# Habituation reverses fear-based ecological effects in brown bears (*Ursus arctos*)

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**Abstract**.  Fear induced by human activity is increasingly becoming recognized to influence both behavior and population biology of wildlife. Exposure to human activity can cause animals to avoid human-dominated areas or shift temporal activity patterns, but repeated, benign exposure can also result in habituation of individuals. Habituation is typically viewed as a negative potential consequence of human interactions with wildlife, with effects such as increased vulnerability of habituated animals to predation. Concurrently, the advancement of the understanding of the ecology of fear has shown reduced fitness in species because of behavioral changes in responses to fear of predators—including humans. Here, we test how habituation and fear drive the foraging ecology of brown bears (*Ursus arctos*) feeding on Pacific salmon (*Oncorhynchus* spp.) in Southeast Alaska, USA. We used motion-detecting trail cameras at salmon spawning areas across a gradient of human disturbance to record human and bear activity at fine spatial and extended temporal scales. Higher human activity was associated with increased nocturnality of non-habituated bears, likely leading to suboptimal foraging, but had no effect on habituated individuals. For the top 20% of sites for which human activity was greatest, an average of 78.7% of the activity of non-habituated bears was nocturnal, compared with an average of only 10.2% of the activity of habituated individuals. Habituation of brown bears in this system alleviated perceived risk and avoidance of human activity, allowing habituated individuals to overcome their fear of human presence and maximize foraging opportunities. While habituation may lessen some of the deleterious effects of human activity on large carnivores, the long-term effects of habituation may be negative, as habituated individuals may be at greater risk of depredation. Future research should examine whether habituated bears and their lower perceived risk of human activity ultimately experience smaller population-level effects of human disturbance than non-habituated individuals.

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## INTRODUCTION

The ecology of fear predicts that individuals will avoid forage patches or times of day where the perceived threat of predation is elevated (Bednekoff 2007, Brown and Kotler 2007). This can cause suboptimal foraging, resulting in increased energetic expenditures (Godin and Sproul 1988, Lima and Dill 1990, Cooke et al. 2003), reduced foraging gains (Bednekoff 2007, Jones and Dornhaus 2011, Eccard and Liesenjohann 2014), and reduced pregnancy rates (Fraser and Gilliam 1992, Creel et al. 2007, Travers et al. 2010). Fear induced directly by humans can influence both the behavior (Wilmers et al. 2013) and population biology of animals (Berger 2007)

with impacts that can cascade through food webs (Hebblewhite et al. 2005, Wang et al. 2015).

As exposure to human activity increases, animals can respond by avoiding human-dominated areas, or by shifting temporal patterns of activity to reduce overlap with human presence (Olson et al. 1998, Frid and Dill 2002, Wang et al. 2015). Some individuals, however, may experience repeated, benign interactions with humans and undergo habituation, leading to some degree of human tolerance (Samia et al. 2015). This is particularly true of animals living in nature-based tourism or ecotourism destinations (Geffroy et al. 2015).

While the advancement of the understanding of the ecology of fear has shown reduced fitness in species because of behavioral changes in responses to fear of humans, habituation may alleviate some of these effects. Habituation is typically viewed as a negative potential consequence of human interactions with wildlife (Higham and Shelton 2011); recent work has indicated that habituation can lead to increased vulnerability of prey animals to predators. For instance, fox squirrels (*Sciurus niger*) habituated to humans were less responsive to predator vocalizations than non-habituated individuals (Mccleery 2009). However, habituation may not be strictly negative if tolerance of humans relieves fear-induced foraging costs, which could potentially benefit species with no natural predators, such as brown bears (*Ursus arctos*).

Here, we examine how fear and habituation influence the foraging patterns of brown bears feeding on Pacific salmon (*Oncorhynchus* spp.) in northern Southeast Alaska, USA. By comparing foraging patterns between known habituated and non-habituated bears, we are able to understand two sides of the same coin—the influence of human-induced fear on the foraging behavior of bears and the degree to which habituation can reduce fear-based effects.

Brown bears, like many other large carnivores, are threatened by human-induced mortality, habitat loss, and habitat fragmentation (e.g., McLellan and Shackleton 1988, Servheen et al. 1990, Paetkau et al. 1998, Proctor et al. 2005, Ordiz et al. 2011). Further, brown bears' feeding activities provide an additional source of human–wildlife conflict; in salmon ecosystems throughout the Pacific Northwest, bears' access to Pacific salmon may be impeded by human recreational activities, such as ecotourism, boating, and sport fishing. Previous studies have identified that bears, like other large carnivores, generally avoid human activities throughout their range (Mace et al. 1996, Rode et al. 2006, Nellemann et al. 2007). While brown bears in salmon ecosystems may perceive areas of high human activity as risky and thus alter their behavior to reduce encounters with humans (e.g., by becoming more nocturnal or avoiding areas with high human activity), they may be limited in the extent of their responses because of the need to be close to salmon spawning areas.

Research suggests that brown bears' ability to successfully capture salmon may vary based on environment and visibility. For example, in the clear-water Glendale River in British Columbia, Klinka and Reimchen (2002) found a marginal trend of increased capture efficiency with reduced light levels, which they suggest is due to reduced evasive behavior of salmon at night. Crupi (2003), however, found that in the glacially turbid Chilkoot watershed in Southeast Alaska, bears had increased capture efficiency with increased light levels, due to better visual detection of salmon during daylight. These findings suggest that in glacially fed systems where visibility of salmon is poor, nighttime foraging is likely suboptimal. Salmon are an extremely important resource for brown bears, as bears avoid winter food limitation by storing fat during pulses of spawning salmon and subsequently hibernating during winter. Bears that consume more salmon have been found to have greater body mass, have larger litters, and subsist at higher population densities (Hilderbrand et al. 1999). If human disturbance limits the amount of time bears spend fishing for and consuming salmon or results in bears foraging suboptimally, weight gain could be restricted, potentially limiting survival or reproductive success.

A clear understanding of the forces that influence bear activity patterns is essential for successful management of human recreational activities and to avoid conflicts between brown bears and recreationists. Olson et al. (1998) identified crepuscular patterns of activity in brown bears within Katmai National Park, Alaska, and suggested that this crepuscular pattern may reflect avoidance of humans. Similarly, Martin et al. (2010) illustrated that brown bear avoidance of human-disturbed areas was most acute during

periods of elevated human activity, particularly during daylight hours.

Human-derived shifts in bear activity patterns, however, may occur unevenly across bear populations (Quinn et al. 2014). While some bears may avoid human activity, others may undergo habituation. Habituation of brown bears can have negative consequences. Habituated individuals are more likely to become food-conditioned, and food-conditioned bears are more likely to be lethally removed from a population than non-habituated, non-food-conditioned individuals (Mattson et al. 1992). Habituated bears are also at higher risk for being injured or killed by motor vehicles or trains (Benn and Herrero 2002). Additionally, habituated individuals are more likely to be approached by humans, which could result in bear-inflicted injury and lethal removal of the bear. Herrero et al. (2005), however, suggest that habituated bears might be better able to access resources that exist near centers of human activity. Bear-to-human habituation could benefit bears as habituation lessens unnecessary energy expenditure associated with avoiding human activity (Smith et al. 2005) and could improve feeding opportunities. In this sense, habituated individuals might overcome fear of humans as perceived top predators, but it is unknown the extent to which habituation influences bear activity patterns.

Quantitative data collection on activity patterns of bears using visual observation is difficult because there are few opportunities to observe individuals across large spatial scales for entire 24-h periods, and visual observation is limited during nighttime hours. Remote, motion-detecting trail cameras operate continuously, can "capture" bears at all times of a 24-h day, can be left unattended for long periods of time, and record information about the times of day bears are active, revealing diel activity patterns. Further, identifying marks on bears can be used to distinguish individuals in photographs, which can be used to compare activity patterns among bears.

Here, we used motion-detecting cameras at salmon spawning areas across a gradient of human disturbance in the Chilkoot watershed in Southeast Alaska to test how habituation and fear drive the foraging ecology of brown bears. We predicted that: (1) fear-based effects of human presence on foraging will be present in non-habituated bears, leading non-habituated individuals to forage suboptimally by becoming increasingly nocturnal as human activity increases, and (2) fear-based effects of human presence on foraging will be reduced in habituated bears, leading to greater temporal overlap in activity between habituated individuals and humans and more optimal foraging.

*Study site*

We conducted our study in the Chilkoot Valley, located 12 km northwest of the community of Haines, Alaska (Fig. 1A). Chilkoot Lake is a glacially turbid lake, approximately 6 km long and 2 km wide. The lower Chilkoot River travels just over 2 km before reaching the ocean. The upper Chilkoot River, originating from the Ferebee Glacier, flows approximately 26 km to the point where it enters Chilkoot Lake. The Valley is narrow, bordered closely to the east by an unnamed mountain range and to the west by the Takshanuk Mountains.

More than 130,000 people visit the Chilkoot River each year, largely for fishing and wildlife viewing opportunities between the months of July and September (Crupi 2003). Human activity is primarily concentrated along a narrow access road that borders the lower river, and a boat landing, picnic area, and campground on the south end of the lake. Access to the eastern side of the lake is possible only by watercraft, but the western side of the lake is accessible via an abandoned two-track dirt road that parallels the western lake and upper river.

The lake and both upper and lower river provide spawning substrate for three species of Pacific salmon. Sockeye salmon (*O. nerka*) return midsummer and spawn primarily along the western shore of the lake and two areas of the upper river. Pink salmon (*O. gorbuscha*) spawn in late summer along the lower river, and coho (*O. kisutch*) follow in early autumn, spawning in the upper river and the northeast corner of the lake. Spawning sites in this area occur in discrete patches, and the rugged terrain surrounding the lake and river largely prevents aggregations of multiple bears feeding simultaneously at spawning sites.

## METHODS

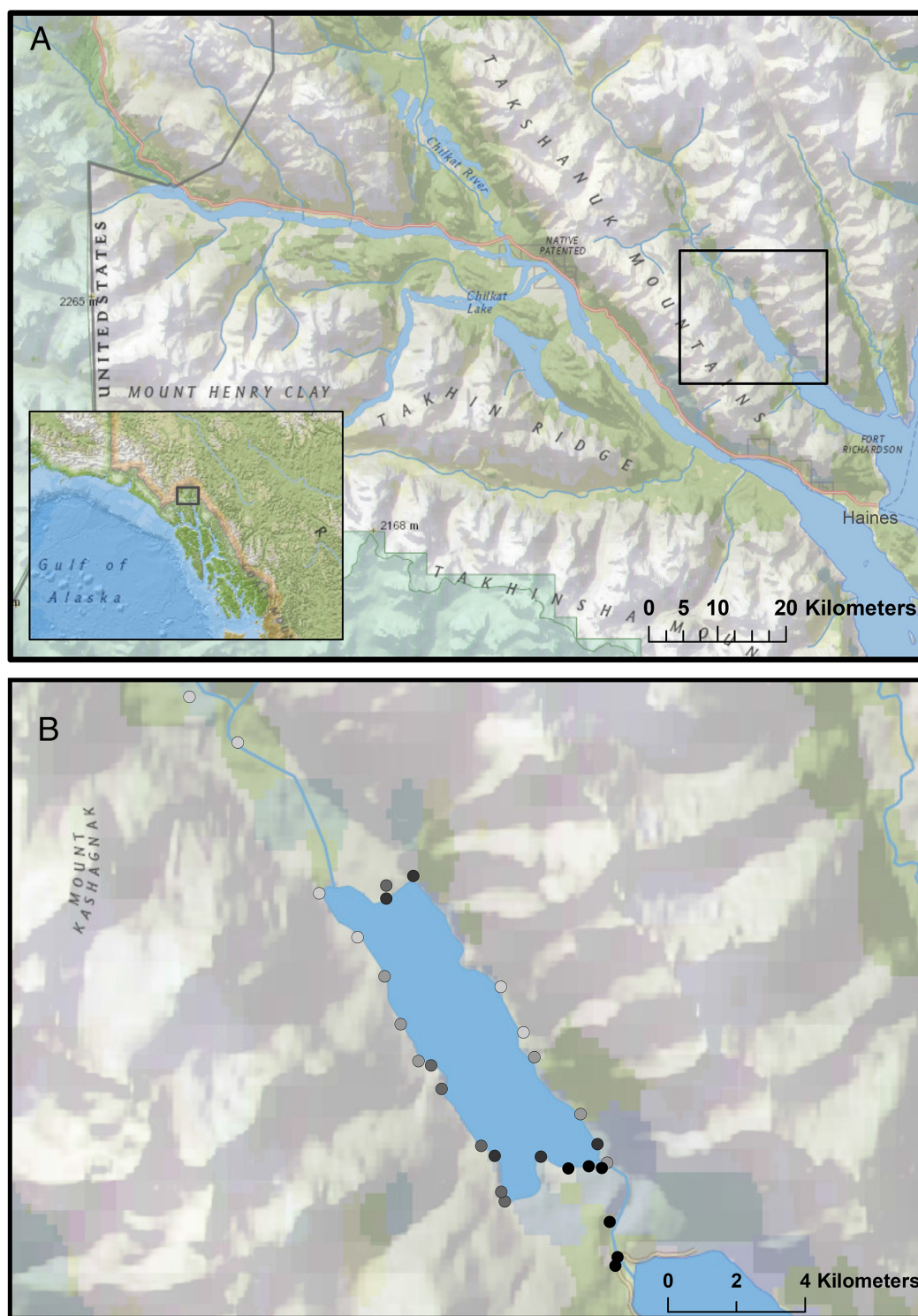We used motion-detecting cameras to observe human and bear activity patterns at fine spatial

Fig. 1.    (A) Chilkoot watershed near Haines, Alaska. (B) Locations of camera trapping sites. The relative levels of human activity are indicated by gradient, with the lowest levels of human activity represented by the lightest shades and the highest levels of human activity represented by the darkest shades of gray.

and extended temporal scales in the Chilkoot watershed (Fig. 1B). We focused our sampling efforts along the river and lake shorelines from the mouth of the lower river to the upper river approximately 4 km upstream of the inlet into the lake. We placed cameras (Bushnell Trophycam; Bushnell Corp., Overland Park, Kansas, USA) at 30 sites to monitor activity from June to October 2014 (Fig. 1B). Cameras were deployed at all known spawning areas. Additional cameras were distributed in the study area at sites that were (1) easily accessible via watercraft and/or foot, (2) along existing game trails, (3) within 50 m of the lakeshore or river, and (4) at least 500 m from an adjacent camera. All cameras were set to take three pictures when triggered with a 1-min delay between successive triggers. Cameras were checked and data were downloaded weekly or every other week, depending on the amount of activity at the site.

For each photograph, we recorded the date, time, location, and species. To reduce pseudoreplication, we defined unique bear visitations as visits with a > 30-min delay between the last photograph from one visit and the first photograph of the next at that site or at any adjacent camera. Family groups were counted as one bear, as cub activity is not independent of its parent.

Two unrelated, adult female bears in the study area were classified as habituated, and both had been previously tagged by the Alaska Department of Fish and Game as part of a study to assess habitat use and movement, thus allowing us to identify them in camera traps. These bears lacked a flight response to humans when foraging, with an overt reaction distance (ORD; Herrero et al. 2005) that was typically < 5 m, even when foraging near large groups of tourists. Non-habituated individuals had higher ORD—while we did not encounter every bear in the study area while in the field, we never personally encountered or observed a non-habituated individual with an ORD less than around 15 m. We identified unique human visits manually. As with the bear photographs, if the camera captured two or more individuals in one photograph, we treated this as one human encounter.

We used several metrics to evaluate the differences in responses to human activity between habituated and non-habituated bears. We used the R package "overlap" for nonparametric kernel density estimation (Ridout and Linkie 2009,

Linkie and Ridout 2011) to first examine temporal partitioning between humans and bears. After converting all time to radians, we used kernel density estimation to generate a probability density distribution of activity patterns for humans, habituated bears, and non-habituated bears based on unique encounters pooled for each sampling site (i.e., camera). We then calculated $\hat{\Delta}$, the overlap term, which is defined as the area under the curve formed by taking the smaller of two density functions at each time point, to compare activity patterns of humans to habituated bears and humans to non-habituated bears (Ridout and Linkie 2009). The overlap term, $\hat{\Delta}$, which ranges from 0 to 1, represents the temporal activity overlap between human and bear activity. If bears and humans share similar activity patterns, we would expect an overlap value ($\hat{\Delta}$) close to 1, whereas dissimilar activity patterns between humans and bears would result in $\hat{\Delta}$ values closer to 0. Ridout and Linkie (2009) outlined three methods for estimating $\hat{\Delta}$ and suggested using $\hat{\Delta}_4$ for larger sample sizes ($n > 75$), which we follow.

Second, we evaluated whether the foraging activity of bears differed among sites with disparate levels of human activity. As foraging at night is suboptimal in this system (Crupi 2003), we calculated the degree of nocturnality observed for bear activity at each camera by identifying the proportion of unique encounters that occurred between sunset and sunrise, using sunrise/sunset times specific to each day of the study. We then ranked camera sites based on the observed number of unique human encounters (i.e., the camera that recorded the highest number of unique human encounters was ranked highest, and the camera that recorded the second highest number of unique encounters was ranked second highest) and compared increasing human presence to the proportion of nighttime encounters observed in bear activity using linear regression, with separate analyses for habituated and for non-habituated bears.

Finally, we assessed differences in diel patterns of bear foraging activity between habituated and non-habituated bears, again using nonparametric kernel density estimation and the coefficient of overlap. We calculated $\hat{\Delta}_4$ for habituated vs. non-habituated bears across all camera sites and across the six sites (top 20%) for which human activity was greatest. We obtained

95% confidence intervals for all overlap estimates from 10,000 bootstrap samples.

## RESULTS

Cameras operated for 4116 cumulative trap nights at the 30 sites. We recorded a total of 154 unique encounters of habituated bears and 1959 unique encounters of non-habituated bears. Human activity was highest along the lower Chilkoot River, boat landing, and campground and decreased sharply toward the north end of the lake and along the upper river (Fig. 1B). Bears were observed at all 30 sites, with the highest numbers of unique encounters occurring at spawning areas along the western shore of the lake and along the lower river.

In accordance with our predictions, temporal partitioning between bear and human activity differed between habituated and non-habituated bears. Overlap between habituated bears and humans was very high (81.3–94.3% overlap; Fig. 2A), whereas overlap between non-habituated bears and humans was less than half that of habituated individuals (40.4–47.7% overlap; Fig. 2B). While habituated bears were primarily active during daylight hours, non-habituated bears were active during crepuscular periods or nocturnally, and most overlap

between non-habituated bears and humans occurred during evening and morning hours.

Additionally, non-habituated bears had less diurnal activity in areas used more heavily by humans. Linear regression revealed that the proportion of nighttime activity for non-habituated bears increased significantly as human activity increased ($P < 0.001$, $R^2 = 0.85$; Fig. 3); in the area of the Chilkoot watershed that sees the highest levels of human activity, non-habituated bears were almost strictly nocturnal. Conversely, there was no relationship between increases in human activity and the proportion of nighttime activity displayed by habituated individuals ($P = 0.49$, $R^2 = 0.07$; Fig. 3).

Overall, the diel patterns of activity of habituated bears differed greatly from diel patterns of non-habituated bears. Particularly in the most human-disturbed areas of the Chilkoot, habituated individuals were primarily diurnal, with activity peaking mid-morning and mid-evening, while the activity patterns of non-habituated bears peaked mid-night. Across all cameras, overlap between habituated and non-habituated bears was low (42.1–54.4% overlap; Fig. 4A), with non-habituated bears consistently displaying more nocturnal activity patterns than habituated individuals. Across the 20% of sites for which human activity was greatest, the overlap between habituated bears and non-habituated
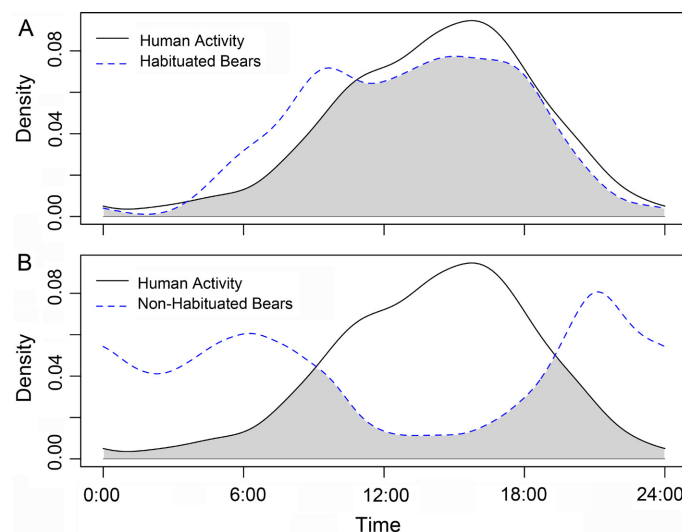


Fig. 2. Overlap of (A) human activity and activity of habituated bears and (B) human activity and activity of non-habituated bears across all camera sites. Gray areas represent periods of time during which both bears and humans are active.
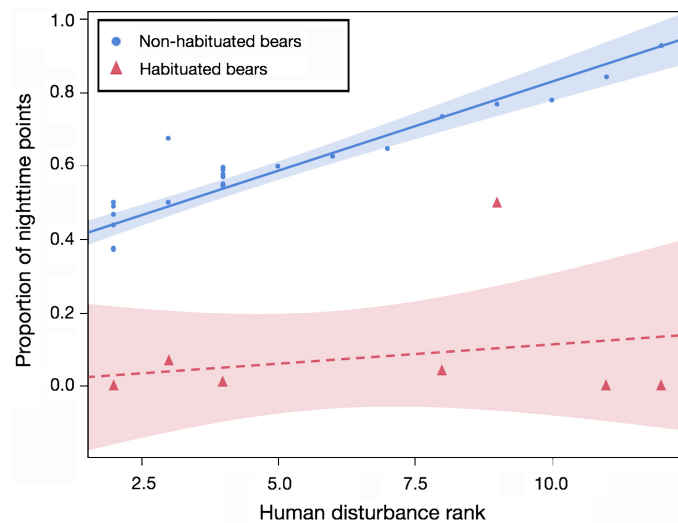
Fig. 3. Linear regression comparing the proportion of nighttime activity displayed by non-habituated (solid line) and habituated (dashed line) bears to the level of human disturbance with 95% confidence intervals (shading). Each point is representative of a single camera site. Cameras were ranked based on the number of unique human encounters observed from the lowest (lowest human disturbance rank) to the highest number of unique human encounters observed (highest human disturbance rank). As human disturbance increased, the proportion of nighttime activity displayed by non-habituated bears increased ($P < 0.001$). There was no relationship between human activity and nighttime activity of habituated individuals ($P = 0.49$).
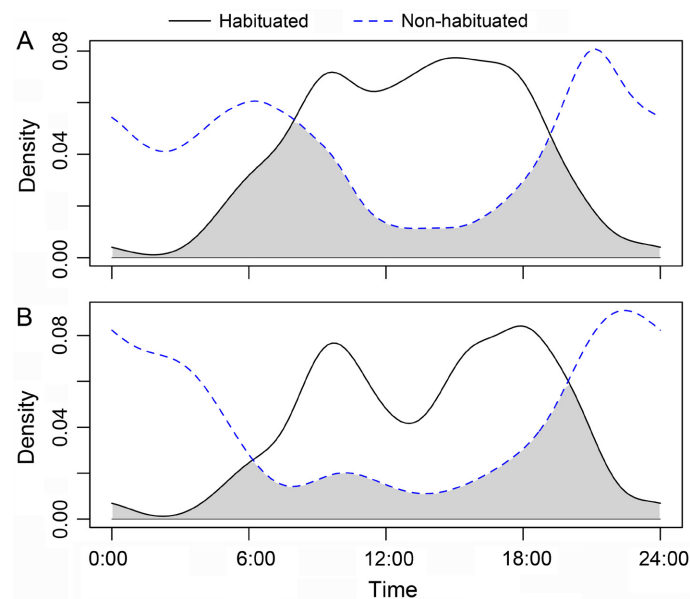


Fig. 4. Comparison of diel activity patterns for habituated vs. non-habituated bears (A) across all camera sites and (B) across the 20% of sites ($n = 6$) at which human activity was greatest. Gray areas represent periods of time during which both habituated and non-habituated bears are active.

bears was even lower, with only 31.5–52.6% overlap (Fig. 4B).

## DISCUSSION

Consistent with our predictions, we found that higher human activity was associated with increased nocturnality for non-habituated bears, which could result in suboptimal foraging, but had no effect on habituated individuals. Habituated bears showed no significant response to differing levels of human disturbance throughout the watershed. Instead, diel patterns of activity for habituated individuals were almost strictly diurnal, suggesting that habituation alleviates fear-based effects in these bears. The two habituated bears in the Chilkoot watershed, with diel activity patterns that were largely diurnal, may benefit from increased daylight during foraging (Crupi 2003), as well as reduced intraspecific competition (Mattson 1990). While previous work has illustrated that habituation of species can either shield animals from predation (Hebblewhite et al. 2005, Berger 2007, Atickem et al. 2014) or make them more

vulnerable to predation (Chan et al. 2010, Geffroy et al. 2015), here we have habituation of a predator alleviating perceived risk and avoidance of human activity, allowing habituated individuals to maximize their foraging opportunities.

Conversely, non-habituated bears displayed fear-based avoidance behavior, feeding almost exclusively during nighttime hours in areas of high human activity. While previous studies have documented shifts toward crepuscular behavior in human-impacted areas, we found that on the lower Chilkoot River, where human activity was highest, non-habituated bears were almost strictly nocturnal, with activity levels peaking in the middle of the night (Fig. 5). Further, proportion of nighttime activity decreased as human activity decreased, suggesting a strong behavioral response by non-habituated bears to human disturbance.

A concurrent genotyping study in the area found that at least 12 of 25 individual bears identified in the study made regular use of the lower Chilkoot River (R. E. Wheat, *unpublished data*). Given that only the two habituated individuals were regularly observed feeding diurnally on the lower Chilkoot River, this suggests that
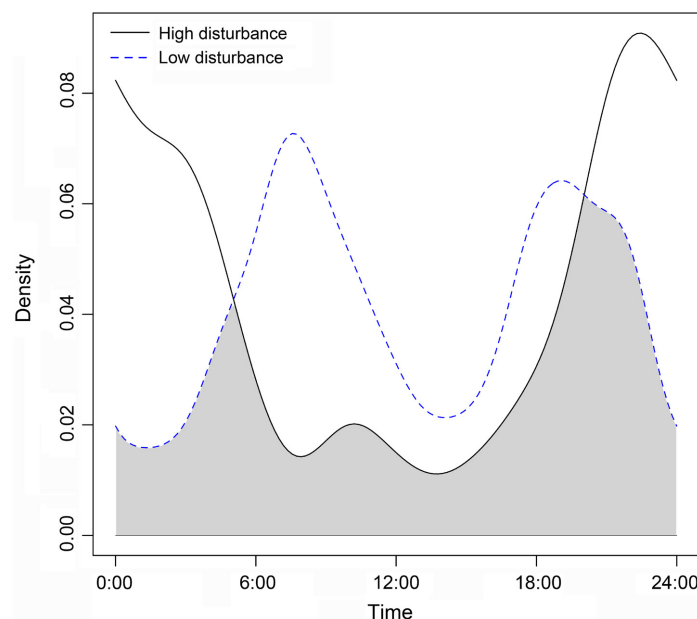


Fig. 5. Diel activity patterns for non-habituated bears across the 20% of sites (*n* = 6) at which human activity was greatest (solid line) and across the 20% of sites (*n* = 6) at which human activity was lowest (dashed line). At high-disturbance sites, activity of non-habituated bears was almost strictly nocturnal, but at sites with low human presence, bears were active diurnally.

a substantial part of the local bear population is being temporally displaced by human activity. Avoidance of human activity could be spatial as well as temporal—at sites in the Chilkoot watershed where human activity was lowest, non-habituated bear activity was distributed more evenly throughout the 24-h day, with the greatest peak in activity occurring mid-morning (Fig. 5). Increased diurnality at sites farther from human-disturbed areas could indicate that at least some individuals avoid human-disturbed areas during daylight but take advantage of foraging opportunities in areas with low human disturbance during these times.

Temporal displacement of non-habituated bears by humans in salmon spawning areas may limit these bears' foraging opportunities. Bears displaced from spawning grounds by human activity can return at alternative times or move to alternative locations to feed on salmon, but availability of salmon may be limited elsewhere depending on the time of year and the size of returning salmon populations—salmon runs returning to the Chilkoot watershed are somewhat asynchronous, with sockeye salmon returning mid-season, followed by a later season run of pink salmon and a late season run of coho, and different salmon species require different spawning substrates and spawn in different locations throughout the watershed. Habituation to human presence allows bears to overcome this displacement, providing extensive access to spawning areas even when recreational use is high.

Limitation to nocturnal foraging opportunities may influence non-habituated bears' ability to maintain adequate food intake. While one previous study found a marginal trend of increased salmon capture efficiency with reduced daylight levels in a clear-water river (Klinka and Reimchen 2002), a study of bear foraging success on salmon spawning grounds in the glacially turbid Chilkoot watershed between 2000 and 2002 found that bears' capture rates of salmon decreased significantly with diminishing daylight and increased significantly with increasing daylight, likely due to better visual detection of salmon during daylight hours (Crupi 2003). These findings suggest that in this system, temporal displacement of non-habituated bears by human activity may have a detrimental effect on bears' foraging success, while habituation releases bears from fear-based

effects of human presence and thus improves foraging opportunities for habituated individuals.

While greater access to spawning salmon and reduced competition for habituated bears may contribute to greater body mass and larger litter sizes (Hilderbrand et al. 1999), the long-term effects of habituation may be negative. In the past 16 yr in the Chilkoot watershed, several of the offspring of the two habituated females in this study have been lethally removed as a result of conflicts with local residents and a lack of wary behavior around humans (A. Crupi, *personal communication*).

Habituation, and the ensuing tolerance of human presence that results, represents one potential outcome of low perceived risk of human activity. Here, we illustrated that habituation of individual brown bears alleviated fear of human presence at a popular recreational fishing and wildlife viewing site, likely leading to improved foraging opportunities for these individuals when compared with non-habituated bears. Nature-based tourism and ecotourism are becoming increasingly popular recreational activities (Knight 2009), and as demand for this type of leisure grows, so too will interactions between humans and wildlife in natural landscapes. Our findings suggest that in some cases habituation may alleviate some of the deleterious effects of human activity on large carnivores, as habituated individuals are more tolerant of human activity. Further research should examine population-level effects of habituation in areas with high human traffic.

## Acknowledgments

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