

Effects of Human Activity on the Distribution of Desert Bighorn Sheep Along the Border in
Southwestern Arizona and Northern Sonora

By

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DEDICATION

For my wife Cassie and our daughter Winifred

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ABSTRACT

Changes in species distribution in areas with human activity may be the result of either spatial-temporal avoidance of those areas, or as the result of a decrease in survival and recruitment within those areas. My research examined the effects of human activity on the distribution of desert bighorn sheep (*Ovis canadensis mexicana*) along the border in southwestern Arizona, USA and northern Sonora, Mexico. I surveyed 33 transects (256 sites) on foot from February 2017 to January 2018, with 8 of 33 transects re-surveyed during this period. Human use at each site was indexed by trash category (0 pieces of trash, 1-10 pieces of trash, >10 pieces of trash). Bighorn sheep fecal pellets were used as detections of bighorn sheep. This study used a novel approach to survey replication. Old, white fecal pellets and newer, brown fecal pellets were used as the first and second temporal replicates of a survey, respectively. I used a hierarchical occupancy model to estimate probability of detection and occupancy, with human activity and environmental covariates as explanatory variables. Human activity as indexed by trash had a non-statistically significant but potentially biologically significant negative effect on occupancy. Elevational site position on mountain was positively related to occupancy in Mexico, but not in the USA. Height of the mountain above adjacent valley bottom was positively related to occupancy in the USA, but not in Mexico. These results suggest that bighorn sheep use habitat differently in the USA than in Mexico, likely due to the differences in human activity within each country. Small mountains should be recognized as habitat for desert bighorn sheep, even though in some areas, those features may be infrequently selected by sheep. Conservation efforts should recognize that 'atypical' bighorn sheep habitat may hold value for restoring or maintaining bighorn sheep populations.

INTRODUCTION

The increase in human populations over the last century and the subsequent expansion of the human activities into wild areas has consequences for the conservation of native plant and animal species (Dietz et al. 2007, Benítez-López et al. 2010). The effects of human activity are not limited to urban or highly modified areas, increasingly impacts to wildlife occur in protected areas (Southworth et al. 2006). Anthropogenic modification of wild areas has resulted in habitat loss for many species, the effects of habitat loss on species distribution and abundance are direct and observable (Fahrig 1997, 2001). Less easily observed are the indirect effects of human activity on wildlife. Many prey species perceive human activity as predation risk and respond to human activities by exhibiting anti-predator behaviors, such as fleeing, shifts in activity budgets, and changes in habitat selection (Frid and Dill 2002). Response to human activity may also have physiological effects, such as increased heart rate, increased energy expenditure, adrenal gland enlargement, increased stress hormones, and increased susceptibility to disease (MacArthur et al. 1982, Hayes et al. 1994, Creel et al. 2002, Keller and Bender 2007). Behavioral and physiological responses to human activity may divert time and energy away from behaviors that increase an individual's fitness (e.g., foraging, mating) (Frid and Dill 2002). Collectively, changes to individual survival and reproduction may result in changes to population attributes, such as abundance and distribution (Frid and Dill 2002). Studying species response to human activity is complex, as responses can occur at multiple levels of biological organization (e.g., cells, individuals, populations) and across time and space. For example, some species may exhibit a spatial avoidance strategy by avoiding areas with high levels of human activity, such as areas near busy roads, hiking trails, or anthropogenic noise (Papouchis et al. 2001, Keller and Bender 2007). Individuals may also display a temporal avoidance strategy to acquire resources

during times of the day when human activities are reduced in number or are absent (Keller and Bender 2007). Therefore, the distribution of a population may be partly the result of lower survival and recruitment arising from spatial variation in human activity and spatial-temporal avoidance strategies (Benítez-López et al. 2010).

Large mammals may be especially susceptible to the effects of human activity due to the large spatial extents necessary to support large mammals, which increases the likelihood that individuals may encounter human activity when fulfilling their daily resource needs in fragmented landscapes (Benítez-López et al. 2010). For example, caribou (*Rangifer tarandus*) reduce activity 50-95% within 5km of roads, powerlines, and other human activities for months or years (Mahoney and Schaefer 2002, Vistnes and Nellemann 2008). The response of large mammals to human activity may be differential, with some species using areas near human activity and some species avoiding areas near human activity, however this response is likely dependent on the level of human activity within the area (Rogala et al. 2011). Both elk (*Cervus canadensis*) and wolves (*Canis lupus*) avoided areas <50 m from hiking trails in 3 Canadian National Parks, but elk used areas 50-400 m from trails as refugia from wolves, while wolves avoided areas 50-400 m from trails when human activity on the hiking trail was <2 people/hour. As human activity on trails increased to >2 people/hour, both wolves and elk avoided areas 50-400 m from trails (Rogala et al. 2011). This suggests that habitat within protected areas can be indirectly lost to wildlife when even under low-levels of human activity (Rogala et al. 2011). Protected areas are often used as conservation strategies to mitigate or buffer from the effects of human activities such as urbanization, habitat loss and fragmentation (Southworth et al. 2006, McDonald et al. 2008). Indirect loss of habitat from human activities within protected areas may

violate the purpose of protected areas to conserve habitat. Understanding where indirect habitat loss from human activity is occurring has important implications for land managers.

Bighorn sheep (*Ovis canadensis*) may be negatively affected by human activity in protected areas due to their tendency to avoid humans (Geist 1971, Papouchis et al. 2001). In areas with high levels of human activity, bighorn sheep abandon use of water sources and mineral licks, even if the replacement of those lost resources is not immediately available (Leslie and Douglas 1980, Keller and Bender 2007). Vehicle traffic from visitation of protected areas may also influence the distribution of bighorn sheep within protected areas (Papouchis et al. 2001). Bighorn sheep are more likely to be found farther from roads in areas with high vehicle use than in areas with low vehicle use, suggesting bighorn sheep avoid areas close to busy roads (Papouchis et al. 2001). The type of human activity may influence the behavioral response by bighorn sheep, with some types of human activity eliciting stronger behavioral responses than other types of human activity (Papouchis et al. 2001). Bighorn sheep flee greater distances when they encounter hikers than when they encounter vehicles, possibly due to closer approach distances of hikers and unpredictability of encountering hikers off-trail (Papouchis et al. 2001). Collectively, the effects of human activity may result in changes in the abundance and distribution of bighorn sheep populations in protected areas. Declines in bighorn sheep abundance and distribution in the last century, and ongoing efforts to maintain populations, suggest the study of the effects of human activities on this species are worth exploring.

My research investigated the effects of human activity on the distribution of desert bighorn sheep (*Ovis canadensis mexicana*) in two protected areas within the Sonoran Desert. The Sonoran Desert experiences a strong gradient in human activity associated with the U.S./Mexico border. Border security (federal law enforcement), human migration, smuggling,

hunting/poaching, military overflights, land management, and recreation may occur in protected areas along the border, however these border-related human activities are generally higher in the U.S. Human activities associated with border security, human migration, smuggling, and military overflights are practically non-existent or occur at much lower levels in protected areas along the border in Mexico. The differences in human activity levels by nation facilitates comparison between areas with high levels of human activity (U.S.) and low levels of human activity (Mexico). I employed a novel application of occupancy modeling to understand the relationships between human activity and use of habitat by desert bighorn sheep along the border. I predicted that desert bighorn sheep distribution was constrained in the U.S. due to generally higher levels of human activity in the U.S. I also predicted that topographic feature traits (terrain) would strongly influence the distribution of desert bighorn sheep, but that the effects of terrain would interact with human activity on both sides of the border and result in very different use of habitat by desert bighorn sheep in each country. Understanding the influencing of human activity on desert bighorn sheep habitat and distribution has important implications for the management of protected areas on both sides of the U.S./Mexico border.

STUDY AREA

Our study area was comprised of two different protected areas, Organ Pipe Cactus National Monument (OPCNM) in southwestern Arizona, U.S.A, and El Pinacate y Gran Desierto de Altar Biosphere Reserve (Pinacate Biosphere Reserve) in northern Sonora, Mexico (Figure 1). The northern boundary of OPCNM is located approximately 20 km south of the city of Ajo, AZ. Organ Pipe Cactus National Monument's southern boundary is 48 km of U.S./Mexico border (Schmidt et al. 2007). Directly across the U.S./Mexico border from OPCNM is the Pinacate Biosphere Reserve in northern Sonora, Mexico. The Pinacate Biosphere Reserve is

approximately 45 km north of the city Puerto Peñasco, Sonora, Mexico. The U.S./Mexico border forms the Pinacate Biosphere Reserve's northern boundary.

Organ Pipe Cactus National Monument is 133,830 ha and is administered by the U.S. National Park Service (Schmidt et al. 2007, NPS 2016). Organ Pipe Cactus National Monument falls within the Basin and Range Geologic Province and is characterized by steep, rugged mountains separated by wide alluvial valleys (Schmidt et al. 2007). Elevation ranges from 305 m in the valleys to 1465 m at Mount Ajo, the highest point within OPCNM (Schmidt et al. 2007). Weather observations during the study were taken from Bull Pasture weather station (elevation 970 m) in the Ajo Mountains of OPCNM. The annual precipitation during the study was 27.0 cm (NPS unpublished data). Temperatures ranged from a minimum of 1.2 °C in January 2017 to a maximum of 43.0 °C in June 2017 (NPS unpublished data). Vegetation in the mountainous areas is characterized as Arizona Upland Subdivision of Sonoran Desert Scrub (Brown 1994, Felger et al. 2012). Common tree species of the Arizona Upland Subdivision include foothill palo verde (*Cercidium microphyllum*), mesquite (*Prosopis spp.*), and ironwood (*Olneya tesota*) (Brown 1994). Dwarf juniper (*Juniperus arizonica*), scrub oak (*Quercus turbinella*) and rosewood (*Vauquelinia californica*) can be found sporadically at the highest elevations (Felger et al. 2012).

The Pinacate Biosphere Reserve is 714,556 ha and is administered by Comisión Nacional de Áreas Naturales Protegidas (CONANP) (CONANP 1995, Esqueda et al. 2006). Our study was conducted primarily on the 228,112 ha El Pinacate core zone ('zona núcleo') (Esqueda et al. 2006). Weather observations during the study were taken from the Pinacate Biosphere Reserve biological station's weather station (elevation 130 m). The annual precipitation during the study was 14.5 cm (Pinacate Biosphere Reserve unpublished data). Temperatures ranged from a minimum of 3.8 °C in January 2017 to a maximum of 46.5 °C in June 2017 (Pinacate Biosphere

Reserve unpublished data). Vegetation in the El Pinacate core zone, specifically the hills and mountains of the volcanic shield is characterized by brittlebush (*Encelia farinosa*), ocotillo (*Fouquieria splendens*), teddybear cholla (*Cylindropuntia bigelovii*) at higher elevations such as Pinacate peak (elevation ~1000m) (Ezcurra et al. 1987). Additional species such as saguaro (*Carnegie gigantean*), desert ironwood (*Olneya tesota*), and foothill palo verde (*Ceridium microphyllum*) are found at lower elevations (~250 m) near El Elegante crater (Ezcurra et al. 1987).

METHODS

I selected 'mountains' to survey in both countries using broad criteria that identified many topographical features as potential survey areas. A 'mountain' was defined as any topographical feature that had: (1) >10m difference between the max elevation of the topographical feature and the elevation of the adjacent valley bottom and (2) a slope >10%. These criteria identified very small 'mountains' with the explicit purpose of surveying areas not typically considered bighorn sheep habitat. Potential survey areas also had to be accessible by road and foot, and capable of being surveyed in a single day, which reduced the total number of potential survey areas. I identified 30 areas to survey in the U.S. and 30 areas to survey in Mexico, however I was unable to survey all of the selected areas due to safety concerns.

My survey methods were designed to measure sheep occupancy, elevation, position on terrain feature, and human activity at multiple areas within each mountain. I established transects the first time I hiked each mountain. Transects varied considerably in both length and time required to survey each transect. Transects generally began from the nearest access road or parking lot for each mountain, ascended a prominent ridge or slope, and traversed a central ridge before descending to the base of the mountain, returning to same place where I started the

transect (Figure 2). Whenever a transect required backtracking over previously surveyed ground, I temporarily suspended the transect before resuming the transect on ground not previously surveyed. I split transects into smaller segments to collect data at a finer spatial scale within each transect, noting the start and end points for each segment. I used the following criteria to create a new segment:

1. Any change in terrain where a slope change of approximately 10° was sustained for more than 30 meters, determined by the observer while hiking the transect
2. Any change in vegetation type from (or to) grassland, bare rock, shrub, or cacti.
3. After approximately 100 m to break up larger areas

I used rules that delineated segments at a finer scale than I thought necessary for ultimately identifying sites for describing occupancy. I subsequently combined transect segments to determine sites. I identified each site on a transect by combining all segments with end points within 300 m of a previously identified site. The first site on a transect was all segments with end points within 300 m of the transect start point (Figure 3). I used 300 m to combine segments because 300 m maintained large variation in explanatory variables within sites while also maintaining reasonable estimates of detection probability (see Results). Thus, my sites for modelling occupancy are transect segments that were combined post hoc.

Sheep were rarely observed (see Results), which precluded use of bighorn sheep detections alone as indicators of site occupancy. I used bighorn sheep fecal pellet detections as indicators of site occupancy. I categorized sheep detections on each transect segment by fecal pellet pile density in one of three categories: 0 pellet piles, 1-5 pellet piles, or >5 pellet piles (Figure 4). Five pellet piles were chosen as the boundary between the 'sheep present' categories because initial surveys suggested that a boundary of five would evenly split our detections

between two categories. I also categorized pellet counts by age of each pellet pile categorizing both brown pellet piles (more recently deposited) and white pellet piles (older) as 0 pellet piles, 1-5 pellet piles, or >5 pellet piles. I was not certain as to the exact age difference between brown pellets and white pellets but repeat visits to several sites suggest a difference in brown and white pellet age of several months. I obtained fresh bighorn fecal samples from captive bighorn sheep to examine the effects of weathering on pellet color (relative age). I placed fecal pellets into three piles of approximate shape and quantity of pellet piles observed in the field at two sites approximately 100 m apart that differed only in aspect (north vs south). These sites were located on bare ground within the study area and had a slope of approximately 10%.

Human activity in my study area was difficult to quantify because it is sparse, and some human activity is intentionally inconspicuous in nature. Humans were not detected during surveys (see Results), which precluded use of human detections to quantify human activity within a site. Trash has been used in other studies to index human activity in wild landscapes (Berry et al. 2006). I used trash counts as an index for human activity. I categorized each segment of a transect by the amount of trash observed: 0 pieces of trash, 1-10 pieces of trash, and >10 pieces of trash (coded as 0, 1, or 2). A single piece of trash was defined as an item or collective parts of single item such as an article of clothing, bottle, or bag. A single item broken into several parts was recorded as one piece. I used 10 pieces of trash as the boundary between trash categories because initial surveys suggested that a boundary of 10 pieces would evenly split our trash detections between two categories. I averaged the trash index among segments when aggregating segments into sites for occupancy modelling. This allowed me to use trash as a continuous variable in my occupancy model that ranged from 0 to 2.

I also defined two terrain variables for each site, mountain height and site position on the mountain. I first extracted the elevation of each site from a 30m digital elevation model. Mountain height is expressed as the difference between the elevation of the highest site surveyed on a transect minus the elevation of the lowest site surveyed on a transect (Figure 5). The highest site surveyed on a transect typically occurred along ridgelines in the middle of a transect. The lowest site surveyed usually occurred at the beginning or end of a transect. Mountain height varied only at the transect-level. Site position was expressed as the elevation of each site on a mountain divided by the elevation of the highest site surveyed on a transect (mountain height), with the highest site surveyed on mountain having a value of 1 and the lowest site surveyed on a mountain having a value of 0. Site position described the relative elevational position of each site on a mountain (Figure 5).

DATA ANALYSIS

I fit a hierarchical occupancy model with the *unmarked* package in R (Fiske and Chandler 2011, *R Core Team* 2017). Occupancy models are an effective tool to gain insight into factors influencing the distribution of a population of interest (Pavlacky et al. 2012). Hierarchical occupancy models in the *unmarked* package model both detection probability and occupancy, to account for the effect of imperfect detection on occupancy estimates (Fiske and Chandler 2011). The logit link function is used to model a binomial response for both detection (i.e. 0 = non-detection, 1 = detection) and occupancy (i.e. 0 = not occupied, 1 = occupied) (Fiske and Chandler 2011).

Hierarchical models allowed me to estimate and explain sheep occupancy while accounting for imperfect detection of sheep pellets. Hierarchical models require replication from multiple site visits to account for imperfect detection (Fiske and Chandler 2011). I was only able

to temporally replicate surveys in 8 out of 33 transects due to limited funding. Estimates of occupancy can be biased if replication is low (i.e. 2 replicates) unless detection probability is 0.5 or higher (MacKenzie et al. 2002). Therefore, I explored a novel approach for to increase replication of my surveys. I treated presence/absence of white pellets as a first replicate of each site and presence/absence of brown pellets as the second replicate. For surveys with true temporal replicates (those 8 of 33 transects actually surveyed a second time, at least 6-months after the first survey), white and brown pellet presence/absence data during the second survey were treated as third and fourth replicates, respectively.

Because relative fecal age has not been used in this manner to estimate detection, I included the color of the fecal pellet (i.e. white or brown) in my detection model. I predicted that white fecal pellets would be more difficult to detect on light-colored substrates. White fecal pellets might also persist at lower rates than brown pellets (due to natural degradation). Observers also tend to develop ‘search images’ for brown fecal pellets over white fecal pellets. I thought it likely that as observer experience increased, detection probability would also increase on those transects that were truly surveyed more than once, so I included a survey period term (1 or 2) in my detection model. Lastly, my detection model included an interaction term for the color of pellets and survey time to determine if the probability of detecting fecal pellets varied by color and survey period.

To model occupancy, I included nation (i.e. USA or Mexico), mountain height, site position, and trash index as model terms. I also included mountain height interacting with nation, and site position interacting with nation. I included nation because occupancy is likely different in Mexico than in the USA due to different land management practices and amount of human activity within each area (Piekielek 2016). Trash index served as an index of human

activity within each site. Mountain height was included in the occupancy model as bighorn sheep prefer higher topographic features and occupancy is likely to increase as height of terrain feature increases (Bleich et al. 2009). I included site position as an index for the elevational position of each site along a transect as sites near the top of a mountain were predicted to have higher occupancy. Finally, I included interaction terms to test whether terrain had weaker or stronger effects on bighorn sheep occupancy in the USA than in Mexico. I scaled the (logged) mountain height and site position covariates, so that the mean of each covariate was 0 with standard deviation of 1, to facilitate parameter estimation and comparison. I used the predict function in R to examine the effect of each covariate on occupancy while holding the other covariates at their mean levels (*R Core Team 2017*).

RESULTS

I surveyed 33 transects totaling 256 sites (Table 1). The number of sites per transect ranged from 1 to 22. I completed temporal replicates 6 months later on 8 of 33 transects for a total of 338 site-surveys. I detected brown or white pellets in 104 sites. Of these, white pellets were detected in 64 surveys and brown pellets were detected in 93 surveys. In 550 hours observing, I detected a desert bighorn sheep 9 times (61 hours/detection). Surveys were generally distributed across a range of trash abundances (Figure 6), and mountain heights (Figure 7), and site positions in each nation, but sites in Mexico generally had less trash (Figure 6) and were on smaller features (Figure 7). Trash and site position was not strongly correlated (0.027), neither was trash and mountain height (0.042), suggesting that trash abundance was not a function of mountain height or site position.

I found effects of sheep pellet color and survey period on detection probably (Table 2). Detection probability varied dramatically and generally increased from survey 1 to survey 2 (for

those sites truly surveyed more than once) and decreased with pellet age (from brown to white). For example, detection probably (p) of white sheep pellets in the first temporal replicate was 0.229 (0.166, 0.307 95% CI) but for brown pellets was 0.347 (0.267, 0.435 95% CI) and detection for both types of pellet increased in the second time-period, but retained differences with $p = 0.593$ (0.442, 0.728 95% CI) and $p = 0.813$ (0.658, 0.907 95% CI), for white and brown pellets, respectively.

I found effects on occupancy from site position and mountain height interacting with nation (Table 3). Effects on occupancy were largely consistent with predictions with generally negative effects of USA on occupancy. Mean expected occupancy of USA sites (given the observed level of trash, site position, and mountain height) was 0.590 (0.464, 0.706, 95% CI) while in Mexico, mean expected occupancy was 0.861 (0.460, 0.978 95% CI). Occupancy was lower in the USA than in Mexico. Interestingly, we found positive effects of site position (Figure 8), but only in Mexico, and positive effects of mountain height but only in USA (Figure 9). Trash also had a negative effect on sheep occupancy that was not statistically significant but appears to perhaps be biologically significant (Figure 10).

DISCUSSION

I used a hierarchical occupancy model to understand the effects of human activity on the distribution of desert bighorn sheep in two protected areas along the border. Occupancy models are an effective tool to gain insight into factors influencing the distribution of a population of interest (Pavlacky et al. 2012). My occupancy modelling approach used bighorn sheep fecal pellets as indicators of site presence and as temporal replicates to solve the problem of low detectability of desert bighorn sheep and low replication of surveys. My approach using fecal pellets as the temporal replicates seemed to work well, as detection probabilities were relatively high (Table 2). With this approach, I was able to achieve reasonably high detection probabilities

and could examine the influence of terrain and human activity covariates on site occupancy. In future work, it might be worthwhile to consider the differences in vegetation between sites and include some measure of vegetation as an occupancy model covariate. My methods proved to be relatively low-cost and could prove useful to the study of bighorn sheep and other sparse species in other areas.

However, there are a several things to consider when using fecal pellets are temporal replicates. On my 2nd survey (of 8 transects), it is likely that at least some of the white fecal pellets detections were formerly brown fecal pellets detections from the 1st survey that turned white due to weathering processes. This creates a problem of unknown fecal pellet persistence at each site. Observations from my study of fecal pellet weathering processes indicates that fecal pellets gradually lighten in color, going from dark brown to light tan after 4 months of exposure. However, it is still not clear exactly when fecal pellets turn white and how long on average white fecal pellets persist at a site. A longer-term (>5 months) study of fecal pellet weathering processes should give better insight into these uncertainties. A potential solution to this problem is to exclude the white pellet observations from the 2nd survey. Including a freshness index indicating the relative age of each pellet pile may help account for fecal pellets undergoing weathering processes within each site.

I made several assumptions using fecal pellets as a detection method for desert bighorn sheep. I assumed that all fecal pellet detections were from desert bighorn sheep. This assumption may be violated in areas where the habitat of desert mule deer (*Odocoileus hemionus*) and Coues' white-tailed deer (*Odocoileus virginiana couesii*) overlap that of desert bighorn sheep. Coues' white-tailed deer only are only found within the study area at high elevations in the Ajo Mountains of OPCNM (Henry 1979). Desert mule deer in the Picacho Mountains west of

Tucson, Arizona were found at an average elevations of 750 m for males and 820 m for females during the winter (Ordway and Krausman 1986). However, the average elevation used by desert mule deer within my study area was not known. I did make note of which fecal samples I thought were likely from desert mule deer, but I did not exclude these detections from the occupancy model. Future genetic work with fecal samples collected from the field will provide insight into my error rate in mis-identifying desert bighorn sheep fecal pellets when in truth the fecal pellets originated from desert mule deer. Additionally, my fecal pellet detection model indicated that detection probability increased with the number of temporal replicates which may be a product of increasing observer experience during the study. An individual observer covariate could be included in future detection models to examine the influence of individual observer experience on detection probability.

My occupancy model assumed that the occupancy ‘state’ of each site did not change during between temporal replicates (Fiske and Chandler 2011). Through additional sampling, dynamic occupancy models might be possible. Dynamic models would allow the occupied ‘state’ to change within a site between sampling seasons. However, the methods employed in this study may not be conducive for dynamic models. Fecal pellets may persist on a site for >6 months as indicated from the observations taken from my study of fecal pellet weathering processes (Figure 11). Because fecal pellets can persist for an unknown length of time, possibly years, my survey method may encounter difficulty when trying to estimate occupancy in a dynamic system.

My results suggest that the distribution of bighorn sheep in the OPCNM (USA) is constrained due to high-levels of human activity. Bighorn sheep were less likely occupy sites as human activity (as indexed by trash) increased, which suggests that bighorn sheep avoided areas

with human activity potentially as a spatial avoidance strategy. Avoidance of areas with human activity may indicate indirect loss of bighorn sheep habitat within OPCNM. This is problematic as it violates the purpose of the protected area to function as a conservation strategy to mitigate or buffer from the effects of human activities (Southworth et al. 2006, McDonald et al. 2008, NPS 2016). Resource managers should recognize the importance of reducing human activity in protected areas to ensure bighorn sheep and other wildlife use all available habitat. Occupancy was negatively related to amount of human activity (indexed by trash) within each site, which was consistent with my predictions. The strong influence of terrain on bighorn sheep occupancy was also consistent with my predictions. Bighorn sheep displayed markedly different use of habitat between nations, which is best explained by the differences in human activity levels in each nation (high levels USA vs. low levels Mexico). Bighorn sheep in the USA were more likely to use only large mountains and where they are on those large mountains was not important. Desert bighorn sheep in Mexico use a much wider variety of sizes of mountains, including very small mountains, which may explain why their position on the mountains is important (Figure 8). Bighorn sheep in Mexico are more likely to occupy sites near the top of mountains, possibly as a predator detection and avoidance strategy (Berger 1991, Bleich 1999). My results indicate the importance of recognizing small mountains as potential habitat for desert bighorn sheep, even though in some areas, those features may be infrequently selected by sheep. Conservation efforts should recognize that 'atypical' bighorn sheep habitat may hold value for restoring or maintaining bighorn sheep populations.

FIGURES

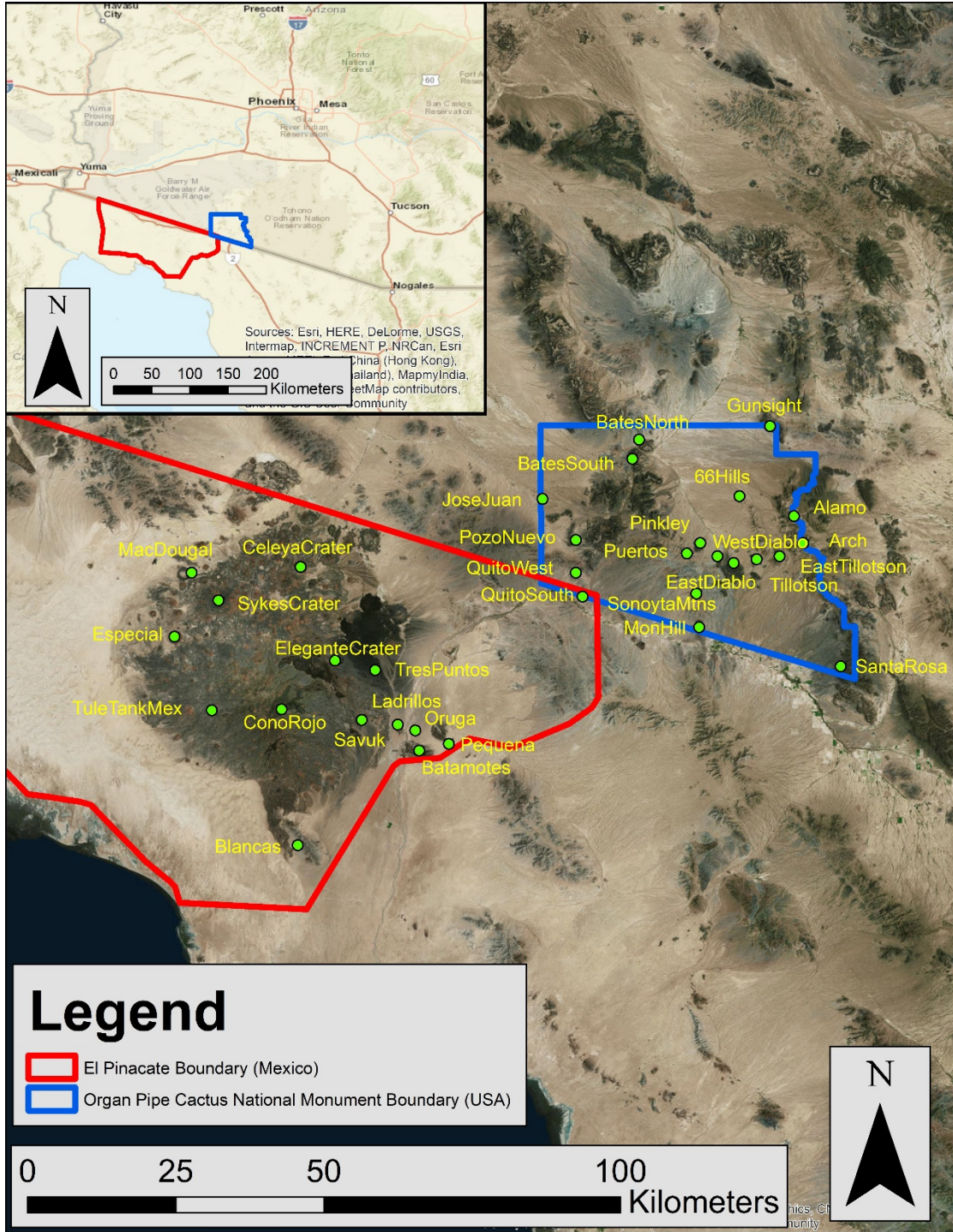


Figure 1. The study area was comprised of 2 land management units, Organ Pipe Cactus National Monument (OPCNM) in southwestern Arizona, USA, and El Pinacate y Gran Desierto de Altar Biosphere Reserve (Pinacate Biosphere Reserve) in northern Sonora, Mexico. Desert bighorn sheep (*Ovis canadensis mexicana*) transects (green dots) surveyed a wide variety of mountain sizes throughout OPCNM and the Pinacate Biosphere Reserve.

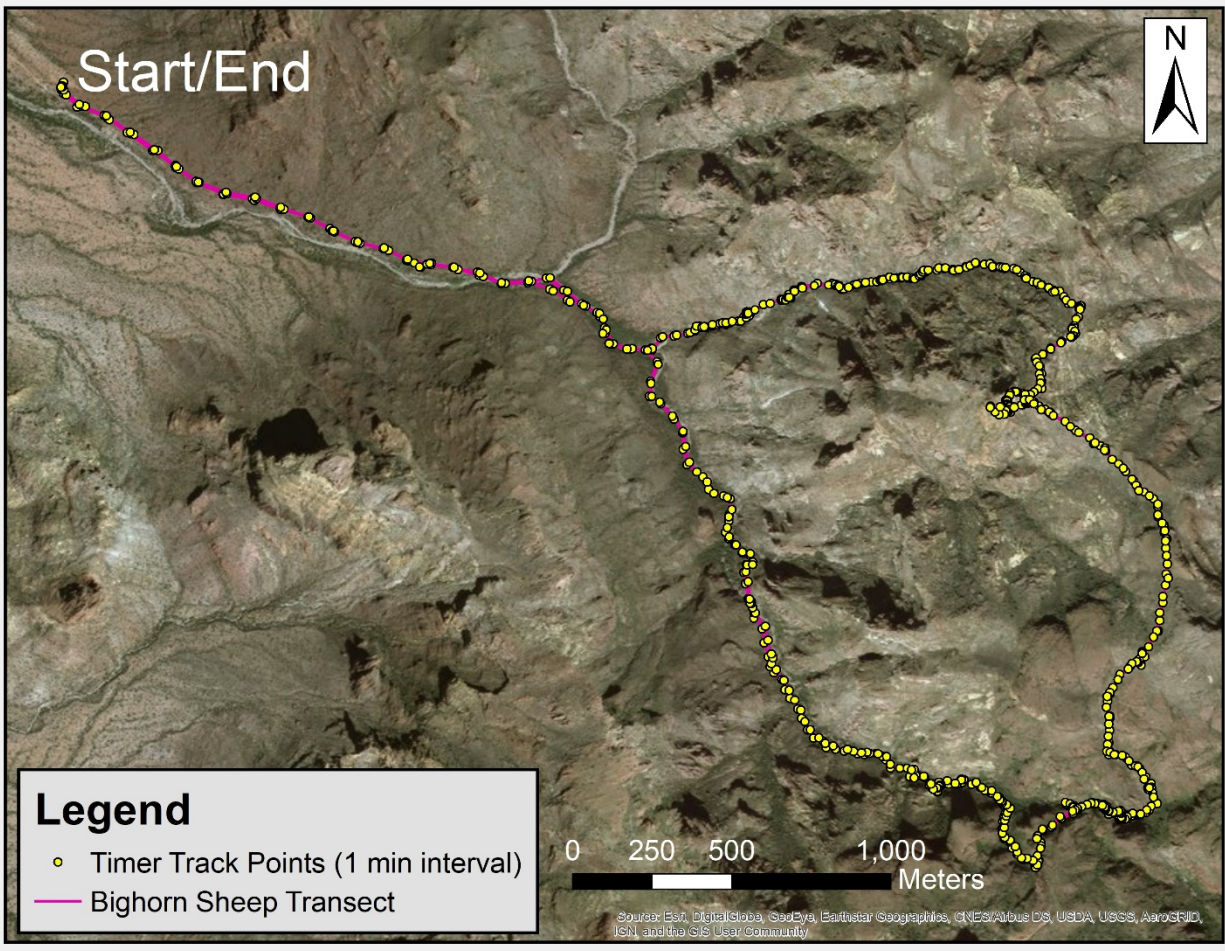


Figure 2. Example of a transect used to survey for bighorn sheep. Transects were established the first time we surveyed each mountain. Transects varied considerably in both length and amount of time required to survey. Transects typically began at the base of a mountain from the nearest road or parking area, continued up a ridgeline, traversed a central ridge, and then ended where they started.

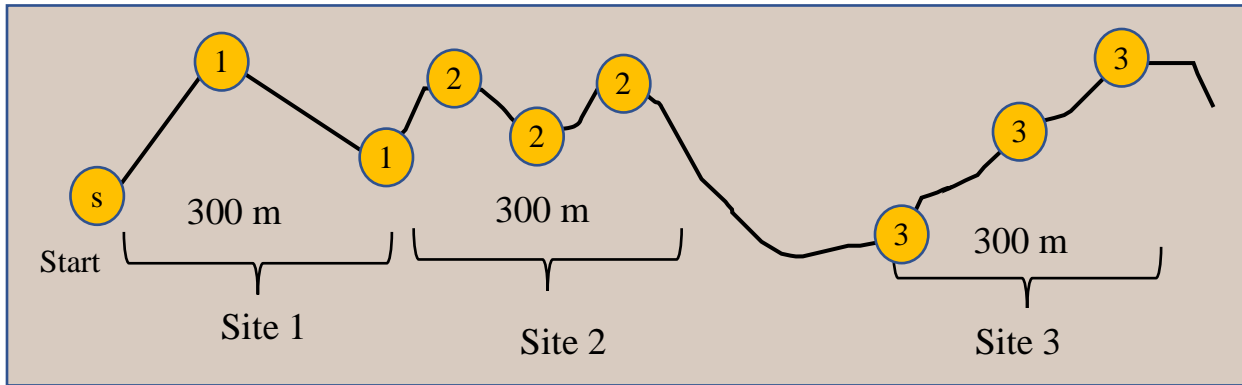


Figure 3. Schematic of a transect illustrating that each transect is split into multiple segments based on the either a change in slope or vegetation type. A new segment was also created to break up large topographical features so that segments were generally <100 m in length. Site were identified on a transect by combining all segments with end points within 300 m of a previously identified site. The first site on a transect was all segment end points within 300 m of the transect start point.

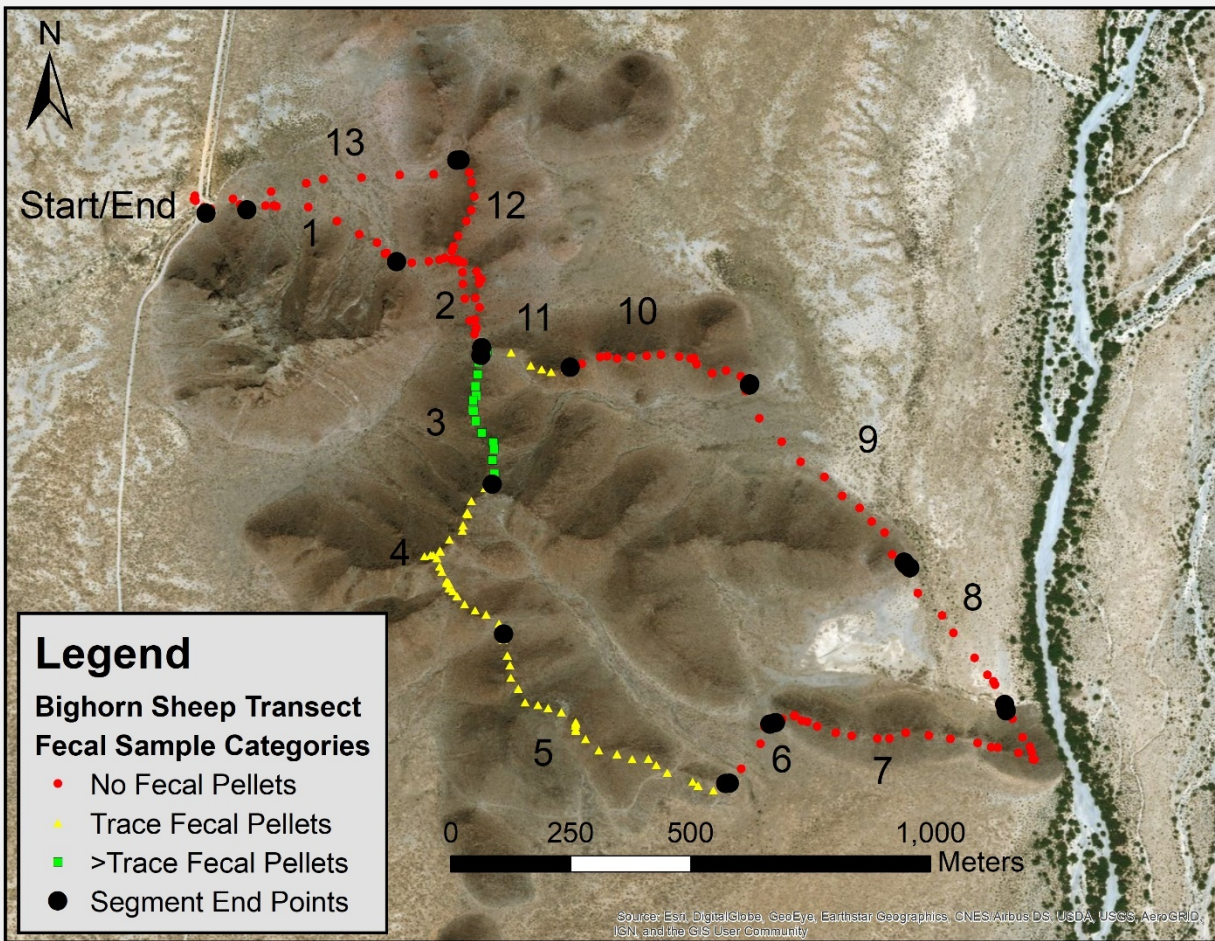


Figure 4. Example of a transect in the Ladrillo Mountains of the Pinacate Biosphere Reserve, northern Sonora, Mexico. Transects were split into multiple segments based on changes in slope or vegetation, and bighorn sheep fecal pellet detections, trash counts, detections of bighorn sheep and humans were recorded along each segment.

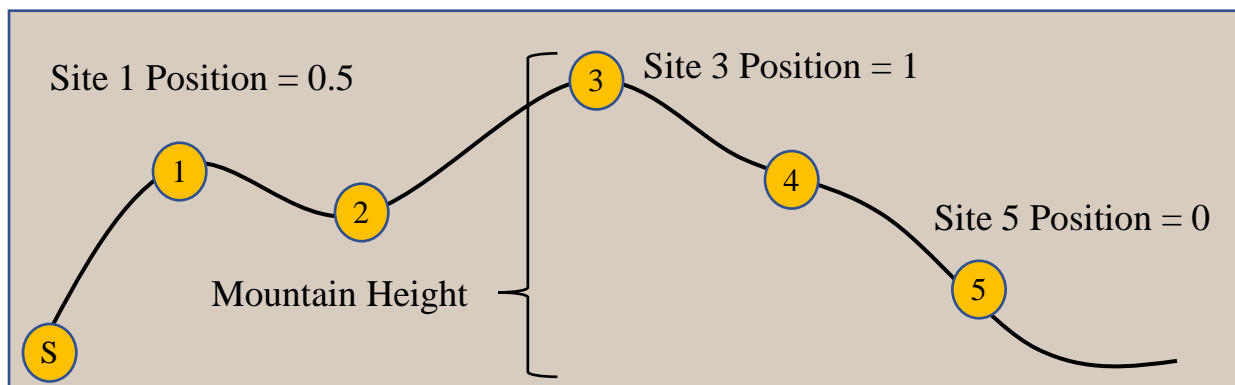


Figure 5. Schematic of a typical transect illustrating how site position and mountain height terrain variables were measured in the occupancy model. Mountain height is expressed as the difference between the elevation of the highest site surveyed on a transect minus the elevation of the lowest site surveyed on a transect. The highest site surveyed on a transect typically occurred along ridgelines in the middle of a transect. The lowest site surveyed usually occurred at the beginning or end of a transect. Mountain height varied only at the transect-level. Site position was expressed as the elevation of each site on a mountain divided by the elevation of the highest site surveyed on a transect (mountain height), with the highest site surveyed on mountain having a value of 1 and the lowest site surveyed on a mountain having a value of 0. Site position described the relative elevational position of each site on a mountain. The lowest site on this example mountain (site 5) has a site position = 0 and the highest site (site 3) has a site position of 1.

Table 1. I surveyed 256 sites along 33 transects. I surveyed 14 transects in the Pinacate Biosphere Reserve, northern Sonoran, Mexico and 19 transects in Organ Pipe Cactus National Monument (OPCNM), southwestern Arizona, U.S.A. Transects varied in length and number of sites. Transects were placed within areas potentially occupied by sheep to capture the variation in topographic features throughout OPCNM and the Pinacate Biosphere Reserve.

Transect Name	Number of Sites	Country
66Hills	7	USA
Alamo	6	USA
Arch	12	USA
Batamotes	11	Mexico
Bates North	8	USA
Bates South	8	USA
Blancas	10	Mexico
Celeya Crater	8	Mexico
Cono Rojo	11	Mexico
East Diablo	8	USA
East Tillotson	10	USA
Elegante Crater	5	Mexico
Especial	6	Mexico
Gunsight	9	USA
Jose Juan	2	USA
Ladrillos	8	Mexico
MacDougal	1	Mexico
Mon Hill	9	USA
Oruga	4	Mexico
Pequena	1	Mexico
Pinkley	5	USA
Pozo Nuevo	3	USA
Puertos	22	USA
Quito South	2	USA
Quito West	13	USA
Santa Rosa	14	USA
Savuk	2	Mexico
Sonoyta Mtns	10	USA
Sykes Crater	9	Mexico
Tillotson	20	USA
Tres Puntos	2	Mexico
Tule Tank Mex	10	Mexico
West Diablo	10	USA

Table 2. Detection model terms, estimate of coefficients, standard errors and p-values.

Model Term	Estimate	SE	P-value
Intercept	-0.634	0.191	<0.001
Pellet Color	-0.580	0.250	<0.001
Time	2.102	0.445	<0.001
Pellet Color * Time	-0.511	0.552	<0.001

$$\text{Detection (p)} = \beta_0 + \beta_1(\text{pellet color}) + \beta_2(\text{time}) + \beta_3(\text{pellet color*time})$$

Table 3. Occupancy model terms, estimate of coefficients, standard errors and p-values.

Model Terms	Estimate	SE	P-value
Intercept	1.571	1.013	0.121
Nation	-1.185	0.998	0.235
Max Height	-0.496	0.467	0.288
Trash	-0.883	0.600	0.141
Site Position	1.610	0.893	0.071
Nation*Height	1.862	0.623	0.003
Nation*Site Position	-1.765	0.922	0.055

$$\text{Occupancy } (\Psi) = \beta_0 + \beta_1(\text{nation}) + \beta_2(\text{height}) + \beta_3(\text{trash}) + \beta_4(\text{site position}) + \beta_5(\text{nation*height}) + \beta_6(\text{nation*site position})$$

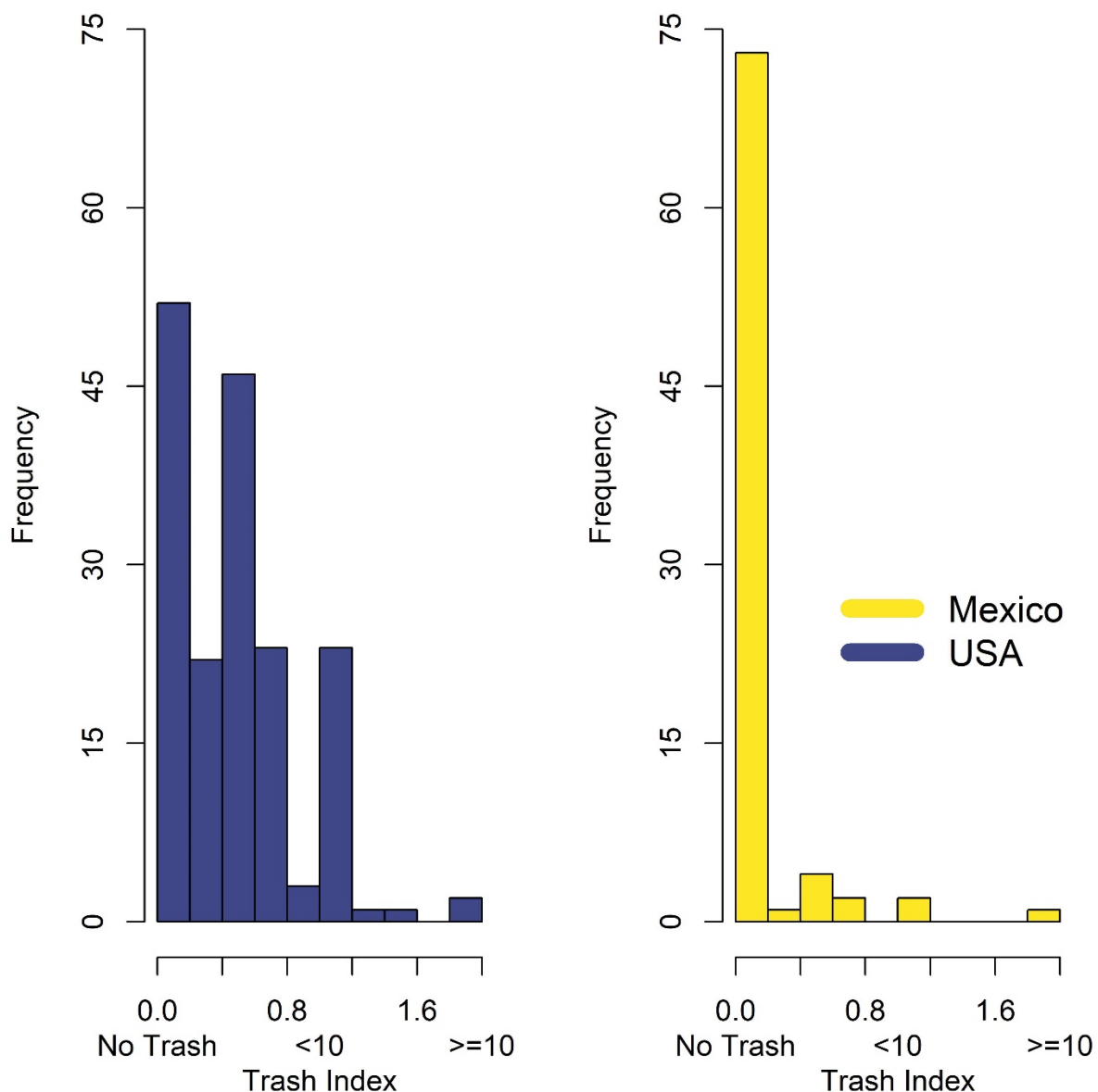


Figure 6. Frequency distribution of the average trash index observed at 256 sites for desert bighorn sheep (*Ovis canadensis mexicana*) in southwestern Arizona and northern Sonora Mexico. Trash index grouped the amount of trash at each site into 3 categories: 0 pieces of trash, 1-10 pieces of trash, and >10 pieces of trash (coded as a 0, 1, or 2, respectively). Trash observations were taken at each transect segment and then averaged together when combining segments into sites to generate a single trash value for each site. Three trash categories seemed to serve as adequate bin ranges for the amount of trash observed on the landscape. Transects in the USA tended to have more trash than sites in Mexico.

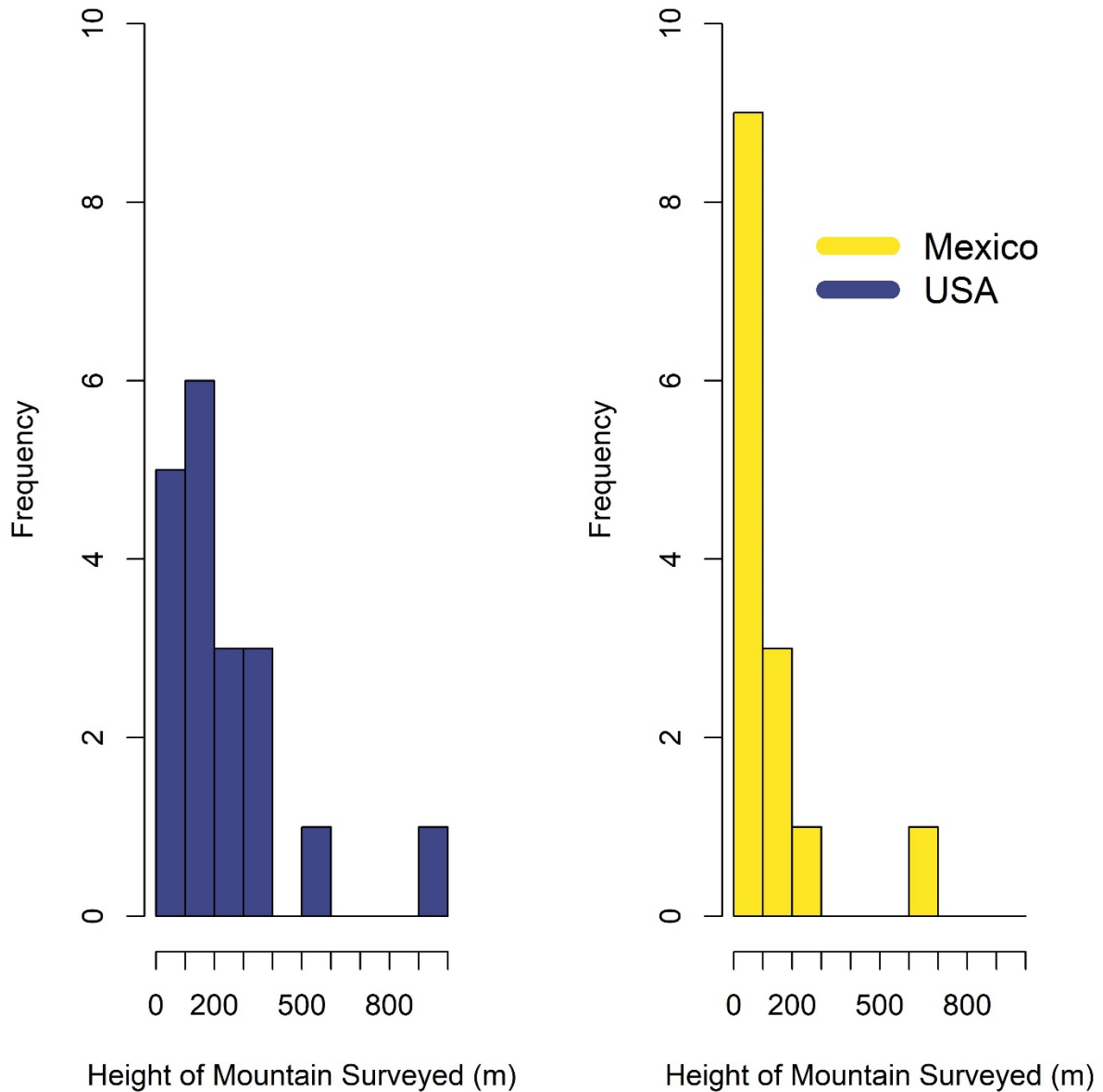


Figure 7. Frequency distribution of the mountain height for 33 transects surveyed for desert bighorn sheep (*Ovis canadensis mexicana*) in southwestern Arizona and northern Sonora. Mountain height is expressed as the difference between the elevation of the highest site surveyed on a transect minus the elevation of the lowest site surveyed on a transect. The highest site surveyed on a transect typically occurred along ridgelines in the middle of a transect. The lowest site surveyed usually occurred at the beginning or end of a transect. Mountain height varied only at the transect-level. Transects in the USA tended to be distributed across higher mountains than in Mexico.

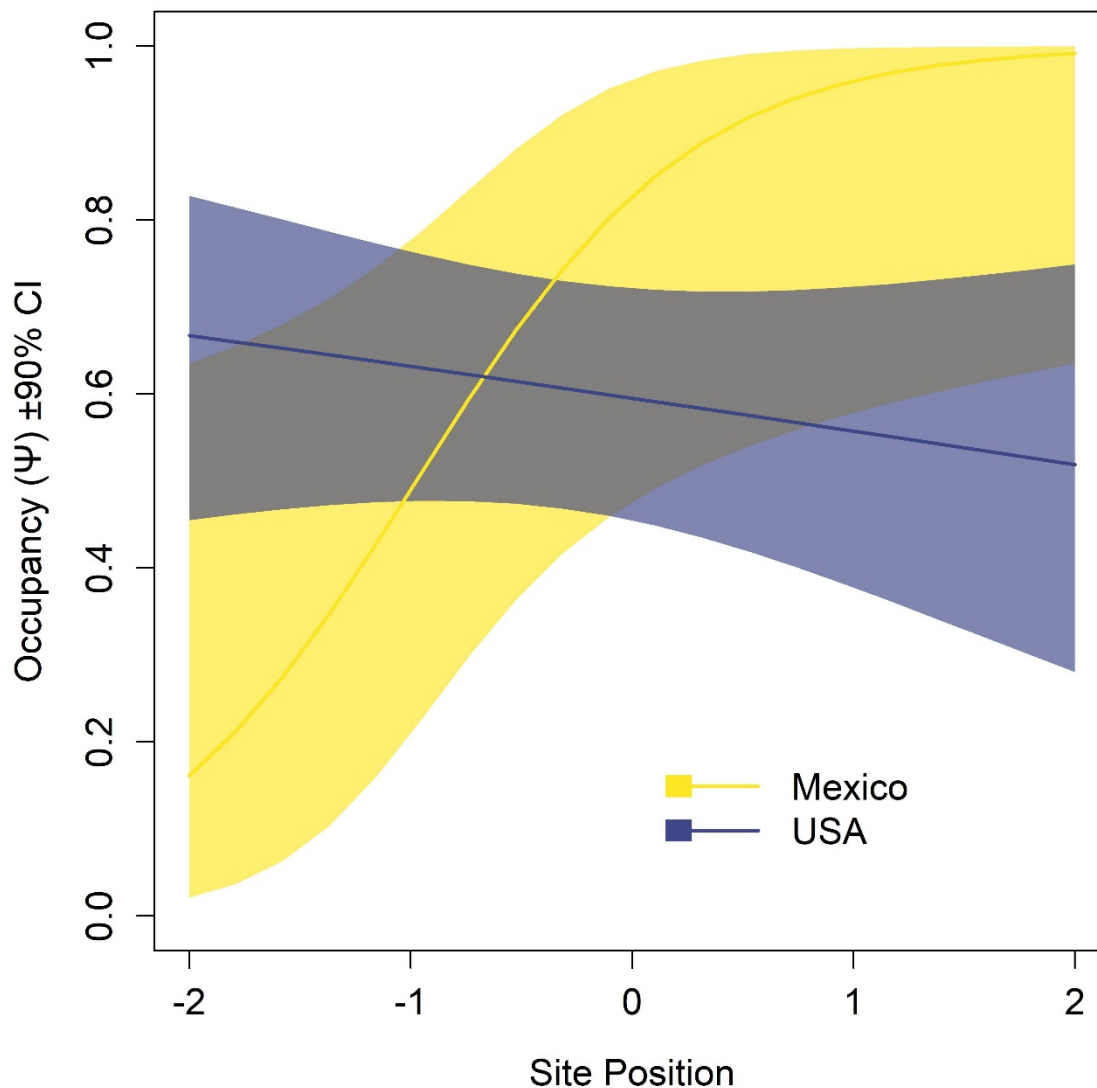


Figure 8. Expected desert bighorn sheep (*Ovis canadensis mexicana*) site occupancy in southwestern and northern Sonora Mexico as a function of site position. Site position was expressed as the (scaled) fraction of elevation of each site on a mountain divided by the maximum elevation of the mountain (mountain height), with the highest site surveyed on mountain having a value of 1 and the lowest site surveyed on a mountain having a value of 0. Site position described the relative elevational position of each site on a mountain. Expected occupancy was produced using regression coefficients from a hierarchical model of occupancy with detection varying by survey period and fecal pellet type and occupancy varying by nation, trash index, height of each transect and site position of each site (with interactions). Height of mountain and trash index were fixed at their mean values (223.035, 0.342 respectively) for these expectations.

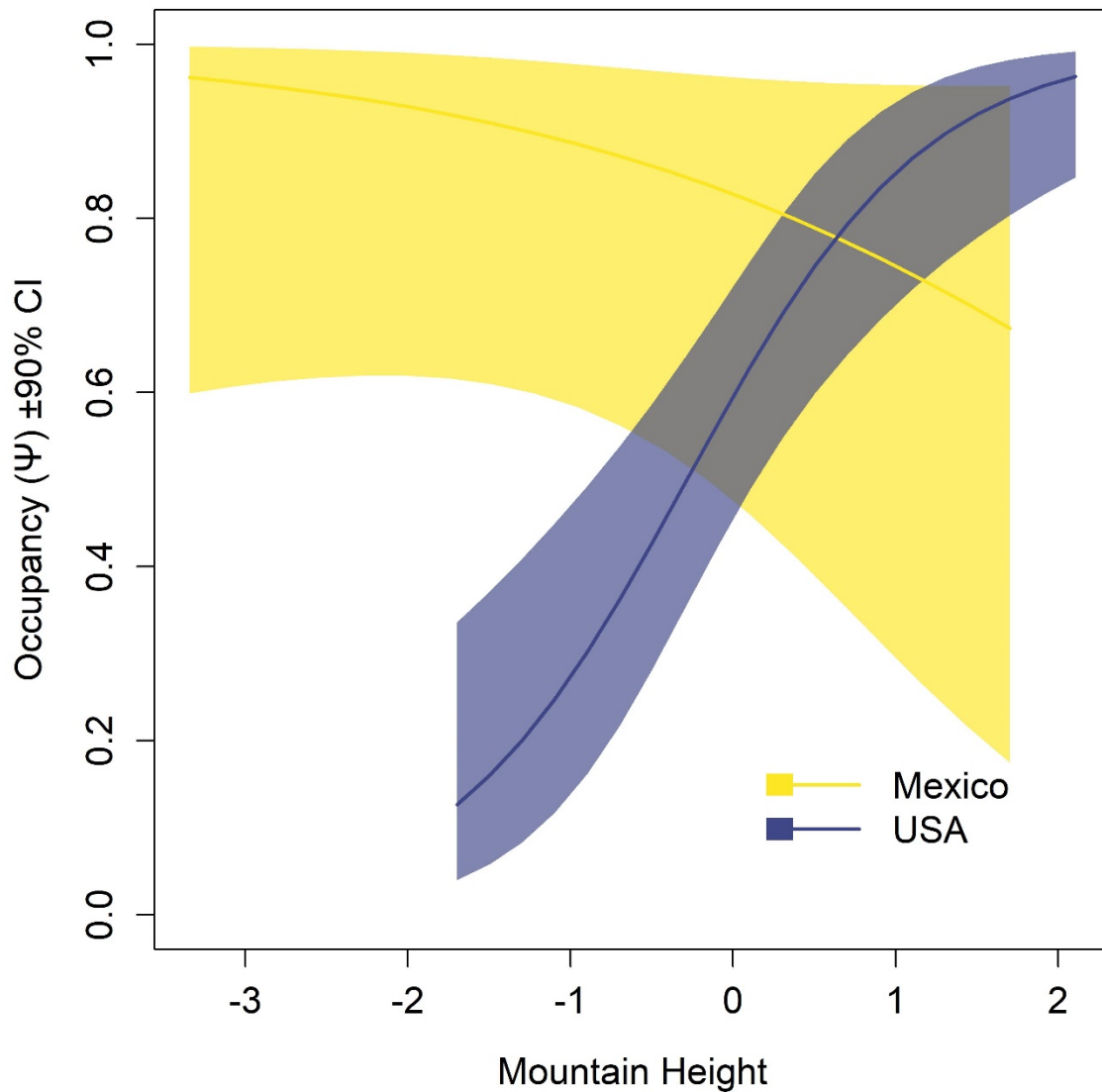


Figure 9. Expected desert bighorn sheep (*Ovis canadensis mexicana*) site occupancy in southwestern Arizona and northern Sonora Mexico as a function of (scaled) mountain height surveyed on each transect. Mountain height is expressed as the difference between the elevation of the highest site surveyed on a transect minus the elevation of the lowest site surveyed on a transect. The highest site surveyed on a transect typically occurred along ridgelines in the middle of a transect. The lowest site surveyed usually occurred at the beginning or end of a transect. Expected occupancy was produced using regression coefficients from a hierarchical model of occupancy with detection varying by survey period and fecal pellet type and occupancy varying by nation, trash index, mountain height and site position (with interactions). Site position and trash index were fixed at their mean values (0.360, 0.342 respectively) for these expectations.

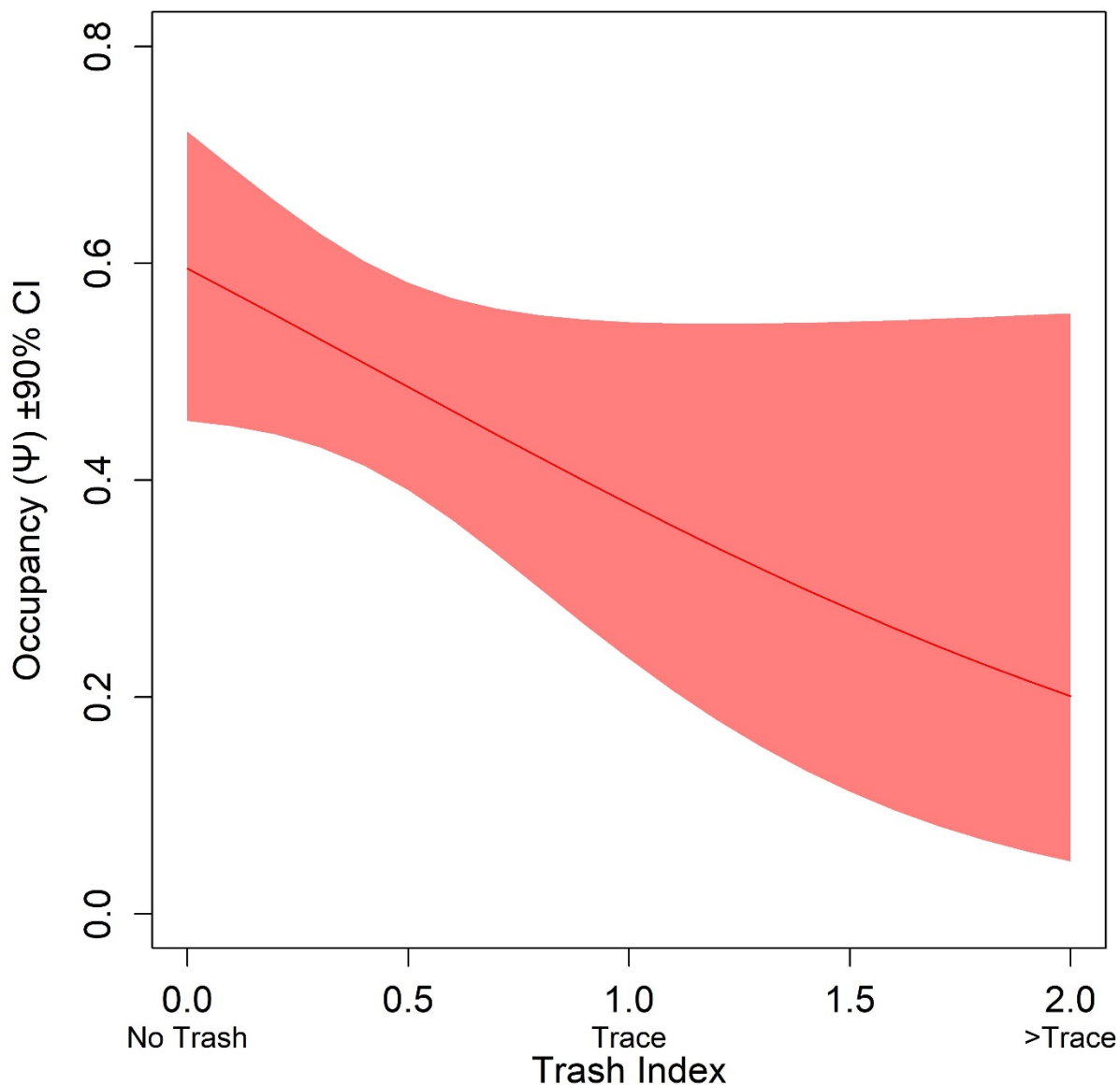


Figure 10. Expected desert bighorn sheep (*Ovis canadensis mexicana*) site occupancy in southwestern Arizona and northern Sonora Mexico as a function of average trash index of each site. The trash index grouped the amount of trash into categories: 0 pieces of trash, 1-10 pieces, and >10 pieces of trash (coded as 0, 1, 2 respectively). Trash observations were recorded for each transect segment then averaged together when combining segments into sites to generate a single trash value for each site. Expected occupancy was produced using regression coefficients from a hierarchical model of occupancy with detection varying by surveyed period and fecal pellet type and occupancy varying by nation, trash index, height of each transect and site position (with interactions). Site position and height were fixed at their mean values (0.360, 223.035 respectively) for these expectations.

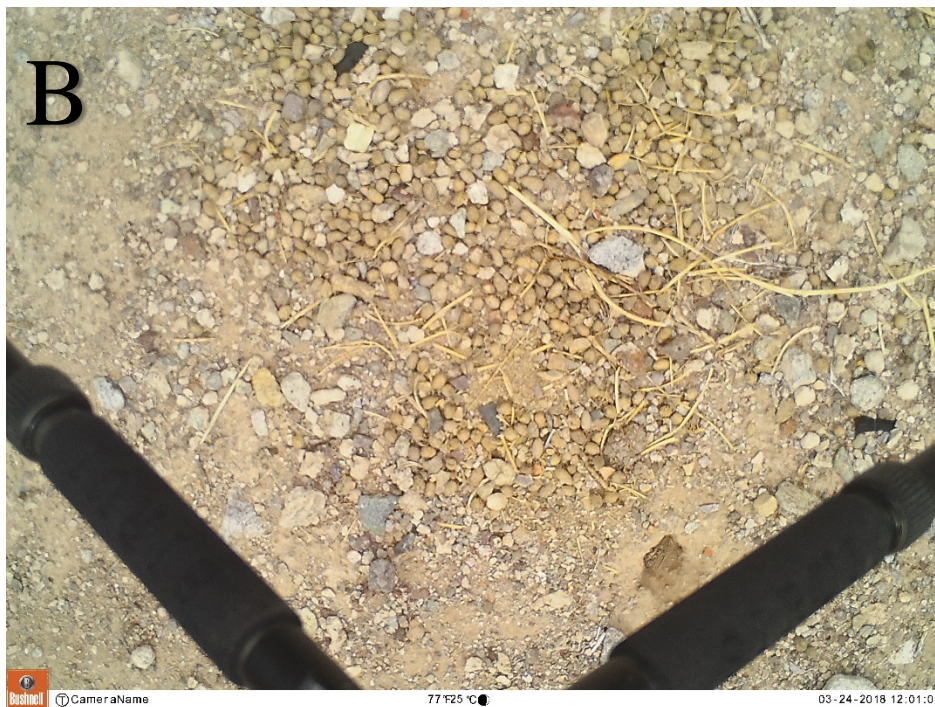


Figure 11. Paired photos of the weathering process on 3 piles of bighorn sheep fecal pellet piles. Photo A: Relatively fresh (<1-week old) bighorn sheep fecal pellet piles. Photo A taken on November 30, 2017. Photo B: the same bighorn sheep fecal pellet piles after approximately 4 months of weathering. Photo B taken on March 24, 2018. Fecal pellets generally lighten in color from dark brown to tan to white when undergoing weathering processes. Given enough time (>5 months) these fecal pellet piles will likely turn white from weathering processes.

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