

RESEARCH ARTICLE

Low levels of outdoor recreation alter wildlife behaviour

Mira L. T. Sytsma¹  | Tania Lewis²  | Beth Gardner¹  | Laura R. Prugh¹ 

¹School of Environmental and Forest Sciences, University of Washington, Seattle, Washington, USA

²Glacier Bay National Park and Preserve, Gustavus, Alaska, USA

Correspondence

Mira L. T. Sytsma

Email: mirasytsma@gmail.com

Funding information

National Park Service

Handling Editor: Barry Brook

Abstract

1. Public interest in nature-based recreation is growing, including visitation to protected areas. However, the level of recreation in these areas that causes detectable changes in wildlife behaviour remains unknown, and many studies that investigate wildlife responses to humans do so in high-visitation areas.
2. We used camera traps to investigate the spatial and temporal responses of brown bears (*Ursus arctos*), black bears (*Ursus americanus*), moose (*Alces alces*) and wolves (*Canis lupus*) to experimentally manipulated levels of human activity in Glacier Bay National Park, Alaska during summers 2017 and 2018. Human activity was restricted at some sites and concentrated at others, and these human impact treatments were swapped mid-season. The park has very low on-land visitation (~40,000 on-land tourists per year), making it a unique study system to investigate wildlife responses to low levels of human activity.
3. Detections did not exceed five per week for any species unless human activity was absent (zero photos of humans were taken). However, spatial and temporal patterns of wildlife activity in relation to human activity were nuanced and species specific. Moose shifted their activity patterns to better align with when people were most active. Black bears were more likely to be detected in areas of high human activity but used high-use areas less intensely than low-use areas. Wolves used areas of high human impact more intensely, but shifted their activity to be more strongly nocturnal.
4. Our results highlight the importance of considering both spatial and temporal responses of wildlife to human activity. Additionally, and arguably most importantly, we detected changes in wildlife behaviour in response to humans in a national park with relatively low tourism. Although natural processes may dominate in protected areas, our results indicate that even low levels of human activity can alter wildlife behaviour.
5. *Synthesis and applications.* We demonstrated that nearly any level of human activity in a protected area may alter wildlife behaviour. However, it is unreasonable to expect protected areas to be completely devoid of human activity. Thus, management of these areas will need to balance the desires of humans to view wildlife with the likely impacts.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *People and Nature* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

KEYWORDS

fear effects, human shield effect, human–wildlife interaction, occupancy, protected areas

1 | INTRODUCTION

Public interest in nature-based recreation is high and growing—terrestrial-protected areas receive an astounding 8 billion visits per year worldwide (Balmford et al., 2015). Over 14% of the world's terrestrial area has protected status (UNEP-WCMC and IUCN, 2016), but visitation rates are outpacing recent expansions of protected area networks: visitation to wilderness areas increased 17.7% from 1999 to 2009 and will likely accelerate (White et al., 2016). Outdoor recreation is the fourth leading threat to at-risk species in North America (Czech et al., 2000; Prugh et al., 2010), raising concerns about the sustainability of growth in nature-based recreation.

Maintaining protected areas is a key component of preserving biodiversity and mitigating anthropogenically caused habitat alteration (Jacobson et al., 2019), and understanding how wildlife respond to human activity in protected areas is important for measuring the effectiveness of these areas.

Some level of human impacts is inevitable in protected areas, and managers are tasked with providing meaningful experiences for visitors without compromising ecological integrity (UNEP-WCMC and IUCN, 2016). Many land management agencies strive to allow for visitor enjoyment while protecting natural resources, and most wildlife viewers likely wish to minimize their own disturbance to the animals they are viewing. To mitigate human disturbance impacts, managers can adopt 'land sparing' or 'land sharing' strategies. Land sparing concentrates human use in certain parts of protected areas to limit the areal extent of human impacts (Cole, 1992; Leung & Marion, 1999). Alternatively, land sharing is used in areas of low human use, with the rationale that human impacts are sufficiently low that areas do not need to be 'sacrificed' to maintain ecological integrity elsewhere (Marion & Farrell, 2002). However, the level of human activity that elicits detectable changes in wildlife behaviour has not been identified, which increases the difficulty of making science-based visitor management decisions.

Wildlife can respond spatially and temporally to human disturbances. Avoidance manifests as short-term changes in wildlife behaviour such as fleeing and interruption of foraging (Bateman & Flemming, 2017), and long-term impacts including decreased reproduction or survival, increased stress, displacement and shifts in diel cycles (Gaynor et al., 2018; Taylor & Knight, 2003). If human disturbance is considered analogous to predation risk (Frid & Dill, 2002), the effects of avoidance or 'fear' of humans may outweigh the effect that predators have on wildlife (Bleicher, 2017; Ciuti et al., 2012). Alternatively, some species of wildlife have demonstrated 'human shield effects', whereby activity increases around humans because they provide some protection, or buffer, against predators that typically avoid people (Berger, 2007). Human activity can thus displace predators and prey and alter ecological interactions between them (Berger, 2007; Sarmiento & Berger, 2017; Suraci et al., 2019).

Knowing the level of human activity that elicits detectable responses by wildlife—and whether responses are spatial, temporal or both—is necessary to effectively manage protected areas as visitation rates increase.

We used remote cameras to quantify spatial and temporal activity patterns of large mammals in response to human activity in Glacier Bay National Park, Alaska (hereafter, Glacier Bay). Glacier Bay provides a unique opportunity to study wildlife responses to relatively low levels of ground-based tourism in a large protected area. Despite low visitation, tourism on the land and water of Glacier Bay has almost doubled in the past 20 years. Due to concerns about visitor impacts, park managers implemented new tour vessel operating plans in 2016 that allowed for the designation of 'high-impact' locations to concentrate human activity in specified areas and restrict human activity in others. These plans provided the unique opportunity to experimentally manipulate human visitation and examine responses by wildlife.

Large mammals may be especially sensitive to human impacts due to their large space requirements, low population densities and/or low birth rates (George & Crooks, 2006). We therefore focused on four large terrestrial mammals: brown bears (*Ursus arctos*), black bears (*Ursus americanus*), moose (*Alces alces*) and wolves (*Canis lupus*). We hypothesized that moose would demonstrate behaviour consistent with the human shield effect (i.e. 'attraction' to human activity), as demonstrated in other systems with higher levels of human use (Hebblewhite et al., 2005; Sarmiento & Berger, 2017; Shannon et al., 2014; Thorsen, 2016). As the apex predators in this system, we hypothesized that brown bears and wolves would avoid humans because prior studies have demonstrated this behaviour in large carnivores (Gibeau et al., 2002; MacHutchon et al., 1998; Shannon et al., 2014; Smith et al., 2017). As a mid-ranked predator in the Glacier Bay system, we expected black bears to respond similarly to moose if they perceive risk from apex predators to be greater than risk from humans (MacHutchon et al., 1998). Alternatively, black bears might respond similarly to brown bears and wolves if their perceived risk from human 'super predators' outweighs their perceived risk from apex predators. Lastly, because human activity in Glacier Bay is low, controlled and fairly predictable, we expected wildlife to demonstrate a stronger temporal response than spatial response to park visitors.

2 | MATERIALS AND METHODS

Glacier Bay National Park is a 13,000 km² portion of a 100,000 km² World Heritage Site (Figure 1). Glacier Bay fjord is a product of the Little Ice Age and glaciation that reached a maximum around 1750 and was followed by a dramatic deglaciation over the past several

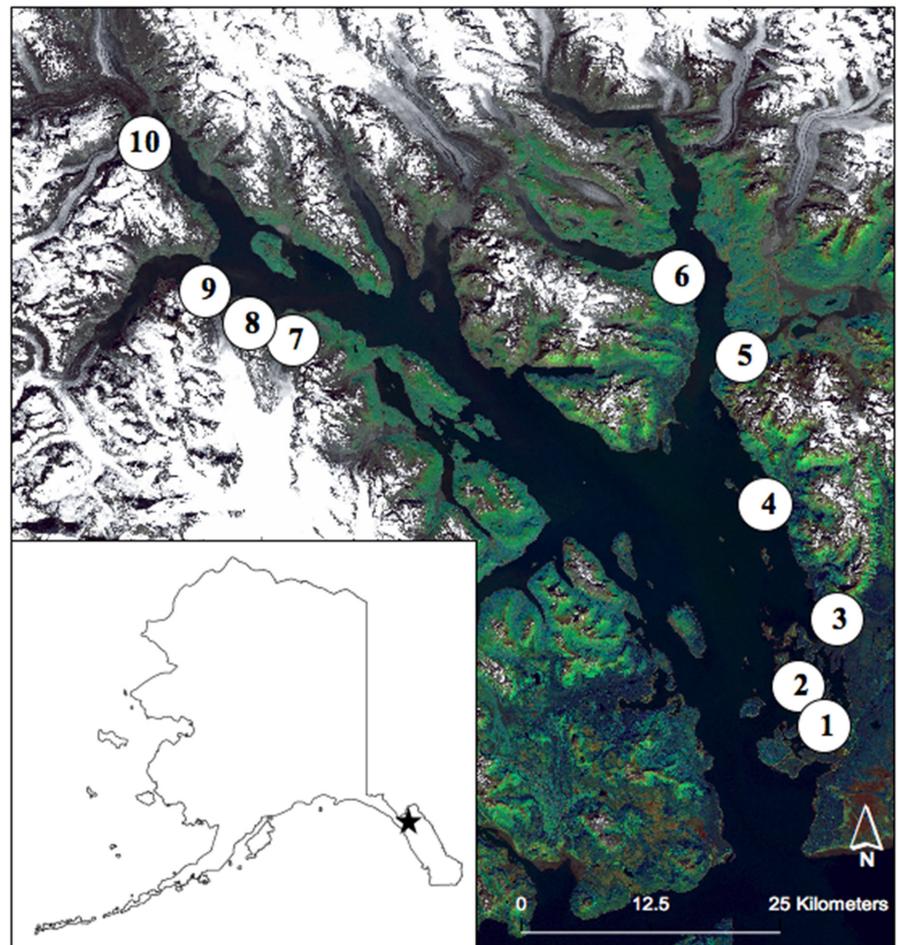


FIGURE 1 Map of Glacier Bay National Park, AK study area. White numbered circles represent study sites, described in Table 1, where four cameras were placed per site (40 total cameras) to capture photos of brown bears, black bears, moose, wolves and humans. The study was conducted during summers of 2017 and 2018

TABLE 1 Characteristics of experimental sites in Glacier Bay National Park, Alaska, including site numbers, names, pairing information, average tree diameter at breast height (DBH), treatment designations and average minutes of human activity per week per site. 'High' and 'low' refer to impact treatment levels (e.g. tour vessels were allowed to drop tourists off at high-impact sites during certain times of the summer and were not allowed to drop tourists of low-impact sites). Early season was June 1–July 14, and late season was July 15–September 1. Site numbers correspond to Figure 1

Site #	Site name	Early 2017	Late 2017	Early 2018	Late 2018	DBH (cm)	HumanActivity (camera minutes)
1	Bartlett Cove	High	High	High	High	47.1	42.59
2	Lester Island	Low	Low	Low	Low	24.9	0.002
3	Beartrack Cove	Low	High	High	Low	32.4	0.33
4	South Sandy Cove	High	Low	Low	High	28.7	2.74
5	Adams Inlet	High	Low	Low	High	53.8	0.05
6	Hunter Cove	Low	High	High	Low	37.2	0.02
7	Reid East	High	Low	Low	High	0.0	0.88
8	Reid West	Low	High	High	Low	0.0	1.10
9	Lamplugh	High	High	High	High	0.0	2.52
10	Upper Tarr	Low	Low	Low	Low	0.0	0.005

hundred years (Connor et al., 2009). The park can be accessed by boat or plane only, and 94% of tourism to Glacier Bay occurs on cruise ships where passengers never disembark. There are approximately 40,000 on-land tourists to Glacier Bay per year. In 2018, 13,000 of those visited the park on tour vessels that drop visitors on shore for day hikes, and the remainder of visitors either stayed within the frontcountry developed area or visited the backcountry by kayak or private vessel (National Park Service IRMA Portal, accessed 5/14/2020). There are no maintained trails or campgrounds outside of the park frontcountry area in Bartlett Cove.

We conducted this study during summers (June–August) in 2017 and 2018 using a crossover, paired-plot experimental design with five replicate pairs. Within two sets of pairs (sites 3, 4, 7 and 8), one site received a high-impact treatment from tour vessels for half of the summer, while human use via tour vessels was prohibited at the other site (Table 1). The third pair of sites (sites 5 and 6) were largely camping destinations and the treatment was applied by changing access via a drop-off vessel. The timing (early vs. late summer) of the high-impact treatment was randomly determined for each pair and reversed in 2018 to control for seasonal effects. We were unable

to manipulate human activity for two pairs of sites (sites 1, 2, 9 and 10), so one site in each pair was considered the treatment and one site the control based on known levels of visitor numbers. This management decision was included as a categorical variable (high versus low) called *HumanTreatment* in statistical analyses. This study did not require ethics approval.

We installed four camera traps (Reconyx HC600 Hyperfire Covert IR) at each study site (40 total), two in shoreline habitat and two in inland habitat. Cameras were approximately 0.5 km away from one another, forming as close to a square grid at each study site as the landscape allowed. Cameras were programmed to take three photos when motion triggered, with no delay between the three photos, and there was no 'quiet period' between triggers. Two cameras at each site were also set to take a timelapse photo every 15 min to increase the chance we would capture photos of wildlife that may not have been travelling close enough to the cameras to trigger a detection. Cameras were placed approximately 0.5 m above ground and along game trails where available (and one human trail in Bartlett Cove) or in expected areas of wildlife concentration to maximize detection probabilities. We identified individuals detected to species and processed photos using Timelapse2 software (Greenberg & Godin, 2015).

We calculated a *HumanActivity* covariate by summing the number of humans detected at each camera during each sampling week, including those detected in timelapse photos. We then divided the total by 60 since each photo roughly represented a second, creating an index of minutes of human activity per week per camera. To calibrate this index with actual numbers of shore excursion tourists, we ran a linear regression between *HumanActivity* and number of tourists at sites reported by the tour vessels. Additionally, to determine the efficacy of the management designations, we conducted a paired *t*-test to compare *HumanActivity* levels across *HumanTreatment* categories.

We visually examined plots of weekly detection rates for each species in relation to *HumanActivity* values at each camera station to identify potential thresholds of human activity resulting in marked changes in detection rates. Our aim was to identify a

human activity threshold that altered wildlife behaviour in a 'pristine' system, so we separated Bartlett Cove (park frontcountry) detections from the other (backcountry) sites. Due to the zero-inflated nature of the data, statistical methods for threshold detection (e.g. segmented regression) were not possible (Toms & Lesperance, 2003), and occupancy models which assume logit-linear relationships between predictors and response variables also could not be used.

We assessed temporal activity patterns of the four focal species using the R (version 1.1.463) package *OVERLAP* (version 0.3.2; Meredith & Ridout, 2017). Photographic events of the same species at each camera were considered independent if they were separated by more than 30 min (Carter et al., 2012). We fit kernel density functions to temporal data (Rowcliffe et al., 2014), calculated the percent overlap of activity patterns between high-impact and low-impact *HumanTreatment* categories for each species and generated confidence intervals of overlap coefficients from 10,000 smoothed bootstrap samples.

We examined spatial activity patterns using an occupancy modelling framework that estimated the probability of species occupancy while accounting for detection probability, where occupancy is defined as the probability that a randomly selected site contains at least one individual of a species (MacKenzie et al., 2006). We considered each camera trap to be a 'site' within the occupancy framework, we refer to these as 'camera sites' to distinguish from the larger study sites (e.g. Bartlett Cove). We partitioned detection histories into 7-day increments (encounter histories) for each species (Rovero et al., 2014) at each camera site using the package *CAMTRAPR* (version 0.99.9; Niedballa et al., 2017). A 7-day increment represented a trade-off between allowing enough time to for wildlife that were truly occupying a camera site to be captured on camera while reducing the number of non-detections (which would likely occur with a shorter encounter history). We estimated detection and occupancy probabilities using single-season occupancy models based on detection histories and covariates (Table 2) using package *UNMARKED* (version 0.12-0; Fiske & Chandler, 2011). We expected humans to primarily affect detection probabilities instead of site occupancy

TABLE 2 Description of covariates on detection and occupancy probabilities used in occupancy models. The 'Brown' covariate was included in black bear models only

Covariate	Definition	Range
Occupancy (ψ)		
DBH	Average tree diameter at breast height (cm)	0.0–53.8
Detection (p)		
HumanTreatment	High- or low-impact treatment	Y, N
Year	Year data collected	2017, 2018
Season	Early or late summer season. Corresponds to switching of treatment/control	Early, Late
Habitat	Shore or inland	Shore, Inland
HumanActivity	'Human camera minutes' of activity/week by camera	0.0–180.5
Brown	Number of independent brown bear photos/week by camera	0–8

Abbreviation: DBH, diameter at breast height.

because relatively low levels of human activity at Glacier Bay even at high-impact treatment areas were unlikely to cause individuals to completely abandon sites. As a proxy for the maturity of the vegetation community at each study site that may have affected wildlife occupancy, we measured tree diameters at breast height (DBH) in the inland habitat. We took four DBH measurements every 10 m (40 measurements total) at one of the inland camera sites at each study site.

We used a two-step model selection process to obtain the most parsimonious occupancy model for each species. First, we compared models with and without tree DBH as a covariate on occupancy, using an intercept-only detection model. If the Akaike information criterion (ΔAIC) between the two models was less than or equal to 2 and DBH significantly impacted occupancy probability, we retained it in the model moving forward. Second, we selected the best-supported detection model, using the occupancy model identified in step one and the detection covariates

in Table 2. We included an additional covariate for black bears, *Brown* (Table 2), to test for potential avoidance of brown bears by black bears in areas where species are sympatric. We ran all possible additive models and tested two-way interactions based on a-priori hypotheses including interactions between *Habitat* and *HumanActivity*, *Habitat* and *HumanTreatment*, *HumanActivity* and *Season*, *HumanActivity* and *Year*, and *Brown* and *Habitat*. We selected the top model for each species based on AIC. If there were multiple top models within 2 ΔAIC of each other, we examined them to see if any of the human-related variables were included and were significant. If either or both human-related variables were significant, we selected that model as the top model. If neither of the human-related variables were significant, we selected the most parsimonious model as the top model (i.e. the model that best fits the data with the fewest parameters; Dingemanse et al., 2004; Burnham & Anderson, 2002; Appendix S1: Table S1). Due to the relative sparseness of wolf detections, wolf models with

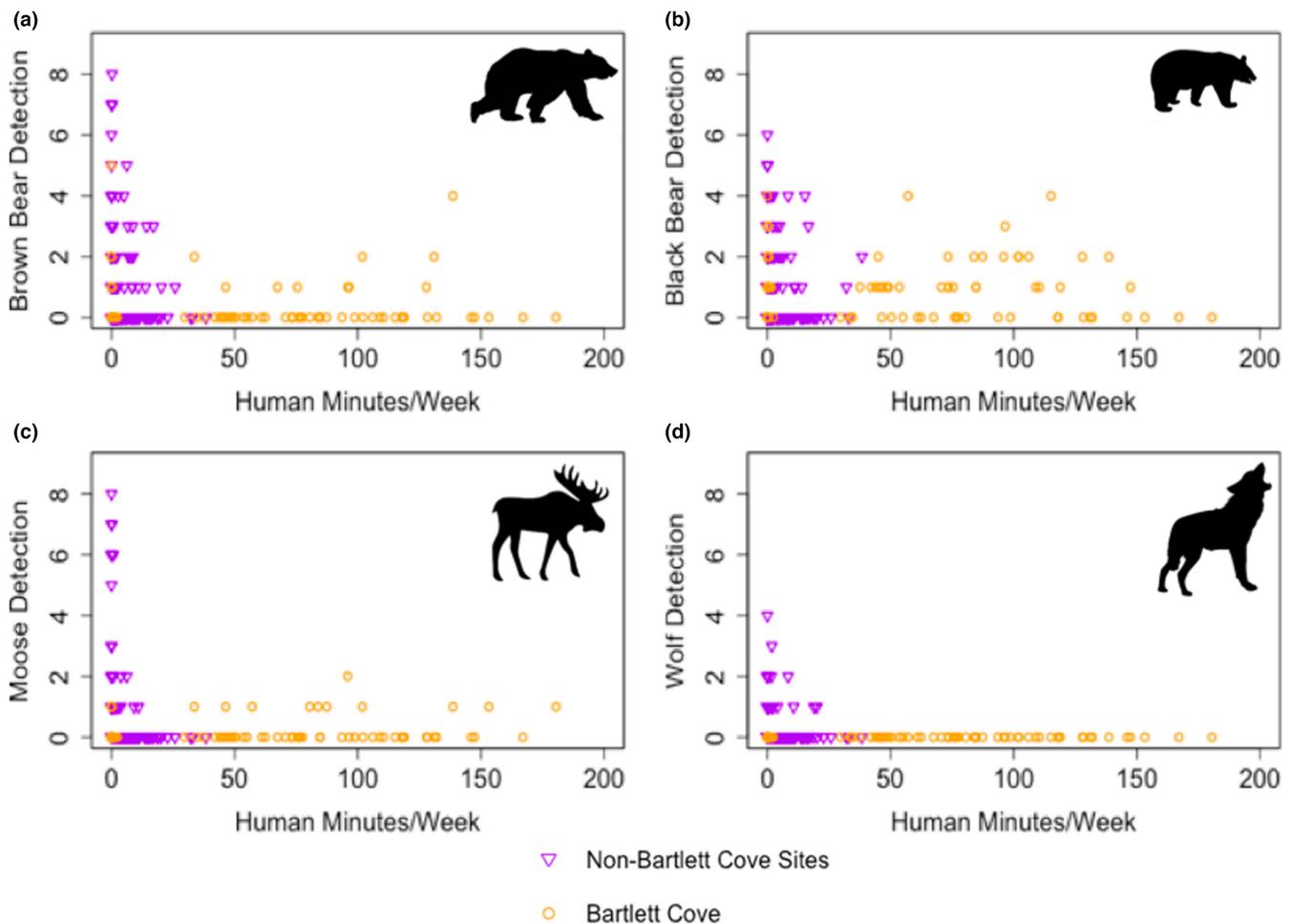


FIGURE 2 Influence of human activity on independent detections of brown bears (a), black bears (b), moose (c) and wolves (d) per week at Bartlett Cove (orange) versus the other sites (purple). Bartlett Cove represents a ‘frontcountry’ site, while the other sites are considered ‘backcountry’. On the x-axis is the number of ‘human camera minutes’ detected each week on the cameras. This was calculated by summing the number of humans detected at each camera during each sampling week (including those detected in timelapse photos) and dividing the total by 60, since each photo roughly represented a second. On the y-axis are independent detections of each species, which were calculated by screening remote camera data such that photographs of the same species at each camera were independent if they were separated by more than 30 min

more than five parameters appeared to be over-parameterized, so only models with a maximum of five parameters were considered.

The close proximity of the four camera sites to each other at each of the 10 study sites violated the assumption of camera site independence within the occupancy model. We used a Bayesian modelling framework to test the effects of this violation and found no effect on our results (Appendix S1: Table S2).

Occupancy models require condensing detection data into temporal sampling occasions, which can result in loss of data regarding intensity of wildlife use (hereafter, use-intensity). Use-intensity differs from estimating occupancy probability, which can remain constant even while use-intensity varies (Keim et al., 2019). To capture this variation, we examined spatial activity of each species using a generalized linear mixed model with a negative binomial distribution and a site random effect. We used independent photographic events (described above) for each species per week as a 'count' response

variable and ran full models for each species with the covariates used in the detection models. The negative binomial model did not converge for wolves due to low sample size, so we fit a Poisson linear mixed model.

3 | RESULTS

We obtained 183,012 photos of humans and wildlife, including 154,444 photos of humans (84% taken at Bartlett Cove), 5860 photos of brown bears, 3452 photos of black bears, 6927 photos of moose and 570 photos of wolves. Independent detections of each species per camera ranged from 0–8 per week. *HumanActivity* ranged from 0–180 min per week, decreasing to a maximum of 30 min per week when excluding Bartlett Cove (Figure 2). Detections of all species declined markedly as *HumanActivity* increased from 0–20

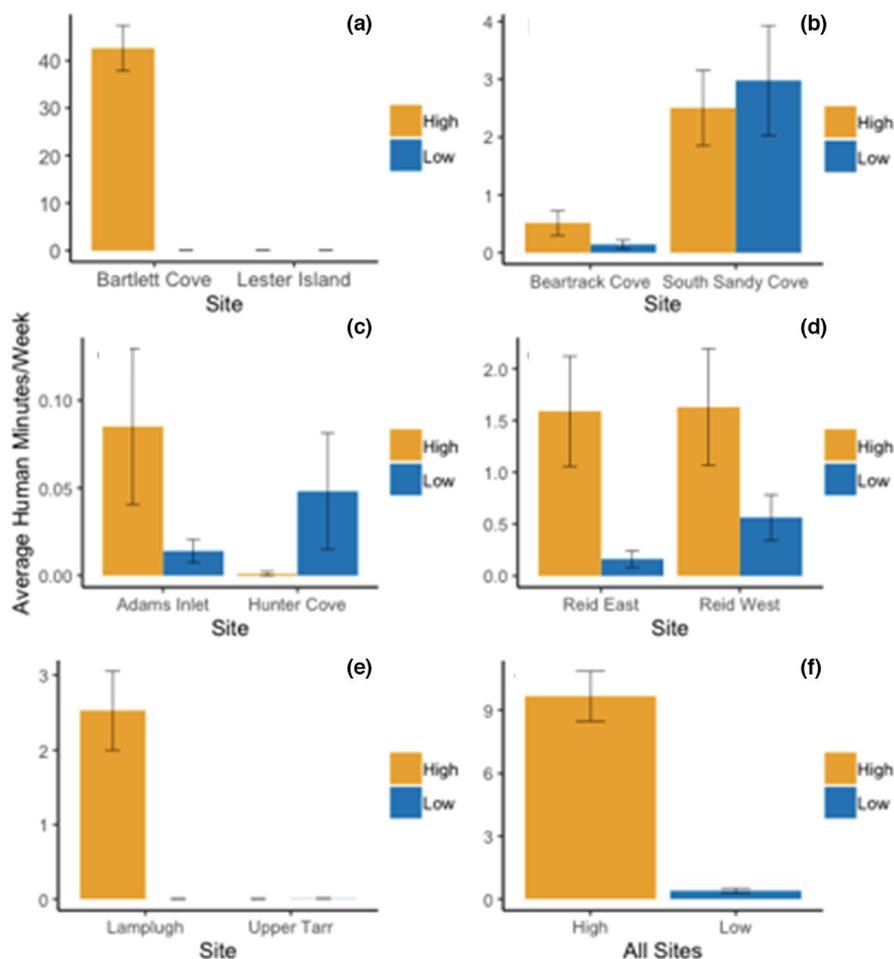


FIGURE 3 Average 'human camera minutes' per week at (a) Bartlett cove/Lester Island, (b) Beartrack Cove/South Sandy Cove, (c) Adams Inlet/Hunter cove, (d) Reid East/Reid West, (e) Lamplugh/Upper Tarr and (f) all sites combined when sites were in a high-impact treatment (orange) or in a low-impact treatment (blue). The human camera minutes represent the *HumanActivity* covariate, which we by summing the number of humans detected at each camera during each sampling week, including those detected in timelapse photos. We then divided the total by 60 since each photo roughly represented a second, creating an index of minutes of human activity per week per camera. The treatment (high impact versus low impact) was largely successful, however two sites had higher levels of *HumanActivity* during low-impact treatments than high-impact treatments (3b, 3c). While we were able to mandate that tour vessels follow our experimental design (and only drop tourists off at sites that were in a high-impact treatment phase), we could not mandate what other vessels in Glacier Bay did (e.g. charter boats or other private vessels), which contributed to this pattern. Error bars represent ± 1 SE

camera minutes per week (Figure 2). There were no more than five brown bear, four black bear and two moose or wolf detections per week unless *HumanActivity* was 0. Wolves were not detected at any camera stations when human activity exceeded 20 min per week. Both bear species had moderate detection rates at Bartlett Cove, whereas detections of moose were low, and wolves were absent at this site (Figure 2). Average *HumanActivity* across cameras at each site ranged from 0.002–42.59 camera minutes per week (Table 1).

Average *HumanActivity* in high-impact treatments (mean = 9.655, SE = 1.189) was 24 times higher than low-impact treatments (mean = 0.393, SE = 0.104), indicating that implementation of the management design was largely successful (Figure 3f; $t_{559} = 7.7$, $p < 0.001$). When excluding the Bartlett Cove outlier (mean = 42.594, SE = 4.779), *HumanActivity* in remaining high-impact treatments (mean = 1.421, SE = 0.189) was 3.6 times higher than in low-impact treatments. Despite the overall success of the treatment, two sites had higher levels of *HumanActivity* during low-impact treatments than high-impact treatments (Figure 3b,c). While we were able

to mandate that tour vessels follow our experimental design (and only drop tourists off at sites that were in a high-impact treatment phase), we could not mandate what other vessels in Glacier Bay did (e.g. charter boats or other private vessels), which contributed to this pattern. We found a significant positive relationship between *HumanActivity* and the number of visitors reported by tour boats, though substantial variation in *HumanActivity* remained unexplained by reported visitor numbers ($R^2 = 0.1921$, $p < 0.001$, Appendix S1: Figure S1). This relationship indicates that a *HumanActivity* level of 30 human camera minutes per week roughly corresponded to 40 visitors per week.

Estimates of temporal activity overlap between high- and low-impact treatments ranged from 0.64–0.87 across species. Moose and wolves had the lowest overlap between treatments, indicating a strong temporal response to the high-impact treatment, whereas brown and black bears had more similar patterns among treatments (Figure 4; Appendix S1: Table S3). Human activity in Glacier Bay was diurnal and highest in midday (Figure 4). Moose activity

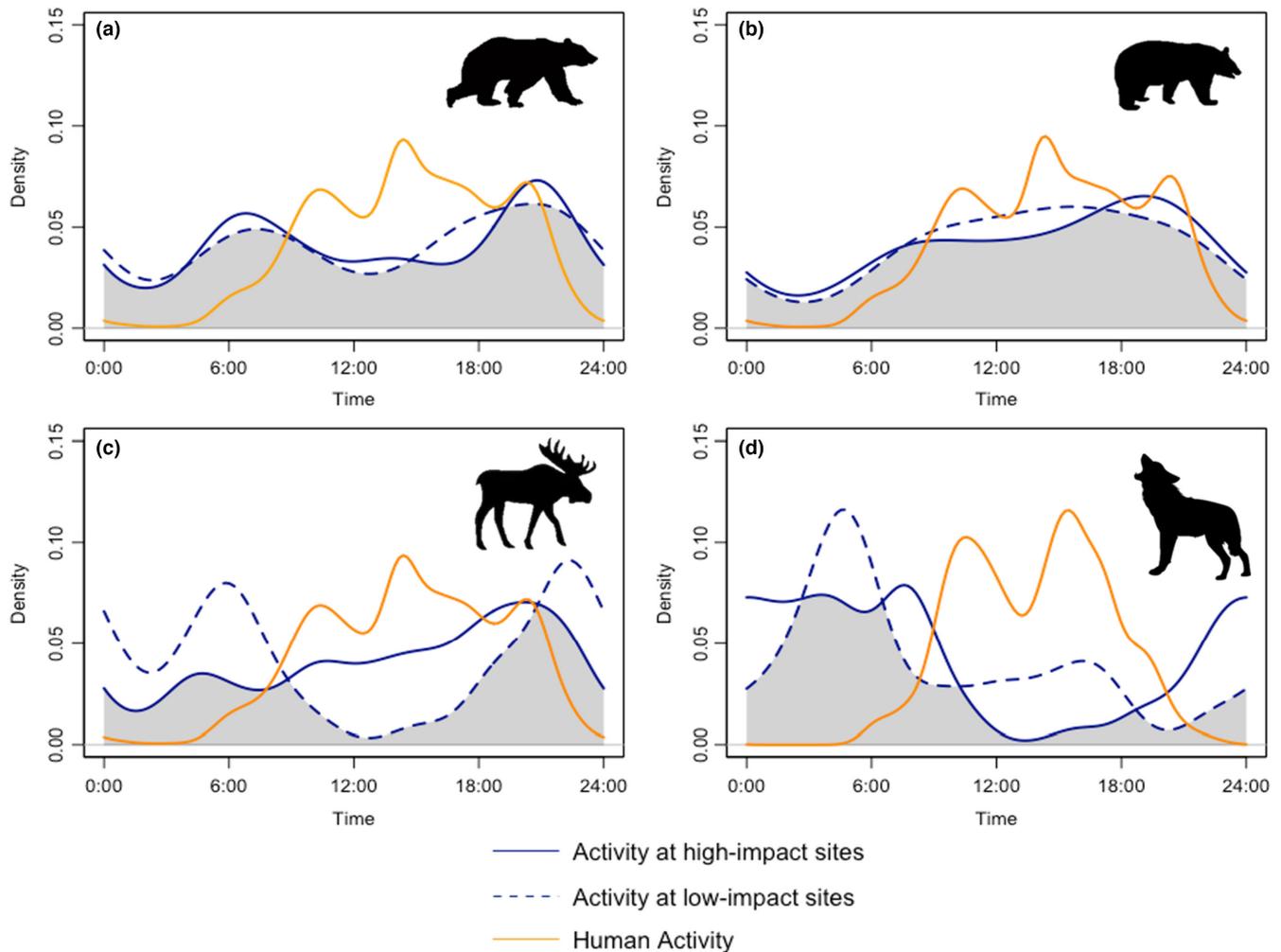


FIGURE 4 Temporal activity patterns of (a) brown bears, (b) black bears, (c) moose and (d) wolves during high-impact (dashed blue line) and low-impact (solid blue line) treatments. Since not all wildlife species were detected at the same sites, human activity patterns (orange) were taken from the corresponding cameras that each species activity data were taken from. The grey shading illustrates the overlap between high- and low-impact site activity. Brown bears and black bears decreased temporal overlap with humans by 5% and 9%, respectively. Moose increased overlap with human temporal activity by 47%, and wolves decreased overlap by 63%

TABLE 3 Top occupancy model results for each species, showing which covariates impacted occupancy and detection probabilities. Tree diameter at breast height (DBH) significantly impacted occupancy for black bears and moose but did not impact occupancy for brown bears and wolves—instead, those species have an intercept-only occupancy model. All covariates are categorical, except for *HumanActivity*, which we standardized

Species	Process	Covariate	Estimate	SE	Z value	p-value
Brown Bear	Occupancy	(Intercept)	0.824	0.212	3.89	<0.001
		Detection	(Intercept)	-0.854	0.21	-4.08
	Detection	Habitat (shore)	0.447	0.19	2.35	0.019
		Season (late)	-0.455	0.178	-2.55	0.011
		Year (2018)	0.424	0.182	2.33	0.020
Black Bear	Occupancy	(Intercept)	-0.41	0.179	-2.29	0.022
		DBH	0.876	0.189	4.63	<0.001
	Detection	(Intercept)	0.671	0.246	2.73	0.006
		HumanTreatment (high)	-0.651	0.232	-2.81	0.005
		Season (late)	-0.5	0.223	-2.24	0.025
		Year (2018)	0.537	0.219	2.45	0.014
HumanActivity		0.463	0.234	1.98	0.047	
Moose	Occupancy	(Intercept)	-0.194	0.215	-0.904	0.366
		DBH	0.532	0.205	2.594	0.009
	Detection	(Intercept)	-0.691	0.15	-4.59	<0.001
		Season (late)	-0.531	0.284	-1.87	0.062
Wolf	Occupancy	(Intercept)	-0.811	0.266	-3.04	0.002
		Detection	(Intercept)	-2.25	0.344	-6.53
	Detection	Habitat (shore)	1.13	0.393	2.88	0.004

shifted from crepuscular in low-impact treatments to steady activity throughout the day in high-impact treatments (overlap = 0.64, 95% CI = 0.52–0.73), increasing overlap with human temporal activity by 47% (Appendix S1: Table S3). During high-impact treatments, black bear activity decreased after noon when human activity was highest, and increased in the evening with declining human activity (overlap = 0.87, 95% CI = 0.81–0.94). Likewise, the peak activity of brown bears shifted towards evening during high-impact treatments (overlap = 0.85, 95% CI = 0.79–0.91). Daytime activity of wolves decreased during high-impact treatments, decreasing to zero when human activity was highest—a 63% change in overlap with human activity (overlap = 0.68, 95% CI = 0.50–0.82; Appendix S1: Table S3).

Occupancy probabilities ranged from 0.70 (brown bears) to 0.31 (wolves) and black bears and moose were more likely to occupy areas with higher tree DBH (Table 3, Appendix S1: Tables S1 and S4). Only the black bear model included significant human-use-related covariates. Black bear detection increased with increasing *HumanActivity* but was lower in high-impact *HumanTreatment* areas (Table 3; Figure 5). When we reran the black bear occupancy model with *HumanTreatment* designations switched for the two site pairs impacted by the imperfect treatment application, detection increased with increasing *HumanActivity* and was higher in high-impact *HumanTreatment* sites (Appendix S1: Table S6). While black bears were more likely to be detected in areas with greater human presence, they used these areas less intensely than low-impact *HumanTreatment* sites (Table 4; Figure 5b). Wolves were

no more likely to be detected in high-impact than low-impact treatments but did use high-impact treatment areas more frequently (Table 4; Figure 5b). Bartlett Cove had much higher human activity than other sites, so we reran use-intensity models with Bartlett Cove excluded to determine if its inclusion impacted results (Appendix S1: Table S5). When this outlier was excluded, moose use-intensity changed—they used areas of high human activity less frequently—but results for other species did not change. Lastly, visual inspection of the detection data indicated that in all backcountry sites, wildlife detections dropped to zero as *HumanActivity* approached 30 camera minutes per week. In Bartlett Cove, detections continued for black bears, brown bears and moose after this threshold was reached (Figure 2).

4 | DISCUSSION

Wildlife responses to human activity have been documented in ecosystems around the world (Gunther et al., 2015; Sarmento & Berger, 2017), and protected areas are often used to quantify these impacts (White et al., 2016). Although protected areas may have reduced human impacts (Beissinger et al., 2017), they can receive millions of visitors a year and visitation is increasing rapidly, calling into question their ability to achieve wildlife conservation objectives in the future. In this study, we experimentally demonstrated that wildlife respond spatially and temporally to low levels of human activity

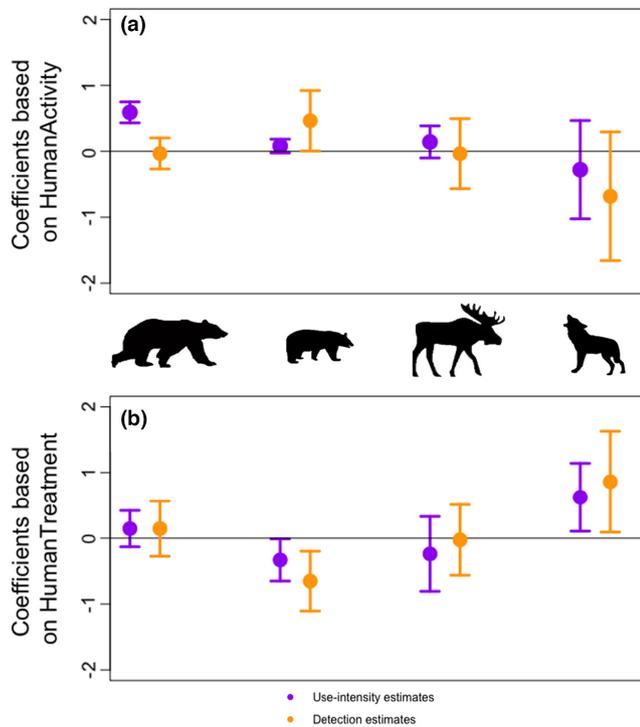


FIGURE 5 Depiction of how *HumanActivity* (panel a) and *HumanTreatment* (panel b) affected all species. In purple is the impact of both variables on wildlife use-intensity (taken from negative binomial regressions of brown bear, black bear and moose data, and a Poisson regression of wolf data). Estimates were obtained by running full models for all species (Appendix S1: Table S5). In orange is the impact of both variables on detection estimates, which we obtained from running full detection models for each species (see Table 2 for variables) with a null occupancy model (brown bear, wolf) or accounting for the impact of tree diameter at breast height (DBH; black bear, moose) on occupancy. Estimates are below zero if the species were less likely to be detected in areas of higher *HumanActivity* or were less likely to be detected in a high-impact *HumanTreatment* area, and estimates are above zero if either human-use-related variable (high human activity or high-impact treatment) positively impacted the probability of detection. Error bars represent ± 1 SE. A table of all coefficients from the full detection models for each species is shown in Table S7

in a protected area. Visual inspection of the detection data revealed two important thresholds: detections did not exceed five per week for any of our four focal species unless human activity was absent, and detections at all backcountry sites dropped to zero per week at *HumanActivity* levels higher than approximately 30 camera minutes (Figure 2), roughly corresponding to 40 visitors per week (Figure S1). This pattern was especially pronounced in wolves, which were not detected at all at the site with the most human use. Additionally, our findings indicate that wildlife responses to human activity may be underestimated unless both spatial and temporal responses are examined, and management of protected areas should consider both when making visitor management decisions.

Moose were unaffected by humans spatially, but in sites that were in a high-impact treatment, moose shifted their activity patterns to

align with when humans were most active (Figure 6). This pattern, in combination with the strong temporal avoidance of humans by wolves, supports the hypothesis that moose may be using human activity as a temporal shield to protect them from predation. Atickem et al. (2014) similarly found that mountain nyala (*Tragelaphus buxtoni*) used humans as a temporal shield during the day—leveraging the fact that predators were avoiding humans during that time. Our results contrast with a meta-analysis that found substantial increases in herbivore nocturnality in response to humans (Gaynor et al., 2018). A temporal human shield is difficult to demonstrate using observational studies because differences in temporal activity patterns between wildlife and humans may be due to natural differences in diel cycles rather than avoidance or attraction responses. In sites where we were able to implement it, our experimental cross-over design removed the influence of potentially confounding site-specific effects and controlled for natural diel patterns, allowing us to rigorously assess the influence of human activity on the spatial and temporal activity patterns of wildlife.

Despite their use of humans as temporal shields, moose did not use humans as spatial shield (Figure 6)—contrasting other studies of ungulates (Berger, 2007; Hebblewhite et al., 2005; Sarmento & Berger, 2017). Furthermore, when the Bartlett Cove outlier was removed from the use-intensity analyses, moose used areas of high human activity less intensely, indicating some level of spatial avoidance outside of the site with the most human activity, and potential habituation within the Bartlett Cove area. These contrasting patterns of moose responses to humans may signify substantial variation among individuals, whereby most individuals use areas of human activity less intensely, but when they cannot avoid these areas spatially, they may use human presence as a ‘shield’ from predators. Over time, this process may lead to a habituated population, especially in protected areas where recurring benign encounters with humans can facilitate habituation (Found, 2019). Analysis of individual variation in diel patterns and boldness behaviour among individuals, facilitated by GPS tracking technology, would shed new light on the mechanisms by which wildlife responses to recreation can change over time (Marion et al., 2020).

Black bears also had opposing temporal and spatial responses to humans: they slightly shifted their activity patterns throughout the day to avoid when humans were most active but were more likely to be detected in areas of higher *HumanActivity* and used high-impact *HumanTreatment* sites areas more frequently than low-impact ones (Figure 6). MacHutchon et al. (1998) similarly found that diurnal black bears may become nocturnal in response to humans, but also reported that black bears avoided areas with high brown bear occurrence and that the presence of humans may have offered black bears protection from brown bears. Our findings support this, and while the *Brown* covariate was not included in the top black bear occupancy model, black bear detection probability tended to decrease with increasing detections of brown bears. Black bear avoidance of people temporally—by shifting their activity throughout a day to avoid coinciding with when humans are most active—may facilitate spatial coexistence, and inspection of black bear detection

TABLE 4 Estimates of space use-intensity for each species. Use-intensity differs from estimating occupancy probability, which can remain constant even while use-intensity varies, and we were interested in understanding how frequently wildlife used the study areas when humans were around versus when they were not. To capture this variation, we examined spatial activity of each species using a negative binomial regression with a site random effect for brown bears, black bears and moose, and a Poisson regression with a site random effect for wolves. Intercept is listed first, then data are sorted by the absolute value of z score for each species (highest to lowest). Human-related variables are bolded

Species	Estimate	SE	Z value	p-value
Brown Bear				
(Intercept)	-1.636	0.268	-6.102	<0.0001
Habitat (Shore)	0.561	0.127	4.412	<0.0001
Year (2018)	0.521	0.127	4.117	<0.0001
Season (Late)	-0.374	0.126	-2.975	0.0029
DBH	0.261	0.228	1.145	0.2523
HumanTreatment (High)	0.146	0.141	1.034	0.3009
HumanActivity	0.059	0.081	0.73	0.4656
Black Bear				
(Intercept)	-5.354	2.006	-2.669	0.0076
Year (2018)	0.489	0.118	4.15	<0.0001
Season (Late)	-0.313	0.117	-2.681	0.0073
Habitat (Shore)	-0.255	0.117	-2.191	0.0285
HumanTreatment (High)	-0.33	0.164	-2.018	0.0436
HumanActivity	0.08	0.053	1.517	0.1293
DBH	0.087	0.058	1.491	0.1359
Moose				
(Intercept)	-1.869	0.445	-4.195	<0.0001
Season (Late)	-0.852	0.204	-4.175	<0.0001
Year (2018)	0.319	0.213	1.494	0.135
HumanActivity	0.142	0.124	1.146	0.252
HumanTreatment (High)	-0.238	0.291	-0.819	0.413
DBH	0.155	0.4	0.387	0.699
Habitat (Shore)	0.06	0.212	0.283	0.777
Wolf				
(Intercept)	-4.593	0.439	-10.455	<0.0001
Habitat (Shore)	1.088	0.268	4.058	<0.0001
Year (2018)	0.677	0.246	2.747	0.006
HumanTreatment (High)	0.624	0.264	2.367	0.0179
DBH	-0.319	0.275	-1.16	0.2462
HumanActivity	-0.279	0.381	-0.733	0.4639
Season (Late)	0.16	0.235	0.682	0.495

Abbreviation: DBH, diameter at breast height.

data showed an increase in detections at Bartlett Cove (the site with highest human use), potentially indicating a shift to habituation when exposed to more constant human activity. The contrasting spatial and temporal responses of black bears and moose to humans highlight the complexity of wildlife-human interactions, and future research combining multiple sampling approaches may be necessary to tease apart factors that influence wildlife responses to recreation.

We did not detect a strong spatial or temporal response of brown bears to humans (Figure 6), contrasting studies that showed brown bear avoidance (both spatially and temporally) of areas with high human-use (Gibeau et al., 2002; Nevin & Gilbert, 2005). We may not have detected this avoidance behaviour because certain brown bears may be habituated to people in Glacier Bay such that human presence is not a strong deterrent. Wheat and Wilmers (2016) found

that fear-based avoidance in brown bears was alleviated by habituation in southeast Alaska, whereas non-habituated bears avoided humans. Habituation can occur in protected areas where the bears are protected from hunting and human activity is more controlled (Smith et al., 2005). Similar to black bears, brown bear detection slightly increased at Bartlett Cove, further indicating their potential habituation. Wildlife habituation in areas of concentrated human use may be a consequence of land sparing management techniques, as demonstrated in Denali National Park where visitor use is extremely concentrated along Denali Park road, and in Yellowstone and Grand Teton national parks where bear habituation in roadside habitat has increased (Albert & Bowyer, 1991; Gunther et al., 2015; Smith et al., 2005). Our results indicate that wildlife habituation to humans may begin at surprisingly low levels of human activity.

Main questions:				
Occupancy model: How do humans impact the probability that each species is detected at a site?				
Use-intensity model: How do humans impact how intensely/frequently wildlife use an area?				
Temporal model: Do wildlife increase or decrease their activity levels when humans are most active during the day?				

↓

Common to all species

- Wildlife detections did not exceed 5 per week unless people were absent
- Wildlife detections dropped to zero at backcountry sites as human activity approached 30 camera minutes, or ~40 people per week

FIGURE 6 Species-specific responses to humans spatially (as demonstrated by occupancy model results and use-intensity model results) and temporally. The magnitude of the arrows represents the relative magnitude of the effect of humans on wildlife. Brown bears were unaffected spatially or temporal by human activity. Black bears were more likely to be detected in areas of human activity but used those areas less intensely, and when humans were around, black bears shifted their activity patterns slightly to avoid when people were most active. Moose were no more likely to be detected in high-impact treatment versus low-impact treatments and did not use either of those areas more frequently than the other. However, when humans were around, moose shifted their activity patterns to align with when people were most active. Wolves were no more likely to be detected in areas of high-impact treatment versus low-impact treatment; however, they used the high-impact treatment areas more frequently. Wolves also strongly avoided humans temporally—dropping their activity to nearly zero during midday when humans were most active

Species that are most sensitive to humans may be the most difficult to demonstrate avoidance due to low detections (Gaynor et al., 2018). We rarely detected wolves on our camera traps (Appendix S1: Table S3) and suspect the lack of significant human-related covariates in wolf models was due primarily to low statistical power. Wolves were not detected at all in the highest human use site (Bartlett Cove), or at any site when *HumanActivity* exceeded 20 camera minutes (roughly corresponding to 30 visitors per week; Figure 2; Figure S1). This strong spatial avoidance of humans is consistent with other studies (Karttinen et al., 2005; Whittington et al., 2005). Additionally, while low sample size likely impacted our results, during high-impact treatments wolves increased their activity at night and avoided humans during midday (Figure 4d), consistent with the findings of Gaynor et al. (2018). However, when unable to avoid human spatially, wolves used high-impact treatment areas more frequently (Figure 6). This again highlights the potential impact that individual variation may have on our results—potentially compounded by low sample size of detections of wolves.

The imperfect application of the high-impact versus low-impact treatment in this study emphasizes the challenge of using an experimental approach in studies of recreational impacts on wildlife. In Glacier Bay, only tour vessels were mandated to follow our experimental design and use of study sites by private and charter vessels

(which also drop tourists off on shoreline areas) was not regulated, thereby leading to increased human activity at two sites, Sandy Cove and Hunter Cove, during low-impact treatments (Figure 3b,c). This impacted our black bear occupancy model results (they were the only species for which *HumanTreatment* was included in the top model) such that *HumanActivity* and *HumanTreatment* had opposite impacts on detection. We accounted for this imperfect application of treatment by switching the *HumanTreatment* designations for the two impacted sites—and their respective paired sites—to align with how many human camera minutes (*HumanActivity*) were recorded. When we did this, contradictory black bear occupancy model results were no longer detected: black bear detection was higher in areas with higher *HumanActivity* and in high-impact treatment sites (Appendix S1: Table S6).

We showed that even low levels of outdoor recreation can alter wildlife spatial and temporal activity; however, land sparing and land sharing strategies are exclusively informed by spatial ecology (Pressey et al., 2007) and do not currently address temporal disturbance. 'Temporal zoning' can mitigate consequences of wildlife temporal partitioning in response to human activity (Gaynor et al., 2018) and is currently used in protected areas to limit human activity during breeding seasons (Larson et al., 2016). However, here we demonstrated that low levels of human activity can alter wildlife behaviour

throughout a day; therefore, some combination of spatial and more granular temporal zoning may be necessary to promote human-wildlife coexistence in protected areas. This is a challenging task, and in Glacier Bay it means balancing the contrasting temporal responses of moose versus black bears and wolves with the fact that all species demonstrated some level of spatial avoidance of humans (Figure 2). Further complicating the situation is a growing population of people who seek to visit wild places and view wildlife without displacing the very animals they hope to watch. One solution is to continue to utilize the water-based wildlife viewing that occurs in Glacier Bay. Allowing people to view wildlife from a vessel, rather than on land, would allow wildlife to more freely use their space while providing people with a memorable wilderness experience. Another potential solution is to use threshold metrics to determine which management strategy—or combination of strategies—to use and where. And while we detected species-specific responses to humans in Glacier Bay, it would be difficult to manage a protected area for each species individually. Instead, management can focus on what species have in common. For instance, our results indicate that a threshold level of *HumanActivity* roughly corresponding to 40 visitors per week potentially displaced all four wildlife species. Land sharing management techniques (or ‘business as usual’ in Glacier Bay) may adequately mitigate human disturbance to wildlife up to that threshold. In areas of Glacier Bay where visitation commonly exceed 40 people per week, land sparing strategies that concentrate use in specific areas—perhaps in combination with temporal zoning that restrict human use during important times of year—may be necessary to promote coexistence.

AUTHOR CONTRIBUTIONS

Mira L. T. Sytsma, Laura R. Prugh and Tania Lewis conceived the ideas, designed the methodology and collected the data; Mira L. T. Sytsma analysed the data with guidance from Beth Gardner and Laura R. Prugh; Mira L. T. Sytsma and Laura R. Prugh led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data used for the analysis are uploaded in a Dryad repository (<https://doi.org/10.5061/dryad.hx3ffbghb>).

ORCID

Mira L. T. Sytsma  <https://orcid.org/0000-0002-4250-7286>

Tania Lewis  <https://orcid.org/0000-0001-5687-3722>

Beth Gardner  <https://orcid.org/0000-0002-9624-2981>

Laura R. Prugh  <https://orcid.org/0000-0001-9045-3107>

REFERENCES

- Albert, D. M., & Bowyer, R. T. (1991). Factors related to grizzly bear-human interactions in Denali National Park. *Wildlife Society Bulletin*, 19, 339–349.
- Atickem, A., Loe, L. E., & Stenseth, N. C. (2014). Individual heterogeneity in use of human shields by mountain Nyala. *Ethology*, 120, 715–725. <https://doi.org/10.1111/eth.12242>
- Balmford, A., Green, J. M. H., Anderson, M., Beresford, J., Huang, C., Naidoo, T., Walpole, M., & Manica, A. (2015). Walk on the wild side: Estimating the global magnitude of visits to protected areas. *PLoS Biology*, 13, e1002074. <https://doi.org/10.1371/journal.pbio.1002074>
- Bateman, P. W., & Flemming, P. A. (2017). Are negative effects of tourist activities on wildlife over-reported? A review of assessment methods and empirical results. *Biological Conservation*, 211, 10–19. <https://doi.org/10.1016/j.biocon.2017.05.003>
- Beissinger, S. R., Ackerly, D. D., Doremus, H., & Machlis, G. (2017). *Science, conservation and National Parks* (p. 440). University of Chicago Press.
- Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, 3, 620–623. <https://doi.org/10.1098/rsbl.2007.0415>
- Bleicher, S. (2017). The landscape of fear conceptual framework: Definition and review of current applications and misuses. *PeerJ*, 5, e3772. <https://doi.org/10.7717/peerj.3772>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference. A practical information-theoretic approach* (2nd ed.). Springer.
- Carter, N. H., Shrestha, B. K., Karki, J. B., Pradhan, N. M., & Liu, J. (2012). Coexistence between wildlife and humans at fine spatial scales. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 15360–15365. <https://doi.org/10.1073/pnas.1210490109>
- Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., & Boyce, M. S. (2012). Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS ONE*, 7, e50611. <https://doi.org/10.1371/journal.pone.0050611>
- Cole, D. N. (1992). Modeling wilderness campsites: Factors that influence amount of impact. *Environmental Management*, 16, 255–264. <https://doi.org/10.1007/BF02393831>
- Connor, C., Streveler, G., Post, A., Monteith, D., & Howell, W. (2009). The neoglacial landscape and human history of Glacier Bay, Glacier Bay National Park and preserve, southeast Alaska, USA. *Holocene*, 19, 381–393. <https://doi.org/10.1177/0959683608101389>
- Czech, B., Krausman, P. R., & Devers, P. K. (2000). Economic associations among causes of species endangerment in the United States. *Bioscience*, 50, 593–601. [https://doi.org/10.1641/0006-3568\(2000\)050\[0593:eaacos\]2.0.co;2](https://doi.org/10.1641/0006-3568(2000)050[0593:eaacos]2.0.co;2)
- Dingemans, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society B: Biological Sciences*, 271, 847–852. <https://doi.org/10.1098/rspb.2004.2680>
- Fiske, I., & Chandler, R. (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, 43, 1–23. <https://doi.org/10.18637/jss.v043.i10>
- Found, R. (2019). Personality influences habituation behavior in ungulates. *Journal of Ethology*, 37, 47–58. <https://doi.org/10.1007/s10164-018-0567-7>
- Frid, A., & Dill, L. M. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, 6, 11–26. <https://doi.org/10.5751/es-00404-060111>
- Gaynor, K. M., Hohnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, 80, 1232–1235. <https://doi.org/10.1126/science.aar7121>
- George, S. L., & Crooks, K. R. (2006). Recreation and large mammal activity in an urban nature reserve. *Biological Conservation*, 133, 107–117. <https://doi.org/10.1016/j.biocon.2006.05.024>

- Gibeau, M. L., Clevenger, A. P., Herrero, S., & Wierzchowski, J. (2002). Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. *Biological Conservation*, 103, 227–236. [https://doi.org/10.1016/S0006-3207\(01\)00131-8](https://doi.org/10.1016/S0006-3207(01)00131-8)
- Greenberg, S., & Godin, T. (2015). A tool supporting the extraction of angling effort data from remote camera image. *Fisheries Magazine*, 40, 276–287. <https://doi.org/10.1080/03632415.2015.1038380>
- Gunther, K. A., Wilmot, K. R., Cain, S. L., Wyman, T., Reinertson, E. G., & Bramblett, A. M. (2015). Habituated grizzly bears: A natural response to increasing visitation in Yellowstone & Grand Teton National Parks. *Yellowstone Science*, 23, 33–39.
- Hebblewhite, M., White, C. A., Nietvelt, C. J., Mckenzie, J. A., Hurd, T. E., Fryxell, J. M., Bayley, S., & Paquet, P. C. (2005). Human activity mediates a trophic cascade caused by wolves. *Ecology*, 86, 2135–2144. <https://doi.org/10.1890/04-1269>
- Jacobson, A. P., Riggio, J., Tait, A. M., & Baillie, J. E. M. (2019). Global areas of low human impact ('low impact areas') and fragmentation of the natural world. *Scientific Reports*, 9(14179), 14179. <https://doi.org/10.1038/s41598-019-50558-6>
- Kaartinen, S., Kojala, I., & Colpaert, A. (2005). Finnish wolves avoid roads and settlements. *Annales Zoologici Fennici*, 42, 523–532.
- Keim, J. L., Lele, S. R., DeWitt, P. D., Fitzpatrick, J. J., & Jenni, N. S. (2019). Estimating the intensity of use by interacting predators and prey using camera traps. *Journal of Animal Ecology*, 88(5), 690–701. <https://doi.org/10.1111/1365-2656.12960>
- Larson, C. L., Reed, S. E., Merenlender, A. M., & Crooks, K. R. (2016). Effects of recreation on animals revealed as widespread through a global systematic review. *PLoS ONE*, 11(12), e0167259. <https://doi.org/10.1371/journal.pone.0167259>
- Leung, Y., & Marion, J. L. (1999). Spatial strategies for managing visitor impacts in national parks. *Journal of Park and Recreation Administration*, 17, 20–38.
- MacHutchon, A. G., Himmer, S., Davis, H., & Gallagher, M. (1998). Temporal and spatial activity patterns among coastal bear populations. *Ursus*, 10, 539–546.
- MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2006). *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence*. Elsevier Publishing, Inc.
- Marion, J. L., & Farrell, T. A. (2002). Management practices that concentrate visitor activities: Camping impact management at Isle Royale National Park. *Journal of Environmental Management*, 66, 201–212. <https://doi.org/10.1006/jema.2002.0584>
- Marion, S., Davies, A., Demšar, U., Irvine, R. J., Stephens, P. A., & Long, J. (2020). A systematic review of methods for studying the impacts of outdoor recreation on terrestrial wildlife. *Global Ecology and Conservation*, 22, e00917. <https://doi.org/10.1016/j.gecco.2020.e00917>
- Meredith, M., & Ridout, M. (2017). *Overlap: Estimates of coefficient of overlapping for animal activity patterns*. R package version 0.3.0. <http://CRAN.R-project.org/package=overlap>
- National Park Service IRMA Portal (Integrated Resource Management Applications). (2020). <https://irma.nps.gov>
- Nevin, O. T., & Gilbert, B. K. (2005). Perceived risk, displacement, and refuging in brown bears: Positive impacts of ecotourism? *Biological Conservation*, 121, 611–622. <https://doi.org/10.1016/j.biocon.2004.06.011>
- Niedballa, J., Courtiol, A., & Sollmann, R. (2017). *camtrapR: Camera trap data management and preparation of occupancy and spatial capture-recapture analyses*. R package version 0.99.9. <https://CRAN.R-project.org/package=camtrapR>
- Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M., & Wilson, K. A. (2007). Conservation planning in a changing world. *Trends in Ecology & Evolution*, 22, 583–592. <https://doi.org/10.1016/j.tree.2007.10.001>
- Prugh, L. R., Sinclair, A. R. E., Hodges, K. E., Jacob, A. L., & Wilcove, D. S. (2010). Reducing threats to species: Threat reversibility and links to industry. *Conservation Letters*, 3, 267–276. <https://doi.org/10.1111/j.1755-263X.2010.00111.x>
- Rovero, R., Martin, E., Rosa, M., Ahumada, J. A., & Spitale, D. (2014). Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. *PLoS ONE*, 9, 1–12. <https://doi.org/10.1371/journal.pone.0103300>
- Rowcliffe, J. M., Kays, R., Kranstauber, B., Carbone, C., & Jansen, P. A. (2014). Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, 5, 1170–1179. <https://doi.org/10.1111/2041-210x.12278>
- Sarmento, W. M., & Berger, J. (2017). Human visitation limits the utility of protected areas as ecological baselines. *Biological Conservation*, 212A, 316–326. <https://doi.org/10.1016/j.biocon.2017.06.032>
- Shannon, G., Cordes, L. S., Hardy, A. R., Angeloni, L. M., & Crooks, K. R. (2014). Behavioral responses associated with a human-mediated predator shelter. *PLoS ONE*, 9, e94630. <https://doi.org/10.1371/journal.pone.0094630>
- Smith, J. A., Suraci, J. P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L. Y., & Wilmers, C. C. (2017). Fear of the human 'super predator' reduces feeding time in large carnivores. *Proceedings of the Royal Society B: Biological Sciences*, 284, 1857. <https://doi.org/10.1098/rspb.2017.0433>
- Smith, T. S., Herrero, S., & DeBruyn, T. D. (2005). Alaskan brown bears: Habituation and humans. *Ursus*, 16, 1–10. [https://doi.org/10.2192/1537-6176\(2005\)016\[0001:abbhah\]2.0.co;2](https://doi.org/10.2192/1537-6176(2005)016[0001:abbhah]2.0.co;2)
- Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, 22(10), 1578–1586. <https://doi.org/10.1111/ele.13344>
- Taylor, A. R., & Knight, R. L. (2003). Wildlife responses to recreation and associated visitor perceptions. *Ecological Applications*, 13, 951–963. [https://doi.org/10.1890/1051-0761\(2003\)13\[951:WRTRA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)13[951:WRTRA]2.0.CO;2)
- Thorsen, N. H. (2016). *Anthropogenic effects on spatiotemporal activity patterns and interactions in a predator-prey assemblage* (Master's thesis). Norwegian University of Life Sciences.
- Toms, J. D., & Lesperance, M. L. (2003). Piecewise regression: A tool for identifying ecological thresholds. *Ecology*, 84, 2034–2041. <https://doi.org/10.1890/02-0472>
- UNEP-WCMC and IUCN. (2016). *Protected planet report 2016*. UNEP-WCMC and IUCN.
- Wheat, R. E., & Wilmers, C. C. (2016). Habitation reverses fear-based ecological effects in brown bears (*Ursus arctos*). *Ecosphere*, 7(7), e01408. <https://doi.org/10.1002/ecs2.1408>
- White, E. M., Bowker, J. M., Askew, A. E., Langner, L. L., Arnold, J. R., & English, D. B. K. (2016). *Federal outdoor recreation trends: Effects on economic opportunities*. Gen. Tech. Rep. PNW-GTR-945. U.S. Department of Agriculture, Forest Service, Pacific Northwest Station. 46 p.
- Whittington, J., St Clair, C. C., & Mercer, G. (2005). Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications*, 15, 543–553. <https://doi.org/10.1890/03-5317>

SUPPORTING INFORMATION

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

How to cite this article: Sytsma, M. L. T., Lewis, T., Gardner, B., & Prugh, L. R. (2022). Low levels of outdoor recreation alter wildlife behaviour. *People and Nature*, 00, 1–13. <https://doi.org/10.1002/pan3.10402>