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

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Abstract

Ecotourism management can draw on theory and data related to non-consumptive effects of risk on wildlife. The asset protection principle (APP) predicts that variable food supply and its associated risks will affect antipredator behavior; responses to predation risk should dominate when food reserves are high, while nutritional risk becomes more important when food reserves are limited. Additionally, the human shield hypothesis (HSH) describes how some individuals might seek human presence if it repels potential sources of risk. Using camera traps, we used generalized linear mixed effects and multinomial regression models to test components of the APP and HSH where ecotourism co-occurs with grizzly bear (*Ursus arctos*) foraging during hyperphagia. When salmon abundance was high (+1 SD), bear activity (weekly detections) decreased by 13% with every 100 visitors/week. Under low salmon conditions, bear activity increased with visitor numbers, creating 'high bear-high visitor' conditions. Consistent with HSH, detection data revealed an increased likelihood of detecting subordinate age-sex classes compared with adult males when visitor numbers were high. Our findings suggest that when salmon are low, managers might consider limiting visitors to mitigate disturbance. More broadly, understanding how wildlife allocate antipredator behavior as a function of risk and food can inform conservation science and practice.

KEYWORDS

asset protection principle, behavior, camera traps, evidence-based management, human shield hypothesis

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1 | INTRODUCTION

Research approaches that incorporate animal behavior (Berger-Tal et al., 2011; Blumstein & Fernández-Juricic, 2004) can lead to a better understanding of non-consumptive human–wildlife interactions that can support evidence-based management. Wildlife ecotourism—an industry built on purpose-driven human–wildlife encounters—continues to grow rapidly as demand by ecotourists increases (Balmford et al., 2015; Tapper, 2006). Evidence for social merits of wildlife ecotourism is clear. Whereas the effects on species targeted for ecotourism vary (Penteriani et al., 2017), behavioral data can inform policy that seeks to reduce and minimize potential impacts. For example, ecotourism policies informed by behavioral research reduced rhinoceros (*Diceros bicornis*) displacement by 80% while maintaining 95% positive feedback from guests (Muntifering et al., 2019). Such evidence-informed outcomes rely in part upon a relevant theoretical background and data. Here we draw on a body of theory that identifies how wildlife can respond to human-caused disturbance in a similar way to how prey respond to predation risk.

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

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

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

Finally, how prey balance asset protection and risk exposure trade-offs may also vary with characteristics of predators. For example, the ‘dynamic landscape of fear’ body of theory suggests that the predictability of predator activity in space, time, or both will influence the dynamics of prey responses (Palmer et al., 2022). If predation is predictable in space and time, the allocation of anti-predator response can be matched accordingly, thereby minimizing risk effects on prey. For example, the sensitivity of Yellowstone elk (*Cervus elaphus*) to spatially and temporally predictable risk from wolves (*Canis lupus*) resulted in negligible net effects on body condition and pregnancy rates (Kohl et al., 2018). On the other hand, such behavioral responses can bear costs with enduring effects, including reduced foraging time and neurobiological effects (Brown & Kotler, 2004; Zanette & Clinchy, 2020), which can exert non-consumptive effects on prey survival. As another example, although humans clearly induce antipredator responses (Frid & Dill, 2002), their generally diurnal activity patterns and fidelity to their own built environments might be particularly predictable in time and space compared with other risks. Prey, however, evidently respond to such human-associated risk. Recent meta-analyses have revealed how wildlife have shifted temporal patterns to avoid largely diurnal activity of humans (Gaynor et al., 2019) as well as spatial patterns to avoid human features of the landscape in which human activity is concentrated (Tucker et al., 2018).

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

Here we test hypotheses related to the APP and HSH in a system comprising grizzly bear–ecotourism interactions along the Atnarko River in the unceded territory of the Nuxalk First Nation. Insight regarding ecotourism-associated effects on individual- and population-level fitness in other systems vary from positive to negative (Penteriani et al., 2017). For example, bears constrained to foraging opportunities close to viewing sites may increase vigilance behavior and divert time away from fitness-enhancing behaviors. Nevin and Gilbert (2005), however, suggested positive population-level effects of viewing, whereby temporal avoidance of human activity by males created a temporal refuge for subordinate age/sex classes that might have increased their survival. Wildlife ecotourism on the Atnarko River co-occurs with grizzly bear pre-denning, and provides a system in which non-lethal human stimuli occurs in predictable ways over space and time. Each year, wildlife ecotourism occurs in the same places and weeks, with varied numbers of humans and methods for viewing (see Section 2), providing a relatively predictable pattern of human activity for bears, especially pronounced in certain times (daylight, during peak visitor periods) and places (ecotourism sites). The Atnarko River provides bears access to aggregations of spawning salmon (*Oncorhynchus* spp.) during hyperphagia—a critical period to amass large amounts of energy before denning. Foraging is directly and strongly related to reproductive asset enhancement; pre-denning fat reserves from salmon and other meats are positively correlated with over-winter survival and reproduction in the following year (Hilderbrand et al., 2000). Grizzly bears with access to salmon have higher population density, body size, and litter size (Hilderbrand et al., 1999). Accordingly, salmon acquisition strongly links to reproductive asset in the context of APP.

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

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

2 | METHODS

2.1 | Study area

The study occurred in the Atnarko River corridor (herein ‘Atnarko’; Figure 1). Located on what is now gazetted by colonial settlers as the central coast of British Columbia, Canada, in Tweedsmuir Provincial Park (9896 km^2), the Atnarko spans the transition between Coastal Western Hemlock and Interior Douglas Fir biogeoclimatic zones. Grizzly bears congregate each summer and fall (~July–November) on the Atnarko and its tributaries to forage on spawning salmon. Resident spawning salmon species include Chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), sockeye (*O. nerka*), and pink (*O. gorbuscha*).

Human presence and activities in the corridor vary during the spawning season (Appendix S1; Figures S1 and S2), with most forms having the potential to interact with grizzly bear foraging. Visitors to the Atnarko seek commercial and self-guided recreational activities. Examples include angling, paddling, hiking, camping, swimming, picnicking, and several modes of bear viewing. We defined ‘spatial treatments’ according to where bear viewing occurred: a ‘no tour’ reference area; a ‘land-based tour’ area; and a ‘land- and boat-based tour’ area. These are management-based categories in which specific activities occur or not. Human visitation in the ‘no tour’ area was mostly limited to backcountry hikers and crews monitoring fish and wildlife via a rough 4 × 4-only access road. The ‘land-based tour’ area has some trail access to the river and light but consistent use by professionally-guided ecotours. The ‘land- and boat-based tour’ area hosted ~2 orders of magnitude more visitors than the ‘no tour’ area (average weekly visitors to ‘land- and boat-based tour’ area was 1363 across years, compared with 11 in the ‘no-tour’ area); it contained a privately regulated platform on the grounds of a commercial ecotourism lodge, and two areas where bear viewing is self-pursued by visitors. One site is a purpose-built platform managed by BC Parks and the Nuxalk Nation with an electric fence and a regulated entry and exit system. The second is a BC Parks campground that is actively used by the public for bear viewing, but was neither managed for bear viewing nor formally designated as such at the time of the study. This latter site also includes a recreation and picnic area. Along this ‘land- and boat-based tour’ stretch, up to 11 commercially operated and professionally guided ‘drifts’ (slow-pace rafting-base viewing) were permitted per day between August 15 and October 15. There were currently no limits on the number of boat launches permitted for public recreation (e.g., self-guided boating) at the time of the study.

2.2 | Camera trap sampling design

We used a camera trap array to estimate weekly patterns of bear activity. We defined our study period as August 15 to October 15 over 3 years (2019–2021). We deployed cameras along the riverbank and adjacent forest, aiming them at bear trails near key fishing locations, such as pools, log jams, and where spawning substrate occurs, as well as at fishing locations (i.e., in-stream locations). We positioned Browning Strike Force HD PRO (Model: BTC-5HDP) and Browning Strike Force Extreme (Model: BTC-5HDX) cameras every ~0.5–2 km along the river.

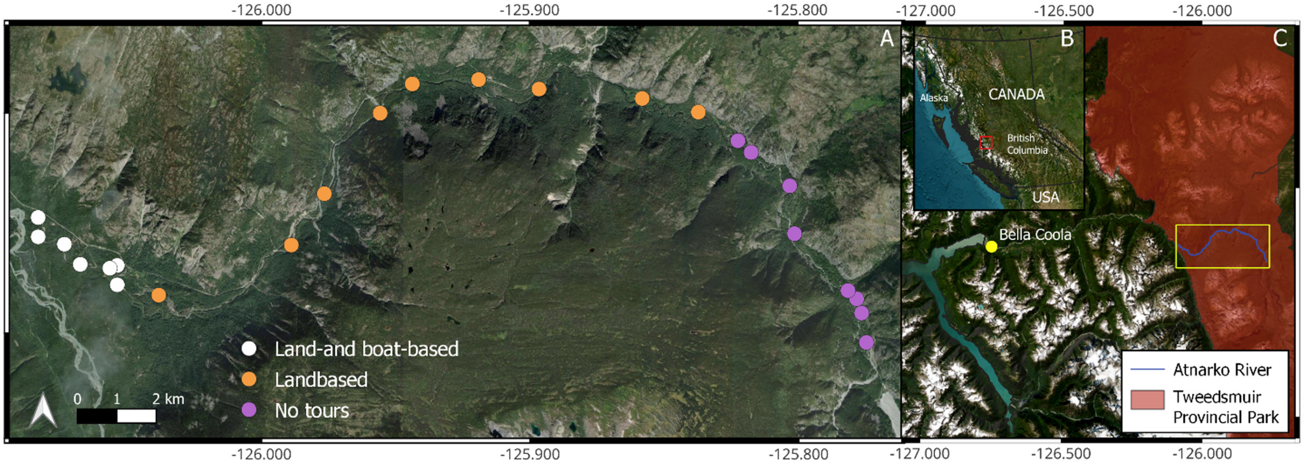

FIGURE 1 Study area: (a) Atnarko River corridor camera trap array by spatial treatment; land- and boat-based tours, land-based tours, and no tours. (b) British Columbia, Canada, with red frame denoting panel (c); (c) Atnarko River and surrounding area, which is located in the unceded Territory of Nuxalk First Nation, with yellow frame denoting panel (a).

We set cameras to record two-minute videos when motion-activated, with cameras operating 24 h a day (see camera trap settings in Appendix S2; Table S1). We checked cameras and downloaded images weekly or bi-weekly, depending on site activity (Wheat & Wilmers, 2016). Cameras were affixed to trees at approximately 1–1.5 m height to maximize detection probability of grizzly bears (Meek et al., 2016), with expected area of bear passage within 20 m.

The camera array consisted of 21, 24, and 24 camera stations in 2019, 2020, and 2021, respectively (Appendix S2, Table S2). Most camera-weeks collected data on all 7 days (85%, $n = 573$ out of 673; Appendix S1, Figure S3), however, some cameras experienced periods of inactivity because of malfunctions and theft. Cameras were active for seven days for more than 80% of camera weeks for each spatial treatment area (Appendix S1; Figures S4, S5, and S6). The lead author and research assistants manually scored all video footage initially before data exploration. We determined sex by observing genitals, whether urine was excreted from between the legs (males) or from below the tail (females), or whether it was a family unit (female with young). Subadults were differentiated from adults via relative size and behavior (Rode et al., 2006). We omitted unknown bear species ($n = 29$ of 2035 total bear detections; 1.4%) from the analysis (e.g., if it was too dark to determine if the detection was a grizzly bear or a black bear, which are much less common in the area during the salmon runs). Research was approved by University of Victoria's Human Research Ethics (19-0036-02) and Animal Care Committees (2019-004).

2.3 | Analyses—general approach

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

2.3.1 | Weekly detection models

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

We used a priori hypotheses to construct a suite of candidate models (Appendix S2; Table S3) and ran generalized linear mixed models using lme4 in R (Bates et al., 2015; R Core Team, 2023) using a Poisson distribution, including site and year as random effects. We centered all predictors and scaled (divided by 2 SDs), backtransforming to raw data in figures, so as to most clearly inform managers of patterns. Given management interest in the potential influence of human activity (metrics of which vary in space and time with ecotourism), we developed candidate model sets that incorporated human and environmental metrics. We included salmon biomass in each model, reasoning that detections will always be influenced by salmon abundance, as related to risk-foraging trade-offs. In some models, we included interaction terms between water level and salmon biomass (because if there is a flood event, we would expect decreased accessibility of salmon to bears) (Quinn et al., 2017). We also included phenological status of fruit-bearing shrubs in some models, given potential attenuation of grizzly bear–salmon interactions when berries are available (i.e., bears may depart salmon-spawning streams to forage on berries on nearby hillsides) (Deacy et al., 2017). In other models, we included visitors and/or spatial treatment, reasoning that one or both of these measures of human influence may affect detections, as related to risk perception. Finally, we included interaction terms between salmon biomass and human influence metrics in some models, reasoning that bears with lower energy reserves will accept greater risk, as predicted by APP. We compared each model set against null and environmental-only models.

2.3.2 | Age-sex class models

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

2.3.3 | Model selection and multimodel inference

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

2.4 | Explanatory variables

2.4.1 | Salmon biomass

We estimated salmon biomass as an index for salmon availability to bears along four river segments during each week of the study. The river segments were defined by whether salmon counts occurred, as dictated by boat-launch accessibility. Salmon biomass estimates for each of the four segments were attributed to each camera site according to the river segment in which it occurred (Appendix S3). We quantified salmon biomass by conducting weekly counts from a non-motorized raft and by drawing from the New Salmon Escapement Database System (NuSEDS; Pacific Region's central database, maintained by Fisheries and Oceans Canada, which stores individual spawner survey data records and spawner abundance estimates). Counts were converted to biomass estimates for each salmon species and sex, assuming a 1:1 sex ratio (Bryan et al., 2014). We included Chinook, pink, and sockeye in our estimates because those were the only species assessed by Fisheries and Oceans Canada during our study period and constituted most of the salmon biomass during that time. Salmon biomass was calculated by multiplying raw counts (or estimates thereof; below) with average species-specific weights. Biomass values per fish used, in kilograms, were: Chinook: 13.6, Pink, odd years: 2.4, Pink, even years: 1.7, Sockeye: 2.7 (Groot & Margolis, 1991). Given missing count data for some river segments and weeks, we used a spatially and temporally explicit approach to impute within- and across-year salmon biomass availability (e.g., Bryan et al., 2014; Ruggerone et al., 2010; Appendix S3).

2.4.2 | Berry availability

We assessed shrub phenology approximately every 2 weeks to estimate berry availability to bears. We counted the number of berry-producing species (from a pre-determined list of 16 on which the area's bears feed; Himmer & Gallagher, 1995; Appendix S2; Table S5) that had ripe berries in each survey. We used this species count as a coarse proxy for berry availability in the valley. Each survey, repeated every 2 weeks, consisted of 16 plots of approximately 5 m^2, spaced at four elevations (Appendix S1; Figure S7) along a ~1300 m elevational gradient. We assumed that bears were able to access any region of the valley for berries, so we applied the same 2-week estimate for each pair of camera site-weeks over our time series (Appendix S1; Figure S8).

2.4.3 | Visitors

We used two measures of human influence. First, we recognized three distinct zones of the river as ‘spatial treatments’ (Figure 1). We defined treatments according to where commercial bear viewing occurred: a ‘no tour’ reference area; a ‘land-based tour’ area; and a ‘land- and boat-based tour’ area (as described above).

Within these three zones, we also derived an index of human foot traffic (i.e., visitors on land; herein ‘visitors’). Specifically, we sampled index sites using ©TRAFx (https://www.trafx.net/) infrared trail counters and camera traps (Reconyx Hyperfire 2 Model: HP2X Professional) placed at one representative spot within each of the three spatial treatments that British Columbia Parks Rangers and Nuxalk Fisheries and Wildlife crew members, both with extensive knowledge of the study system, considered representative of human activity within each spatial treatment (Appendix S3). Camera traps set to index human foot traffic were set to motion activated videos of 30 s durations (see full settings in Appendix S2; Table S1). People were informed of camera trap research in the park through a public notice on the BC Parks website, communication with bear viewing operators, and research signs. We assumed a consistent level of human activity within each treatment, attributing a given week's estimate to all camera trap sites within the same treatment area where we measured bear activity.

2.4.4 | Water level

We estimated water levels along the Atnarko using hydrometric data obtained from the Government of Canada water office, station "ATNARKO RIVER NEAR MOUTH (08FB006)" (https://wateroffice.ec.gc.ca/report/real_time_e.html?stn=08FB006). We summarized the data by year and week, and used the weekly mean as our unit of measure (Appendix S1; Figure S9).

3 | RESULTS

3.1 | Weekly detection models

We found evidence for associations between human activity and grizzly bear activity. Accounting for all other terms, weekly detections were higher in the land- and boat-based area compared with other areas (Figure 2a). As we predicted, the number of visitors had a negative association with bear weekly detections within any spatial treatment (Figure 2a,b). Holding all other variables at their mean values, an additional 100 visitors/week (i.e., ~7% of mean visitors/week in the land- and boat-

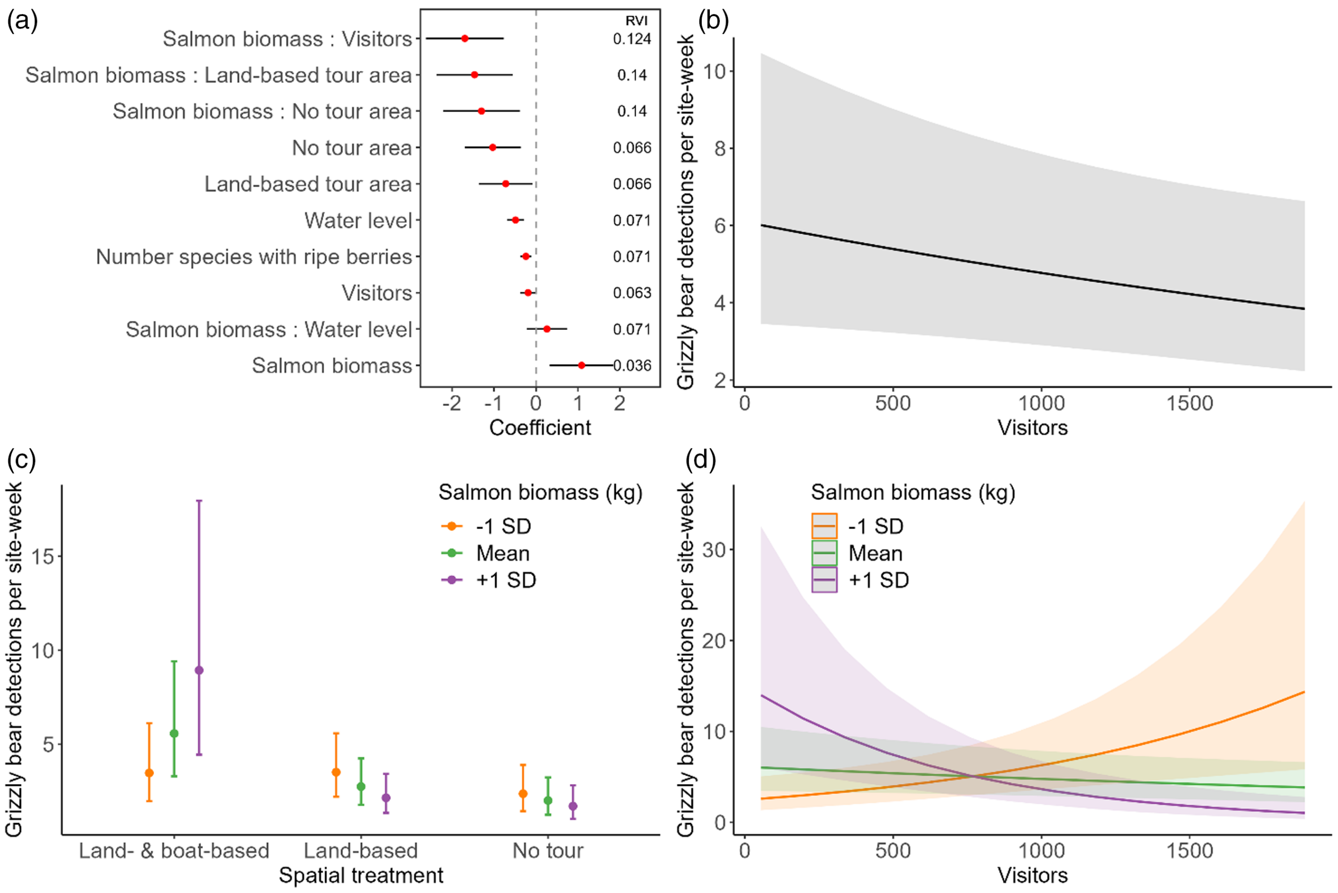

FIGURE 2 Top weekly detection model. (a) Parameter coefficients and CIs for fixed effects, centered and scaled by two standard deviations. Red dots represent parameter coefficients and black lines span 95% CIs. RVI shown for all fixed effects. (b) Weekly detections as a function of the number of visitors;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

based treatment) was associated with a 3% decrease in weekly detections.

The strongest patterns linking human activity to bear activity, however, depended on measures of salmon abundance. An interaction term between spatial treatment and salmon biomass was more than twice as important (RVI = 0.140) as the number of visitors (RVI = 0.063). Contrary to our predictions, when salmon biomass was high (+1 SD), weekly detections were higher in the land- and boat-based treatment; but lower in the other two treatments (Figure 2c). Additionally, an interaction term between visitor numbers and salmon biomass was of similarly high importance (RVI = 0.124), revealing that when salmon abundance was high (+1 SD), weekly detections decreased when more visitors were present, aligning with our predictions. Under this high salmon scenario, weekly detections decreased by 13% with every 100 visitor/week increase (7% of weekly visitor mean [$n = 1363$] in the land- and boat-based treatment). As we predicted, under a low salmon scenario (−1 SD), we observed the opposite pattern: an increase in detections with increased visitors (Figure 2d).

Environmental variables also influenced bear weekly detections. Water level and the number of fruit-bearing plant species with ripe berries were negatively associated with grizzly bear detections (RVI = 0.071; 0.071; Figure 2a), whereas salmon biomass was positively associated with detections (RVI = 0.036). These variables were between ~1.2 and ~2.5 times less important than the human-related variables highlighted above.

We assessed the performance of our top GLMM using both marginal and conditional R^2 values. We obtained marginal R^2 values of 0.197 for our top model, with a corresponding conditional R^2 value of 0.653. We performed a Moran's I test to assess potential spatial autocorrelation in log-transformed residuals. The Moran's I statistic standard deviate was 1.23 ($p = .11$), suggesting no significant spatial autocorrelation in the log-transformed residuals.

3.2 | Age-sex class models

The probability of detections being of certain age-sex classes varied primarily with measures related to human influence, specifically visitor numbers, and diurnality. In line with our predictions, with higher visitor numbers, there was increased likelihood of detections being female with young and sub-adults compared to adult males and females (Figures 3 and 4a). Similarly, with increased diurnality, the likelihood of a detection being all other age-sex classes increased compared with males, which were strongly nocturnal in their detections (Figures 3 and 4b).

Among environmental variables, only berry availability influenced age-sex class detection probabilities. Specifically, compared with males, detections were less likely to be sub-adults when berries were ripe (Figure 3). Salmon biomass did not affect the probability of a detection being a given age-sex class (Figure 3).

4 | DISCUSSION

Our findings revealed varied spatial and temporal relationships among humans, food resources, and grizzly

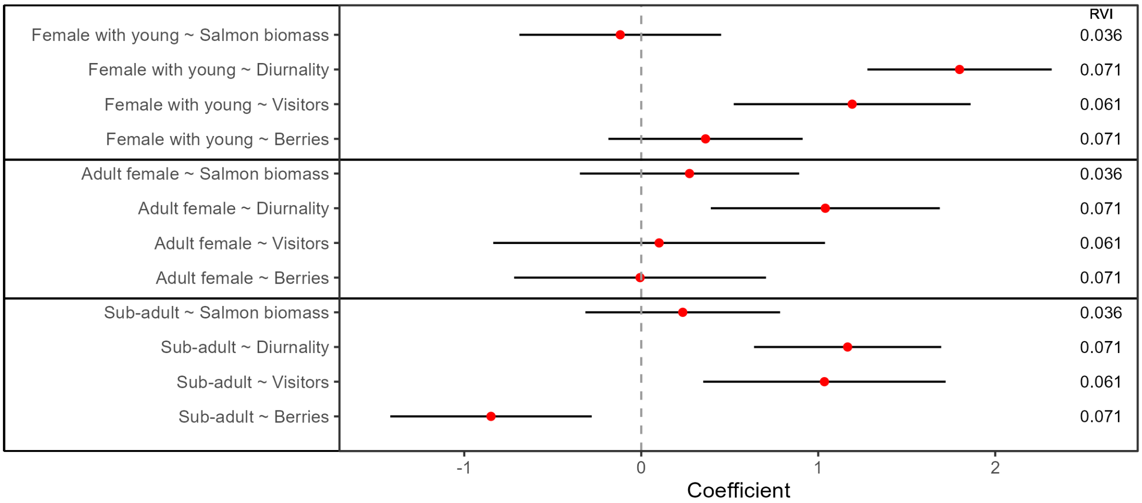

FIGURE 3 Age-sex class top multinomial model. Parameter coefficients and CIs for fixed effects, centered and scaled by two standard deviations. Red dots represent parameter coefficients and black lines span 95% CIs. Atnarko River, Nuxalk Territory, British Columbia (2019–2021).

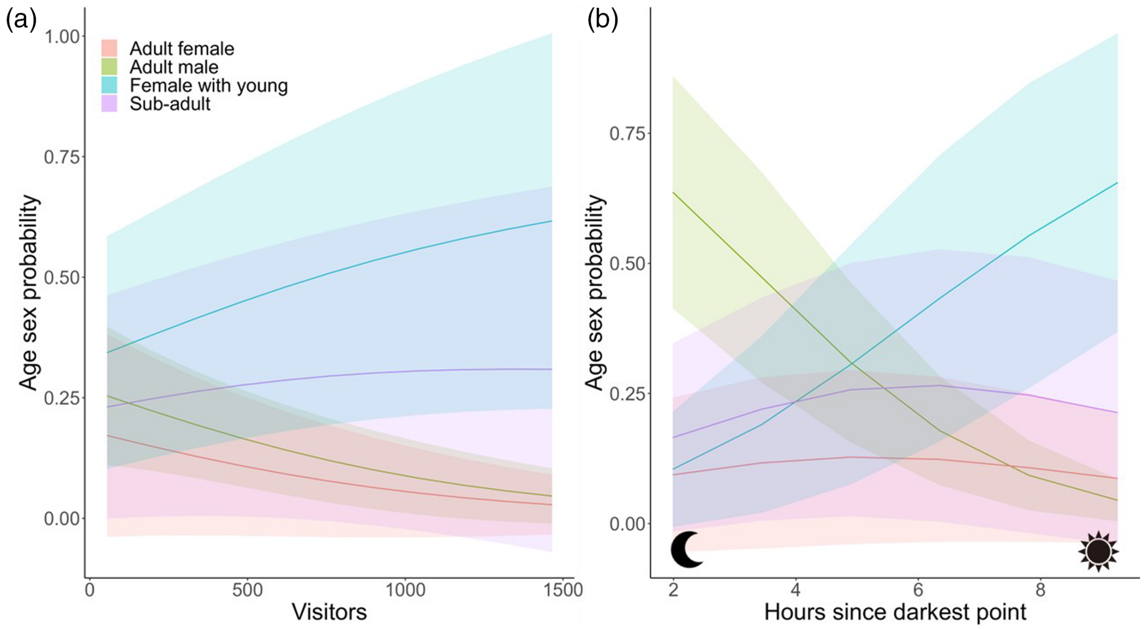

FIGURE 4 Age-sex class top multinomial model. (a) Age-sex probability as a function of number of visitors. (b) Age-sex probability as a function of number hours since the darkest point in the night. Shaded regions represent 95% CIs for model predictions. Atnarko River, Nuxalk Territory, British Columbia (2019–2021).

bear activity. We found several lines of support for the APP and HSHs. Specifically, how bears allocated their spatial–temporal activity varied and interacted across human and environmental contexts, as well as age-sex classes. Generally, bear activity was lower during weeks in which the number of visitors present was higher. Detections during those scenarios were more likely to be females with young and sub-adults. Salmon abundance was especially influential in its interaction with the number of visitors, leading to opposite patterns during periods of low and high salmon. Collectively these patterns of bear activity align with, and can be explained in the context of, risk perception.

The ways weekly detections varied with human activity differed between our two primary measures (number of visitors and spatial treatment). In the spatial treatment with the highest ecotourism activity, bear activity was higher compared with upstream areas where human activity was lower (Figure 2a). This pattern also emerged when salmon abundance was high (Figure 2c). We suspect this result in part occurred because the ecotourism sites occur near the mouth of the Atnarko River, where salmon congregations are dense and highly available to fishing bears. After accounting for the effect of spatial treatment, however, bear activity along the Atnarko declined during weeks with higher visitor numbers (Figure 2d). Owing to varied spatial and temporal human behavior among the types of bear viewing (i.e., professionally-guided tours and tightly managed bear stand versus a comparably unregulated recreation area not designated for bear viewing), we infer that bears generally reduced their activity when and where visitor numbers are high because perceived risk was higher with variable and largely unregulated behavior among visitors, especially in areas with high visitation; namely, the BC Parks recreation area that was actively used by the public for bear viewing, but not formally designated as a bear viewing area. Given that predictable patterns enable wildlife to anticipate risk (Gaynor et al., 2019; Laundré et al., 2001; Palmer et al., 2022), we suspect bears at this site modulate non-consumptive risk-effects of visitor numbers and behavior accordingly, as prey do with varied characteristics of predators.

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

We also found strong support for the HSH. Whereas the probability that a detection was a given age-sex class did not vary by spatial treatment, when visitors increased, the probability of detections being adult male decreased and the probability that a detection was female with young or subadult increased. Whereas, as noted above, activity across detections of all age-sex classes decreased when visitor numbers were high, we infer that the underlying mechanism of this decrease is avoidance of humans by adult males. Indeed, lower weekly bear detections are comprised of a lower proportion of adult males (Figure S10). Additionally, females with young, adult females, and subadults were more likely to be detected during daylight hours than adult males, which were more likely to occur during darker periods of the day (Figure 4b). This pattern was consistent with previous research findings. In Sweden, mother grizzly bears selected human-dominated sites, which were avoided by males (Steyaert et al., 2016). In an ecotourism context elsewhere in coastal British Columbia, males and females with young similarly partitioned their temporal activity in relation to ecotourism periods (Nevin & Gilbert, 2005).

Our approach had several limitations. Logistical constraints (e.g., segments of the river that were inaccessible by boat to count salmon) required us to impute missing spatial and temporal dimensions of salmon data. More broadly, data on spawner abundances of wild salmon are not always consistently collected through space and time for each species, requiring similar estimation via imputation (Bryan et al., 2014; Ruggerone et al., 2010). Nonetheless, that we detected qualitatively similar patterns in datasets with and without imputed data (Appendix S1; Figure S11) suggested our results were not sensitive to our imputation approach. Moreover, we note that we used only two relatively coarse metrics of grizzly bear activity, assessed with a suite of covariates for which variation was expressed over a weekly period. Whereas broad patterns emerged, only a finer-scale ethological approach could evaluate how more specific behaviors (i.e., activity budgets) might be influenced by ecotourism. Such an approach could also assess if fitness-related behaviors (e.g., salmon consumption; Hilderbrand et al., 1999) were influenced by human activity. Finally, and relevant to many ecotourism contexts, genetic sampling over a broader area could identify whether there are risk-adverse and -tolerant individuals in the population of mobile wildlife that avoid or tolerate high-density human presence. Similarly, more comprehensive genetic approaches could assess whether exposure to ecotourism might predispose individuals to subsequent conflict (e.g., Cui et al., 2021). We note that bear culture, personality, and individual capacity for logic and thought (Paquet & Alexander, 2018; Whiten, 2021) might be important individual trait contexts, which are not captured via camera trap weekly detections, a measure that pools the detections of unknown individuals. Whereas this work confronts only one of three lines of inquiry (i.e., broad activity patterns via analysis of camera trap data) associated with our research project and its objectives, subsequent analyses of behavioral and genetics data (as described above) will aim to confront these limitations and yield more detailed inference.

Several specific management implications of this work span both conservation and social domains. If activity levels of bears are important targets for management consideration, the interactive influences of salmon abundance and number of visitors requires special consideration. Specifically, when salmon runs are low, management might consider limiting the number of visitors more than during high salmon weeks. This is because grizzly bears with few alternatives for foraging opportunities during low salmon scenarios may be more vulnerable to non-consumptive risk effects of increased humans (Gill et al., 2001). Indeed, if an animal's riskier behavioral options are also those that result in a higher rate of energy intake, then relatively food-deprived animals would be expected to accept a greater risk while feeding (Lima, 1998, p. 5). Predictions from our top model's output provide insight into how many visitors present under different salmon scenarios would align with several candidate targets of bear activity (Table 1). These options of management interventions allow managers to consider varying visitor numbers under different salmon scenarios to manage for a level of predicted responses in bear activity they consider acceptable. How the human-induced effects and any interventions by managers might scale to measurable changes to population fitness is unknown, but offers an important avenue for future research to address.

Human safety might also be considered by managers. A proactive approach would favor the regulation of times, places and permitted human behavior (e.g., constraining humans to within-site spaces if bear viewing is permitted at multi-use recreation areas), so as to make interactions more predictable for bears and humans alike. Such scenarios not only reduce apparent

TABLE 1 Visitor numbers associated with grizzly bear weekly detection scenarios under high, mean, and low salmon conditions as predicted by the top model.

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

Note: Visitor numbers are rounded to the nearest 50. Note that under low salmon and high visitor scenarios, bear detections increase. In low salmon scenarios, managers might consider limiting visitor numbers to no greater than those associated with mean bear detections to mitigate disturbance when bears have little alternatives for foraging opportunities.

risk perception (Palmer et al., 2022) but also avoid unanticipated encounters, which can underlie cases of human injury by bears (Herrero, 1985). As we suggest, low salmon conditions might present few foraging options for bears, thereby creating congregations at available feeding sites where human activity is high. At the larger British Columbia and yearly scales, Artelle et al. (2016) found that grizzly-human conflict rises in years with poorer salmon returns. Such context presents not only a bear conservation challenge for managers (i.e., managing for disturbance during a critical time for bears to amass large amount of energy to support themselves and offspring during dormancy; Farley & Robbins, 1995; Hilderbrand et al., 1999) but also a safety consideration for managing visitors who are actively pursuing grizzly bear encounters at recreation areas that are not designated for bear viewing.

Although our bear ecotourism system has a unique constellation of properties (i.e., discrete foraging patches [some of which also easily accessible to visitors], high carnivore densities, hyperphagia, potential for human safety issue), our work offers broader implications for conservation science and practise. First, we designed our work to confront and contribute to two bodies of theory (the APP and the HSH) that are relevant to the conservation of any predator–prey system, including the many in which wildlife show prey-like antipredator behavior in the presence of humans. Second, we showcase with rich detail how data from animal behavior can be harnessed to directly inform specific and context-dependent management actions (Table 1).

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

AUTHOR CONTRIBUTIONS

K. A. F., C. T. D., J. E. M., and P. C. P. contributed to the inception and design of the study. Data collection and field program management and coordination was undertaken by K. A. F. and J. E. M. Data analysis was performed by K. A. F. with guidance in design, data preparation, analyses and/or visualization from C. T. D.,

M. L. S., K. A. A., and M. L. B. All authors were involved in drafting the manuscript or revising it critically.

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CONFLICT OF INTEREST STATEMENT

No conflict of interest exists.

DATA AVAILABILITY STATEMENT

Annotated code is uploaded to the project's GitHub repository at https://github.com/fieldka/atnarko-camtraps. Data generated during this study are not publicly available due to confidentiality agreement with Nuxalk Nation, but available from the corresponding author and Nuxalk Nation upon reasonable request.

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SUPPORTING INFORMATION

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

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