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Human visitation limits the utility of protected areas as ecological baselines

Wesley M. Sarmento*, Joel Berger

[a] *205 Natural Sciences, 32 Campus Drive, Missoula, MT 59812, Wildlife Biology Program, The University of Montana, USA*
[b] *Barbara Cox Anthony Chair in FWC Biology, Colorado State University, Fort Collins, CO 80523, USA*
[c] *Wildlife Conservation Society, Bronx, New York 10460, USA*

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ABSTRACT

A key goal of protected areas is the conservation of biodiversity. Increasing visitation, however, can compromise ecological integrity. A fundamental conundrum is that if parks are to serve as our most pristine places, then we must understand how human presence alters biological interactions. Species that redistribute themselves closer to people is of growing management concern both in and out of national parks because of 1) human safety, 2) animal health, and 3) ecological consequences. Drivers of distributional change are often dissimilar but may include increased association with people for predator avoidance – the human shield hypothesis. We examine redistribution patterns with comparative, observational, and experimental approaches contrasting ecological responses of an iconic species in an USA national park - Glacier. Specifically, we focused on the role of predator-avoidance and resource enhancement to test whether a cold-adapted alpine obligate, mountain goats, (*Oreamnos americanus*), mediate their distribution by increasing spatial overlap with humans. Individuals that enhanced mineral acquisition through access to human urine concomitantly reduced behavioral and ecological responses to grizzly bear (*Ursus arctos horribilis*) experiments. Goats near people also displayed reduced group sizes, vigilance, use of escape terrain, and forfeited migrations to naturally occurring minerals. Our findings re-enforce the increasing complexities of natural area management because visitation is altering ecological interactions. While protected areas offer some forms of baselines for scientists and enjoyment for millions of visitors, redistribution of species and associated ecological changes signifies that additional care will be needed in what we perceive as pristine and what is anthropogenically-altered.

1. Introduction

Protected areas are the planet's best hope to maintain vignettes of our past and perhaps to garner public support for the protection of wildlife and associated biodiversity (Chape et al., 2005). Globally, terrestrial protected areas receive approximately 8 billion visits per year (Balmford et al., 2015). Increasing human populations and expansion of settlements along the borders of protected areas is leading to habitat destruction and human-wildlife conflict, which often results in retribution killings (Wittemyer et al., 2008; Young et al., 2010). While protected areas are one of several solutions to enhance wildlife conservation, consequent indirect interactions have received less attention (Inskip and Zimmermann, 2009). For instance, the redistribution of ungulates in protected areas is occurring because millions of visitors interact with wildlife in non-consumptive ways (Arlinghaus et al., 2016). Prey species can sometimes shift to areas around humans to capitalize on novel resources or escape predation (Copper and Blumstein, 2015; Geffroy et al., 2015). With increasing nature-based tourism, little is known about the redistribution of species in protected areas nor broad-scale ecological effects (Geffroy et al., 2015; Penteriani et al., 2017).

Across the US, there are > 400 national park units. Collectively, these attract 280 million visitors annually (Berger et al., 2014), and those like Yosemite, Yellowstone, and Grand Canyon receive more than three million/yr. In protected areas, wildlife often habituate to people (Orams, 2002), where an animal's physiological response to humans becomes dimished after repeated non-negative stimulus. This process leads to increased wildlife tolerance to humans at close distances. Tolerance of animals towards people is not a clean cut classification, but can vary widely across individuals and within narrow temporal and/or spatial scales (Steyaert et al., 2014). Close proximity of wildlife to people may lead to the opportunity for wildlife-caused human injury or death. As a consequence, individual animals are often destroyed. To develop conservation solutions to this emerging issue will require an understanding of why animals enhance proximity to people and the discrete role, if any, of human infrastructure such as roads (Fahrig and

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* Corresponding author.
E-mail address: wmsarmento@gmail.com (W.M. Sarmento).

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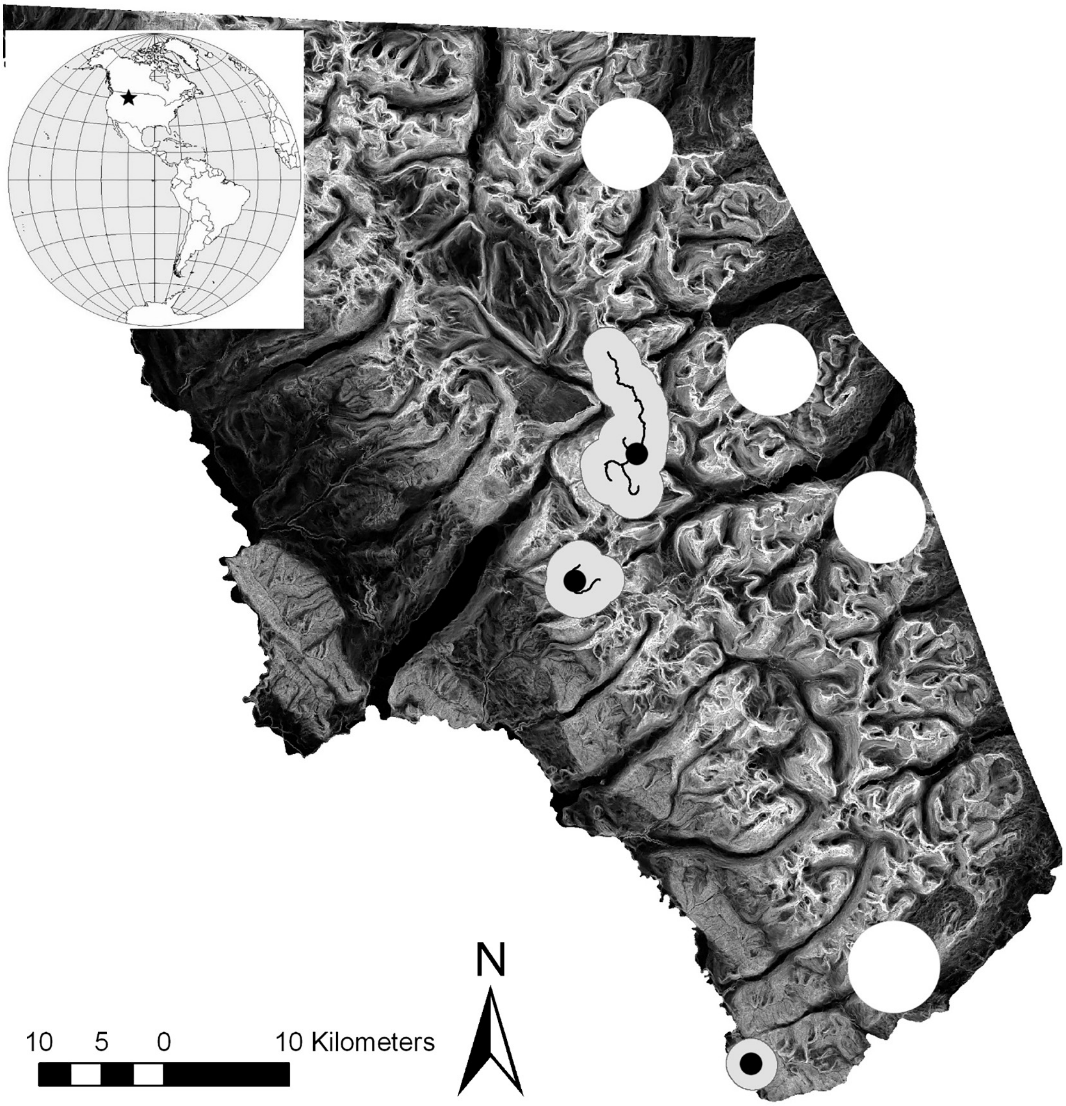

Fig. 1. Map of our study location, Glacier National Park in Montana, USA. The black star on the western hemisphere map denotes the location of our study system on the broader scale. The large white dots represent the general location of our natural mineral sites. The small black dots note the primary place of anthropogenic minerals, while the black lines are trails that goats also used to access human salts. Grey buffers around trails are our 2 km. sampling areas where we defined goats as near people.

Rytwinski, 2009; Ordiz et al., 2014).

The redistribution of populations may occur due to provisioning of novel resources. For example, elk (*Cervus canadensis*) gather on crop lands to access food (Sorensen et al., 2015). Ecological consequences of deliberate food provisioning of wild macaques in a Thailand protected area resulted in reduced home range sizes, core areas, and daily travel (Savini et al., 2015). In other instances, people provide novel nutrients, but only subordinate individuals exploit these resources (Elfström et al., 2014). Evidence suggests that some bears (*Ursus americanus*) do not become food conditioned, but instead reside in towns primarily to escape mortality from dominant conspecifics (Beckmann and Berger, 2003). Choices about habitat selection result from a myriad of competing pressures in which anthropogenic factors become potent.

The human shields hypothesis posits that prey species reduce predation risk by increasing spatiotemporal overlap with people (Berger, 2007). Both in and out of protected areas human shields are noted from at least six sites in North America, Europe, and Africa (Atickem et al., 2014; Elfström et al., 2014; Waser et al., 2014), and likely many more. This three-way interaction of people, predators, and prey may have the strength to cause trophic cascades through changes in prey behavior, distribution, and demographics (Hebblewhite et al., 2005; Shannon et al., 2014). An ecological appreciation of these indirect yet complicated interactions can be improved by understanding 1) its prevalence across taxa and regions, 2) mechanisms that drive redistribution, 3) costs associated if human shields are occurring, and 4) both ecological and social consequences of reduced predation risk. Here we use a case study in which to investigate the potential for human shields in a protected area and then amplify our findings to address the broader issue of ecological baselines in other protected areas.

Mountain goats (*Oreamnos americanus*) are an alpine obligate in mountainous regions of north-western North America. In Glacier National Park (GNP), an area with more than two million annual visitors, goats are not only the local icon but also offer unique opportunities to explore human shield issues, in part because population segments vary dramatically in exposure to people. GNP has a full suite of carnivores including grizzly bears (*Ursus arctos*), which can be important predators of goats (Cote and Beaudoin, 1997; Festa-Bianchet and Côté, 2008). Further, because goats are closely tied to cliff safe terrain (Hamel and Côté, 2007), their ability to adjust to humans may be less than species more catholic in habitat choice.

Goats occasionally leave the security of cliffs to obtain minerals to fulfill their physiological requirements, a behavior most common in summer (Ayotte et al., 2008; Rice, 2010). Natural mineral licks, however, are a limited and patchily distributed (Rice, 2010). In GNP goats are reducing or eliminating their use of natural mineral licks by accessing anthropogenic minerals, often by consuming human urine and sweat. To do this, they presumably tradeoff safety because both human minerals and natural licks are far from cliffs. In other words, the potential for predation is increased by mineral acquisition, especially if predators learn that mineral sites are predictable locales to encounter prey (Rice, 2010). By contrast, predation risk may be lowered by anthropogenic minerals if carnivores avoid sites used by human, hence a human shield.

We tested the human shields hypothesis, and explored alternative explanations, to assess patterns of mountain goat redistribution in Glacier National Park (see Alternative hypotheses in Appendix A). More broadly, however, we investigated the extent to which humans in protected areas modulated the distribution of a native species in part because protected areas form the basis for understanding ecological baselines (Arcese and Sinclair, 1997; Berger, 2008a). We predicted that if a human shield is occurring then in areas of higher human use: 1) predator occurrence will be reduced, and 2) goat sensitivities to potential predators will be lower.

2. Material and methods

2.1. Study area

Glacier National Park (48.6967° N, 113.7183° W), Montana, USA (Fig. 1) contains a full suite of native carnivores including those that prey on mountain goats; wolves (*Canis lupis*), mountain lions (*Puma concolor*), grizzly bears, black bears, and coyotes (*C. latrans*) (Festa-Bianchet and Côté, 2008). The 4100 km^2 park contains 1885–3269 mountain goats (Belt and Krausman, 2012) and is native range for these ungulates.

2.2. Sampling and observations

To test prey reliance on people to escape predation we sampled mountain goat populations from May to September (2013–2015) both near and away from areas of high human visitation. We defined areas near people as those within 2 km of hiking trails at three high human use sites: Logan Pass, Sperry Chalet, and the Walton Lick. We choose a 2 km buffer because at this distance cliff availability was similar between near and away from people sites. Goats near people interacted with visitors on a near daily basis during the summer. Logan Pass receives ~3500 visitors/day during the peak summer season with roughly half of the people hiking the surrounding trails. Sperry Chalet and nearby campgrounds receive over 55 overnight hike-in visitors on an average summer day. Goats near people obtained anthropogenic minerals primarily from small patches (< 0.5 m in diameter) of human urine (Fig. 1). Goats used sweat from backpacks and on handrails to a lesser extent. Goats at the Walton Lick site accessed road salts and natural minerals near this popular (> 1000 people/day) visitor viewing area located off of Montana Highway 2. Both anthropogenic and natural mineral sites were found in meadows, krumholtz forests, and talas fields.

Goats away from people were defined as any goat beyond 2 km from these high visitation areas. Four natural mineral licks were 4–10 ha in size and comprised of mineral pools, springs, and favored soil (Fig. 2). People rarely or never visited these natural mineral licks. Goats away from people at licks were unmarked and sampled once every two weeks. We also sampled goats away from people randomly across GNP and did not revisit these sites within the same year. We avoided the possibility of pseudoreplication in goats near people by concentrating on 44 identifiable goats, which were located on a weekly basis. Twenty-four carried temporary radio (ATS) or satellite (Lotek Wireless) collars. The other 20 goats had unique traits to enable individual recognition. All data collection occurred under an institutional animal care and use committee Animal Use Permit (017-15) from the University of Montana.

We quantified time budgets during 180 s focal bouts. We performed one observation per day on goats near people and once every two weeks on goats away from people. Observer influence was minimized by watching subjects from afar with spotting scopes. Among the abiotic variables we recorded were; cloud cover, wind, and temperature, the latter two with a Kestrel 2000 wind and weather meter. Cloud cover was assessed by partitioning the sky into quadrants and subsequently estimating percentage of cloud cover/section. Location and linear distances to escape terrain and to observer were determined by a Bushnell rangefinder or with topographic map in a Garmin E-Trex Vista Global Positioning System (GPS). We defined escape terrain as cliffs with slopes of 60° or steeper (Sarmento and Berger, in review). Land cover was classified categorically where the focal sample ended (classes included: snow, cliff, ledge, meadow, forest, and scree). The sex and age of individuals were established by examining group structure, horn/body morphology, urination postures, and winter coat shedding patterns.

To examine the human shields hypothesis, we recorded goat patterns of habitat use and grouping. We recorded whether or not a goat bedded on cliffs because sleeping is considered a risky behavior (Lima et al., 2005). Additionally, we used group size as a response variable because of the potential for increased predator detection and the dilution effect (Bednekoff and Lima, 1998; Blumstein, 2010). Group size was assessed by counting every individual within 50 m of the focal subject. We also included nearest neighbor distance (NND) as a response variable (Hamilton, 1971). NND is the distance between a focal goat and the next closest individual.

To evaluate if large carnivores avoided areas of high human visitation, we used camera traps and conducted track surveys in areas near and away from people where goats accessed minerals. Cameras were placed randomly within 200 m of mineral site centers from May–September. Carnivore track and scat presence were assessed during bi-weekly 1 h searches by two observers at mineral acquisition sites. Surveys covered the entire area within 200 m of the center of the mineral site. Additionally, animal trails were followed for 300 m away from the center of mineral sites. Evidence of carnivores was then removed to prevent double counting during subsequent sampling. We pooled track and camera detections, making presence of any mid-large predator for each two week period a binary variable (present or absent). During our track and scat surveys we also recorded the presence of goat skulls as an indirect measure of predation and skulls were moved from the area to prevent double counting.

2.3. Predation risk experiments

We tested whether responses to predation risk differed by goat proximity to people. We tested goat responses to predation risk experiments at locations within 200 m from high-human use areas and at backcountry sites. We predicted goats near people would have dampened responses to predation risk and tested this by using visual models representing differential risk: 1) grizzly bear (potential danger), 2) familiar ungulate (low risk), and 3) a person in ordinary clothes in a quadrupedal posture as if a bear. We expected all goats to respond weakly to the familiar ungulate or quadrupedal human but stronger to a predator model, especially because grizzly bears are predators of goats (Cote and Beaudoin, 1997; Festa-Bianchet and Côté, 2008). The use of such experimental models are common in some field experiments as they offer credible prey responses during presentations (Reimers and Eftestøl, 2012; West and Packer, 2002).

Grizzly bear and ungulate models were used in 2014 and 2015. In 2014 we used a foam bighorn sheep (*Ovis canadensis*) head (Delta Mackenzie Targets, Inc.) and masked our postures by using beige shirt/pants, and foam front legs. The 2014 grizzly bear model was constructed from a Styrofoam head and a furred fabric cape. In 2015 the models were revamped to decrease weight for improved transport and accessibility to remote back-country sites > 15 km distant. In 2015 the ungulate model was a beige white-tailed deer (*Odocoileus virginianus*) cutout (Montana Decoy, Inc.) with foam front legs. The 2015 grizzly bear model was a large dark brown coat, hat and pants combined with a bear mask (Ruby's Costume Company). These models tested goat reaction to risk.

We approached sites quietly through the forest so goats would not perceive our presence. Additionally, experiments were presented downwind of subjects to prevent olfactory detection. Treatments were conducted broadside to prevent an over-threatening direct approach. Experiments were not conducted between a subject and escape terrain (Kramer and Bonenfant, 1997). Presentation order was randomized to control for potential sequence effects during the 2014 pilot period. Because reactions to models were similar within goat proximity to people, we switched to presenting models in increasing order of predicted risk in 2015; 1) familiar ungulate, 2) human, 3) bear. We opted for this ordering to prevent loss of subjects due to cliff escape. To ensure ordering did not bias results we tested year (i.e. random versus ordered) as a variable in analyses – which are described later.

In June, July, and August of 2014–2015, we conducted these experiments via a before-after-control-impact research design where baseline (180 s focal sampling) data were collected on a focal subject prior to model treatments and included the same explanatory variables as described above. Data were recorded by a second person who remained hidden and did not accompany the model during presentation. Response variables included; flight distance, distance fled, time to return to pre-experiment behavior, time until reaching escape terrain, distance to cliffs, latency to response, and time to group clustering. A post-experiment focal sample was then recorded 12 min after the experiment ended.

2.4. Human exclusion experiment

To assess a component of the human shields hypothesis we predicted goat use of anthropogenic substances would decrease if people were excluded but minerals remained. To determine urine attractiveness over time, we placed camera traps at urine deposition sites and measured temporal goat use. We then eliminated human presence in its entirety by reliance on a natural experiment which disentangled the potentially confounding effects of human presence and mineral access. The manipulation involved a weeklong exclusion of all people at Logan Pass between 22 July and 28 July 2015 due to safety concerns during of a 30-day wildfire. Consequently, visitation dropped from ~3500 people/day to functionally zero during the weeklong fire closure. Data from eight GPS collared animals were used to test spatial variation in habitat use before, during, and after the closure. The wildfire did not directly threaten the goats as it was > 5 km distant and burned in the opposite direction.

2.5. Analytical techniques and modeling

Analyses for both observation and experiment data were conducted with the statistical program R (R Development Core Team, 2015). Using the lme4 package, we included predictor covariates into generalized mixed effect models (Bates et al., 2014). For count response data, such as group size, we used generalized linear models with a Poisson distribution and location as a random intercept. If models were over-dispersed (dispersion parameter > 1.5), we then used negative binomial models to account for non-parametric residuals while recognizing that these models fail to include random effects due to limitations of available statistical packages. For binary response data, we used logistic regression with a logit link function and included location as a random intercept (Bates et al., 2014).Model selection was not performed on observational data because we sought to compare explanatory variables across responses. For reactions to predation risk experiments we used backward stepwise selection on models to assess relative strength of the covariates, and employed the small sample size Akaike information criterion (AICc) in model ranking.

To ensure model assumptions were met, we checked residual plots and tested independence of covariates. We tested independence of covariates 1) using a variance inflation factor of less than five, 2) noting whether correlation coefficients were under 40% among parameters, and 3) assessing whether coefficient estimates changed > 20% with the addition of covariates. Wind and distance variables were log-transformed to meet assumptions of normality. We did not include land cover in analyses of observational data since it was confounded by the distribution of licks; natural ones were mainly in talas fields, while anthropogenic minerals were primarily in meadows, krumholtz forests, or on roads/trails. Other explanatory variables from the observational data were not confounded. For our experimental data the variables, wind and distance to treatment were correlated with proximity to people (goats near or away from people). Wind was correlated because natural licks were located in windier locations. Distance to treatment was correlated because we could not approach within 100 m of away from people goats without being detected, while goats near people failed to detect treatments at further distances (> 100 m). Thus, we ran analyses with distance to experiment, wind, and proximity to people separated.

To test if distances fled varied between goats near and away from people we used Welch's *t*-test, a procedure that corrects for unequal variances. We also tested if distances fled varied across treatments, but within goats near or away from people using three-way ANOVAs.

3. Results

3.1. Observations

Our analyses of anti-predator behavior and grouping of goats near and away from people are based on 715 and 276 focal observations, respectively. If human presence is creating a de facto human shield and facilitating ecological redistribution, we predicted reductions in carnivore use of human sites and desensitized goat anti-predator behavior. The presence of a carnivore was 27 time more likely at natural mineral sites compared to anthropogenic mineral locations (Z-value = 3.099, $df = 79$, $P \leq 0.005$). Furthermore, we recorded indirect evidence of predation through a count of 26 mountain goats skulls across the four backcountry mineral lick sites versus only two goat skulls at the three anthropogenic sites.

Whether a goat bedded on cliffs was most influenced by proximity to people, and to a smaller extent group size, temperature, and the presence of young with adult females (Fig. 2). The odds of a goat

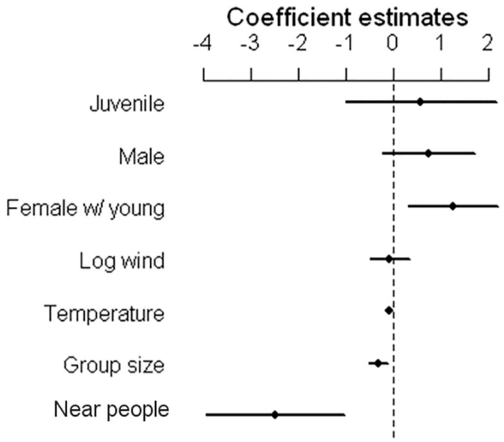

Fig. 2. Coefficient estimates from a logistic regression model explaining mountain goat bed site selection on cliffs in Glacier National Park (2013-15). Bars represent 95% confidence intervals. Location was added as a random effect, goats away people and females without offspring are set as reference.

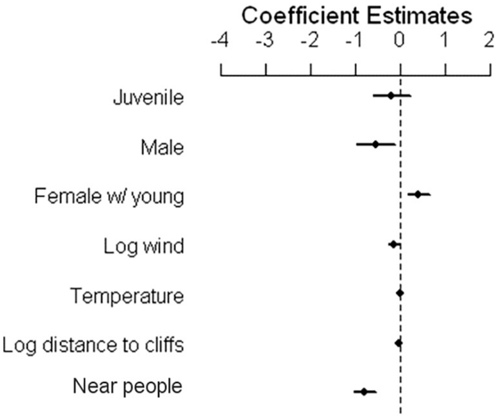

Fig. 3. Coefficient estimates from a negative binomial model explaining mountain goat group size at anthropogenic and natural mineral sites in Glacier National Park (2013-15). Goats away people and females without offspring set as the intercept.

bedding on cliffs increased 18 fold for goats away from people. For animals accessing minerals, group size was explained by proximity to people, and age/sex class (Fig. 3). Age/sex class had the only significant influence on nearest neighbor distances, where adult females with young were found closer together (Appendix Table 2). Distance to escape for goats feeding was most influenced by proximity to people, where goats away from people were found feeding significantly closer to cliffs (Appendix Table 3). Finally, 10 of 24 collared goats near people migrated to a natural lick during late June-early July of 2015 and 2016, while the other individuals strictly used anthropogenic minerals. Goat migrations to mineral licks were approximately 12 km in length and occurred only once per year. Collared goats that migrated eventually returned to human dominated areas to use anthropogenic minerals.

3.2. *Predation risk experiments*

If goats near people benefit from a human shield, responses to grizzly bears should be dampened relative to goats away from people because individuals would be desensitized to carnivore cues as stimuli would not convey realized danger. Both goats near and away from people had an increased flight response to the bear model. Goats away from people, however, fled further from the bear model compared to goats near people ($T = 4.985$, $df = 34.339$, $P \leq 0.001$). Goats away from people fled an average of 184 m further than goats near people when exposed to the grizzly bear imitation. Conversely, goats near and away from people did not differ in flight distance responses from ungulate and human models ($T = 1.360$, $df = 32.963$, $P = 0.183$, and $T = 1.968$, $df = 12$, $P = 0.073$ respectively). Goats away from people differed in their responses between models (ANOVA; $df = [2, 61]$, $F = 14.105$, $P \leq 0.001$), as did goats near people (ANOVA; $df = [2, 62]$ $F = 4.398$, $P = 0.016$; Fig. 4).

Our presentation of a bear model reveals goat responses was largely explained by the intensity of human presence. Proximity to people outperformed the correlated variables, wind and distance to experimental subject, as a predictor of whether goats remained or fled to cliffs (Appendix Table 4). The odds of goats escaping to cliffs after the bear experiment increased 18 fold where people lacked relative to sites associated with people (Appendix Table 5). Similarly, proximity to people best explained whether or not a goat returned to pre-experiment baseline behavioral values after exposure to predation risk (Appendix Table 6). Distance to escape terrain also affected the probability of an individual returning to baseline behavioral values; goats further from cliffs were less likely to return original values (Appendix Table 7).

3.3. *Human exclusion experiment*

A week-long public closure of the Logan Pass area due to a wildfire provided an experimental test to assess the potentially confounding effects of human presence and mineral access on goat redistribution. Because human urine was repeatedly used by goats for an average of 11.4 days ($n = 7$; ± 3.70 SE) after initial deposition, this source if mineral enhancement remained at Logan Pass despite the closure.

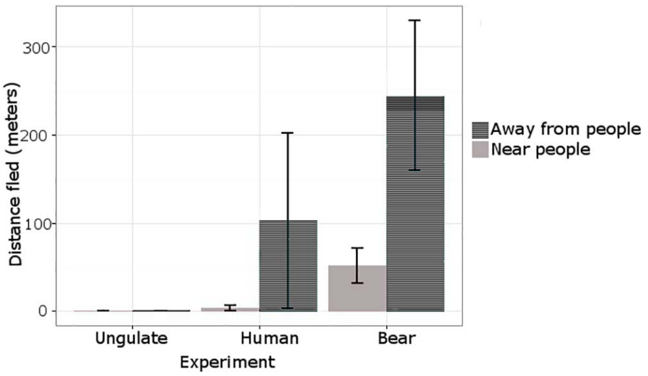

Fig. 4. Relationships between mean distances fled during exposure to three mammalian treatments with bars representing the 95% confidence interval. N, as follows, for goats near people: ungulate = 33, human = 20, and bear = 54; and for goats away from people 30, 22, and 37, respectively.

During the public closure, goats reduced use of Logan Pass significantly although human minerals remained (Fig. 5). Simultaneously, goats shifted to areas closer to cliffs during the public closure relative to the week before ($T = 5.542$, $df = 1476.774$, $P \leq 0.005$), and the week after ($T = -3.823$, $df = 1719.828$, $P \leq 0.005$). The reduction in distance to escape terrain ceased 12 days after the public closure ended, suggesting a lag effect ($T = 1.626$, $df = 1566.51$, $P = 0.104$). Additionally, three of six remote camera detections of predators at the Logan Pass area occurred during the public closure. This suggests the presence of over 3500 people per a day at Logan Pass had a strong influence on goat behavior, distribution, and mineral use. Due to other fires the area was covered in smoke for weeks before and after the closure – thereby eliminating the potentially confounding effect of smoke. Furthermore, the fires were 5 km distant and thus it is unlikely the goats were responding to the fire itself.

4. Discussion

4.1. *Understanding human impact from the mountain goat perspective*

Our study presents experimental and comparative evidence that suggests a prey species is gaining protection from predators through interaction with people. In some cases, people provide urine with minerals that attract goats. But, the additional interaction is more nuanced. Goats near people had significantly weaker responses to predation risk and engaged in risker behavior compared to goats further from human realms. Further, when people were excluded goat presence

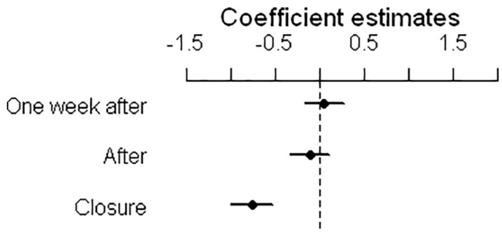

Fig. 5. Coefficient estimates from a logistic regression model explaining mountain goat use of Logan Pass (within 250 m of trails) in Glacier National Park before and after a week-long public closure. Bars represent 95% confidence intervals. Data are from eight GPS collared goats and individual is added as a random effect. The week before closure is set as baseline. “After” refers to the week after the closure ended, and “One week after” denotes the second week past the closure.

was reduced. Goats that accessed a human dominated natural lick along US highway 2 also had reduced predation risk behavior, yet obtained naturally occurring minerals. Our statistical evidence, other than the test for nearest neighbor distances, supports the idea of a human shield. Because mountain goats are known for cliff retreat and high rates of intraspecific aggression we surmise that group clustering (shorter nearest neighbor distances) at the outset of an immediate disturbance is not a mechanism goats employ to mitigate predation risk (Côté, 2000; Côté et al., 1997). Goats often failed to associate with other individuals but instead attempted to reach escape terrain as quickly as possible post exposure to a predator, an observation that aligns with observations of actual bear-goat interactions (Cote and Beaudoin, 1997). Thus, apart from nearest neighbor distances, we present multiple lines of evidence that suggest a prey species receives defense from predators through spatial overlap with protected area visitors.

4.2. Ecological baselines and habituation in reserves

Protected areas are frequently reported as our most pristine places and paramount as baselines to detect ecological change (Arcese and Sinclair, 1997). Yet, change occurs within reserves as well as beyond. An understanding of changes in ecological relationships which includes the redistribution of populations is an important consideration if we wish to fully appreciate alterations fomented by human actions whether direct or indirect. Beyond control samples for science, baselines are valuable at averting shifting baseline syndrome in the public eye, while both visitors and scientists need information on what present conditions reveal about those in the past. Without such information visitors may believe the altered interactions they observe are an accurate presentation of the past and of fully functioning natural processes. Providing a reference of the unimpaired is a goal of protected areas, but altered baselines may distort what is perceived as intact 'natural' processes.

While national parks often reflect ecological processes with reduced human effects relative to elsewhere (Leroux et al., 2010; Beissinger et al., 2017), visitation alters behavior, distribution, and migratory pathways for some species. For instance, the habituation of GNP goats has resulted in the loss of a 12 km annual migration to a natural mineral lick. The majority of our collared goats did not access natural mineral licks, while the goats that did migrate did not do so every year. Because information is likely passed down through generations in at least some ungulates (Berger, 2008b), then individuals that forgo the use of natural licks may not be transferring knowledge of migratory pathways to young (Sweanor and Sandegren, 1988). While direct impediments to migration have been substantiated, migratory loss from indirect effects are less known or documented (Berger, 2004; Sawyer et al., 2009).

In protected areas ecological change associated with wild animals often coincides with habituation because fear is reduced or lost. Habituation presents serious concerns because people are injured, sometimes fatally. Our findings suggest that mountain goat aggressive behavior increases at anthropogenic mineral sites (our unpub. data) and sometimes the aggression is redirected to visitors. A human was killed in Olympic National Park in 2010 when gored by a habituated goat.

Despite the unfortunate fatality, a broader question remains. Do protected area managers have a responsibility to prevent habituation? Understanding the relationships between habituation and redistribution is relevant to the management of protected areas especially if these locales are to remain useful as baselines for conserving biological diversity and ecological processes.

4.3. The context of human shields and conservation

Human shields may be a common yet under-appreciated phenomenon of human-wildlife interactions. In protected areas high-human access may reduce carnivore presence, though not always because tourists of East Africa and in Yellowstone enjoy viewing relatively habituated lions or wolves. In other situations, prey species leave protected areas and make use of locations around human settlements where carnivores are persecuted (Atickem et al., 2014). Similarly, where private lands prevent human hunter access, prey exploits these de facto predation-free refuges, another form of capitalization on a human shield (Berger, 2007; Proffitt et al., 2013). Thus, conservation efforts and an understanding of ecological baselines will be enhanced by consideration of matrices of land ownership since protected areas are often juxtaposed within a broader array of landscapes.

Maintaining natural settings in a way that approximates the past is increasingly difficult given more than eight billion people worldwide visit terrestrial protected areas annually (Geffroy et al., 2015), with over 280 million/year to USA national parks (Berger et al., 2014). The challenge of providing quality experiences in nature seems to come with a cost where the goal is to maintain ecological integrity including "naturally functioning ecological processes such as predation, nutrient cycling, disturbance and recovery, succession, and energy flow" (National Park System Advisory Board Science Committee, 2012). Accordingly, managers must try to balance the seemingly impossible mandate of preservation and visitation incumbent in the foundation legislation of the National Park Service in 1916 (Lemons, 2010; Beissinger et al., 2017). Addressing the conflicting demands and challenges will require both site and species-specific solutions.

At Glacier National Park, two opportunities exist to mitigate redistribution of mountain goats – reducing benefits or increasing risk costs. Risk to goats can be increased by altering carnivore management. For example, GNP grizzly bears are quickly hazed from the Logan Pass area to prevent encounters with people for safety reasons. The presence of people and hazing reduces bear presence and moderates their pursuit of goats. When bears actively pursue goats, however, the individuals quickly respond as the risk of death becomes real. Trail closures are effective at permitting carnivores to stay and pushing goats out, but this option comes at the expense of substantial public dissatisfaction. And, as shown by our results, the use of predation risk cues like bear models will not work to frighten goats because the cost carries no realized predation. Risk to goats might be created by direct human actions. Hazing for instance creates initial fear from stimuli such as noise, dogs, and non-lethal force. The problem with this approach is that animals quickly learn that the stimuli poses no real threat and thus become habituated to hazing itself (Demarais et al., 2012). Fear provoking stimuli can be effective at moving animals out for short time periods. Overall, there is little evidence that manipulating risk without realized costs will permanently displace habituated animals from human dominated locations.

A potentially more sustainable tactic could be to reduce benefits that lure wildlife to human locales (Grosman et al., 2009). In GNP, the removal of anthropogenic minerals might cause goats, over time, to leave human areas. The provisioning of toilets would be a way to reduce human minerals, but it would also be logistically challenging as helicopters are required to remove backcountry waste. Compositing toilets are impractical in areas that receive high human visitation. Conversely, GNP could try to entice goats away from human locations by enhancing the existing mineral licks with salt blocks, however, this may contradict wilderness ideals. Clearly, there is much need for broader policy discussion about how or even why to modulate habituation.

Interactions with wildlife are often the highlights of visitor experiences. As such, habituated wildlife may be beneficial to conservation because they increase appreciation for natural resource initiatives (Hudenko and Decker, 2008; Kretser et al., 2009). Visitors to parks and the parks themselves will either decide through a de facto lack of action or additional planning how much a role habituation will play in shaping future systems.

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Appendix A. Alternative hypotheses

In addition to the human shields hypothesis we considered two additional a priori hypotheses to explain goat occurrence in areas of high-human presence. First, individuals may only use areas near people to access novel mineral resources. We tested the mineral benefits hypothesis using two predictions. If this was the case we expected mineral availability to be higher for anthropogenic sources compared to natural licks. We quantified mineral content from water at three natural mineral licks and the urine of three people (analyses were performed at Stukenholtz Laboratory, Inc.; Twin Falls, ID, USA; Strausbaugh et al., 2004). Because we tested liquid urine, the results of mineral content may be higher as soil percolation occurs quickly (< 30 s). Additionally, if mineral acquisition is driving redistribution then we predicted goat use of cliff safety terrain to be similar across anthropogenic and natural mineral sources. We compared collared goat cliff use at anthropogenic mineral sites and a natural mineral lick site to test for differences in escape terrain use.

Second, we tested the hypothesis that goats occur in areas near people simply because of greater food availability. As a proxy for food availability we used 250 m Moderate-resolution Imaging Spectroradiometer images to calculate Normalized Difference Vegetation Index (NDVI; earthexplorer.usgs.gov, accessed 20 October 2015) as it is highly associated with mountain goat habitat use (Hamel et al., 2009).

Appendix Table 1
Summary of key hypotheses explaining why goats redistribute to areas of high human use.

Hypotheses	Predictions	Tests
Mineral acquisition[a]	Anthropogenic minerals will be better	Compared mineral content of urine and natural licks
	Anti-predator behavior will not differ	Compared collared goat cliff use across mineral sources
Human shields[b]	Predation risk is lower around people (precondition)	Contrasted carnivore presence across mineral sites
	Riskier behavior for goats near people	Compared goat anti-predator behavior from observations
	Absence of people will alter human mineral use	Collared goat use of minerals during a human exclosure
	Damped responses to predators for goats near people	Experimentally presented risk cues to goats
Better forage	Food will be better in human dominated locations	Compared vegetation index near and away from people
Null	No redistribution	Contrasted observational data on mountain goat habitat use

[a] The mineral acquisition hypothesis explains goat redistribution is due to anthropogenic substances providing better minerals than naturally available.

[b] Human shields hypothesis suggests redistribution is due to reduced predation risk in human dominated locations.

Appendix Fig. 1. Photograph goats accessing anthropogenic minerals near people.

Appendix Fig. 2. Photograph of mountain goats at a natural lick away from people.

Appendix B. Alternative hypotheses results

To understand why goats concentrate in areas near people we explored multiple hypotheses (Appendix Table 1).Goat interactions with people may be a simple byproduct of their acquisitioning of a novel mineral. If this were the case, we'd expect goats to mitigate predation risk similarly across mineral sources as both natural licks and anthropogenic substances are far from cliffs. Ten of 24 collared goats accessed a natural lick, enabling an assessment. These collared individuals differed behaviorally when accessing minerals from natural and anthropogenic sources. Goats using natural licks spent proportionally more times on cliffs and only accessed minerals quickly compared to anthropogenic substances ($T = 5.290$, $df = 366.34$, $P < 0.000$). In contrast, individuals accessing human minerals spent the majority of time away from cliffs. We found total soluble salts to be seven time higher in human urine than natural lick water. Natural mineral water, however, had 18 × more volume than anthropogenic mineral liquids. Licks had streams and ponds while urine quickly percolated into soil after deposition.

Further, if food alone was responsible for driving goat redistribution (Appendix Table 1), we expected strong differences in food quality at goat foraging sites with humans versus those elsewhere. However, because differences were not evident (Appendix Table 8), it appears that food was not a key determinant of goat proximity to humans.

Appendix Table 2
Coefficient estimates for distance to escape of mountain goats foraging in Glacier National Park from 2013 to 2015. Results are from a negative binomial model. Goats near people and female goats without kids are set as baseline.

	Estimate	± SE	z-Score	P
Intercept	4.578	0.401	11.405	< 0.000
Proximity to people (away)	− 2.040	0.206	− 9.899	< 0.000
Group size	0.051	0.032	1.579	0.114
Temperature	0.014	0.015	0.918	0.359
Log wind	0.124	0.097	1.281	0.200
Female with young of year	− 0.210	0.223	− 0.943	0.346
Male	− 0.229	0.247	− 0.929	0.353
Juvenile	0.092	0.482	0.191	0.849

Appendix Table 3
Coefficient estimates for nearest neighbor distances of mountain goats accessing natural and anthropogenic minerals in Glacier National Park from 2013 to 2015. Results are from a negative binomial model. Goats near people and female goats without kids are set as baseline.

	Estimate	± SE	z-Score	P
Intercept	0.886	0.570	1.554	0.120
Proximity to people (away)	0.234	0.206	1.138	0.255
Log distance to escape	0.010	0.041	0.249	0.803
Temperature	0.016	0.019	0.874	0.382
Group size	0.146	0.124	1.175	0.240
Log wind	− 0.182	0.102	− 1.790	0.074

Female with young of year	− 0.584	0.177	− 3.298	0.001
Male	− 0.312	0.344	− 0.908	0.364
Juvenile	0.362	0.261	1.388	0.165

Appendix Table 4
Backwards model selection for whether or not individual mountain goats escaped to cliffs after bear experiment was presented. Logistic regression with location as random effect.

Models	k	AICc	ΔAICc	Likelihood	AICc wt	LL	Cum. wt
Proximity to people + log dist. to cliffs	4	68.778	0.000	1.000	0.445	− 30.056	0.445
Proximity to people + log wind + log dist. to cliffs	5	70.118	1.341	0.512	0.227	− 29.551	0.672
Proximity to people	3	70.643	1.865	0.394	0.175	− 32.125	0.847
Proximity to people + log wind + log dist. to cliffs + group size	6	72.426	3.648	0.161	0.072	− 29.489	0.919
Proximity to people + log wind + log dist. to cliffs + sex/age + group size + year	9	74.894	6.116	0.047	0.021	− 26.811	0.940
Proximity to people + log wind + log dist. to cliffs + group size + year	7	74.934	6.156	0.046	0.020	− 29.484	0.960
Log wind + log dist. to cliffs	4	76.396	7.618	0.022	0.010	− 33.865	0.970
Log dist. to cliffs	3	77.087	8.310	0.016	0.007	− 35.347	0.977
Proximity to people + log wind + log dist. to cliffs + log dist. to model + sex/age + group size + year	10	77.222	8.444	0.015	0.007	− 26.574	0.983
Log wind	3	78.137	9.359	0.009	0.004	− 35.872	0.988
Log wind + log dist. to cliffs + group size	5	78.664	9.886	0.007	0.003	− 33.824	0.991
Log wind + log dist. to cliffs + group size + year	6	78.887	10.110	0.006	0.003	− 32.719	0.994
Log wind + log dist. to cliffs + group size + year	6	79.094	10.316	0.006	0.003	− 32.823	0.996
Log dist. to cliffs + group size	4	79.361	10.583	0.005	0.002	− 35.347	0.998
Proximity to people + log wind + log dist. to cliffs + log dist. to model + temp + sex/age + group size + year	11	80.013	11.235	0.004	0.002	− 26.516	1.000

Appendix Table 5
Factors explaining mountain goat flight behavior to cliffs after presentation of a bear model in Glacier National Park (2014-15), with coefficient estimates from a logistic regression top model. Location was added as a random intercept. Sample sizes are 54 for goats near people goats and 37 for goats away from people.

	Estimate	± SE	z-Score	P
Intercept	− 4.158	1.454	− 2.860	0.004
Proximity to people (away)	2.666	0.666	4.003	< 0.000
Log distance to escape	0.532	0.284	1.875	0.061

Appendix Table 6
Backwards model selection for whether or not individual mountain goats returned to pre experiment behavior after bear model experiment was presented. Logistic regression with location as random effect.

Models	k	AICc	ΔAICc	Likelihood	AICcwt	LL	Cum. wt
Proximity to people + log dist. to cliffs	4	77.389	0.000	1.000	0.453	− 34.367	0.453
Proximity to people + log dist. to cliffs + habitat	7	79.843	2.454	0.293	0.133	− 31.956	0.586
Log dist. to cliffs + log wind	4	80.118	2.728	0.256	0.116	− 35.731	0.702
Proximity to people + log dist. to cliffs + sex/age	6	80.833	3.444	0.179	0.081	− 33.705	0.783
Log dist. to cliffs + habitat + sex/age	8	81.282	3.892	0.143	0.065	− 31.378	0.847
Proximity to people	3	81.683	4.293	0.117	0.053	− 37.648	0.900
Proximity to people + log dist. to cliffs + log temp. + sex/age	7	82.798	5.408	0.067	0.030	− 33.433	0.931
Proximity to people + log dist. to cliffs + habitat + sex/age	9	83.656	6.267	0.044	0.020	− 31.221	0.950
Log dist. to cliffs	3	84.067	6.678	0.035	0.016	− 38.840	0.966
Proximity to people + log dist. to cliffs + log temp. + year + sex/age	8	85.006	7.617	0.022	0.010	− 33.240	0.977
Log dist. to cliffs + log dist. to model	4	85.048	7.658	0.022	0.010	− 38.196	0.986
Proximity to people + sex/age	5	85.353	7.964	0.019	0.008	− 37.176	0.995
Proximity to people + group size + log dist. to cliffs + log temp. + year + sex/	9	87.693	10.304	0.006	0.003	− 33.239	0.997

age							
Log dist. to cliffs + year + sex/age	6	88.123	10.734	0.005	0.002	− 37.350	1.000
Proximity to people + habitat + log dist. to cliffs + log temp. + year + sex/age + group size	12	91.280	13.891	0.001	0.000	− 30.696	1.000

Appendix Table 7

Coefficient estimates for probability of an individual mountain goats returning to pre-experiment behavior after a bear model was presented to goats accessing natural and anthropogenic minerals in Glacier National Park from 2013 to 2015. Model selection was performed and these estimates are from the top model. Results are from logistic regression model with location as a random effect. Wind and distance to experiment were correlated with proximity to people, however, proximity to people preformed best.

	Estimate	± SE	z-Score	P
Intercept	4.171	1.464	2.849	0.004
Proximity to people (away)	− 2.119	0.642	− 3.303	0.001
Log distance to escape	− 0.656	0.290	− 2.260	0.024

Appendix Table 8

Coefficient estimates for mean NDVI values at 250 m cell resolution where mountain goats were observed foraging in Glacier National Park from 2013 to 2015. Results are from a linear model with location as a random effect. Goats near people and female goats without kids are set as baseline.

	Estimate	± SE	z-Score	P
Intercept	2.178	0.368	5.914	< 0.000
Proximity to people (away)	− 0.103	0.079	− 1.307	0.193
Elevation	− 0.002	0.000	− 10.739	< 0.000
Log distance to escape	− 0.008	0.016	− 0.502	0.616

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