–415.

Frey, S., J. T. Fisher, A. C. Burton, and J. P. Volpe. 2017. "Investigating Animal Activity Patterns and Temporal Niche Partitioning Using Camera-Trap Data: Challenges and Opportunities." *Remote Sensing in Ecology and Conservation* 3(3): 123–132.

Gaynor, K. M., J. S. Brown, A. D. Middleton, M. E. Power, and J. S. Brashares. 2019. "Landscapes of Fear: Spatial Patterns of Risk Perception and Response." *Trends in Ecology & Evolution* 34(4): 355–368.

Gaynor, K. M., M. J. Cherry, S. L. Gilbert, M. T. Kohl, C. L. Larson, T. M. Newsome, L. R. Prugh, J. P. Suraci, J. K. Young, and J. A. Smith. 2020. "An Applied Ecology of Fear Framework: Linking Theory to Conservation Practice." *Animal Conservation* 24(3): 308–321.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. "The Influence of Human Disturbance on Wildlife Nocturnality." *Science* 360(6394): 1232–35.

Gelman, A. 2008. "Scaling Regression Inputs by Dividing by Two Standard Deviations." *Statistics in Medicine* 27(15): 2865–73. https://doi.org/10.1002/sim.3107.

Groot, C., and L. Margolis. 1991. *Pacific Salmon Life Histories*. Vancouver: University of British Columbia Press.

Hartig, F. 2022. "DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models." R Package Version. https://CRAN.R-project.org/package=DHARMa.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur, and C. Servheen. 1999. "The Importance of Meat, Particularly Salmon, to Body Size, Population Productivity, and Conservation of North American Brown Bears." *Canadian Journal of Zoology* 77(1): 132–38.

Jacobs, M. J., and C. A. Schloeder. 1992. "Managing Brown Bears and Wilderness Recreation on the Kenai Peninsula, Alaska, USA." *Environmental Management* 16(2): 249–254.

Kittle, A. M., J. M. Fryxell, G. E. Desy, and J. Hamr. 2008. "The Scale-Dependent Impact of Wolf Predation Risk on Resource Selection by Three Sympatric Ungulates." *Oecologia* 157(1): 163–175.

Lima, S. L., and L. M. Dill. 1990. "Behavioral Decisions Made under the Risk of Predation: A Review and Prospectus." *Canadian Journal of Zoology* 68(4): 619–640.

Naidoo, R., and C. A. Burton. 2020. "Relative Effects of Recreational Activities on a Temperate Terrestrial Wildlife Assemblage." *Conservation Science and Practice* 2(10): e271.

Nevin, O. T., and B. K. Gilbert. 2005. "Perceived Risk, Displacement and Refuging in Brown Bears: Positive Impacts of Ecotourism?" *Biological Conservation* 121(4): 611–622.

Ordiz, A., O.-G. Støen, S. Sæbø, V. Sahlén, B. E. Pedersen, J. Kindberg, and J. E. Swenson. 2013. "Lasting Behavioural Responses of Brown Bears to Experimental Encounters with Humans." *Journal of Applied Ecology* 50(2): 306–314.

Palmer, M. S., K. M. Gaynor, J. A. Becker, J. O. Abraham, M. A. Mumma, and R. M. Pringle. 2022. "Dynamic Landscapes of Fear: Understanding Spatiotemporal Risk." *Trends in Ecology & Evolution* 37: 911–925.

Penteriani, V., J. V. López-Bao, C. Bettega, F. Dalerum, M. del Mar Delgado, K. Jerina, I. Kojola, M. Krofel, and A. Ordiz. 2017. "Consequences of Brown Bear Viewing Tourism: A Review." *Biological Conservation* 206(2): 169–180.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ridout, M. S., and M. Linkie. 2009. "Estimating Overlap of Daily Activity Patterns from Camera Trap Data." *Journal of Agricultural, Biological, and Environmental Statistics* 14(3): 322–337.

Ripple, W. J., and B. Van Valkenburgh. 2010. "Linking Top-Down Forces to the Pleistocene Megafaunal Extinctions." *Bioscience* 60(7): 516–526.

Robbins, C. T., C. C. Schwartz, and L. A. Felicetti. 2004. "Nutritional Ecology of Ursids: A Review of Newer Methods and Management Implications." *Ursus* 15(2): 161–171.

Ruiz-Mar, M. G., G. Heckel, E. Solana-Arellano, Y. Schramm, M. C. García-Aguilar, and M. C. Arteaga. 2022. "Human Activities Disturb Haul out and Nursing Behavior of Pacific Harbor Seals at Punta Banda Estuary, Mexico." *PLoS One* 17(7): e0270129.

Rutz, C., M.-C. Loretto, A. E. Bates, S. C. Davidson, C. M. Duarte, W. Jetz, M. Johnson, et al. 2020. "COVID-19 Lockdown Allows Researchers to Quantify the Effects of Human Activity on Wildlife." *Nature Ecology & Evolution* 4(9): 1156–59.

Schmidt, K., and D. P. J. Kuijper. 2015. "A 'Death Trap' in the Landscape of Fear." *Mammal Research* 60(4): 275–284.

Short, M. 2024a. "Data from: Ecology of Fear Alters Behaviour of Grizzly Bears Exposed to Bear-Viewing Ecotourism." Dryad, Dataset. https://doi.org/10.5061/dryad.brv15dvcq.

Short, M. 2024b. "Data from: Ecology of Fear Alters Behaviour of Grizzly Bears Exposed to Bear-Viewing Ecotourism." Zenodo, Software. https://doi.org/10.5281/zenodo.7995511.

Smith, J. A., E. Donadio, J. N. Pauli, M. J. Sheriff, O. R. Bidder, and A. D. Middleton. 2019. "Habitat Complexity Mediates the Predator–Prey Space Race." *Ecology* 100(7). https://doi.org/10.1002/ecy.2724.

Spitz, D. B., M. M. Rowland, D. A. Clark, M. J. Wisdom, J. B. Smith, C. L. Brown, and T. Levi. 2019. "Behavioral Changes and Nutritional Consequences to Elk (*Cervus canadensis*) Avoiding Perceived Risk from Human Hunters." *Ecosphere* 10(9): e02864.

Steyaert, S. M. J. G., M. Leclerc, F. Pelletier, J. Kindberg, S. Brunberg, J. E. Swenson, and A. Zedrosser. 2016. "Human Shields Mediate Sexual Conflict in a Top Predator." *Proceedings of the Royal Society B: Biological Sciences* 283(1833): 20160906.

Stillfried, M., J. L. Belant, N. J. Svoboda, D. E. Beyer, and S. Kramer-Schadt. 2015. "When Top Predators Become Prey: Black Bears Alter Movement Behaviour in Response to Hunting Pressure." *Behavioural Processes* 120(11): 30–39.

Suraci, J. P., M. Clinchy, L. Y. Zanette, and C. C. Wilmers. 2019. "Fear of Humans as Apex Predators Has Landscape-Scale Impacts from Mountain Lions to Mice." *Ecology Letters* 22(10): 1578–86.

Suraci, J. P., B. A. Nickel, and C. C. Wilmers. 2020. "Fine-Scale Movement Decisions by a Large Carnivore Inform Conservation Planning in Human-Dominated Landscapes." *Landscape Ecology* 35(7): 1635–49.

Symonds, M. R. E., and A. Moussalli. 2011. "A Brief Guide to Model Selection, Multimodel Inference and Model Averaging in Behavioural Ecology Using Akaike's Information Criterion." *Behavioral Ecology and Sociobiology* 65(1): 13–21.

Zanette, L. Y., and M. Clinchy. 2019. "Ecology of Fear." *Current Biology* 29(9): R309–R313.

SUPPORTING INFORMATION

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

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