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Human shields and redistribution of prey species complicate the utility of protected areas as ecological baselines

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HUMAN SHIELDS AND REDISTRIBUTION OF PREY SPECIES COMPLICATE THE

UTILITY OF PROTECTED AREAS AS ECOLOGICAL BASELINES

By

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HUMAN SHIELDS AND REDISTRIBUTION OF PREY SPECIES COMPLICATE THE

UTILITY OF PROTECTED AREAS AS ECOLOGICAL BASELINES

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Abstract
A key goal of protected areas is the conservation of biodiversity, an aim that garners increasing public support through positive experiences. Increasing visitation, however, can come at the cost of reduced ecological integrity. A fundamental conundrum is that if parks are to serve as our most pristine places, then we must understand how our presence alters species interactions. Species redistributing 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. Across parks drivers of distributional change are often dissimilar, and include movement to people enhance predator avoidance – the human shields hypothesis. We examine these issues with comparative, observational, and experimental approaches contrasting ecological responses of an iconic species in a USA national park where annual visitation exceeds two million people/year. Specifically, we focus on the relative role of predator-avoidance and resource enhancement to test whether a cold-adapted alpine obligate, mountain goats, (*Oreamnos americanus*), mediate their distribution across time by increasing reliance on human presence in a North American national park – Glacier. Individuals that enhanced mineral acquisition through access to human urine concomitantly reduced behavioral responses to predator experiments relative to non-habituated back-country conspecifics. Habituated goats reduced group size, vigilance, and use of cliffs. Such patterns were quickly reversible when human presence was excluded. Our findings hold conservation relevance at three levels. First, human visitation to protected areas is altering species interactions and causing – in this case – the loss of seasonal goat migrations for minerals. Second, habituated animals, including goats, have killed and injured visitors. Third, while protected areas offer baselines for both scientists and visitors, redistribution of species and associated ecological changes means precaution 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, protected areas receive approximately 8 billon visitors 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 wildlife conflict, which results in 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-threatening ways (Arlinghaus et al., 2016). Prey species often 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 and effects on human safety.

In national parks, redistribution coincides with habituation where fear of people is reduced because encounters are not adverse. As a consequence of human injuries and deaths, animals are often destroyed. To develop conservation solutions to this emerging issue will require an understanding of why animals seek people or the byproducts of human infrastructure such as roads.

The redistribution of populations arises due to many factors. It may occur because people provide novel resources, for example, some North American cervids 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. Evidence suggests that some bears do not become food conditioned, but instead reside in towns primarily to escape mortality from dominant conspecifics (Beckmann and Berger, 2003). Therefore, the redistribution of individuals can occur because both resources and predation risk are altered.

The human shields hypothesis posits that prey species reduce predation risk by increasing 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. The 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). At this point, an ecological appreciation of human shields can be improved by understanding 1) its prevalence across taxa and regions, 2) mechanisms that drive redistribution, and 3) both ecological and social consequences of reduced predation risk. Here we test predictions of the human shields hypothesis in a protected area, and relate our findings to what may be considered 'normative' and non-normative' patterns of distribution and behavior.

Across the US, there are more than 400 national park units, and collectively these receive more than 280 million visitors annually (Berger et al., 2014). Several units including Yosemite, Yellowstone, and Grand Canyon receive more than three million visitors yearly. If these units are to serve as preserves and places to gauge ecological change, then we must understand change in distributional and ecological patterns as direct and indirect consequences of associations with people. Here we test three predictions of the human shields hypothesis to

offer a better understanding of the limitations and promise of protected areas to serve as ecological baselines.

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 offer unique opportunities to explore human shield issues, in part because population segments vary dramatically in exposure to people. 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 frequently 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). Mineral licks, however, are a limited and patchily distributed resource (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 licks are predictable places to find vulnerable prey (Rice, 2010). Alternatively, predation risk may be lowered for anthropogenic minerals if a human shield is occurring.

2. Materials and methods

2.1 Study area and sampling framework

Glacier National Park (48.6967° N, 113.7183° W), Montana, USA contains a full suite of native carnivores including wolves (*Canis lupis*), mountain lions (*Puma concolor*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), and coyotes (*Canis latrans*). The 4,100 km^2 park contains 1,885-3,269 mountain goats (Belt and Krausman, 2012). We defined habituated goats as individuals located near high visitor use areas, specifically within 2 km of hiking trails at Logan Pass, Sperry Chalet, and the Goat Lick. Our central area of study for habituated goats was Logan Pass, which receives 3,500 visitors/day on average during the peak summer season. Sperry Chalet and surrounding campgrounds receive over 55 overnight visitors on an average summer day. Wild goats were defined as any goat away from these high-visitation areas.

We focused data collection in areas where goats obtained anthropogenic or natural minerals. Anthropogenic mineral sites were primarily along the Hidden Lake Trail and Highline Trail at Logan Pass, in addition to the Sperry Chalet area. Wild goats at licks were unmarked and sampled once every two weeks. We also sampled wild goats randomly across GNP and did not revisit these sites within the same year. Conversely, we avoided the possibility of pseudoreplication in habituated goats by concentrating on 44 identifiable goats. Twenty four goats 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 Animal Use Permit (017-15).

2.2 Hypotheses

We considered multiple 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 three 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 seconds). To determine urine attractiveness over time, we placed camera traps at urine deposition sites and measured temporal goat use.

Second, under the mineral benefit hypothesis we predicted goat use of anthropogenic substances would not decrease if people were excluded and minerals remained. We capitalized on a natural experiment to assess the potentially confounding effects of human presence and mineral access. The manipulation involved preclusion of all people at Logan Pass between 22 July and 28 July 2015 because of safety concerns during a 30 day wildfire (Photo below). Consequently, visitation dropped from ~3,500 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

Third, 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.Because goats aggressively seek anthropogenic minerals (Hutchins and Geist, 1987) we cannot completely reject mineral benefits as a partial driver of redistribution without experimental manipulation. We tested the

human shields hypothesis as an additive effect to mineral acquisition using observational and experimental efforts. If human shields were occurring we expected habituated goats to 1) engage in riskier behavior, and 2) have a weakened response to predation risk (Table 1).

Finally, we tested the hypothesis that goats occur in areas of high human use simply because of greater food availability. As a proxy for food availability we used 250 meter 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).

2.3 Observations

From May to September (2013-2015) we quantified time budgets during 180 second focal bouts. We performed one observation per day on habituated animals and once every two weeks on wild goats. 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. Location and linear distances (to escape terrain and to observer) were estimated by a Bushnell rangefinder or with topographic map in a Garmin E-Trex Vista Global Positioning System (GPS). We defined escape terrain as rock cliffs with slopes of 60^0 or steeper. 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 sheading patterns.

To examine the above hypotheses, we measured vigilance as individuals accessed minerals. We used vigilance as a surrogate of perceived predation risk since minerals, anthropogenic or natural, are far from cliffs. We also recorded the proportion of goats bedded

on cliffs because sleeping is considered a risky behavior (Lima et al., 2005). Additionally, group size was tested as a response variable because of the potential for increased predator detection and the dilution effect (Bednekoff and Lima, 1998; Blumstein, 2010). Because group geometry is known as an anti-predation mechanism we also included nearest neighbor distance as a response variable (Hamilton, 1971).

To evaluate if large carnivores avoided areas of high human visitation, we used camera traps and conducted track surveys for predators at and away from goat mineral access locations. Track and scat abundance of carnivores were assessed during bi-weekly one hour searches by two observers at natural and anthropogenic licks. Surveys covered game trails within 300 m of licks, and off game trails. Evidence of carnivores was then removed to prevent double counting during subsequent sampling periods. Data were censored if species identity was uncertain. Two cameras were set up at each site. Cameras were placed in areas which received most intensive goat use for minerals. We pooled track and camera detections, making presence of any mid-large predator for each two week period a binary variable (present or absent), and examined this relationship with logistic regression as previously described.

2.4 Experiments

We tested whether responses to predation risk differed by habituation status. We predicted habituated individuals 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 experiments, but more strongly to a predator model as grizzly bears are predators of goats (Cote and Beaudoin, 1997).

Grizzly bear and ungulate models were used in 2014 and 2015. In 2014 the familiar ungulate model consisted of a researcher covered with foam bighorn sheep (*Ovis canadensis*) head (Delta Mackenzie Targets, Inc.), a beige shirt/pants, and a foam front legs. The 2014 grizzly bear model was a Styrofoam bear head and furred fabric cape. Models were revamped in 2015 to decrease weight for improved transport and accessibility to remote back-country sites more than 15 km distant. In 2015 the familiar ungulate model was a researcher dressed in all beige with a white-tailed deer (*Odocoileus virginianus*) cutout (Montana Decoy, Inc.) and foam front legs. The 2015 grizzly bear model was a researcher with a large dark brown coat, hat and pants combined with a bear mask (Ruby's Costume Company). These models tested goat reaction to risk. Treatments were conducted broadside to provide a profile and prevent an over-threatening direct approach. Experiments were not conducted between a subject and escape terrain (Kramer & Bonenfant 1997). Presentation order was randomized to control for potential sequence effects. Because reactions to models were similar within goat habituation status in 2014, we switched to presenting models in increasing order of risk in 2015; 1) familiar ungulate, 2) human, 3) bear. We opted for this ordering to prevent loss of subjects due to cliff escape.

In June, July, and August of 2014-2015, we conducted these experiments via a before-after-control-impact research design where baseline (180 second focal sampling) data were collected 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, detection time, 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 minutes after the experiment ended.

To test if cliff escape varied between wild and habituated goats we used Welch's T-test, a procedure that corrects for unequal variances. We also tested if cliff escape responses varied across treatments, but within wild and habituated goats using three-way ANOVAs.

2.5 Analyses

Analyses for both observation and experimental data were conducted using the statistical program R (R Development Core Team, 2015). Using the lme4 package, we included all predictor covariates into generalized mixed effect models (Bates et al., 2014). For count response data, such as group size, we used general 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 focal data due to our interest in comparing each predictor across responses. For experimental data, however, 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 using methods described above. Wind and distance variables were log-transformed to meet assumptions of normality. 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 more than 20% with the addition of covariates. We did not include land cover in analyses of observational data since it was confounded by the distribution of licks; natural ones were in scree 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 human use level (wild or habituated). Wind was correlated because natural licks were located in windier locations. Distance to treatment was correlated because we could not approach within 100 meters of wild goats without being detected, while habituated goats failed to detect treatments at further distances (>100 meters). Thus, we ran analyses with distance to experiment, wind, and human use level separated.

3. Results

3.1 Observations and Experiments

Our analyses of anti-predator behavior and grouping of habituated and wild individuals 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 vigilance and cliff use.

 Whether a goat bedded on cliffs was most influenced by human-use level, and to a smaller extent; group size, temperature, and the presence of young with adult females (Figure 1). For animals accessing minerals, group size was explained by human-use level, and age/sex class (Appendix Figure 1). Vigilance rates for goats accessing minerals were influenced by nearly every covariate (Appendix Table 1). Age/sex class had the only significant influence on nearest neighbor distances, where adult females with young were found closer together (Appendix

Table 2). Finally, distance to escape for goats feeding was most influenced by human-use levels, where wild goats where found feeding significantly closer to cliffs (Appendix Table 3).

If habituated goats benefit from a human shield, responses to grizzly bears should be dampened relative to wild goats because individuals would be desensitized to carnivore cues as the stimuli would not convey realized danger. Both wild and habituated goats had an increased flight response to the bear model. Wild goats, however, fled further from the bear model compared to habituated goats (T= 4.985, *df*= 34.339, P= <0.000). Wild and habituated goats 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), but wild goats differed in their responses between models (ANOVA; *df* = [2, 61], F=14.105, P=<0.000), as did habituated goats (ANOVA; *df* = [2, 62] F= 4.398, P= 0.016; Figure 2).

Our presentation of a bear model reveals goat responses were largely explained by the intensity of human presence. Human use level 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 a goats escaping to cliffs after the bear experiment increased 18 fold for wild individuals relative to habituated (Appendix Table 5). Similarly, human use level performed best in explaining whether or not a goat returned to pre-experiment behavior after exposed to risk, where wild goats were less likely to return to baseline (Appendix Table 6). Distance to escape also had a significant effect on the probability of an individual returning to baseline behavioral values; goats further from cliffs were less likely to return original values (Appendix Table 7).

Human use level, however, dropped out of models explaining time to detection of the bear. (Appendix Table 8). Subsequently the correlated variable, wind, performed better (natural

licks were windier). Time to detection was also explained by the group size, where individuals

in larger groups were slower to detect the bear but more rapid with wind (Appendix Table 9).

Proximity to cliffs affected detection times of the bear. Adult females had more rapid detection

times.

Habituated and wild goat response to the bear experiments aligned with our observations

of actual goat-grizzly interactions. We observed three interactions between goats and grizzly

bears; two with habituated goats and one with a wild goat. The latter involved a male goat

detecting the bear ~300 meters away and immediately retreating to cliffs. By contrast, the first

habituated goat-grizzly encounter involved a bear fleeing from park visitors. The bear fled past

a female goat and offspring 37 meters away, then ended with the goats bedding 78 meters from

cliffs. The second grizzly-habituated goat encounter occurred with numerous park visitors

around and resulted in no behavioral change in the goats, despite close proximity to the grizzly

(83 meters).

3.2 Hypotheses and Expectations

To understand why goats concentrate in areas of high human use we explored multiple

hypotheses (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 time 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. Additionally, we expected mineral availability to be higher for anthropogenic sources if human substances were a cause for goat redistribution. We found total soluble salts to be seven time higher in human urine than natural lick water. Natural mineral water, however, had 18x more volume than anthropogenic mineral liquids. Licks had streams and ponds while urine quickly percolated into soil after deposition. We also expected goats to remain in high human use areas in the absence of people if mineral acquisition was the primary driver of redistribution.

Human urine is repeatedly used by goats for an average of 11.4 days (n=7; ±3.70 S.E) after deposition. A week-long public closure of the Logan Pass area due to a wildfire provided an experimental test of the influence of novel minerals on redistribution in the absence of visitor presence. During the public closure, goat use of Logan Pass was reduced significantly although human minerals remained (Figure 3). Simultaneously, goats shifted to areas closer to cliffs during the public closure relative to the week before (T= 5.542, df = 1476.774, P= <0.000), and the week after (T= -3.823, df = 1719.828, P= <0.000). 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 3,500 people per a day at Logan Pass had a strong influence on goat behavior, distribution, and mineral use.

Further, if food alone was responsible for driving goat redistribution (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 10), it appears that food was not a key determinant of goat proximity to humans.

4. Discussion

4.1 Redistribution and habituation in reserves

Protected areas are frequently reported as our most pristine places and to be used as ecological baselines to detect change (Arcese and Sinclair, 1997). Yet, change occurs within reserves as well as beyond their boundaries. An understanding of redistribution of populations is an important consideration if we wish to fully appreciate the alterations that humans either directly or indirectly foment. Beyond control samples for science, baselines are valuable at averting shifting baseline syndrome in the public eye and both visitors and scientists need information about how present conditions may not represent those of the past. 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), visitation still 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 seasonal 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, 2008), then individuals that forgo the use of natural licks may be specifically detrimental to offspring that do not learn migratory pathways (Sweanor and Sandegren, 1988). While direct impediments to migration have been substantiated, migratory loss from indirect effects are less known (Berger, 2004; Sawyer et al., 2009).

In protected areas redistribution of populations or species coincides with habituation because visitors interact with wildlife in non-threatening ways. Habituation not only alters

ecology, but it also presents serious concerns because people are injured, sometimes fatally. Our findings suggest that mountain goat aggressive behavior increases at anthropogenic mineral sites (Sarmento unpublished data) and sometimes the aggression is redirected to visitors. A human death occurred in Olympic National Park in 2010 when a visitor was gored. An association between personal human danger and animal habituation may not have been clear, and despite this highly unfortunate incident, a broader question remains. Do protected areas have a responsibility to prevent habituation? Understanding the relationships between habituation and redistribution is crucial for the management of protected areas if these are to remain useful as baselines for conserving biological diversity and ecological processes.

4.2 The context of human shields and conservation

Redistribution of populations or species through human shields may be a common yet under-appreciated phenomenon. In protected areas high-human access reduces carnivore presence. 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 exploit these de facto predation-free refuges, another form of capitalization on a human shield (Berger, 2007; Proffitt et al., 2013). Thus, conservation effots and an understanding of ecological baselines will be enhacned by consdieration of matricies 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 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). Addressing the conflicting demands and challenges may require site and species-specific solutions.

For GNP's habituated goats, two opportunities exist to mitigate redistribution – 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. 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 work, 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 redistribute. The provisioning of toilets would be a way to reduce human minerals, but it would also be logistically challenging as dozens of helicopter flights 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 lick with salt blocks, however, this may contradict wilderness ideals. Clearly, there is much need for broader policy discussion about how or even why to end 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.

Acknowledgments

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Tables

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

Hypotheses	Predictions	Tests
Mineral acquisition[1]	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
	Absence of people will not alter human mineral use	Collared goat use of minerals during a human exclosure
Human shields[2]	Predation risk is lower around people (precondition)	Contrasted carnivore presence across mineral sites
	Riskier behavior for habituated goats	Compared goat anti-predator behavior from observations
	Damped responses to predators for habituated goats	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

[1]The mineral acquisition hypothesis explains goat redistribution is due to anthropogenic substances providing better minerals than naturally available. [2] Human shields hypothesis suggests redistribution is due to reduced predation risk in human dominated locations.

Figures

Figure 1. Coefficient estimates from a logistic regression model explaining mountain goat bed site selection on or away from cliffs Glacier National Park (2013-15). Bars represent 95% confidence intervals. Location was added as a random effect, habituated goats and females without offspring are set as reference.
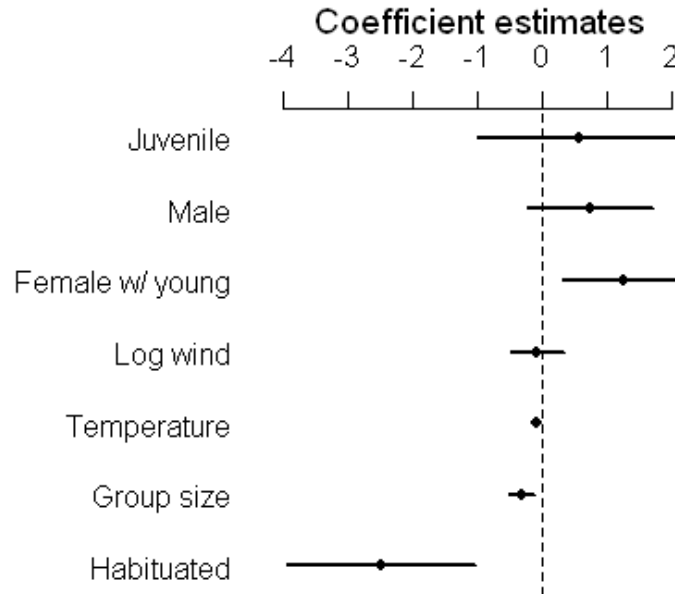
Figure 2. Relationships between mean distances fled during exposure to three mammalian treatments with bars representing the 95% confidence interval. N, as follows, for habituated goats: ungulate – 33, human – 20, and bear – 54; and for wild goats 30, 22, and 37, respectively.
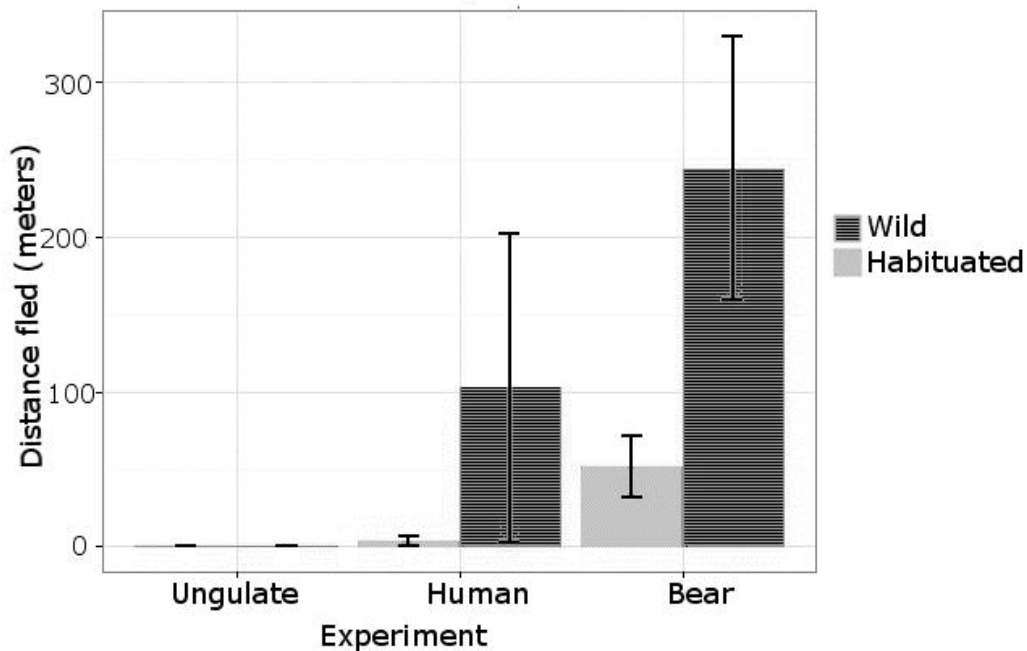
Figure 3. Coefficient estimates from a logistic regression model explaining mountain goat use of Logan Pass (within 250 meters of trails) in Glacier National Park before and after a week-long public closure. Bars represent 95% confidence intervals. Data are from eight GPS collared goats and individual is added as a random effect. The week before closure is set as baseline
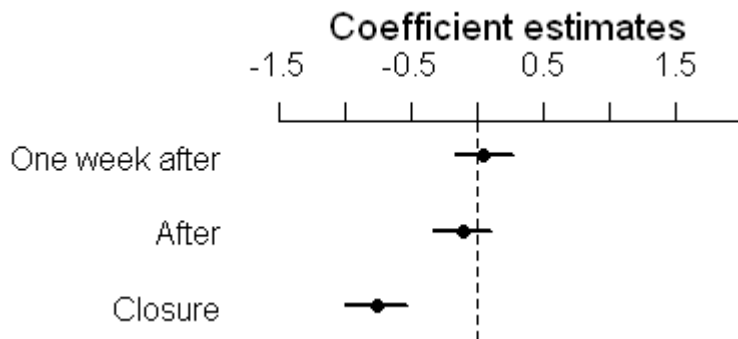
Appendix
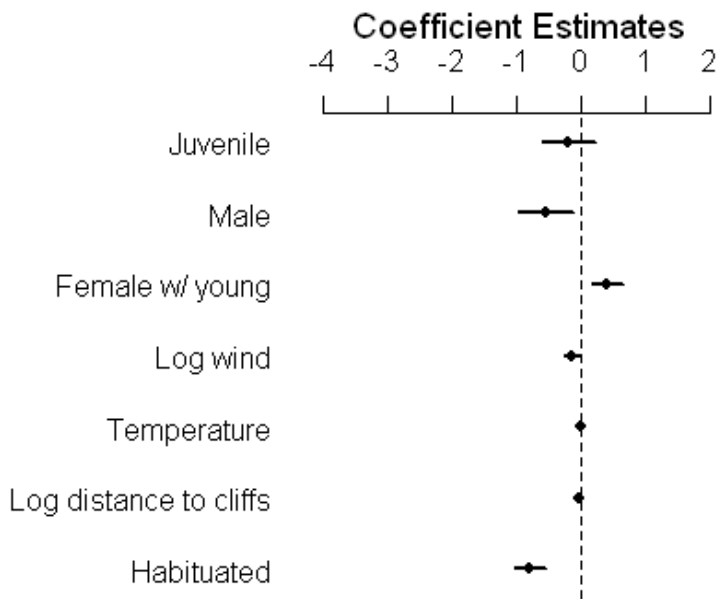
Appendix Figure 1. Coefficient estimates from a negative binomial model explaining mountain goat group size at anthropogenic and natural mineral sites in Glacier National Park (2013-15). Habituated and females without offspring set as the intercept.

Appendix Table 1. Coefficient estimates for vigilance rates during 180 second focal samples on goats accessing natural and anthropogenic minerals in Glacier National Park from 2013-2015. Results are from a general linear model with a Poisson family and location as a random effect. Habituated and female goats without kids are set as baseline.

	estimate	± se	z-score	p
intercept	0.351	0.521	0.675	0.500
low-human use area (wild goats)	1.674	0.826	2.027	0.043
log distance to escape	0.064	0.015	4.376	<0.000
temperature	0.014	0.004	3.581	<0.000
groupsize	0.043	0.005	8.380	<0.000
log wind	0.054	0.026	2.071	0.038
female with young of year	0.024	0.042	0.579	0.563
male	0.200	0.068	2.918	0.004
juvenile	-0.175	0.076	-2.284	0.022

Appendix Table 2. Coefficient estimates for nearest neighbor distances of mountain goats accessing natural and anthropogenic minerals in Glacier National Park from 2013-2015. Results are from a negative binomial model. Habituated and female goats without kids are set as baseline.

	estimate	± se	z-score	p
intercept	0.886	0.570	1.554	0.120
low-human use area (wild goats)	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
groupsize	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 3. Coefficient estimates for distance to escape of mountain goats foraging in Glacier National Park from 2013-2015. Results are from a negative binomial model. Habituated and female goats without kids are set as baseline.

	estimate	± se	z-score	p
intercept	4.578	0.401	11.405	<0.000
low-human use area (wild goats)	-2.040	0.206	-9.899	<0.000
groupsize	0.051	0.032	1.579	0.114
temperature	0.014	0.015	0.918	0.359
logwind	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 4. Backwards model selection for whether or not individual mountain goats escaped to cliffs after bear experiment was presented. Logestic regression with location as random effect.

models	k	AICc	ΔAICc	likelihood	AICc wt	LL	cum. wt
human use level + log dist. to cliffs	4	68.778	0.000	1.000	0.445	-30.056	0.445
human use level + log wind + log dist. to cliffs	5	70.118	1.341	0.512	0.227	-29.551	0.672
human use level	3	70.643	1.865	0.394	0.175	-32.125	0.847
human use level + log wind + log dist. to cliffs + group size	6	72.426	3.648	0.161	0.072	-29.489	0.919
human use level + log wind + log dist. to cliffs + sex/age + group size + year	9	74.894	6.116	0.047	0.021	-26.811	0.940
human use level + 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
human use level + log wind + log dist. to cliffs + log dist. to model + sex/age + group	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
human use level + log wind + log dist. to cliffs + log dist. to model + temp + sex/age	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 habituated goats and 37 for wild goats.

	estimate	± se	z-score	p
intercept	-4.158	1.454	-2.860	0.004
low human use area (wild goats)	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 beahvior after bear model experiment was presented. Logestic regression with location as random effect.

models	k	AICc	ΔAICc	likelihood	AICcwt	LL	cum.wt
human use level + log dist. to cliffs	4	77.389	0.000	1.000	0.453	-34.367	0.453
human use level + 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
human use level + 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
human use level	3	81.683	4.293	0.117	0.053	-37.648	0.900
human use level + log dist. to cliffs + log temp. + sex/age	7	82.798	5.408	0.067	0.030	-33.433	0.931
human use level + 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
human use level + 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
human use level + sex/age	5	85.353	7.964	0.019	0.008	-37.176	0.995
human use level + group size + log dist. to cliffs + log temp. + year + sex/age	9	87.693	10.304	0.006	0.003	-33.239	0.997
log dist. to cliffs + year + sex/age	6	88.123	10.734	0.005	0.002	-37.350	1.000
human use level + habitat + log dist. to cliffs + log temp. + year + sex/age + group si	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 2013-2015. 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 human use level, however, human use level preformed best.

	estimate	± se	z-score	P
intercept	4.171	1.464	2.849	0.004
low human use area (wild goats)	-2.119	0.642	-3.303	0.001
log distance to escape	-0.656	0.290	-2.260	0.024

Appendix Table 8. Backwards model selection on time to bear model detection for indiviudal mountain goats during experimental presentation. General linear model with Poission family and location as random effect.

models	k	AICc	ΔAICc	likelihood	AICcwt	LL	cum.wt
group size + habitat + log dist. to cliffs + temp + sex/age + year + log wind	12	1196.903	0.000	1.000	0.682	-583.393	0.682
group size + habitat + log dist. to cliffs + sex/age + log wind	10	1200.025	3.122	0.210	0.143	-587.937	0.825
group size + habitat + log dist. to cliffs + temp + sex/age + log wind	11	1201.541	4.638	0.098	0.067	-587.232	0.892
group size + habitat + log dist. to cliffs + temp + sex/age + year + log dist. to model	12	1201.798	4.894	0.087	0.059	-585.840	0.951
group size + habitat + log dist. to cliffs + log wind	8	1202.833	5.930	0.052	0.035	-592.107	0.986
group size + habitat + log dist. to cliffs + temp + sex/age + year	11	1205.151	8.247	0.016	0.011	-589.037	0.997
group size + habitat + log dist. to cliffs + temp + sex/age + year + human use level	12	1207.653	10.750	0.005	0.003	-588.768	1.000
group size + log dist. to model + year	5	1232.657	35.753	0.000	0.000	-610.811	1.000
group size + log wind	4	1232.802	35.899	0.000	0.000	-612.062	1.000
group size + log dist. to model	4	1232.974	36.071	0.000	0.000	-612.148	1.000
group size + log dist. to cliffs + temp + sex/age + year	8	1233.245	36.342	0.000	0.000	-607.314	1.000
group size + temp + year	5	1237.550	40.646	0.000	0.000	-613.258	1.000
group size + temp + sex/age + year	7	1239.774	42.871	0.000	0.000	-611.887	1.000
group size	3	1240.095	43.191	0.000	0.000	-616.847	1.000
human use level + log dist. to cliffs	4	1625.148	428.245	0.000	0.000	-808.235	1.000

Appendix Table 9. Coefficient estimates for the time it took an individual mountain goats to detect the bear model that was experimentally presented to goats accessing natural and anthropogenic minerals in Glacier National Park from 2013-2015. To remove outliers, detection times were truncated to less than 180 seconds. Model selection was performed and these estimates are from the top model. Results are from a general liner model with a Poisson family and location as a random effect. Human use level and distance to experiment were correlated with wind, however, wind preformed best.

	estimate	± se	z-score	P
intercept	3.288	0.522	6.295	<0.000
group size	0.157	0.010	15.882	< 2e-16
forest	0.442	0.389	1.135	0.256
meadow	0.019	0.381	0.051	0.959
scree	-0.400	0.397	-1.007	0.314
log distance to escape	-0.168	0.035	-4.857	<0.000
temp	-0.017	0.007	-2.455	0.014
adult female with yonug of year	0.076	0.074	1.026	0.305
adult male	-0.216	0.100	-2.168	0.030
year 2015	0.231	0.084	2.761	0.006
log wind	-0.156	0.046	-3.358	0.001

Appendix Table 10. Coefficient estimates for mean NDVI values at 250 meter cell resolution where mountain goats were observed foraging in Glacier National Park from 2013-2015. Results are from a linear model with location as a random effect. Habituated and female goats without kids are set as baseline.

	estimate	± se	z-score
intercept	1.927	0.384	5.023
low-human use area (wild goats)	-0.197	0.100	-1.965
elevation	-0.002	0.000	-9.483
log distance to escape	-0.006	0.017	-0.366
groupsize	0.013	0.013	0.983
female with young of year	0.005	0.070	0.069
male	-0.024	0.083	-0.282
juvenile	-0.030	0.152	-0.195