DEVELOPMENT OF OCCUPANCY SURVEYS FOR MOUNTAIN UNGULATES

by

Megan O'Reilly

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APPROVAL

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Dr. Robert Garrott

Approved for the Department of Ecology

Dr. David Roberts

Approved for The Graduate School

Dr. Ronald W. Larsen

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ABSTRACT

Bighorn sheep (*Ovis canadensis canadensis*) and mountain goats (*Oreamnos americanus*) overlap in broad food and habitat requirements. In places where mountain goats are non-native there are concerns over potential competition between the two species. The southern Gallatin Mountain range, within and adjacent to the northwest boundary of Yellowstone National Park has both native bighorn sheep and non-native mountain goats. Existing observations of both species for this area vary in spatial precision and there are no records of where observers looked for animals but did not detect them. To gain a better understanding of the relationship between bighorn sheep and mountain goats and their habitat, it is necessary to understand resource selection and the extent of overlap in resource use at fine spatial and temporal scales. I used logistic regression to relate existing presence-only bighorn sheep and mountain goat data for this area to landscape features I expected would be important to both species. Using resulting coefficient estimates, I constructed a relative habitat suitability map and used it to define four survey regions within the study area. The crew of four spent 113 observer days afield and hiked 210 miles recording occupancy data for both mountain ungulates within these four survey regions. Observers surveyed 6,603 100 x 100 meter grid cells, with 15 groups of bighorn sheep and 34 groups of mountain goats observed during surveys. Because there were more mountain goat observations available, I used only mountain goat data to conduct formal occupancy analyses. Mountain goat occupancy was positively associated with ruggedness at the 100 meter scale and there was an important interaction between distance to escape terrain and tree cover at the 500 meter scale. As the distance to escape terrain increased mountain goats were less likely to occupy treed areas. The ruggedness index used in my presence-only modeling effort was based on the rate of change in slope. By using a ruggedness index which included changes in slope and aspect I improved model performance. This research demonstrates the feasibility of conducting occupancy surveys in mountainous terrain and provides interesting biological insights regarding mountain goats and their habitat.

INTRODUCTION

An organism's ecological niche is defined by its role in relation to intra-community resources and other species within the community, which limit where it can survive, develop, and reproduce (Elton 1927, Hutchinson 1957). In the absence of competitors, an organism can occupy a larger ecological niche than when the use of some primary resource is restricted by individuals of another species. When two species have overlapping niches, interspecific competition will occur resulting in one species using limited resources more efficiently (Begon et al. 2006). In some instances interspecific competition may lead to local elimination of the inferior competitor, which is known as competitive exclusion (Gause 1934, Begon et al. 2006). The extent of interspecific competition is dependent on the extent of niche overlap and is expected to lead to evolution towards niche divergence (Lack 1947, Schluter et al. 1985) allowing both species to coexist.

In some situations interspecific competition can be caused by intentional or accidental introduction of non-native species by human activities (Cox 1999). When occupying a niche similar to that of native species, non-native species may compete for resources indirectly through resource exploitation, or directly through interference by individuals (Pianka 1981, Noss and Cooperrider 1994, Poling and Hayslette 2006). Native species competing with non-natives may be forced to modify their use of resources, resulting in decreased individual fitness and less abundant populations (Gause 1934, Hobbs et al. 1990, Mack et al. 2000). Non-native species may also serve as vectors for disease transmission (Reed and Green 1994, Daszak et al. 2000) which may further limit the fitness of native species. In some cases, competition with non-native species may lead to competitive exclusion of native species. When assessing potential competition between native and non-native species, it is important to consider other potential determinants of the distribution, abundance, and fitness of a native species such as human exploitation, predator effects, climate change and disease outbreaks (Fritts and Rodda 1998).

In some parts of North America mountain goats (*Oreamnos americanus*) are not native causing concern about their potential impact on native plant and animal populations, particularly Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) (Laundre 1994, Varley and Varley 1996). Mountain goats are native to North America with historic ranges throughout British Columbia, Alberta, the Yukon Territories, southern Alaska and the northwestern United States, west of the Continental Divide (Guenzel 1980, Picton and Lonner 2008, Rideout and Hoffmann 1975). Native populations in the United States are restricted to Alaska, northern Idaho, western Montana and western Washington (Guenzel 1980, Picton and Lonner 2008). Mountain goat habitat is frequently characterized by remote, mountainous, steep and cliffy terrain. In an effort to increase hunting opportunities in the early and mid-1900s, state wildlife agencies in the northwestern United States transplanted mountain goats to numerous mountain ranges outside their historical range (Picton and Lonner 2008). Introduced populations of mountain goats have expanded their range substantially making it critical to examine the potential effects of mountain goats on bighorn sheep.

Rocky Mountain bighorn sheep are native to the mountainous regions of western North America from Alberta and British Columbia south as far as northern New Mexico (Beecham et al. 2007; E. Goldstein, New Mexico Game & Fish, personal communication). Bighorn sheep prefer areas of open landscape with stable plant communities, dominated by grasses and sedges in close proximity to steep, mountainous terrain (Adams et al. 1982, Risenhoover and Bailey 1985, Smith et al. 1991, Laundre 1994, Varley 1994). Both mountain goats and bighorn sheep are generalist herbivores that overlap extensively in broad food and habitat requirements. Although bighorn sheep and mountain goats are adapted to various habitats, it appears they most frequently overlap in subalpine and alpine areas. Similarities in foraging and habitat use could lead to competition between the two species (Pianka 1981, Noss and Cooperrider 1994, Mack et al. 2000, Poling and Hayslette 2006).

To date, there have been few studies examining the potential for competition between mountain goats and bighorn sheep. The majority of studies on these two species have examined feeding habits and habitat use of only allopatric populations and attempts have been made to demonstrate the potential for competition based on broad use of similar resources (Laundre 1994). Resulting literature indicates possible, indirect competition between the two species as a result of dietary overlap in some seasons as well as dominance of mountain goats over bighorn sheep when direct interactions occur (Chadwick 1983, Reed 1986).

Both mountain goats and bighorn sheep have some distinctive physical adaptations which should allow them to successfully exploit different niches within alpine and subalpine habitats. Mountain goats have short, heavily muscled limbs and broad hooves with special traction pads that help grip on smooth surfaces, such as rock and ice. They are not well-suited to outrun predators (Geist 1971, Adams et al. 1982, Chadwick 1983) and in many cases avoid predation by escaping to steeper, more rugged terrain. This requires mountain goats to forage alone or in small groups, where food resources are frequently patchy and/or sparse in very rugged terrain (Adams et al. 1982). Bighorn sheep are morphologically well-adapted to outrun predators over broken terrain (Geist 1971) with longer limbs and leaner bodies. As a result, they tend to feed in larger groups in areas of continuous, dense forage with unobstructed visibility and in close proximity to open areas where they can outrun predators (Shannon et al. 1975, Adams et al. 1982). Bighorn sheep and mountain goats are naturally sympatric in some areas west of the Continental Divide and both species in these areas seem to have partitioned their use of resources in such a manner that they are able to coexist. In other areas, bighorn sheep have persisted in the absence of competition from native mountain goat populations. The possibility exists that in these areas bighorn sheep have expanded their niche to encompass some of the resources that would typically be used by mountain goats in their native habitat. In these instances the potential for competition between the two species may be increased as a result of greater overlap in resource use. To gain a better understanding of the relationship between bighorn sheep and mountain goats and their habitat, it is necessary to understand resource selection and the extent of overlap in resource use, over time, among both allopatric and sympatric populations on a fine spatial scale.

Several types of data may be used to examine resource selection by animals; however, each has strengths and limitations. Most commonly, presence-only data are collected which consist of animal locations from radio-telemetry collars, transect surveys or opportunistic sightings and do not include records for areas where observers looked for but did not detect animals. These data may be used to produce coarse spatial representations of animal distributions (Elith et al. 2006, Gormley et al. 2011) but do not allow for predictions or comparisons between places where the species of interest is present and absent (Hirzel et al. 2006). In these situations, where non-detection points do not exist, random "available" points may be generated for the study area and compared to points of use, in order to allow for the estimation of the probability that a species of interest will use a given resource, based on some combination of ecological variables, such as food or escape terrain (Lele and Keim 2006, Lele 2010). This method is less likely to identify sites of true absence than formal survey methods (Loiselle et al. 2003, Keating and Cherry 2004). Presence-only data are frequently not collected as part of systematic, standardized surveys and, as a result, are likely subject to spatial and detection biases (Hijmans et al. 2000, Reese et al. 2005, and Gormley et al. 2011).

A second type of data used to assess resource selection is presence-absence data. These data are most often collected as part of formal surveys, during which observer's record areas of both detection and non-detection of animals, within defined survey units. These data may be used in much the same way as presence-only data with the added advantage of the ability to make comparisons and predictions between places where the species of interest is present and absent (Hirzel et al. 2006). These data are collected as part of systematic, standardized surveys and as a result are likely subject to fewer spatial and detection biases (Hijmans et al. 2000, Reese et al. 2005, and Gormley et al. 2011).

Occupancy data combines the probability that an animal is present with the probability that it was detected, when present in a survey unit. Animals present on a site might not always be detected by observers, so we cannot safely interpret non-detection of an animal as a true absence. Failure to account for imperfect detection can result in the underestimation of occupancy and false inferences about the relationship between actual occupancy and habitat characteristics. There is typically variation in the probability among survey units that an animal will be detected when present. By visiting survey units repeatedly over a short period of time and conducting multiple surveys it is possible to use patterns of detection and non-detection to estimate detection probabilities (MacKenzie et al. 2002).

My study area represents a portion of the southern Gallatin Mountain range within and adjacent to the northwest boundary of Yellowstone National Park (Figure 1), which provides year-round habitat for native bighorn sheep and non-native mountain goats. Based on historical observation data, I know that bighorn sheep and mountain goats have been sympatric in the area since 1967 (MTFWP, unpublished data; Wild Things Unlimited, unpublished data); however existing animal location data have been collected in many different ways resulting in observations that vary greatly in spatial precision. Most of these observations were recorded by managers during annual population surveys and are comprised of presence-only data.

The objectives of this study were to: 1) use existing management presence-only data to develop habitat models to define regions within the general study area to be intensively sampled during formal occupancy surveys; 2) intensively sample individual regions within the study area in an effort to develop, test and refine ground-based field methodology for collection of spatially explicit occupancy data for bighorn sheep and mountain goats in mountainous terrain; and 3) develop preliminary habitat selection models to predict distributions of bighorn sheep and mountain goats by including additional habitat covariates, multiple scales of selection, and spatially-explicit occupancy and detection data obtained during the 2011 field season.

METHODS

Study Area

The general study area (1342 km^2) used for the presence-only habitat selection modeling effort was located in the southern portion of the Gallatin Range in Montana and Wyoming and encompassed areas east of the Yellowstone River (Figure 1). The area was chosen based on historic data which indicated local sympatry of native bighorn sheep and introduced mountain goats.

Land ownership was a mosaic of U.S. Forest Service (Gallatin National Forest), National Park Service (Yellowstone National Park), Bureau of Land Management and private lands. Topography varied from rolling hills and flats with winding streams to abrupt, steep slopes. Elevations in the area ranged from 1,501 meters at the Yellowstone River to 3,334 meters on Electric Peak. The area experiences short summers and harsh long winters, snow frequently persisting in the higher portions of the study area into July. Average annual precipitation is 118.6 centimeters as measured at 2469 meters elevation by the Shower Falls weather station in the northern Gallatin Range, Montana. Mean annual temperature is 1.1degrees Celsius.

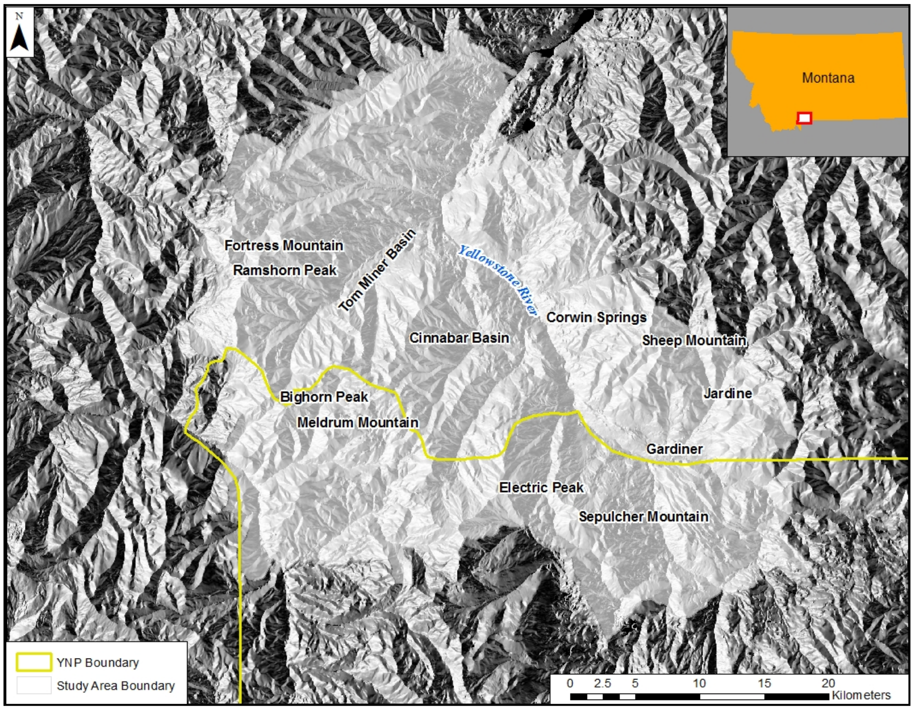


Figure 1. Study area located in the southern Gallatin Range in Montana and Wyoming.

Presence-Only Modeling Effort

Management Point Data

To determine the area to be sampled via formal occupancy surveys in the summer of 2011, summer season habitat selection modeling was conducted using a subset of existing bighorn sheep and mountain goat presence-only observation data which were previously compiled into a point database of all available bighorn sheep and mountain goat locations for the Greater Yellowstone Area (GYA). Data were collected by multiple agencies including Montana Fish, Wildlife and Parks, Yellowstone National Park, Montana State University, and private wildlife consultants beginning in 1967 and continuing to 2010. Animals were observed from various survey platforms including airplanes, helicopters and ground locations. Many of these data were not collected as part of structured surveys, resulting in various spatial resolutions of animal locations. Records considered for these analyses were restricted to observations in my general study area and with quarter section or finer spatial resolution, resulting in a total of 160 mountain goat locations and 377 bighorn sheep locations (Figure 2a). There were very few mountain goat records available to examine habitat use in winter or lambing seasons, so I opted to focus analyses on summer and rut location data for mountain goats and summer location data for bighorn sheep. Bighorn sheep appeared to move into lower elevation habitat during the rut, however mountain goats appeared to inhabit similar areas during both summer and rut seasons (Figure 2a). As a result, mountain goat location data from these two seasons were combined and included for development of summer habitat models. A total of 1000 available points were randomly distributed (Figure 2b) within the study area to define characteristics of available habitat and to compare available to used habitat locations. This number was chosen as it provided reasonable coverage of the study area and was anticipated to capture heterogeneity in the landscape. The same set of available points was employed in modeling for both species. Around each point, a 300-m radius buffer was created for data extraction from the related covariate layers to quantify habitat characteristics. This buffer size was chosen based on the judgment of wildlife professionals and was expected to capture the area of habitat that was available to animals at these observed locations.

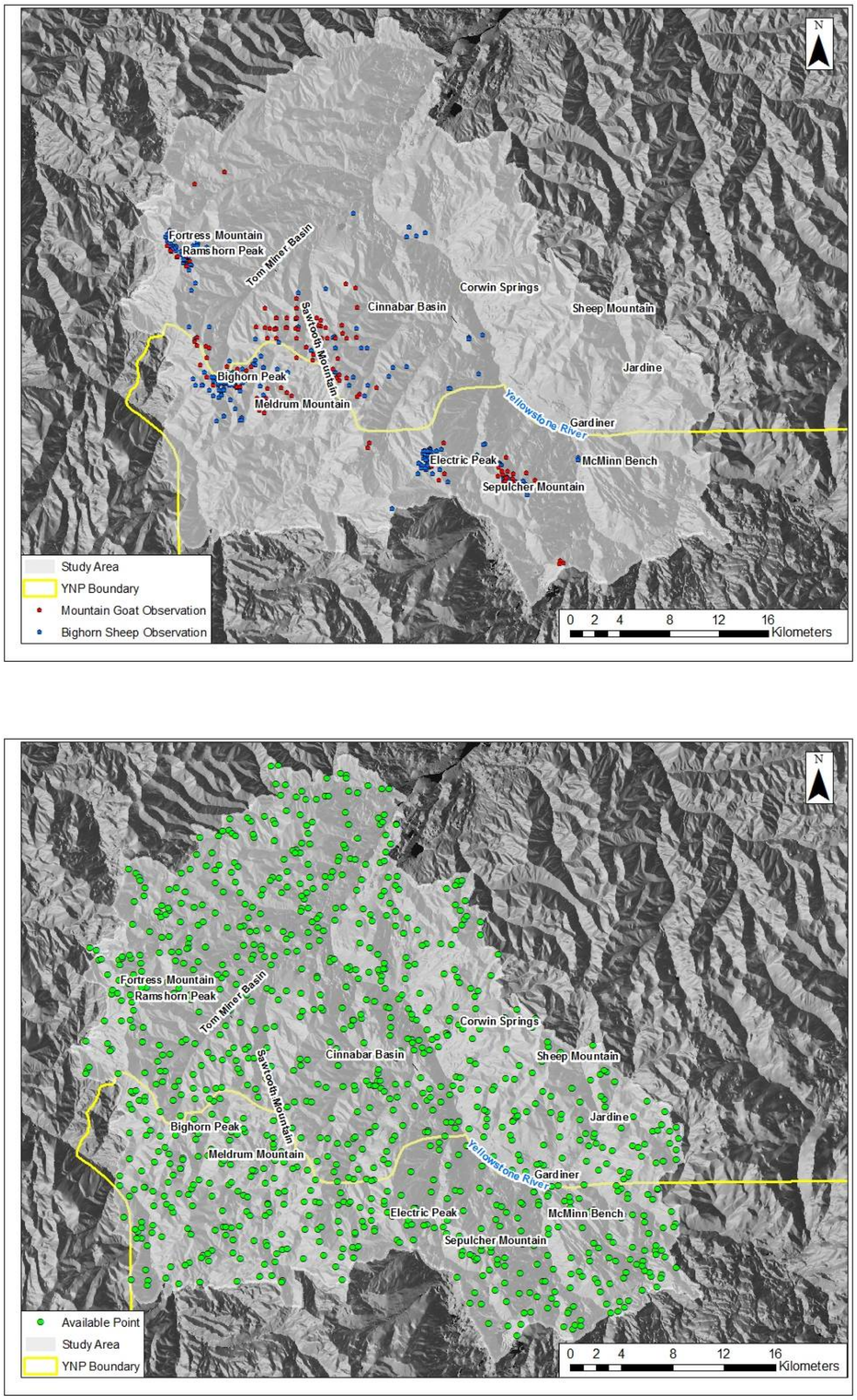


Figure 2. (a) Bighorn sheep summer and mountain goat summer and rut locations used in summer season, presence-only habitat models in the general study area. (b) Randomly distributed “available” points used in summer season, presence-only habitat models for bighorn sheep and mountain goats in the general study area.

Covariate Development

All covariates used for the presence-only modeling effort were developed as part of preliminary analyses conducted in 2010 for the Greater Yellowstone Area Mountain Ungulate unpublished report (available from: http://www.gyamountainungulateproject.com/science.html) and were based on bighorn sheep and mountain goat biology, published literature and readily accessible GIS layers. Each of seven habitat parameters (Table 1) was measured using 30-by-30 meter grid-cell resolution, as this was the most common resolution of available data sources and allowed for reasonable spatial resolution and feasible data processing. All related layers were compiled and analyzed in a geographic information system (GIS). GIS analyses and modeling were completed using ESRI's ArcMap Ver. 9.1 software (available from: http://www.esri.com). Hawth's Analysis Tools extension (available from: http://www.spatialecology.com/htools) was also used to allow extraction of statistics from various GIS layers concurrently.

Table 1. List of covariates considered in presence-only modeling effort.

Covariate List	Covariate Abbreviation	Description
Distance to escape terrain	Escape	Distance to terrain with a slope > 36 degrees
Elevation	Elev	Meters
East/West Aspect	E/W Asp	Gross et al. 2002
North/South Aspect	N/S Asp	Gross et al. 2002
Percent tree	Tree	MODIS data re-sampled to 30 meters
Ruggedness	ORug	rate of change in slope (Poole et al. 2009)
TCAP wetness	Wet	tasseled cap wetness (band 3), Landsat derivative (July 2000)

Habitat characteristics within the study area were represented using a Digital Elevation Model (DEM), Landsat Enhanced Thematic Mapper (ETM) satellite imagery and a MODIS scene. DEM layers were obtained from the Montana Natural Resource Information System (NRIS) (http://nris.mt.gov). Landsat imagery data were obtained from the Global Land Cover Facility website (www.landcover.org) and MODIS data were obtained from Montana State University's Landscape Biodiversity Lab (http://www.montana.edu/hansen/). Distance to escape terrain (Escape), elevation (Elev), aspect (Asp) and ruggedness (ORug) were developed using DEM layers. Escape terrain has been defined in existing literature using a range of slopes from 27 degrees to > 40 degrees (Zeigenfuss et al. 2000, Gross et al. 2002, DeCesare and Pletscher 2006, Poole et al. 2009). For these analyses I defined escape terrain as > 36 degrees. A distance layer was created for the entire study area to determine the distance to the nearest escape terrain pixel. Two continuous covariates were derived from an aspect layer created for the study area. These covariates described N-S and E-W exposures and ranged from 0 to 180, with 0 indicating north or east, respectively, and 180 indicating south or west, respectively (Gross et al. 2002).

The data layer created from a MODIS scene captured in 2001, covered the entire GYA and contained a percent tree cover (Tree) for each pixel. The original spatial resolution of the MODIS scene was 250 meters; however, it was resampled to 30 meters to ensure the resolution was comparable to other data layers used for analyses. Terrain ruggedness was calculated using the curvature function in ArcView 9.1. A curvature grid of 30-meter resolution was generated and run through a moving window analysis for standard deviation within a 100 meter radius of each grid cell. The result was a measure of the variability of the rate of change in slope for each grid cell. A high value was considered to be more rugged habitat as it would be indicative of a high degree of change in slope and complexity of surrounding cliffs (Poole et al. 2009).

Landsat data are multispectral images of the earth with high spatial resolution which are recorded via satellites equipped with remote sensors. Landsat data are used for many different applications from monitoring sea-ice (Meir 1973, Bindschlader et al. 2001) and water quality (Carpenter and Carpenter 1983) to land-use changes and population growth (Tan et al. 2009). For this project, Landsat data were converted from digital numbers to at-sensor reflectance values for normalization across scenes prior to use in data transformation and covariate creation. Landsat imagery for the study area consisted of three scenes collected in July of 2000. Preprocessing of Landsat imagery and creation of remotely sensed variables was done using Research System's Inc. ENVI. v4.1. (personal communication: M. Zambon). The TCAP transformation was used to convert the original covariant Landsat data into new bands making up three unrelated indices: brightness, greenness and wetness which can reflect the condition of soil and vegetation (Sheng et al. 2011). Tasseled Cap Transformation Band 3 from Landsat ETM + imagery (Wet) was included as a surrogate for the amount of moisture found across the study area, where lower values indicate wetter habitat (Crist and Kauth 1986).

Statistical Modeling

Assessing Collinearity Between Covariates

Including two or more strongly correlated covariates in the same model may confound results and make interpretation difficult (Farrar and Glauber 1967). Before constructing a global model, all seven covariates (Table 1) were evaluated for collinearity, through inspection of pairwise plots (see Figure 1B, Appendix B) and corresponding correlation coefficients. All correlation coefficients were < |0.65| and as a result I included all possible combinations of covariates in my modeling efforts.

Overview of Model Development and Analyses

Using all seven covariates, I constructed a global model: logit $\pi = \beta_0 + \beta_1$ (Escape) + β_2 (Elev) + β_3 (E/W Asp) + β_4 (N/S Asp) + β_5 (Tree) + β_6 (ORug) + β_7 (Wet). I then used logistic regression to relate the relative probabilities of use by bighorn sheep and mountain goats to the covariates of interest (Manly et al. 2002). Because these were exploratory analyses, all possible additive combinations of covariates in the global model were considered in program R (R Development Core Team 2011) extension package MuMIn. The strength of support that the data gave to each model was evaluated by ranking models with Akaike's Information Criterion and model weights (Burnham and Anderson 2002). Models within four ΔAIC_c units of the top model were considered to have received comparable support from the data. For each of the coefficient estimates resulting from top models, 95% confidence intervals were constructed.

Model outputs were in log odd units and were used for presentation of summer distribution maps. The ArcGIS raster calculator was used to apply regression coefficients from the top models to the covariates for the study area to create summer habitat suitability maps for mountain goats and bighorn sheep. The habitat suitability map constructed during this modeling exercise was used to identify regions within the general study area to be intensively sampled during formal occupancy surveys during the summer of 2011. Each survey area was stratified into four categories of relative probabilities of species occurrence: very low (40%), low, medium and high (20%). Due to the logistical and practical constraints of conducting ground surveys in mountainous terrain, occupancy survey sampling was limited to all areas predicted as high (20%) and medium (20%) suitability habitats and approximately half (10%) of the low suitability habitat defined by these models.

In addition to formal logistic regression modeling and evaluation, I constructed plots of the use and available locations for each of the seven covariates included in the modeling effort. These plots depict the range of covariate conditions sampled and allow for easy interpretation of data distributions. If distributions of use and available points are comparable, it is unlikely that the covariate in question represents a selection criterion. Where use and available distributions are different, there is evidence that the covariate may be influential to animal distributions.

Occupancy Modeling Efforts

Development of Formal Occupancy Surveys

In order to divide the landscape into discrete sampling units for occupancy surveys, a 100 x 100 meter grid cell system was placed over an aerial photo of each of the survey regions (Figure 3). The grid cell system was designed to allow observers to record animal locations with fine spatial resolution (within 100 meters) and to record areas where they looked for, but did not detect animals.

The field computers used for data collection were the Geo Mesa by Juniper Systems (see Figure 1A, Appendix A). ArcPad was loaded onto each of four field computers and custom modifications were made to ArcPad software to allow observers to enter animal locations, group sex-age composition, and behavior data accurately and efficiently into field computers during surveys (see Figure 2A, Appendix A).

Observers conducted occupancy surveys within each of the four survey regions. A survey event consisted of three to four day backpacking trips in each of these regions. Travel routes were placed along trails and ridges, based on what was logistically feasible and safe for observer travel, while affording observers a reasonable field of view. Observation points were systematically placed every three kilometers along travel routes using ArcGIS. A random number generator was used to select a starting point within the first three kilometers of the intended travel route. Observation points were then systematically selected every three kilometers from the starting point, as this distance allowed the survey crew to traverse a reasonable amount of the survey area during a three to four day trip.

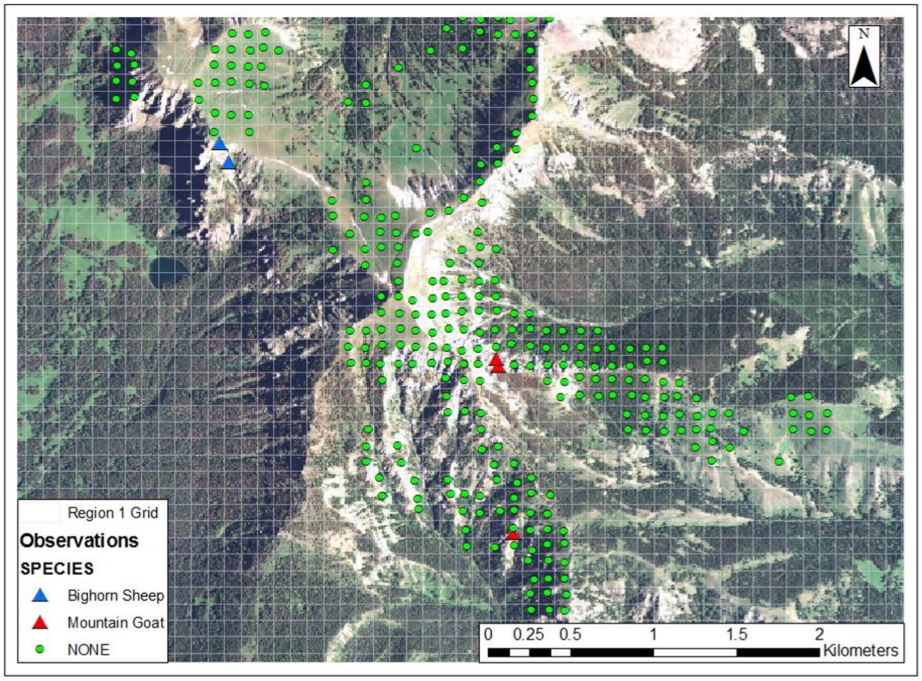


Figure 3. Screen shot of ArcPad in Juniper Systems Geo Mesa field computers. Grid overlay is made up of 100x100 meter cells, which define the individual units surveyed for bighorn sheep and mountain goat presence-absence. Green dots indicate grid cells where observers looked but did not detect bighorn sheep or mountain goats, blue triangles indicate bighorn sheep observations and red triangles indicate mountain goat observations.

A 500 meter radius buffer was placed around each observation point to allow observers to select a site for conducting an occupancy survey that afforded maximum visibility of the landscape. The surrounding viewsheds were surveyed and observations recorded into field computers. The duration of surveys varied according to the size of viewsheds and the ability of observers, however no specific survey duration was dictated. If there were multiple options for survey travel routes (i.e., a fork in the trail) direction of travel was based on logistics. Upon arrival at each systematically-selected observation point, a coin was flipped to determine which observers would survey a given viewshed (e.g., east or west side of a ridgeline) from the observation point. The exception was when an observer had already surveyed parts of the adjacent area. In order to avoid confusion about which areas were previously surveyed by another observer the original observer surveyed the aforementioned adjacent area. Observers attempted to visit each predetermined observation point during a survey event. Certain pre-selected observation points were not visited, due to logistical constraints in the field (i.e., weather, challenging terrain, etc). Observers made every attempt to visit these points and survey visible viewsheds on subsequent visits.

Animals will not always be detected when they are present in a sampling unit. Patterns of detection and non-detection accrued through repeat surveys in a short period of time may be used to estimate detection probabilities (MacKenzie et al. 2002, 2003, MacKenzie and Royle 2005, MacKenzie et al. 2006). In an effort to accrue adequate animal detections for estimation of detection probabilities and still cover a reasonable amount of ground, observers alternated between double and single observation methods. During double observer surveys, two observers independently and simultaneously surveyed the same area. Observers positioned themselves on opposite sides of a natural barrier (i.e., rock, vegetation) when possible and did not communicate or view the field computer of the other observer once a survey period had begun. These measures helped to ensure that data collected by each observer were independent. After surveys at selected observation points were completed, team members reconvened and determined which groups of animals were detected by both observers and which animal groups were only detected by one observer. Data were recorded onto detection probability worksheets (see Figure 3A, Appendix A). Observers then traveled together to the next systematically selected observation point until all possible observation points had been visited and the associated visible viewsheds had been surveyed. Efforts were focused on visiting more sampling units rather than conducting more visits per sampling unit during a survey event, as additional visits do not always notably increase the accuracy of detection probability estimates (MacKenzie and Royle 2005). If previously surveyed grid cells were visible on a future trip, those grid cells were re-surveyed.

Before scanning grid cells within a viewshed for animals, observers agreed on a reasonable topographic boundary defining the area to be surveyed. This was done at the start of both single and double observer surveys to ensure observers were covering a comparable amount of land so survey duration was not drastically different. Date, survey point ID, survey start and end times and observer location (UTM, WGS-1984) were recorded. Average wind-speed (meters/second) over a ten-second period and temperature (degrees Fahrenheit) were measured using a Kestrel 2000 Pocket Weather meter at the beginning and end of each survey period. Data were recorded into field notebooks. Observers then scanned all grid cells within the viewshed for mountain goats and bighorn sheep using 10x42 binoculars and 20x60 spotting scopes. When animals were detected, the predominant behavior of the group at first observation (feeding, resting, traveling, or other) was recorded and each group was assigned a unique number for the day. A group was considered a single animal or individuals of a species within approximately 250 meters of each other. Animals separated by more than 250 meters at first detection were considered separate groups. Group numbers allowed us to record animals as they traveled through multiple grid cells and minimize the chance of animals being counted multiple times. Any grid cell that was traversed by an animal, during a survey event was considered occupied. Animals were counted before any attempt at age/sex classification was made in an effort to increase the likelihood of recording all visible animals before they moved out of sight. Counts and point locations of detected animals were recorded directly into the field computers.

Using binoculars and spotting scopes, observers attempted to classify individual animals within a group by age and sex classes, including mature male, young male, female, yearling or young of year. Bighorn sheep classes were determined using methods described by Geist (1971) (see Figure 4A, Appendix A) and were based on a combination of possible identifying features including horn size, body size and positive identifying features, including urination posture and external genitalia. It is frequently difficult to differentiate between yearling males and ewes. If an observer was unable to differentiate between the two, the animal was classified as a female. Methods described by Chadwick (1983) were used to classify mountain goats (see Figure 5A, Appendix A) and were based on a combination of possible identifying features including horn mass and shape, body size, rump cleanliness and positive identifying features, including external genitalia and urination posture. If it was not possible to determine the age or sex of an animal, it was recorded as unknown.

Each grid cell surveyed by an observer was assigned a ranking from 1-4 based on the percentage of the grid cell visible to the observer: 1- 1%-25%, 2- 26%-50%, 3- 51%-75% and 4- 76%-100%. This ranking system was based on topography (i.e., a cell going over a ridgeline or in a draw) and was not affected by cover or ruggedness. Due to high snow levels in 2011 and my inability to quantify snow cover using a GIS layer, we did not survey large areas of the landscape fully covered in snow.

All surveyed grid cells where no bighorn sheep or mountain goats were detected were identified and recorded in the field computer by placing a non-detection point in approximately, the middle of the grid cell. If a group of animals moved into a previously unoccupied grid cell during a survey, the observer changed the status of the grid cell and included relevant animal information. If groups of animals were encountered while observers were traveling between the pre-determined observation points, they were counted and classified and their point location recorded as an opportunistic sighting. Surveys were not conducted during periods of extreme inclement weather (i.e., high winds, heavy rain) due to a decrease in observer ability to locate animals on the landscape. Upon returning from the field, all supplementary data recorded in field notebooks were logged onto data sheets to ensure consistency of recorded data and to streamline data entry (see Figure 6A, Appendix A).

Survey Data Entry

Data from field computers were downloaded after each field data collection event, upon return to the office. The Access database designed for this study consisted of four main tables to store the point and demography data for bighorn sheep and mountain goat observations (Figure 4). The first table, Field Computer, stored all of the survey data downloaded from field computers. The second table, Notebook, stored all of the survey information not recorded directly into field computers. The third table, Detection Probability, stored survey data related to groups of animals detected during double observer surveys. The fourth table, Opportunistic, stored the attribute data and the demography data associated with each opportunistic animal point location recorded outside of a survey event. The Field Computer table was linked to the Notebook table through the Survey ID, a unique ID code generated for each survey conducted. The Detection Probability table was also linked to the Notebook table through the Survey ID.

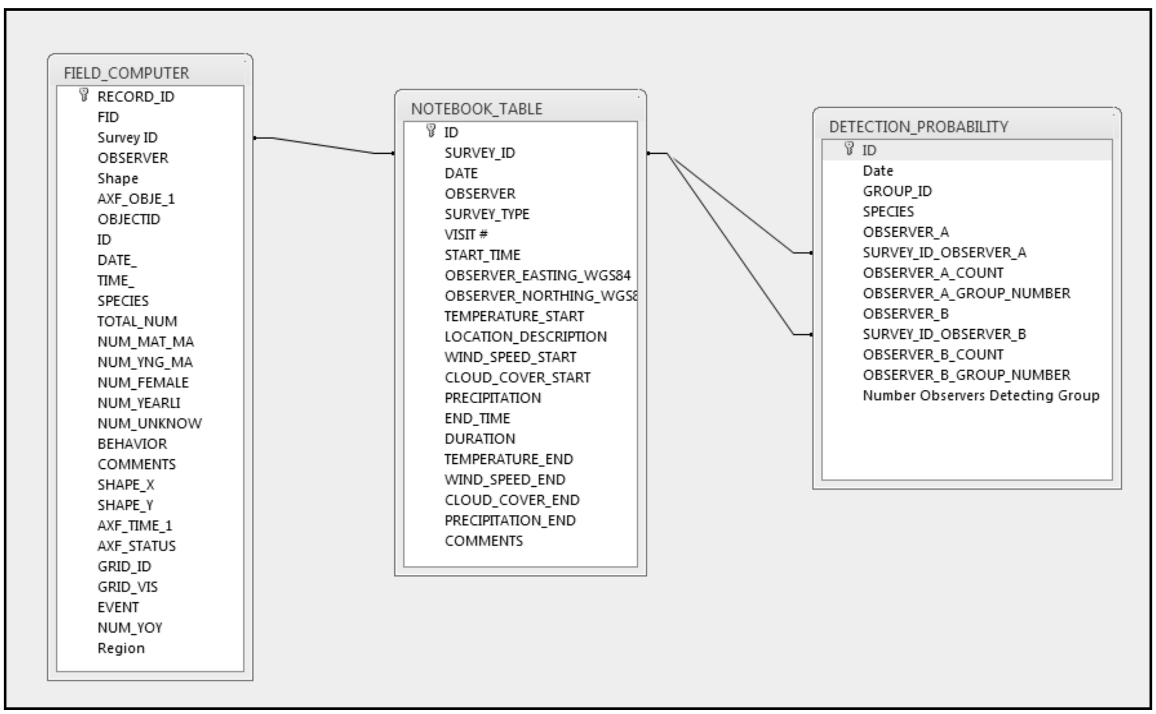


Figure 4. A screenshot of three of the four main tables (Field Computer, Notebook Data and Detection Probability) are displayed as well as the relationships between them. The Opportunistic table was not related to the other tables in the database.

Development of Additional Covariates

Frequently, habitat studies include covariates such as aspect as a proxy for solar radiation, rather than including it as a distinct covariate (Keating et al. 2007). I found it difficult to determine the biological significance of the aspect covariates as used in previous modeling efforts. As a result, I decided to exclude these covariates from further modeling efforts and I instead canvassed the literature for a more direct way to measure solar radiation. I decided to calculate solar radiation using a DEM and Spatial Analyst Extension (Fu and Rich 2002) in the ArcGIS Solar Radiation toolset. These tools have been employed by previous wildlife habitat studies (Singleton et al. 2010, Ruesch et al. 2012) and allow the user to process a huge amount of information including atmospheric effects, site latitude, elevation, slope, aspect, daily sun angle shift and adjacent topographical shading, which would otherwise be too time consuming. The resulting product is a measure of the cumulative solar energy in watt hours per meter squared. The related calculations can be performed for individual points or over large geographic areas and are carried out in a multi-step process. The process begins with calculation of an upward-looking hemispherical viewshed and is calculated based on topography. This viewshed is then laid over a direct sunmap and a diffuse skymap, allowing for estimation of direct radiation and diffuse radiation, respectively. This process is then repeated for every point or area of interest and used to produce a map of insolation (Huang and Fu 2009). I used the time period from July 8th 2011 to September 20th 2011 to estimate the amount of solar radiation on my study area during the field season. Inclusion of these site specific features may help capture some of the factors affecting spatial distribution patterns of air and soil temperatures, patterns of snow melt, moisture content of soil and the amount of light available to enable plant productivity.

The basic ruggedness measure (ORug) used in previous presence-only modeling included only the variability of the rate of change in slope for each grid cell. Using layers previously generated in ArcView 9.3 including slope, aspect and contour and an ArcView Script developed by Sappington et al. (2007), I created a new, more complex layer of vector ruggedness measures (Rug) which combined variation in aspect and slope into a single measure (script available online from the Environmental Systems Research Institute ArcScripts website: www.esri.com/arcscripts). It seems logical to quantify ruggedness based on changes in both aspect and slope to truly capture features of surrounding topography important to animals (Sappington et al. 2007). This method may capture more heterogeneity in the landscape than indices based only on changes in slope or elevation.

The scale at which an animal selects a resource is dependent on many variables some of which include vulnerability to predation, the cost of foraging and the spatial distribution of the resource (Senft et al. 1987, Gustafason 1998, Johnson et al. 2002, Kie et al. 2002). Scale is defined here as spatial extent or area as opposed to grain or resolution of measured landscape features (Kie et al. 2002). Our ability to capture differences in resource selection and to make associations between animals and their habitat will vary with scale (Boyce 2006). If data are not explored at the scales which are important to animals, we are likely to misinterpret the results of habitat suitability analyses (Wiens 1989). Examining too large of an area may preclude detection of habitat heterogeneity and examining too small of an area may cause under-sampling of variance in local habitat characteristics (Boyce 2006).

In an effort to account for heterogeneity of the habitat and local variation of habitat characteristics, I examined habitat selection at two different spatial scales. Hawth's Analysis Tools extension was used to create 100 meter and 500 meter buffers around both detection and non-detection records as well as to extract covariate values within each buffer. In grid cells where animals were not detected, observers placed an observation point in the approximate center of the grid cell. If there were multiple observation points in the same grid cell, covariate values were averaged across the buffers placed around each of the observation points. Subscripts were used ($_1$=100 meters or $_5$=500 meters) to denote at which scale a covariate was being considered in a given model.

Statistical Modeling

Assessing Collinearity Between Covariates

Before developing an *a priori* model list, all seven covariates (Table 2) were evaluated for collinearity, at both the 100 and 500 meter scales, through inspection of pairwise plots (see Figure 2B, Appendix B) and corresponding correlation coefficients. Any combination of covariates with correlations > |0.6| were determined to be highly collinear and were not included together in models. These included $Tree_1$ and $Elev_1$, $Tree_5$ and both Wet_5 and $Elev_5$ and finally $Escape_5$ and Rug_5. $Tree_5$ was excluded from all models as it was correlated with multiple covariates. All covariates at the 100 meter scale were highly correlated with the same covariates at the 500 meter scale. As a result, no covariate was included at both scales in the same model.

Table 2. List of covariates considered in occupancy modeling effort. All covariates except ORug were examined at both 100 meter and 500 meter scales.

Covariate List	Covariate Abbreviation	Description
Distance to escape terrain	Escape	Distance to terrain with a slope > 36 degrees
Elevation	Elev	meters
SRI	SRI	Fu and Rich 2002
Percent tree	Tree	MODIS data re-sampled to 30 meters
New Ruggedness	Rug	slope/aspect (Sappington et al. 2007)
TCAP wetness	Wet	tasseled cap wetness (band 3), Landsat derivative (July 2000)
Old Ruggedness	ORug	rate of change in slope (Poole et al. 2009)

Covariate Predictions and Interactions

Animals select landscape features at various spatial scales ranging from geographic areas to individual plants (Johnson 1980). I predicted that different habitat features would be important to mountain goat habitat selection at different scales. Mountain goats are associated with steep, rugged, sloped terrain which they use to escape from potential predators (Adams et al.1982, Chadwick 1983, Laundre 1994, Varley 1994, Gross et al. 2002, Poole et al. 2009). I predicted an increase in the probability of occupancy as terrain ruggedness values increased and a decrease in the probability of occupancy when the distance to escape terrain (slope > 36 degrees) increased. I also predicted that the effect of distance to escape terrain would depend on ruggedness indices in the area, with higher ruggedness indices minimizing the need for mountain goats to have access to additional escape terrain.

Species distributions and habitat selection depend on various biological processes, many of which are affected by solar radiation (SRI). For example, Sargeant et al. (1994) found that mule deer (*Odocoileus hemionus*) were selecting different exposures and slope positions on clear summer days, versus overcast or winter days. They also found that bedded deer frequently moved when changes in cloud cover or solar angle exposed them to the sun. Selection of bed sites sheltered by vegetative cover or adjacent topography was linked to season and cloud cover, with selection of more sheltered areas on clear summer days. Solar radiation indices may also be indicative of some of the resources available to animals in the form of plant productivity and snow melt patterns, influenced by soil and air temperatures. I hypothesized that there would be a negative relationship between SRI and mountain goat occupancy. Areas with higher SRI values are hotter and plants used for forage in these areas likely experience a shorter growing season, greening up and senescing earlier than plants in cooler areas, particularly during the summer.

TCAP wetness is used as a surrogate for moisture in the study area, the lower the value the wetter the area (Crist and Kauth 1986). Wetter areas are likely to produce more forage than hot dry areas, over a longer period of time during the summer months. For this reason I predicted that mountain goats would select for wetter areas resulting in a negative relationship between TCAP wetness and the probability of occupancy by mountain goats. Percent tree cover can affect an animal's ability to detect predators (Risenhoover and Bailey 1985, DeCesare and Pletscher 2006, Riginos and Grace 2008). Festa-Bianchet and Cote (2007) found that the majority of successful predation attempts on mountain goats were either in forested habitat or within 50 meters of forested habitat.

Mountain goats frequently remain within or near escape terrain where it is difficult for predators to keep up (Geist 1971, Adams et al. 1982, Chadwick 1983), however tree cover can provide shelter from the heat of the sun resulting in a longer growing period for forage plants. I expected the effect of tree cover on mountain goat occupancy to depend on the distance to escape terrain. I predicted that in areas closer to escape terrain, tree cover would be more important. Tree cover provides cooler areas allowing moisture to persist in the soil for longer periods of time. With this increase in moisture, I would again expect a longer growing period for plants used as forage. I also predicted that the effect of tree cover on occupancy would depend on SRI, with an increase in the probability of occupancy for densely treed areas where solar radiation indices were higher. Mountain goats use high-elevation habitat, particularly during the summer, as high quality vegetation becomes available at increasing altitudes (Festa-Bianchet and Cote 2007). For this reason, I expected an increase in the probability of occupancy by mountain goats as elevation increased. Of the six covariates I examined during *a priori* modeling efforts, I expected that as both ruggedness and tree cover values increased, the probability of detection of mountain goats would decrease.

To help with the interpretation and biological significance of the results, I constructed plots illustrating predicted occupancy as a function of selected covariates based on coefficient estimates from top models. Several combinations of covariates were examined prior to construction of prediction plots to ensure I used only covariate values within the observed range (see Figure 3B and Figure 4B, Appendix B) allowing me to stay within the appropriate inference space.

Overview of Model Development

Using only those covariates that I found to be sufficiently uncorrelated and that I predicted *a priori* to be related to occupancy and/or probability of detection of mountain goats by observers, I developed two suites of *a priori* candidate models at the 100 meter and 500 meter scales, respectively. These two model suites were based on prior knowledge of the study system and existing literature. All covariates were centered and scaled to enable comparisons and interpretation of covariate coefficients. Pearson's chi-squared goodness-of-fit test for the richest *a priori*, 100 meter model (*p*-value = 0.376) and 500 meter model (*p*-value = 0.099) indicated that the model fit the data reasonably well. Ideally, the Pearson's chi-squared goodness-of-fit tests would be followed up by some assessment of the predictive power of the models using cross validation. The idea is to evaluate the performance of the model with data that were not used in its creation to see if it remains valid (Williams et al. 2002). I did not cross validate models as part of this effort.

Because animals select different resources at different scales and I did not examine all possible combinations of scale for covariates in my *a priori* modeling effort, I ran a post-hoc exploratory analysis to examine the possible effects of scale on individual covariates. I substituted the scale of the covariates in the top-ranking model with all possible combinations of scale. I included only the new, complex ruggedness covariate in my *a priori* modeling effort. In order to validate my inclusion of this covariate, I conducted a post-hoc exploratory analysis where I compared the top-ranking model using the complex ruggedness covariate to the same model including the more basic ruggedness covariate.

Model Analysis

Single-species, single-season occupancy modeling was used to estimate occupancy and detection probability (MacKenzie et al. 2006). Occupancy rate (ψ) was defined as the proportion of all survey units that were occupied by mountain goats. This method accounts for the probability that an individual will occupy a site (ψ) and be detected by observers during a survey (p). I completed model analysis using R (R Development Core Team 2011) extension package unmarked (Fiske and Chandler 2011). Occupancy survey observation data were limited for all survey sites for both bighorn sheep (n=21 grid cells) and mountain goats (n=47 grid cells). I decided to use only mountain goat observation data for this modeling effort. Of the 55 grid cells occupied by mountain goats during occupancy surveys, eight were excluded from analyses, as they were repeat observations of the same animal or group of animals among multiple grid cells and could not be considered spatially or temporally independent. In an effort to include my entire model lists for anaylses, I supplied starting values and increased the maximum number of iterations for any models that would not converge. If models were still unable to converge I excluded them from my analyses. The strength of support that the data gave to each model was evaluated by ranking models with Akaike's Information Criterion and model weights (Burnham and Anderson 2002). Models within four ΔAIC_c units of the top model were considered to have received comparable support from the data. To evaluate the effect of each of the covariates on occupancy or detection, I constructed 95% confidence intervals for each of the coefficient estimates resulting from top-ranking models. Many of the models were nested so I considered parameters uninformative if their addition to the model did not explain as much variation as necessary to overcome the two ΔAIC_c parameter penalty incurred and their 95% confidence interval spanned zero (Arnold 2010).

Investigation of Potential Violations of Assumptions

Several critical assumptions are made when modeling single-species, single-season occupancy (MacKenzie et al. 2006). It is assumed that a survey site is "closed" to changes in occupancy status for each site during the survey period, which means that occupancy status of a site does not change during the survey period. Despite conducting double observer surveys in an effort to accrue data for independent, closed survey events, I did not have enough data to consider each of these events independently. As a result, detection probability and occupancy data were pooled across all visits to a site and sites were considered closed to changes in occupancy status throughout the survey season, possibly violating this assumption. There have been few studies examining the sensitivity of occupancy models to violations of the closure assumption (Rota et al. 2009); however there are strong similarities between occupancy estimators and closed mark-recapture estimators (MacKenzie et al. 2006, Rota et al. 2009). Based on existing literature, violations of the closure assumption are likely to result in overestimates of occupancy (Kendall 1999, MacKenzie et al. 2006, Rota et al. 2009).

Constant probability of occupancy and detection are assumed across all sites unless differences can be modeled using covariates. I included multiple covariates that I expected would affect occupancy by mountain goats, as well as the probability of detection given a site was occupied, in order to address these assumptions. Although I recorded several covariates which were likely to vary over time, I did not include them in my analyses and as a result I may have failed to capture some of the variation in the probability of detection among sites and surveys. Violation of this assumption is likely to result in a negatively biased estimate of occupancy (MacKenzie and Bailey 2004, MacKenzie 2005). The final assumption for occupancy modeling is that detection of the species and detection histories at each site are independent. At each survey point observers would be randomly assigned a viewshed to survey in an effort to minimize the chance of an observer repeatedly surveying the same viewshed and looking for animals where they had seen them in the past. I also used only the first grid cell an animal or group of animals was observed in, for my occupancy analyses. This assumption was reasonable for this study.

RESULTS

Presence-Only Modeling Effort

The use versus available covariate distributions for mountain goats during the summer season (see Figure 1C, Appendix C) suggested mountain goats selected for areas closer to escape terrain, slightly drier, rugged, higher elevation terrain than what was available. There was also some evidence for selection of areas with greater tree cover. Interpretations of the density plot patterns were supported by results of model selection. The two top models accounted for nearly all of the model weight (Table 3). Both of these models included five of the seven covariates, with only east/west aspect not appearing in both models. Coefficient estimates were similar for both models and the only coefficient confidence intervals that spanned zero were wetness and EWAsp, in one of the two top models (Table 4).

The use versus available covariate distributions for bighorn sheep during the summer season (see Figure 1C, Appendix C) suggested bighorn sheep and mountain goats selected for similar locations in rugged habitat, closer to escape terrain and at high elevations. Bighorn sheep also appeared to select for drier areas with fewer trees compared to areas selected by mountain goats. Model comparisons resulted in one top model receiving 91% of the model weight (Table 3). The top model included six of the seven covariates considered. Point estimates and associated 95% confidence intervals for the six covariate coefficients appearing in the model did not span zero (Table 4). The resulting habitat suitability maps were very similar for both species so I only present the mountain goat suitability map in this document (Figure 5).

Based on this map and the ability of an occupancy survey field crew to cover a given area with the resources available during three to four day backpacking trips I selected four regions (Region 1, Region 2, Region 3 and Region 4) to be utilized for development of field methods and data collection for formal occupancy surveys in the summer of 2011. These four survey regions extended from Fortress Mountain south to Sepulcher Mountain covering a total area of 250 km^2 and were restricted to areas west of the Yellowstone River (Figure 5).

Table 3. Model selection results for resource selection probability function models examining the effects of seven landscape covariates on bighorn sheep and mountain goat summer and rut habitat selection. Models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i).

Bighorn Sheep					
Model ID	Model	k	AIC_c	ΔAIC_c	ω_i
1	Escape + Elev + EWAsp + NSAsp + Rug + Wet	7	3494.00	0	0.91
2	Escape + Elev + EWAsp + NSAsp + Tree + Rug + Wet	8	3499.00	5.20	0.07
Mountain Goat					
Model ID	Model	k	AIC_c	ΔAIC_c	ω_i
1	Escape + Elev + EWAsp + Tree + Rug + Wet	7	1523.00	0	0.48
2	Escape + Elev + Tree + Rug + Wet	6	1523.00	0.17	0.44
3	Escape + Elev + EWAsp + NSAsp + Tree + Rug + Wet	8	1528.00	5.05	0.04

Table 4. Coefficient estimates of all models within four AIC_c units of the top model for bighorn sheep and mountain goat summer habitat selection. Coefficient estimates in bold font include confidence intervals that do not span zero.

	Bighorn Sheep	Mountain Goat	
Model ID	1	1	2
Covariate			
Intercept	**-17.3**	**-23.07**	**-27.69**
	(-18.9, -15.7)	**(-37.96, -18.35)**	**(-37.97, -18.44)**
Escape	**-0.006**	**-0.005**	**-0.005**
	(-0.009, -0.005)	**(-0.008, -0.003)**	**(-0.007, -0.003)**
Elev	**0.003**	**0.003**	**0.003**
	(0.003, 0.004)	**(0.002, 0.004)**	**(0.003, 0.004)**
EWAsp	**0.008**	0.002	-
	(0.005, 0.011)	(-0.004, 0.008)	
NSAsp	**-0.005**	-	-
	(-0.009, -0.002)		
Tree	-	**0.027**	**0.026**
		(0.018, 0.039)	**(0.017, 0.034)**
Rug	**2.66**	**3.856**	**3.887**
	(2.02, 3.24)	**(3.093, 4.685)**	**(3.109, 4.709)**
Wet	**122.6**	-17.56	**-34.06**
	(122.5, 138.7)	(-31.82, 18.72)	**(-50.17, -14.53**)

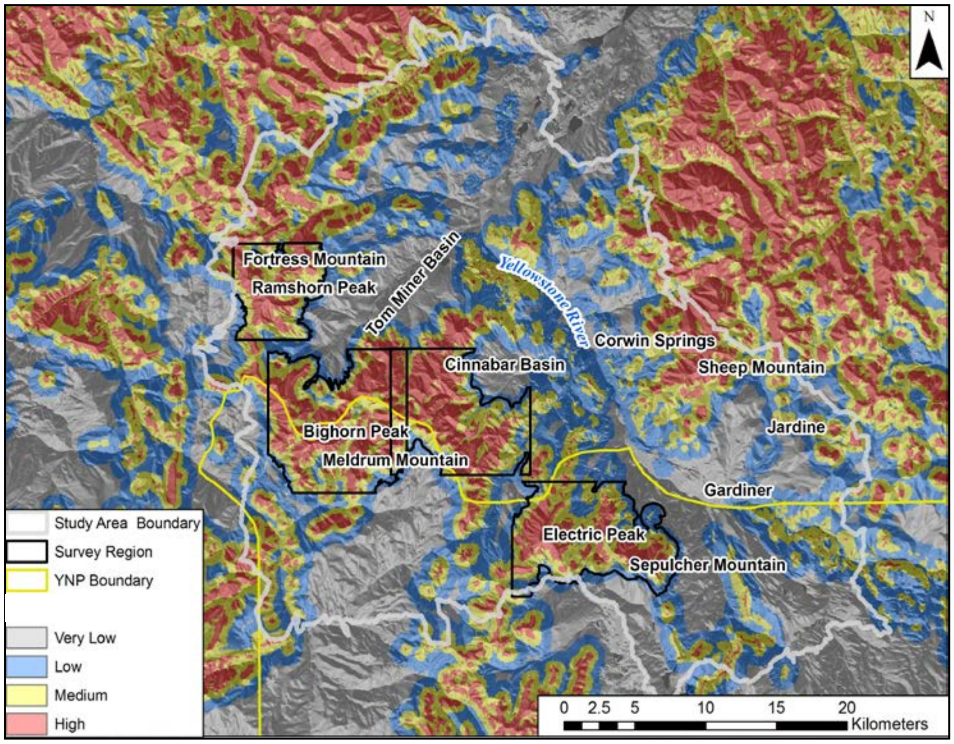


Figure 5. Habitat suitability map, depicting relative habitat selection by mountain goats in summer, across the study area and surrounding areas. Estimates from the top, presence-only, logistic regression model for mountain goats were used to create this map. Also depicted are the four survey regions within the area that were developed based on results from the presence-only modeling effort. These four survey regions were sampled during occupancy surveys in 2011.

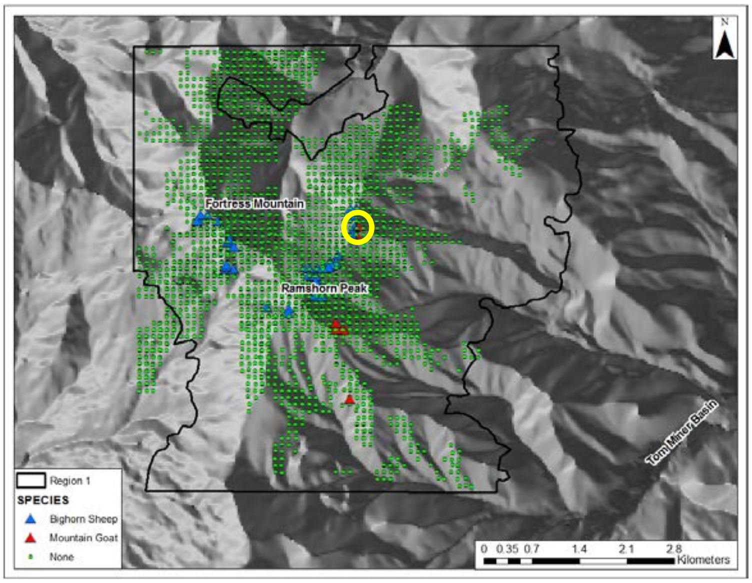
Formal Occupancy Field Surveys

From 8th of July to the 20th of September 2011 the total number of observer days in the field was 113, resulting in approximately 240 hours of occupancy survey effort. Fifty-seven viewsheds were surveyed by a single observer and an additional 77 viewsheds were surveyed by two, independent observers. A total of 6,603 100x100 meter grid cells were surveyed (Figure 6) on at least one occasion with 3,392 of those grid cells visited on multiple occasions during the season.

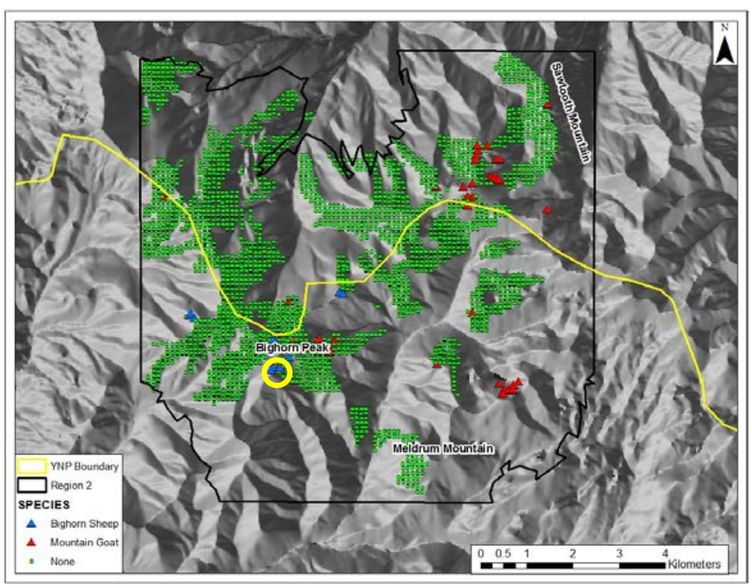
Fifteen groups of bighorn sheep were detected during occupancy surveys with an average group size of 10.3 individuals, a median group size of 7.0 individuals, and a group size range of 44.0 individuals with a SD of 10.9 individuals. One hundred fifty four individual bighorn sheep were observed and classified during occupancy surveys with 81 females, 57 young of the year, 1 mature male, 9 yearlings, and 6 unknown. Fifty grid cells were occupied by bighorn sheep during surveys, resulting in a naïve occupancy rate of 0.008 in 2011. Observers recorded bighorn sheep in an additional 18 grid cells while traveling between surveys. A total of 13 groups of bighorn sheep were detected during double observer surveys and 10 of these groups were detected by both observers (76.9%).

Thirty-four groups of mountain goats were detected during surveys with an average group size of 2.3 individuals, a median group size of 1.0 individual, and a group size range of 17.0 individuals with a SD of 3.2 individuals. Seventy individual mountain goats were observed and classified during occupancy surveys with 16 females, 12 young of the year, 5 yearlings and 37 unknown. Fifty-five grid cells were occupied by mountain goats during surveys, resulting in a naïve occupancy rate of 0.008. Observers recorded mountain goats in an additional 36 grid cells while traveling between surveys. A total of 22 groups of mountain goats were detected during double observer surveys and 12 groups were detected by both observers (54.5%).

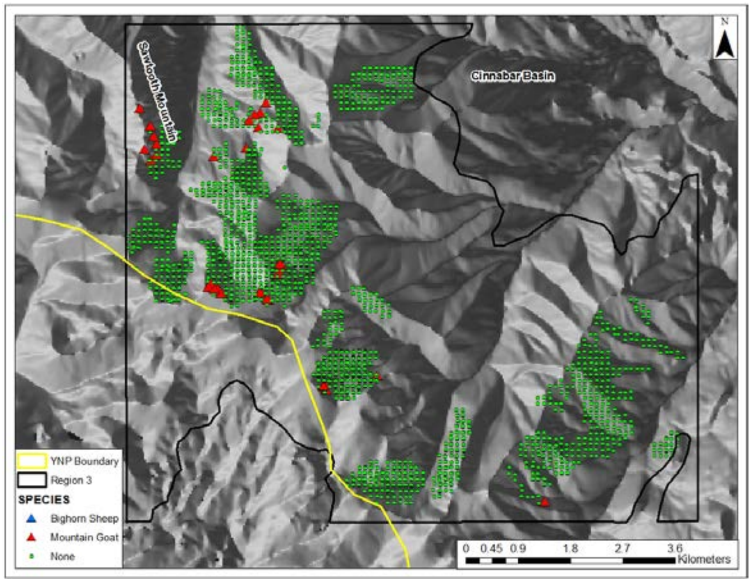
Scatter-plots, frequency plots and detection versus non-detection plots constructed using raw covariate and observation data (see Figures 3B-4B in Appendix B and Figure 2C in Appendix C) suggested that mountain goats were more frequently observed at rugged, high elevations and in drier areas than areas of non-detection. Mountain goats were also more frequently detected in locations near escape terrain with low SRI indices. There was some evidence for selection of areas with greater tree cover and no evidence for selection related to the older, basic ruggedness covariate.



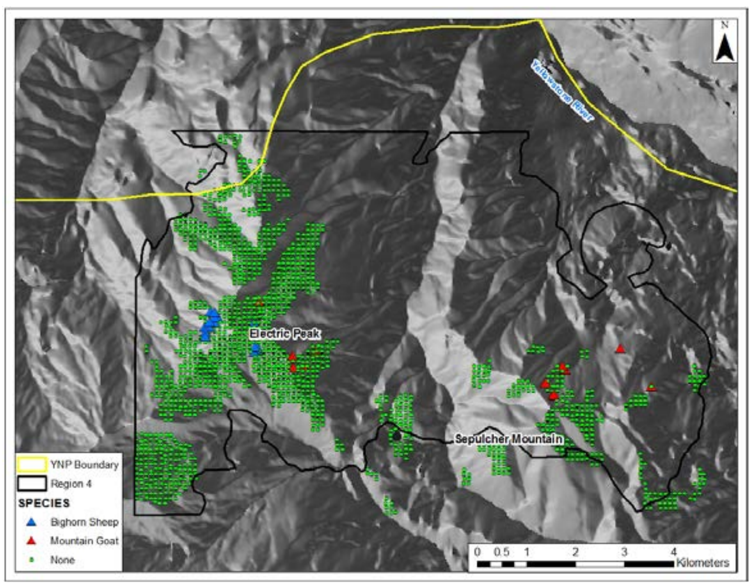
Region 1



Region 2



Region 3



Region 4

Figure 6. Maps of each individual survey region (Region 1, Region 2, Region 3 and Region 4) and the observations recorded in each, during the 2011 field season. Green dots indicate neither bighorn sheep nor mountain goats were observed, blue triangles indicate bighorn sheep observations and red triangles indicate mountain goat observations. There were two grid-cells where both mountain goats and bighorn sheep were observed at the same time and these areas are denoted by yellow circles.

A priori Modeling Suite (100 meter)

I fit 194 *a priori* models which included covariates at the100 meter scale to evaluate which were affecting the probability of occupancy and detection for mountain goats. I only present here the ΔAIC_c table and coefficient estimates for models within four ΔAIC_c units of the top model. The entire model selection table is presented in Appendix D, Figure 1D. There was considerable model selection uncertainty, as results supported eleven models within four ΔAIC_c of the top model (Akaike model weight for the top model = 0.18). The next ten models combined, accounted for most of the remaining model weight (0.68) (Table 5). This was a result of models being nested and receiving greater support because they contained the important occupancy covariates of $Escape_1$, Rug_1, and in most instances $Tree_1$. Coefficient estimates for Rug_1 were consistent and in the predicted, positive direction (β_{Rug1} = 0.49, 95% CI = 0.25 to 0.73). $Escape_1$ appeared in all models within four ΔAIC_c of the top model and $Tree_1$ appeared in nine of these eleven models. These two covariates were part of an important interaction term ($Escape_1$*$Tree_1$) indicating that the use of tree cover depended on the distance to escape terrain. All coefficient estimates for the interaction between $Escape_1$*$Tree_1$ were negative ($\beta_{Escape1\ *Tree1=}$ -4.00, 95% CI -7.04 to -0.95) such that as the amount of tree cover increased the probability of use by mountain goats decreased, however the effect was greater in areas farther away from escape terrain compared to those closer to escape terrain (Figure 7). Mountain goats were more likely to be present in areas of higher tree cover when they were closer to escape terrain. Covariates included for the estimation of detection probability appeared in several models, however in all instances the 95% confidence interval spanned zero. Based on the top *a priori* model, at the minimum value for $Escape_1$ (0), the 3rd quartile value for $Rugg_1$ (0.01) and the mean value for $Tree_1$ (37.0%), $\psi = 0.09$, 95% CI = 0.04 to 0.24, p = 0.23, 95% CI = 0.07 to 0.38.

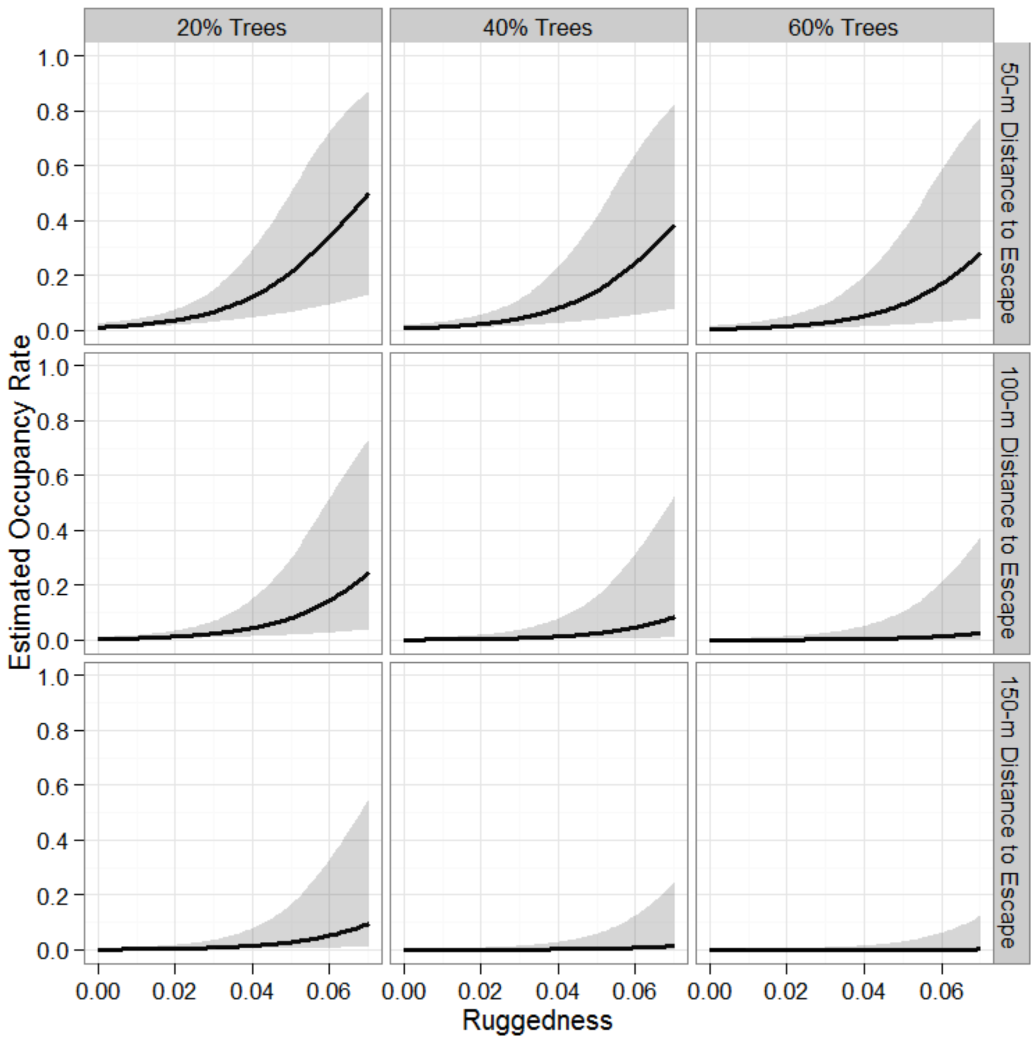


Figure 7. Predicted occupancy rate (ψ) for mountain goats (solid line) at various covariate values for distance to escape terrain ($Escape_1$), Ruggedness (Rug_1), and percent tree cover ($Tree_1$). The grey bands represent the 95% confidence intervals. These plots are based on the original coefficients from the top *a priori* occupancy model (Model 42).

Table 5. Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of six landscape covariates on mountain goat summer occupancy rate (ψ) and detection probability (p) at the 100 meter scale. All models within four ΔAIC_c units of the top model are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
42	$\psi(Escape_1+Rug_1+Tree_1+Escape_1*Tree_1)p(.)$	6	507.02	0.00	0.18
142	$\psi(Escape_1+Rug_1+SRI_1+Tree_1+ Escape_1*Tree_1)$ $p(Rug_1)$	8	508.72	1.70	0.08
75	$\psi(Escape_1+Rug_1+Tree_1+ Escape_1*Tree_1)p(Tree_1)$	7	508.93	1.91	0.07
143	$\psi(Escape_1+Rug_1+SRI_1+Tree_1+ Escape_1*Tree_1$ $+Escape_1*Rug_1)p(Rug_1)$	9	509.31	2.29	0.06
128	$\psi(Escape_1+Rug_1+Wet_1+Tree_1+Escape_1*Tree_1)p(Tree_1)$	8	509.51	2.49	0.05
131	$\psi(Escape_1+Rug_1+SRI_1+Tree_1+Escape_1*Tree_1)p(Tree_1)$	8	509.54	2.52	0.05
77	$\psi(Escape_1+Rug_1+Tree_1+Escape_1*Rug_1$ $+Escape_1*Tree_1)p(Tree_1)$	8	509.55	2.53	0.05
9	$\psi(Rug_1+Escape_1+Rug_1*Escape_1)p(.)$	5	510.09	3.07	0.04
121	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1+ Escape_1*Tree_1)$ $p(Rug_1)$	9	510.12	3.10	0.04
59	$\psi(Escape_1+Rug_1+Escape_1*Rug_1)p(Rug_1)$	6	510.42	3.40	0.03
189	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1+Escape_1*Tree_1)$ $p(Tree_1+Rug_1)$	10	510.96	3.94	0.03

Table 6. Coefficient estimates of all 100 meter *a priori* models within four ΔAIC_c units of the top model for mountain goat summer occupancy modeling. Coefficient estimates in bold font include confidence intervals that do not span zero.

Model ID	42	142	75	143	128	131
ψ Covariate						
Intercept	**-11.23 (-15.06, -7.39)**	**-11.16 (-14.94, -7.28)**	**-11.23 (-15.06, -7.40)**	**-10.46 (-14.17, -6.75)**	**-11.37 (-15.28, -7.47)**	**-10.85 (-14.67, -7.04)**
$Escape_1$	**-9.05 (-13.37, -4.72)**	**-8.37 (-12.74, -4.00)**	**-9.01 (-13.33, -4.70)**	**-7.61 (-11.87, -3.36)**	**-9.25 (-13.66, -4.83)**	**-8.41 (-12.77, -4.05)**
Rug_1	**0.49 (0.25, 0.73)**	**0.68 (0.26, 1.09)**	**0.50 (0.24, 0.74)**	-0.51 (-2.53, 1.51)	**0.51 (0.25, 0.78)**	**0.49 (0.24, 0.74)**
$Tree_1$	**-3.54 (-6.25, -0.84)**	**-3.47 (-6.14, -0.80)**	**-3.60 (-6.33, -0.87)**	**-2.94 (-5.63, -0.26)**	**-3.78 (-6.58, -0.98)**	**-3.50 (-6.19, -0.81)**
SRI_1	-	-0.16 (-0.46, 0.13)	-	-0.14 (-0.44, 0.16)	-	-0.18 (-0.48, 0.11)
Wet_1	-	-	-	-	-0.17 (-0.47, 0.12)	-
$Escape_1$ x Rug_1	-	-	-	-1.39 (-3.69, 0.90)	-	-
$Escape_1$ x $Tree_1$	**-4.00 (-7.04, -0.95)**	**-3.84 (-6.85, -0.82)**	**-3.95 (-7.00, -0.91)**	**-3.24 (-6.27, -0.21)**	**-4.03 (-7.14, -0.91)**	**-3.76 (-6.77, -0.75)**

Table 6. Coefficient estimates of all 100 meter *a priori* models within four ΔAIC_c units of the top model for mountain goat summer occupancy modeling. Coefficient estimates in bold font include confidence intervals that do not span zero (continued).

Model ID	42	142	75	143	128	131
p Covariate						
Intercept	**-1.22 (-2.14, -0.29)**	-0.79 (-1.93, 0.33)	**-1.18 (-2.16, -0.20)**	-0.77 (-1.91, 0.35)	**-1.23 (-2.25, -0.21)**	**-1.17 (-2.13, -0.20)**
$Tree_1$	-	-	0.11 (-0.63, 0.87)	-	0.13 (-0.63, 0.91)	0.14 (-0.60, 0.88)
Rug_1	-	-0.19 (-0.53, 0.14)	-	-0.22 (-0.55, 0.10)	-	
Intercept	**-10.47 (-14.27, -6.67)**	**-7.89 (-9.99, -5.78)**	**-11.43 (-15.43, -7.42)**	**-8.16 (-10.14, -6.16)**	**-11.58 (-15.59, -7.56)**	
$Escape_1$	**-8.18 (-12.45, -3.92)**	**-5.39 (-7.83, -2.95)**	**-8.83 (-13.45, -4.21)**	**-5.19 (-7.56, -2.82)**	**-8.75 (-13.38, -4.12)**	
Rug_1	-0.70 (-2.76, 1.34)	**-1.29 (-3.29, 0.72)**	**0.71 (0.29, 1.13)**	-1.27 (-3.21, 0.68)	**0.78 (0.37, 1.18)**	
$Tree_1$	**-3.09 (-5.83, -0.35)**	**-**	**-3.67 (-6.45, -0.89)**	**-**	**-3.80 (-6.61, -0.99)**	
SRI_1	**-**	-	-0.08 (-0.45, 0.28)	-	-0.08 (-0.45, 0.28)	
Wet_1	**-**	-	-0.14 (-0.50, 0.22)	-	-0.15 (-0.51, 0.21)	

Table 6. Coefficient estimates of all 100 meter *a priori* models within four ΔAIC_c units of the top model for mountain goat summer occupancy modeling. Coefficient estimates in bold font include confidence intervals that do not span zero (continued).

Model ID	77	9	121	59	189
ψ Covariate					
$Escape_1$ x Rug_1	-1.37 (-3.69, 0.95)	-2.02 (-4.30, 0.25)	-	**-2.27 (-4.49, -0.04)**	-
$Escape_1$ x $Tree_1$	**-3.33 (-6.43, -0.23)**	**-**	**-4.00 (-7.11, -0.88)**	**-**	**-3.85 (-6.98, -0.71)**
pCovariate					
Intercept	**-1.25 (-2.29, -0.21)**	**-1.39 (-2.41, -0.35)**	**-0.80 (-1.94, 0.33)**	-0.85 (-2.01, 0.30)	-0.46 (-1.70, 0.77)
$Tree_1$	0.16 (-0.62, 0.95)	-	-	-	0.35 (-0.25, 0.97)
Rug_1	**-**	-	-0.21 (-0.54, 0.12)	-0.22 (-0.54, 0.09)	-0.28 (-0.62, 0.05)

<u>*A priori* Modeling Suite (500 meter)</u>

I fit 34 *a priori* models which included covariates at the 500 meter scale to evaluate which were affecting the probability of occupancy and detection for mountain goats. There was some model selection uncertainty, as results supported six models within four ΔAIC_c of the top model (Akaike model weight top model = 0.38) (Table 7). The entire model selection table is presented in Appendix D, Figure 2D. There were three models within two ΔAIC_c units of the top model each of which contained one additional covariate different from the top model. The only covariate included in the top model for this suite was $Escape_5$ and the relationship was in the expected, negative direction ($\beta_{Escape5}$ = -6.03, 95% CI = -7.85 to -4.19) (Table 8). The top model in the 500 meter suite (AIC_c = 536.66) was 29.64 AIC_c units away from the top model in the 100 meter suite (AIC_c = 507.02)(Table 5).

Table 7. Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of five landscape covariates on mountain goat summer occupancy (ψ) and detection probability (p) at the 500 meter scale. All models within four ΔAIC_c units of the top model are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
8	$\psi(Escape_5)p(.)$	3	536.66	0	0.38
15	$\psi(Escape_5+Wet_5)p(.)$	4	538.50	1.84	0.15
17	$\psi(Escape_5+Elev_5)p(.)$	4	538.60	1.94	0.14
16	$\psi(Escape_5+SRI_5)p(.)$	4	538.65	1.99	0.14
26	$\psi(Escape_5+Wet_5+SRI_5)p(.)$	5	540.47	3.81	0.06
27	$\psi(Escape_5+Wet_5+Elev_5)p(.)$	5	540.50	3.84	0.06
28	$\psi(Escape_5+SRI_5+Elev_5)p(.)$	5	540.60	3.94	0.05

Table 8. Coefficient estimates of all 500 meter a priori models within four ΔAIC_c units of the top model for mountain goat summer occupancy modeling. Coefficient estimates in bold font include confidence intervals that do not span zero.

Model ID	8	15	17	16
ψ Covariate				
Intercept	**-7.57 (-9.14, -5.99)**	**-7.57 (-9.15, -5.99)**	**-7.55 (-9.13, -5.97)**	**-7.54 (-9.20, -5.87)**
$Escape_5$	**-6.03 (-7.85, -4.19)**	**-6.06 (-7.90, -4.22)**	**-6.03 (-7.85, -4.20)**	**-5.97 (-8.01, -3.93)**
Wet_5	-	-0.05 (-0.30, 0.19)	-	-
SRI_5	**-**	-	-	-0.01 (-0.35, 0.31)
$Elev_5$	**-**	-	-0.04 (-0.38, 0.29)	-
p Covariate				
Intercept	**-1.35 (-2.27, -0.42)**	**-1.36 (-2.27, -0.44)**	**-1.36 (-2.27, -0.43)**	**-1.36 (-2.27, -0.43)**

Model ID	26	27	28
ψ Covariate			
Intercept	**-7.63 (-9.38, -5.89)**	**-7.57 (-9.17, -5.98)**	**-7.55 (-9.23, -5.88)**
$Escape_5$	**-6.18 (-8.47, -3.90)**	**-6.06 (-7.91, -4.22)**	**-6.03 (-8.14, -3.92)**
Wet_5	-0.07 (-0.39, 0.25)	-0.05 (-0.40, 0.29)	-
SRI_5	0.03 (-0.38, 0.46)	-	0.00 (-0.37, 0.38)
$Elev_5$	**-**	0.01 (-0.47, 0.49)	-0.04 (-0.43, 0.34)
p Covariate			
Intercept	**-1.35 (-2.27, -0.43)**	**-1.36 (-2.27, -0.44)**	**-1.36 (-2.27, -0.43)**

Exploratory Modeling Suite

I constructed a suite of six, post-hoc, exploratory models, using the habitat covariates included in the top *a priori* model, to examine the effects of scale on overall model performance. I included all possible combinations of scale for the covariates included. This exercise resulted in an improved overall top model which was 4.02 ΔAIC_c units better (AIC_c = 503.00) (Table 9) than the top model from the 100 meter *a priori* model suite (AICc = 507.02) (Table 5). All models within four ΔAIC_c of the top-ranking model included Rug_1. The top-ranking model for this exploratory suite accounted for 65% of the model weight and the second-ranking model (AIC_c = 505.42) accounted for 20% of the model weight. Coefficient estimates for all covariates, at both the 100 and 500 meter scales were stable, and in the expected direction with related 95% confidence intervals that did not span zero (Table 10). Based on this top exploratory model, at the minimum value for $Escape_5$, the 3rd quartile value for Rug_1 and the mean value for $Tree_5$, ψ = 0.08, 95% CI = 0.04 to 0.18, p = 0.25, 95% CI =0.10 to 0.39. As the amount of tree cover increased the probability of use by mountain goats decreased, however the effect was greater in areas farther away from escape terrain compared to those closer to escape terrain (Figure 8).

I also conducted a post-hoc exploratory analysis to examine whether the new, more complex ruggedness covariate outperformed the basic ruggedness covariate. I substituted the basic ruggedness covariate (ORug) for the more complex ruggedness covariate (Rug) in the overall top model. This exercise resulted in a model which was

19.7 ΔAIC_c units greater (AIC_c = 522.70) than the top model (AIC_c = 503.00) indicating that use of the more complex ruggedness covariate improved model performance.

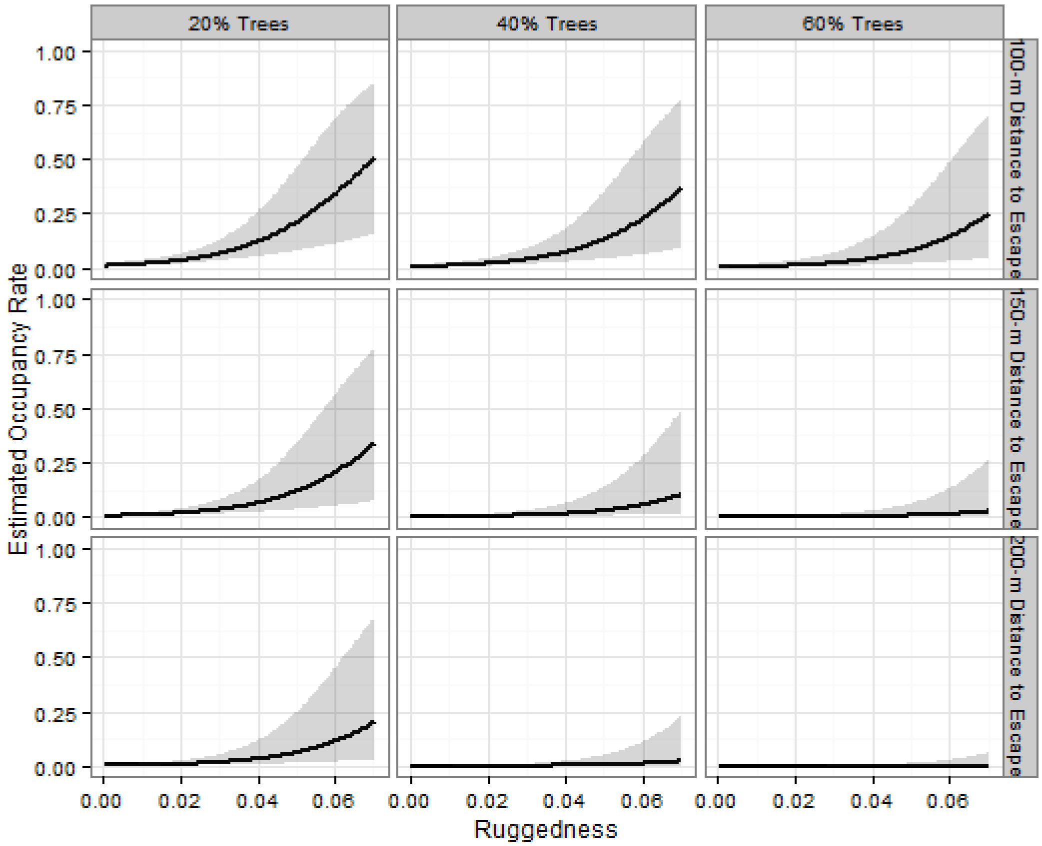


Figure 8. Predicted occupancy rate (ψ) for mountain goats (solid line) at various covariate values for distance to escape terrain (DET_5), Ruggedness (Rug_1), and percent tree cover ($Tree_5$). The grey bands represent the 95% confidence intervals. These plots are based on the original coefficients from the overall top occupancy model.

Table 9. Model selection results from an exploratory model list for a single-season occupancy analysis examining the effects of various combinations of scale on mountain goat summer occupancy rates (ψ). All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
5	$\psi(Escape_5+Rug_1+Tree_5+Escape_5*Tree_5)p(.)$	6	503.00	0.00	0.65
4	$\psi(Escape_1+Rug_1+Tree_5+Escape_1*Tree_5)p(.)$	6	505.42	2.42	0.20
1	$\psi(Escape_1+Rug_1+Tree_1+Escape_1*Tree_1)p(.)$	6	507.02	4.02	0.09
2	$\psi(Escape_5+Rug_1+Tree_1+Escape_5*Tree_1)p(.)$	6	507.62	4.61	0.06
6	$\psi(Escape_1+Rug_5+Tree_5+Escape_1*Tree_5)p(.)$	6	516.23	13.23	0.00
3	$\psi(Escape_1+Rug_5+Tree_1+Escape_1*Tree_1)p(.)$	6	517.29	14.29	0.00

Table 10. Coefficient estimates from an exploratory model list for a single-season occupancy analysis examining the effects of various combinations of scale on mountain goat summer occupancy. Coefficient estimates in bold font include confidence intervals that do not span zero.

Model ID	5	4	1	2	6	3
ψ Covariate						
Intercept	**-9.15 (-11.40, -6.90)**	**-11.27 (-14.97, -7.57)**	**-11.23 (-15.06, -7.39)**	**-8.98 (-11.28, -6.68)**	**-11.31 (-14.86, -7.77)**	**-11.27 (-14.93, -7.61)**
Escape$_1$	-	**-9.12 (-13.31, -4.94)**	**-9.05 (-13.37, -4.72)**	-	**-9.34 (-13.40, -5.26)**	**-9.23 (-13.40, -5.05)**
Escape$_5$	**-6.67 (-9.28, -4.05)**	-	-	**-6.50 (-9.16, -3.85)**	-	-
Rug$_1$	**0.49 (0.27, 0.72)**	**0.49 (0.25, 0.73)**	**0.49 (0.25, 0.73)**	**0.48 (0.25, 0.71)**	-	-
Rug$_5$	-	-	-	-	**0.49 (0.16, 0.82)**	**0.50 (0.17, 0.83)**
Tree$_1$	-	-	**-3.54 (-6.25, -0.84)**	**-2.83 (-4.47, -1.17)**	-	**-3.28 (-5.91, -0.66)**
Tree$_5$	**-3.05 (-4.57, -1.53)**	**-3.57 (-5.97, -1.17)**	-	-	**-3.31 (-5.67, -0.96)**	-
Escape$_1$ x Tree$_1$	-	-	**-4.00 (-7.04, -0.95)**	-	-	**-3.64 (-6.59, -0.68)**
Escape$_1$ x Tree$_5$	-	**-4.11 (-6.82, -1.40)**	-	-	**-3.77 (-6.43, -1.11)**	-

Table 10. Coefficient estimates from an exploratory model list for a single-season occupancy analysis examining the effects of various combinations of scale on mountain goat summer occupancy. Coefficient estimates in bold font include confidence intervals that do not span zero (continued).

Model ID	5	4	1	2	6	3
ψ Covariate						
$Escape_5$ x $Tree_1$	-	-	-	**-3.23 (-5.10, -1.35)**	-	-
$Escape_5$ x $Tree_5$	**-3.58 (-5.30, -1.86)**	-	-	-	-	-
p Covariate						
Intercept	**-1.13 (-1.90, -0.34)**	**-1.24 (-2.16, -0.32)**	**-1.22 (-2.14, -0.29)**	**-1.13 (-1.92, -0.32)**	**-1.26 (-2.18, -0.34)**	**-1.23 (-2.15, -0.31)**

DISCUSSION

In my presence-only modeling efforts, I considered all possible, additive combinations of covariates in exploratory analyses. As a result, I did not state any formal predictions. My findings were, however, consistent with those from previous studies. For instance, both mountain goats and bighorn sheep use rugged escape terrain in an effort to avoid predation (Geist 1971, Shannon et al. 1975, Adams et al. 1982, Chadwick 1983). All of the top-ranking, presence-only models for both species included distance to escape terrain and ruggedness. As the distance to escape terrain increased, the relative probability of use by both species decreased and as ruggedness values increased, the relative probability of use by both species increased.

Mountain ungulates move to areas of higher elevation during the warm summer months (Festa-Bianchet and Cote 2007) and the top presence-only models for both species included the well-supported covariate, elevation, with positive coefficient estimates. Tree cover was important only in top mountain goat models and estimates for this covariate were well supported and positive, indicating that as the percentage of tree cover increased, so did the relative probability of use by mountain goats. Festa-Bianchet and Cote (2007) found that tree cover provided shelter from the wind and allowed moisture to persist in the soil longer, resulting in plentiful forage from June through August. This is a likely reason for mountain goats to use these habitats during the summer months in my study area, as well.

TCAP wetness was present in top presence-only models for both species and was well-supported for bighorn sheep with positive estimates, indicating that bighorn sheep preferred drier areas. This relationship coincides with the tendency of bighorn sheep to use open areas for forage (Shannon et al. 1975, Adams et al. 1982). TCAP wetness was in both of the top mountain goat models and was well supported in one of these. Estimates were in the expected negative direction, indicating that mountain goats were selecting for wetter areas. This may be a result of continuous snow melt in some of the more rugged terrain used for forage by mountain goats in the summer.

The covariates used to estimate aspect were included based on previous studies that considered them to be a means of capturing topographic features that may be important to mountain ungulates (Gross et al. 2002). Both the N/S and the E/W aspect covariates were well supported in the top presence-only model for bighorn sheep and coefficient estimates were negative and positive, respectively. Only the E/W aspect covariate appeared in the top mountain goat model and it was not well supported. Aspect is strongly tied to both vegetative composition (Armesto and Martinez 1978, Desta et al. 2004) and solar radiation (Fu and Rich 2002) and will almost certainly have an effect on forage opportunities, as well as the ability of ungulates to thermo-regulate. Regardless of the amount of support for each of these two covariates, I was unable to interpret their biological importance in the format which I included them here. It seems reasonable to expect that both mountain goats and bighorn sheep are likely to select areas in a particular range of aspects and it would be useful to examine this landscape feature in future modeling efforts. However, aspect must be included in models in a biologically interpretable form. Alexander et al. (2006) created four continuous covariates, one for each cardinal direction. Each covariate represented a range of degrees in aspect. For example, aspects ranging from 315-44 degrees were categorized as north aspect. This appears to be a much more straightforward approach to accounting for aspect in habitat modeling and results would likely be interpretable.

My analyses of the presence-only management data were very informative, despite lacking fine spatial resolution and information on areas where observers looked for mountain goats and bighorn sheep but did not detect them. The results allowed me to construct a coarse representation of habitat use across the study area and to reconsider which covariates would be included in my subsequent modeling efforts. The maps that I generated using these estimates allowed me to key in on which geographic areas to focus my occupancy field-sampling efforts. Through this exercise I also gained many of the skills and much of the knowledge that I would need to design effective field sampling methods for formal occupancy surveys and to analyze the resulting data.

There were many complexities involved in designing and implementing ground-based occupancy survey methods for mountain ungulates. Challenges presented themselves in various forms including technical difficulties with field computers and software, as well as the need for continual modifications to the software to better fit our needs. The crew was constantly encountering new situations, asking questions and discussing possible outcomes in order to refine the original plan for field-data collection. For example, should we include grid cells that were covered in snow during early season surveys, despite not having any covariate data to capture snow cover? If we approach a given viewshed by traveling along an adjacent ridge, will we have pushed mountain goats or bighorn sheep out of the area before having surveyed it? As we progressed through the season we discussed our thoughts on these and many other topics and became more familiar with the study system and field equipment. Terrain navigation and weather conditions frequently dictated how much ground could be covered in a day and as with any field project, particularly during a pilot year, we were constantly adapting to changing circumstances and new ideas. As a result, I modified my survey protocol to reflect those changes that I expected would allow this and future field efforts to provide quality data, in an efficient manner. Established protocols are reasonably easy to teach or learn and can be broadly applied to most landscapes and many species of interest.

Once I had completed my initial *a priori* modeling effort I conducted a post-hoc exploratory analysis during which I substituted all possible combinations of covariate scales into my top *a priori* model to explore how this may be affecting mountain goat occupancy. As expected, the results of my formal occupancy analyses suggest that mountain goats are selecting different resources at different scales. Based on the overall top model both the distance to escape terrain and the percent tree cover were more important at the 500 meter scale, while ruggedness appeared to be more important at the 100 meter scale. Previous studies have indicated that ungulates may select habitat on a coarse scale to reduce the risk of predation, while selecting forage on a finer scale (Bergerud et al. 1990, Rettie and Messier 2000). Both distance to escape terrain and tree cover are likely to affect the ability of mountain goats to avoid predation. On a finer scale, perhaps the ruggedness index is indicative of the quantities and varieties of available forage.

Overall, distance to escape terrain, tree cover and ruggedness were the three most important landscape features predicting the probability of occupancy by mountain goats, with an important interaction term between the distance to escape terrain and tree cover. When tree cover was held at the mean value (37.0%) and distance to escape terrain increased, the probability of occupancy decreased dramatically, as was evidenced in both of my predicted occupancy plots as well as my raw data plots. When distance to escape terrain was held at the mean value (244 meters) and the percent of tree cover increased, the probability of occupancy also decreased. However, this was more pronounced if the distance to escape terrain increased along with increasing tree cover. When distance to escape terrain decreased, while tree cover was increased there was a much smaller drop in the probability of occupancy, indicating that mountain goats were more likely to be present in areas of higher tree cover the nearer they were to escape terrain. I also predicted that there may be an interaction between tree cover and solar radiation indices; however this interaction received virtually no support.

The importance of ruggedness in my top models was expected. Earlier studies have demonstrated that mountain goats prefer to occupy rugged terrain, where they can easily escape predators (Adams et al.1982, Chadwick 1983, Laundre 1994, Varley 1994, Gross et al. 2002, Poole et al. 2009). Ruggedness may also be indicative of the type and quantity of forage available on a smaller scale (Rettie and Messier 2000). This covariate was included in all of my, top-ranking 100 meter *a priori* models and was well supported in the majority. I also expected that there may be an interaction between distance to escape terrain and ruggedness with the need for additional escape terrain minimized in areas with higher ruggedness indices. This interaction did appear in several models within four ΔAIC_c of the top-model but was overall not well supported.

Solar radiation indices appeared in several of the top, *a priori* models and all estimates were negative, as predicted. However, all estimated 95% confidence intervals spanned zero and overall it was not well supported in any of the models. Sargeant et al. (1994) found that mule deer were selecting different exposures and slope positions depending on cloud cover and time of year. Perhaps this covariate will be better supported with more data or there is some alternate index such as temperature, distance to snowfields, time of day, or some combination of these that may better capture how mountain goats are selecting habitat. This is certainly worth considering for future analyses.

I expected that there would be a negative relationship between the probability of occupancy for mountain goats and TCAP wetness, because I expected they would prefer areas with more moisture, likely indicative of increased forage. As predicted, the relationship was negative. However this covariate appeared in only three of the top, *a priori* models and in all instances it received little support, with estimated 95% confidence intervals that spanned zero.

The covariates I expected would affect detection probability received little support. Tree cover appeared in five of the eleven top, *a priori* models and all estimates were positive, however estimates were close to zero and estimated 95% confidence intervals spanned zero. The relationship between tree cover and the probability of detection is not one that I expected to be positive, as this would indicate that an increase in tree cover leads to an increase in the probability that observers will detect animals. Ruggedness was included as a covariate affecting detection in five of the eleven top, *a priori* models and coefficient estimates were negative, however estimates were near zero and 95% confidence intervals for this coefficient spanned zero. I expected a negative relationship for estimates of this covariate, as ruggedness would likely make it more difficult for an observer to see an animal on the landscape.

In an effort to better determine which covariates may be affecting detection probability, it may be wise to conduct only double observer surveys. To increase the amount of surveys completed, while still allowing for estimation of detection probability, I decided to alternate between double and single observer survey methods. Given the low number of animal observations and the need to detect animals during double observer surveys for use in estimating detection probabilities, it would be worthwhile to increase the number of double observer surveys.

There were several time varying measurements taken in the field, including temperature, wind speed, grid visibility ranking, and observer which I expected may affect the probability of detection of mountain goats. I did not include these in my modeling efforts due to time constraints, but they should certainly be considered, where possible, in future modeling efforts. Detection probabilities are likely to differ with observers due to hearing, vision and experience disparities among individuals. Accounting for observer effect in future modeling efforts would be wise. Observers noted that mountain goats were more likely to bed down in the shade, out of sight when temperatures were higher, likely resulting in decreased probabilities of detection.

Therefore, it may be useful to include temperature as a covariate or to restrict surveys to certain times of day when temperatures are lower. Despite having a protocol which requires surveys to cease during periods of prolonged, high winds, it was sometimes difficult to keep optics steady throughout a survey when winds were intermittently high. Although I would expect wind speed to be less important in modeling efforts it would be worth further consideration. The grid cell visibility ranking system was devised to allow observers to account for grid cells which were not completely physically available to survey. For example, if part of a grid cell went over the top of a ridge and only half of it was visible to an observer it was given a lower visibility ranking. Not including this as a covariate in modeling failed to account for habitat that observers were certain they could not see and may have contributed to overestimates of detection probability and underestimates of occupancy.

Results of the post-hoc exploratory analysis during which I substituted the more complex ruggedness covariate (Rug) with the basic ruggedness covariate (ORug) into my overall top model, resulted in an increase in ΔAIC_c score. This supported my prediction that the more complex ruggedness covariate would improve model performance. By taking into account complexity in the landscape, rather than just considering the change in slope, we are likely capturing more attributes of the landscape important to mountain goats.

Occupancy surveys were only conducted during ideal weather conditions when there was little wind or rain. As a result, potential inferences regarding mountain goat occupancy and habitat were limited to only those weather conditions observed during surveys.

There are many other factors which are likely to influence occupancy by mountain goats. Some of these I considered, but I did not have time or resources to explore as part of this thesis. The distance to sites where non-native mountain goats were transplanted to, may have some effect on the probability of mountain goat occupancy. I would expect that survey sites closer to transplant sites may have a higher probability of occupancy. The scale of my study area may be too small to detect any differences based on this covariate, but in the case of expansion of mountain goat occupancy surveys to multiple study sites, it may be worthwhile to explore. Male and female mountain goats use habitat in different ways. Females are frequently part of nursery groups during the summer and this will likely influence their movements (Festa-Bianchet and Cote 2007). It is oftentimes difficult to identify the sex of mountain goats in the field, with 42 of the 70 mountain goats observed during my occupancy surveys classified as unknown sex. Perhaps it will be possible to include this as a covariate in future modeling efforts if enough data become available, and if so, it will be worthwhile to explore possible relationships. Lastly, animals will behave differently under threats of predation, whether they are from natural predators or human hunting pressures (Sparrowe and Springer 1970, Root et al. 1988, Mitchell and Lima 2002). There are several natural predators of mountain goats present in my study area including mountain lions (*Felis concolor*), grizzly bears (*Ursus arctos horribilis*), wolves (*Canis lupus*), and golden eagles (*Aguila chrysaetos*). Despite much of my study area being located in Yellowstone National Park where hunting is not allowed, there are several areas, which are open for hunting of both mountain goats and bighorn sheep beginning in early to mid-September and continuing until November 25th. Predator densities and behavior are likely to influence mountain goat movements and it would be informative to include this information in future analyses, if possible.

There are several data analyses topics that I would recommend revisiting for future efforts. I potentially violated two of the four assumptions of occupancy modeling. Violations of the closure assumption most frequently bias estimates of occupancy positively, while failure to account for the variation in the probability of detection among sites and surveys will frequently bias estimates of occupancy negatively. The possible violation of both of these assumptions limits the potential inferences that may be made for my estimates of both occupancy and detection. In the future it may be useful to treat repeat visits after some predetermined length of time as a new season for analyses, provided the number of observations allow. Because of similarities between mark-recapture data and occupancy data it is possible to use robust occupancy estimation methods following MacKenzie et al. (2003). By setting up surveys to consist of primary sampling periods of a closed duration and then conducting repeat, secondary surveys within that closed period, it may be possible to avoid violation of the closure assumption. The structure of my data collection allowed for either of these options for analyses, as repeat visits to survey regions could have been treated as individual seasons or double observer surveys considered secondary sampling periods. Because of the limited amount of animal observations I had to work with I was unable to analyze my data using multiple seasons or primary and secondary periods and rather I collapsed the data across all surveys.

The issue of heterogeneity in the variation of detection among sites and surveys is more straightforward. As mentioned previously, data have been collected for multiple covariates, particularly those that vary over time. Inclusion of these covariates in future modeling efforts would likely help to avoid violations of this assumption and may better explain what is affecting the probability that observers will detect animals if they are present. Regardless of the strategy employed, more data will be required before any robust inferences may be made about the study system.

I used 100 meter grid cells for both my field survey units and my occupancy analyses units, as this was the finest spatial resolution I felt comfortable assigning to animal locations. If I had combined multiple 100 meter grid cells to create larger grid cells my estimated occupancy rates would have increased. For example, if I combined 100 meter grid cells to make 400 meter grid cells for analyses, my naïve occupancy estimate would have increased from 0.008 to 0.030. I was not able to manipulate the data to explore this option, prior to completing my analyses, but strongly recommend exploring this in the future and determining what size unit on the landscape is biologically meaningful for use in occupancy analyses for mountain ungulates.

I used over forty years of existing management data to determine what would be an effective area to sample, based on coarse relative habitat suitability analyses. I demonstrated the feasibility of conducting formal occupancy surveys for mountain ungulates, from the ground across a reasonably large and rugged study area. Despite having minimal data, I was able to draw some broad conclusions regarding habitat selection by mountain goats in my study area and to shed light on some of the covariates and analyses methods which would likely benefit from future additions and/or modifications. Continued research investigating habitat characteristics is likely to further elucidate what landscape components are associated with the probability of occupancy and detection for both mountain goats and bighorn sheep.

Management Implications

The methods developed during this project for conducting occupancy surveys may be applied to most wildlife surveys conducted by managers from the air or the ground. Even with budgetary and manpower constraints it is feasible to use these methods to differentiate between places where animals are detected on the landscape and places were observers look for animals, but do not detect them. It would require a relatively small increase in time and money to place a grid system with the desired size survey units over aerial photos of the landscape and then to use these photos to record detection and non-detection data, while in the field. It may not always be possible to revisit a location during a closed period or to have multiple observers in an effort to calculate detection probabilities; however recording areas where managers looked for animals, but did not detect them would allow for some comparisons that have not been possible in the past. There would be inherent biases when not accounting for detection probabilities, but managers would be aware of these biases and could ensure that they discuss potential implications when interpreting results.

Both mountain goats and bighorn sheep are important wildlife resources for a variety of reasons. Despite mountain goats being non-native in this study area they, as well as bighorn sheep, are a coveted game species and a thrill for wildlife watchers. It is the mission of the U.S. National Park Service to manage for the original faunal and floral communities within our national parks and therefore it is important that we continue to gain a better understanding of the relationships between non-native and native species and how each uses the resources available. There is currently a dearth of detailed, resource use data from comparative studies of sympatric populations of mountain goats and bighorn sheep, from which we can draw conclusions about the extent of resource overlap or the possibility that the two species may be competing for resources. Despite only one, pilot-year of data collection for the occupancy analyses I present here I provide a foundation. With continued data collection and additional animal locations the options for analyses will increase and results will help to inform future management of native bighorn sheep and non-native mountain goats within Yellowstone National Park and surrounding areas.

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APPENDICES

APPENDIX A

PHOTOS OF GEO-MESA FIELD COMPUTER BASIC FEATURES,
FIELD DATA ENTRY DISPLAY FOR GEO-MESA FIELD COMPUTER,
DETECTION PROBABILITY WORKSHEET, CRITERIA FOR BIGHORN SHEEP
AGE AND SEX CLASSIFICATION AND MOUNTAIN GOAT SEX
CLASSIFICATION, AND SUPPLEMENTARY FIELD DATA FORM

Figure 1A: Geo Mesa Unit Basic Features

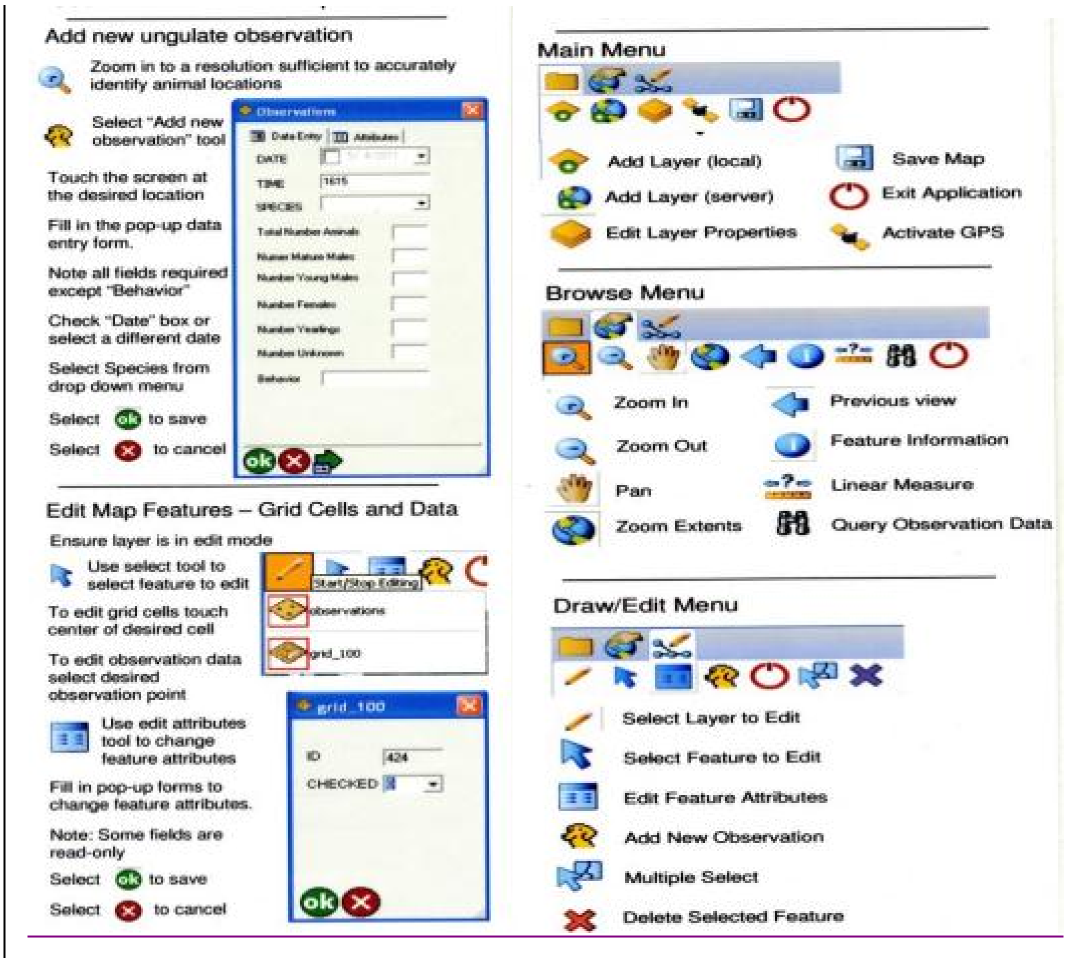


Figure 2A: Menu display for custom data entry into Geo Mesa field computers.

Bighorn Sheep/Mountain Goat

Detection Probability Worksheet

Date	GROUP_ID	OBSERVER_A	SURVEY_ID_OBSERVER_A	OBSERVER_A_COUNT	OBSERVER_A_GROUP_NUMBER
Species		OBSERVER_B	SURVEY_ID_OBSERVER_B	OBSERVER_B_COUNT	OBSERVER_B_GROUP_NUMBER

Date	GROUP_ID	OBSERVER_A	SURVEY_ID_OBSERVER_A	OBSERVER_A_COUNT	OBSERVER_A_GROUP_NUMBER
Species		OBSERVER_B	SURVEY_ID_OBSERVER_B	OBSERVER_B_COUNT	OBSERVER_B_GROUP_NUMBER

Date	GROUP_ID	OBSERVER_A	SURVEY_ID_OBSERVER_A	OBSERVER_A_COUNT	OBSERVER_A_GROUP_NUMBER
Species		OBSERVER_B	SURVEY_ID_OBSERVER_B	OBSERVER_B_COUNT	OBSERVER_B_GROUP_NUMBER

Date	GROUP_ID	OBSERVER_A	SURVEY_ID_OBSERVER_A	OBSERVER_A_COUNT	OBSERVER_A_GROUP_NUMBER
Species		OBSERVER_B	SURVEY_ID_OBSERVER_B	OBSERVER_B_COUNT	OBSERVER_B_GROUP_NUMBER

Figure 3A: Detection probability worksheet.

Possible Features	Positive Features
-Horn size and shape	-External genitalia
-Body size	-Urinating Posture (females squat, males stand)
-Group size	

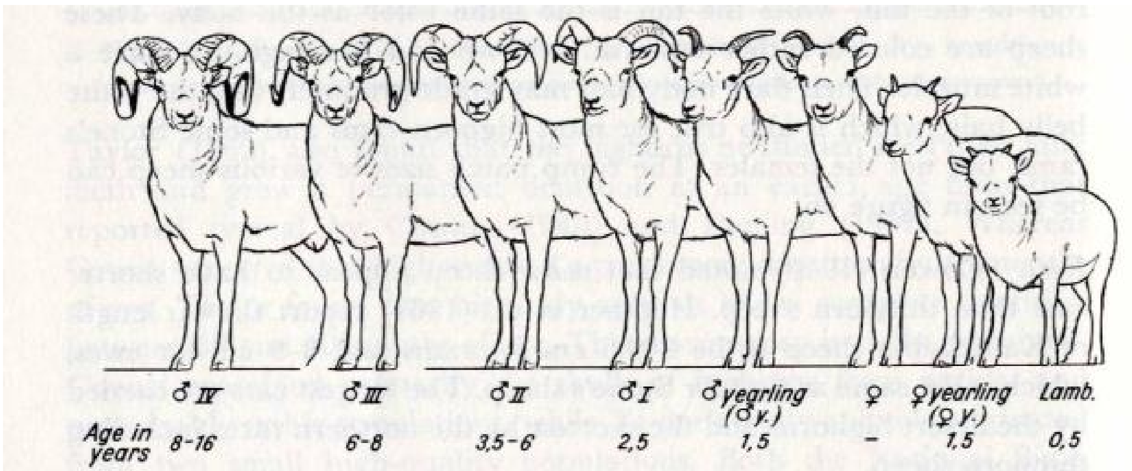


Figure 4A: Bighorn sheep age and sex classification

Possible Features

-Horn mass and shape

-Body size

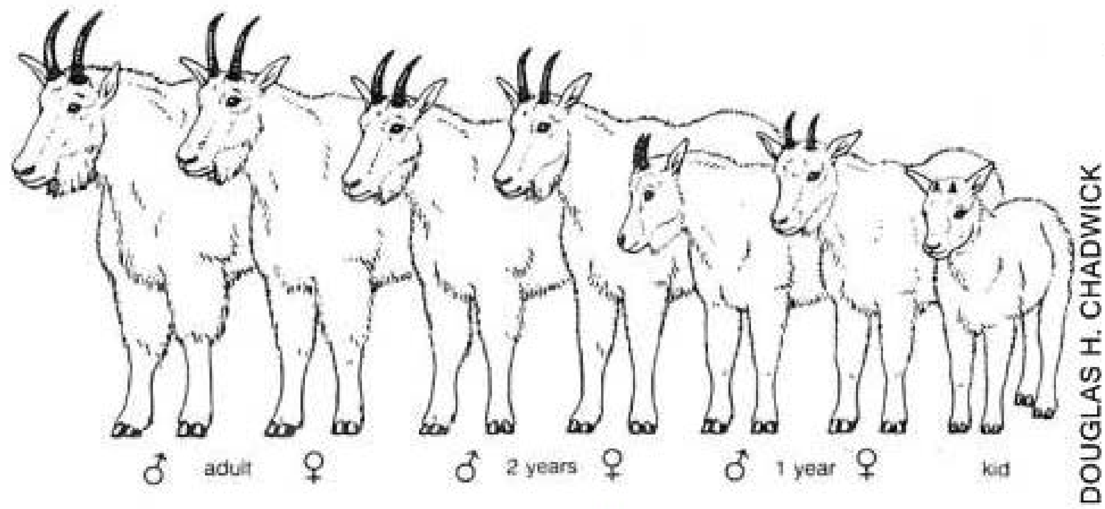
-Group size

-Rump cleanliness

Positive Features

-External genitalia

-Urination posture



Male and female goats at different ages.

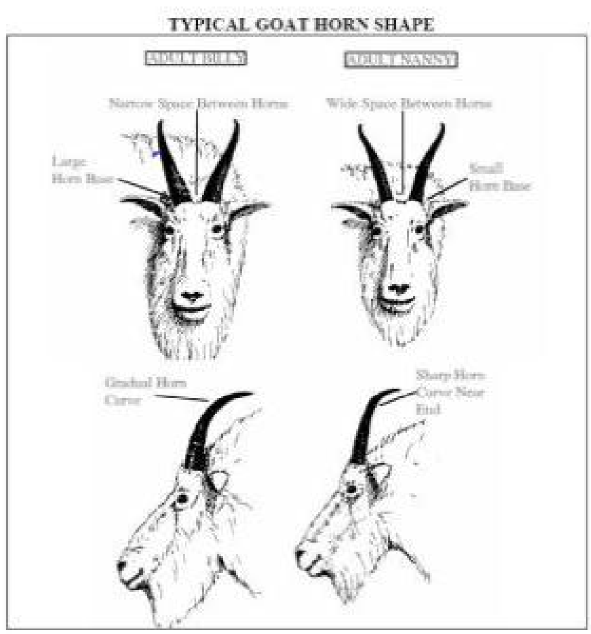


Figure 5A. Male and Female Goats at Different Ages.

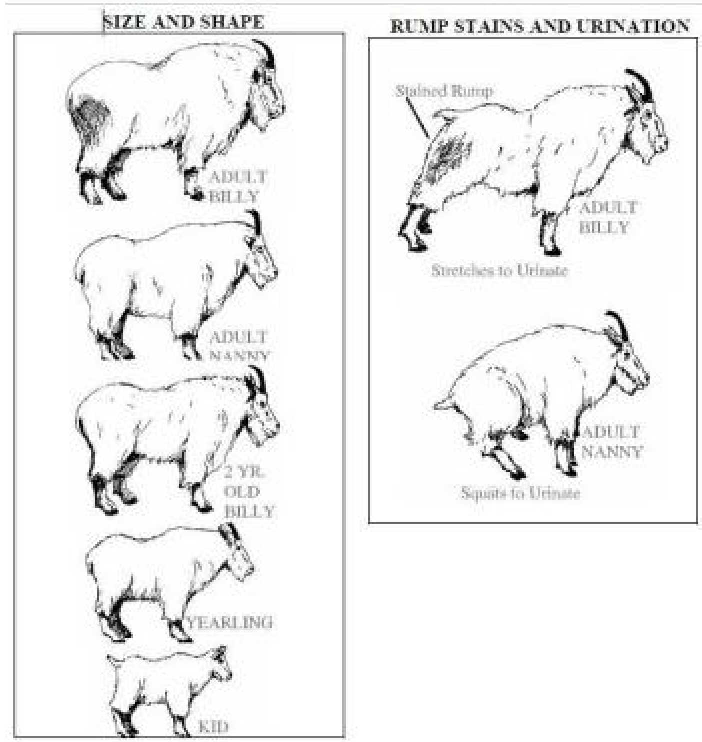


Figure 5A: Male and Female Goats at Different Ages (continued).

Bighorn Sheep/Mountain Goat Supplementary Field Data Collection Sheet

<table>
<tr><td>Date (mmddyy)</td><td>OBS</td><td>SurveyType:
Single /
Double</td><td colspan="2">Survey Point ID</td><td>VISIT
#</td><td>Start
Time:</td></tr>
<tr><td colspan="6">Observer UTMs (WGS_1984):</td><td>Temp (°F)</td></tr>
<tr><td colspan="7">Location Description</td></tr>
<tr><td>Avg. Wind Speed (m/s)</td><td colspan="3">*Cloud cover (0-4)</td><td colspan="3">*Precip (0-5)</td></tr>
<tr><td colspan="3">End Time:</td><td colspan="3">Duration:</td><td>Temp (°F)</td></tr>
<tr><td>Wind Speed (m/s)</td><td colspan="3">*Cloud cover (0-4)</td><td colspan="3">*Precip (0-5)</td></tr>
<tr><td colspan="7">Comments:</td></tr>
</table>

Figure 6A: Bighorn Sheep and Mountain Goat Supplementary Data Form.

APPENDIX B

HISTOGRAMS, PEARSON ABSOLUTE CORRELATION COEFFICIENTS, X-Y SCATTER PLOTS, AND RAW DATA PLOTS FOR INDIVIDUAL AND PAIRED COVARIATE VALUES

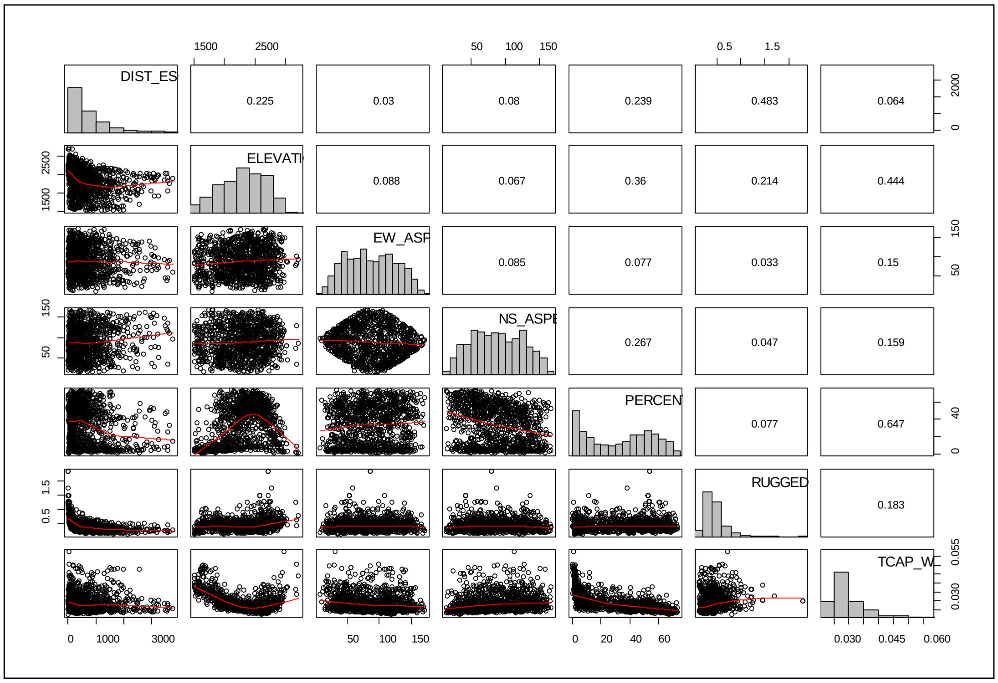


Figure 1B: Histograms, Pearson absolute correlation coefficients, and x-y scatter plots of habitat and landscape variables used in mountain goat presence-only models.

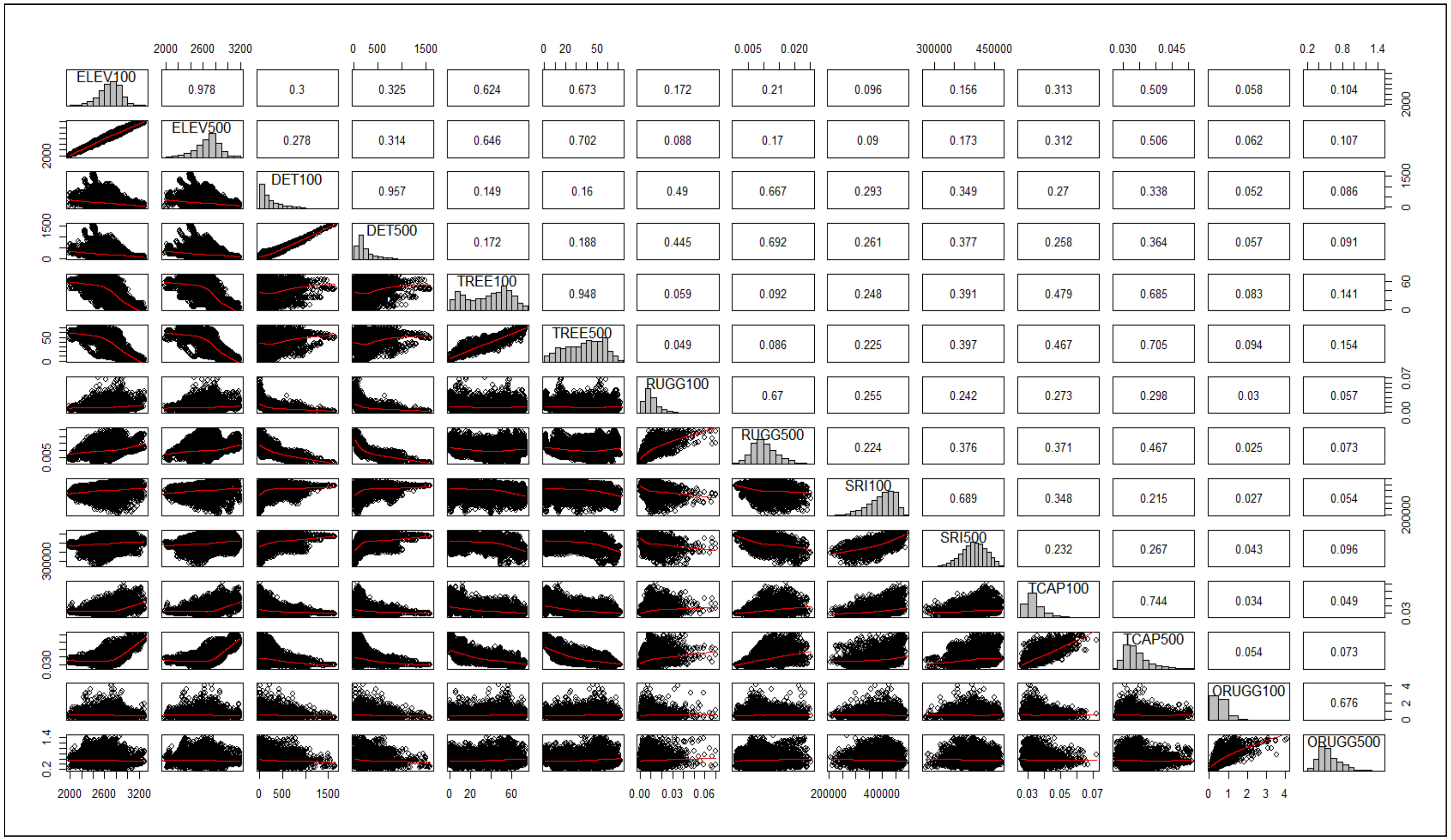


Figure 2B: Histograms, Pearson absolute correlation coefficients, and x-y scatter plots of habitat and landscape variables used in mountain goat occupancy models.

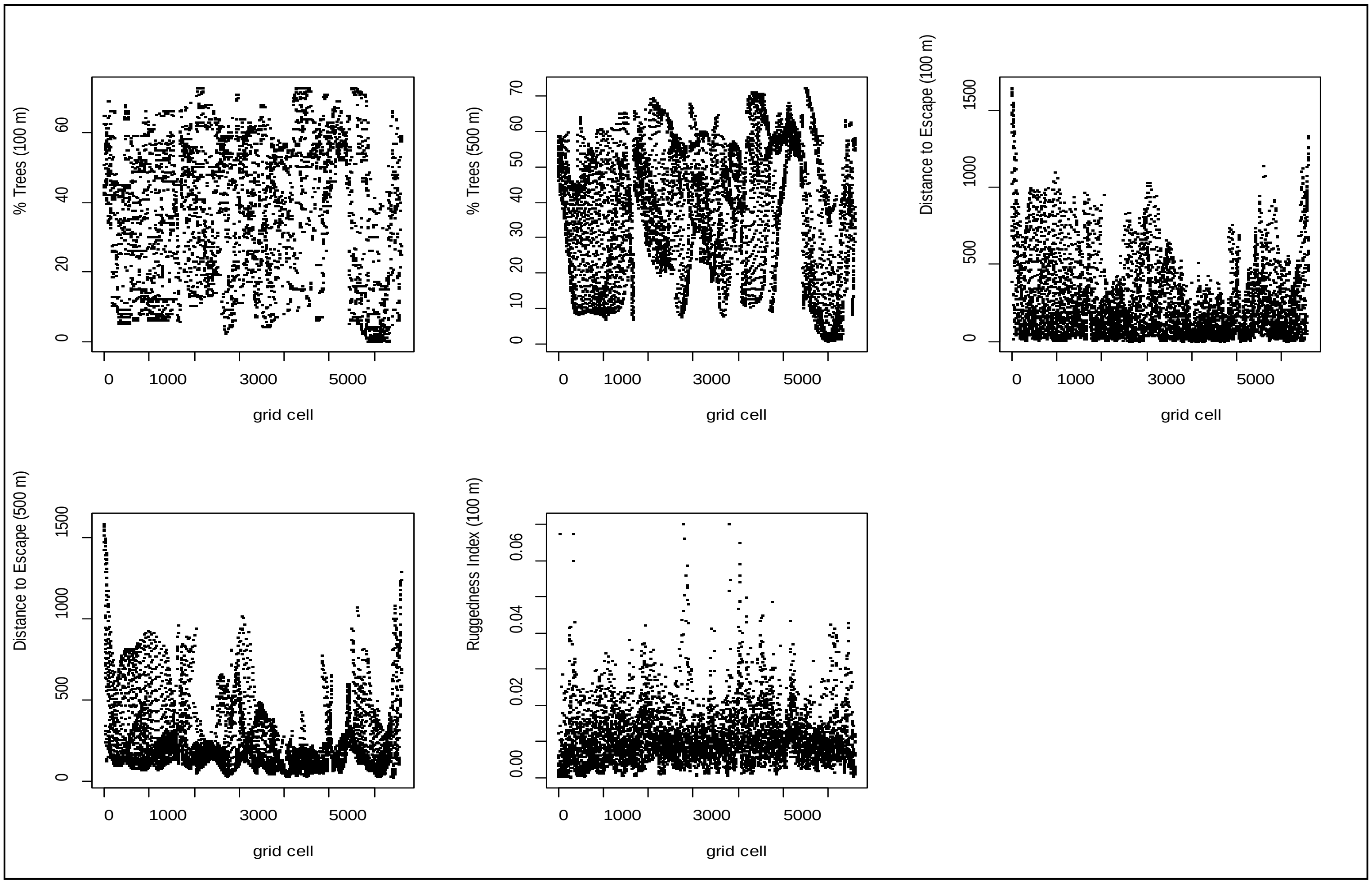


Figure 3B: Scatterplots of raw data observed during occupancy surveys for covariates included in top models. Each point represents a grid cell that was surveyed and the corresponding covariate value for that grid cell.

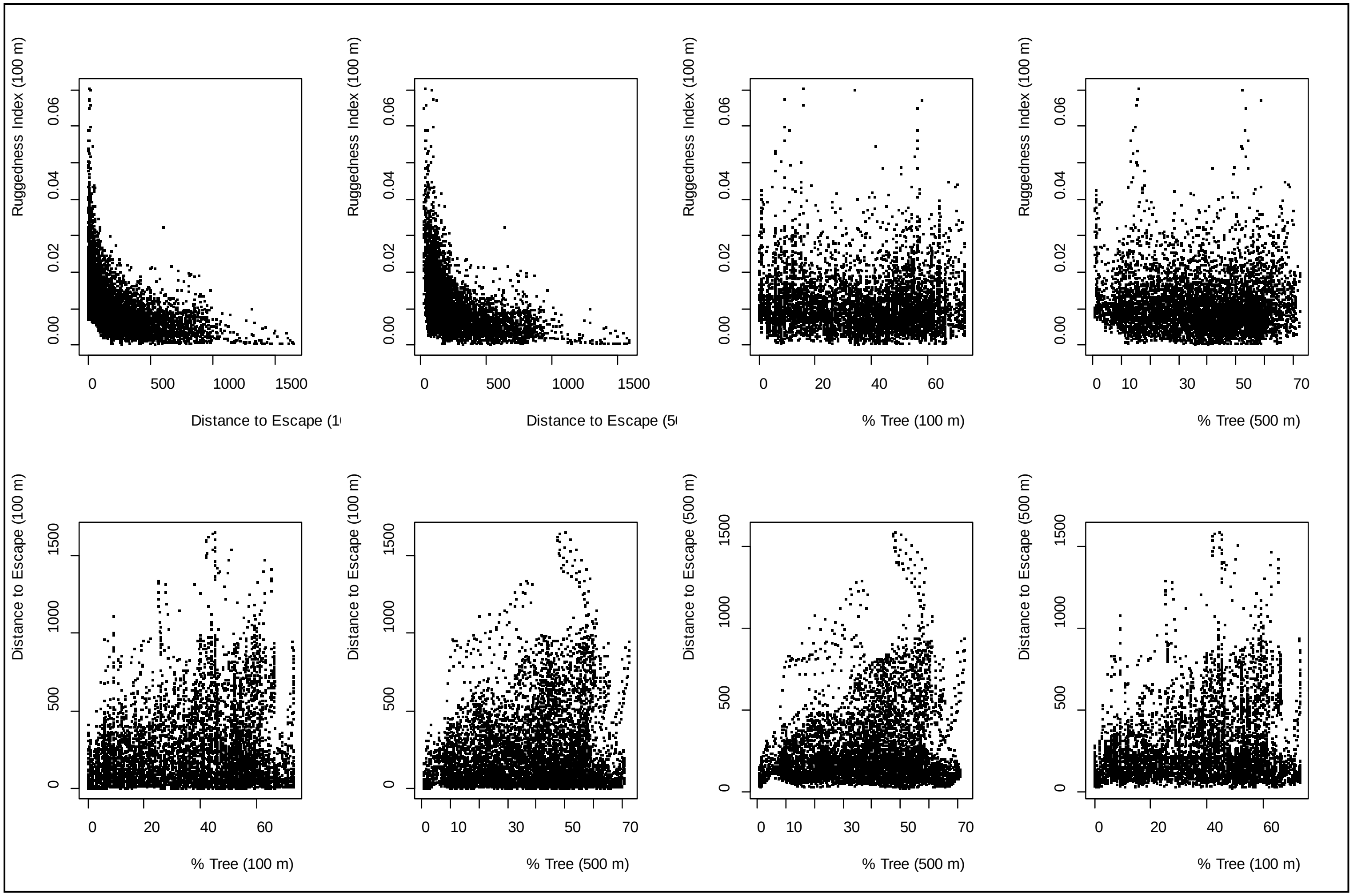


Figure 4B: Scatterplots of raw data observed during occupancy surveys for pairs of covariates included in top models. Each point represents the covariate values for a grid cell that was surveyed.

APPENDIX C

USED VS. AVAILABLE PLOTS

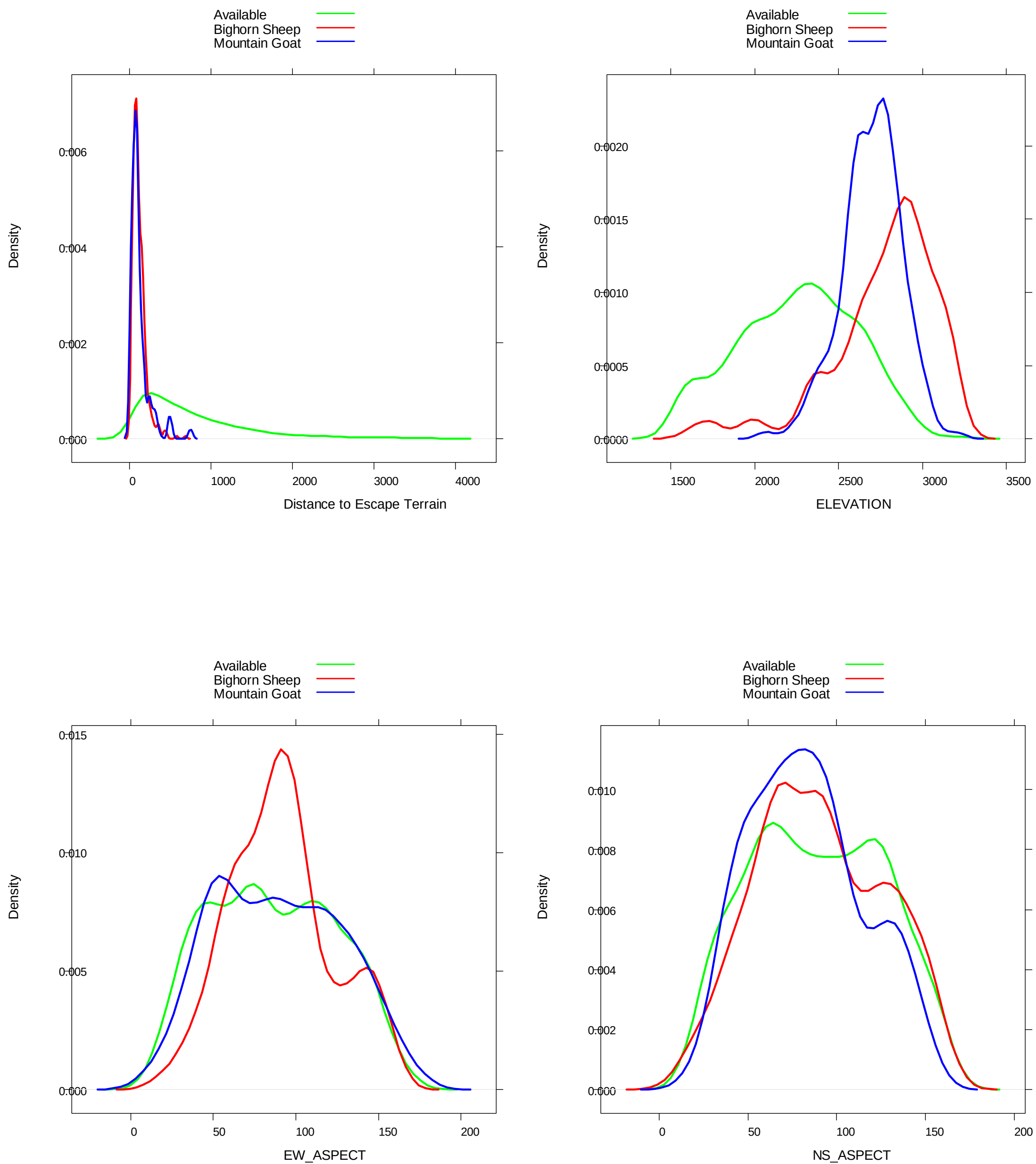


Figure 1C: Comparison of mountain goat use (n=160), bighorn sheep use (n=377) and available (n=999) for each of seven landscape covariates used in resource selection probability (logistic regression) analyses to explore relative habitat selection by mountain goats and bighorn sheep during the summer.

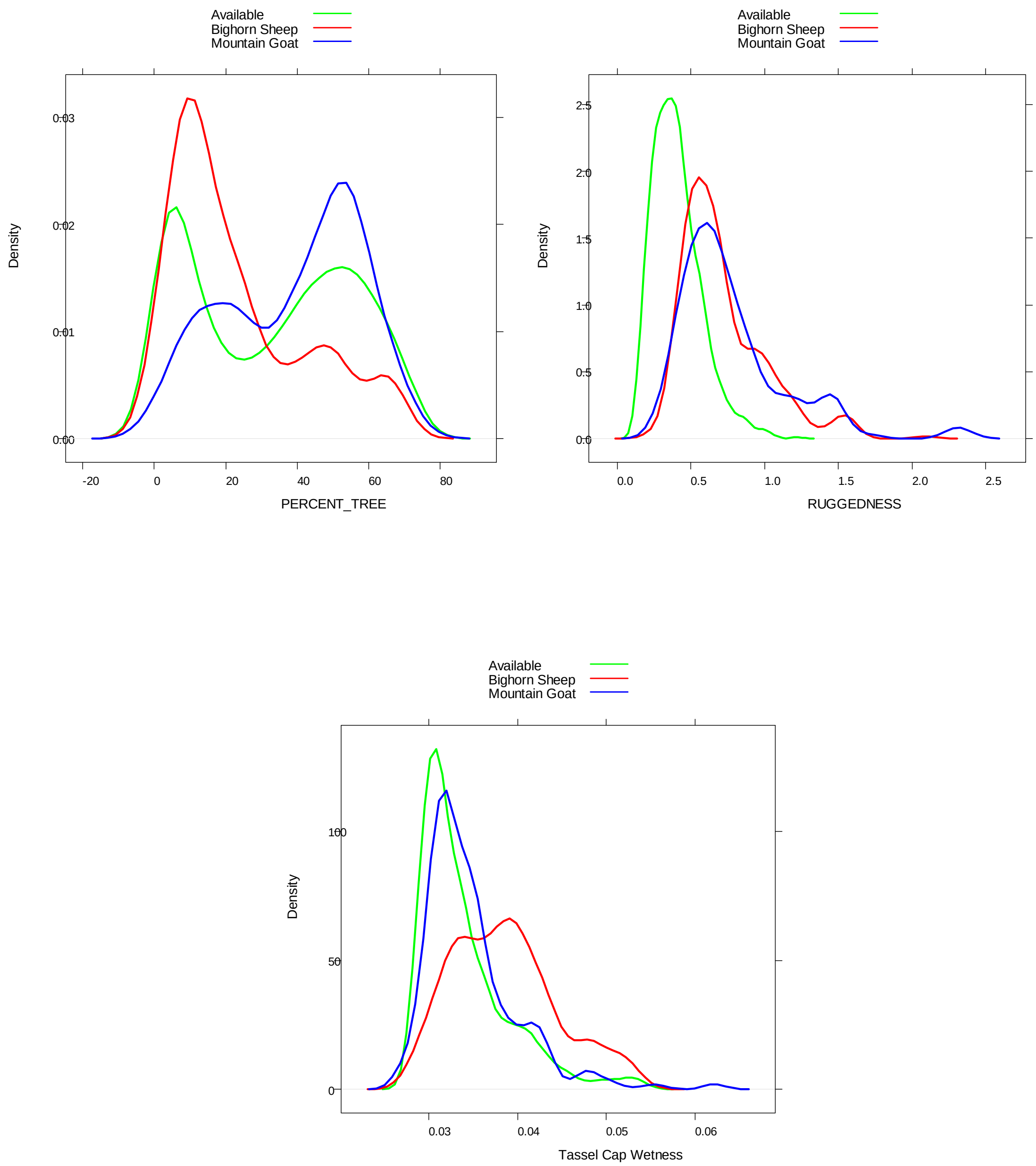


Figure 1C: Comparison of mountain goat use (n=160), bighorn sheep use (n=377) and available (n=999) for each of seven landscape covariates used in resource selection probability (logistic regression) analyses to explore relative habitat selection by mountain goats and bighorn sheep during the summer (continued).

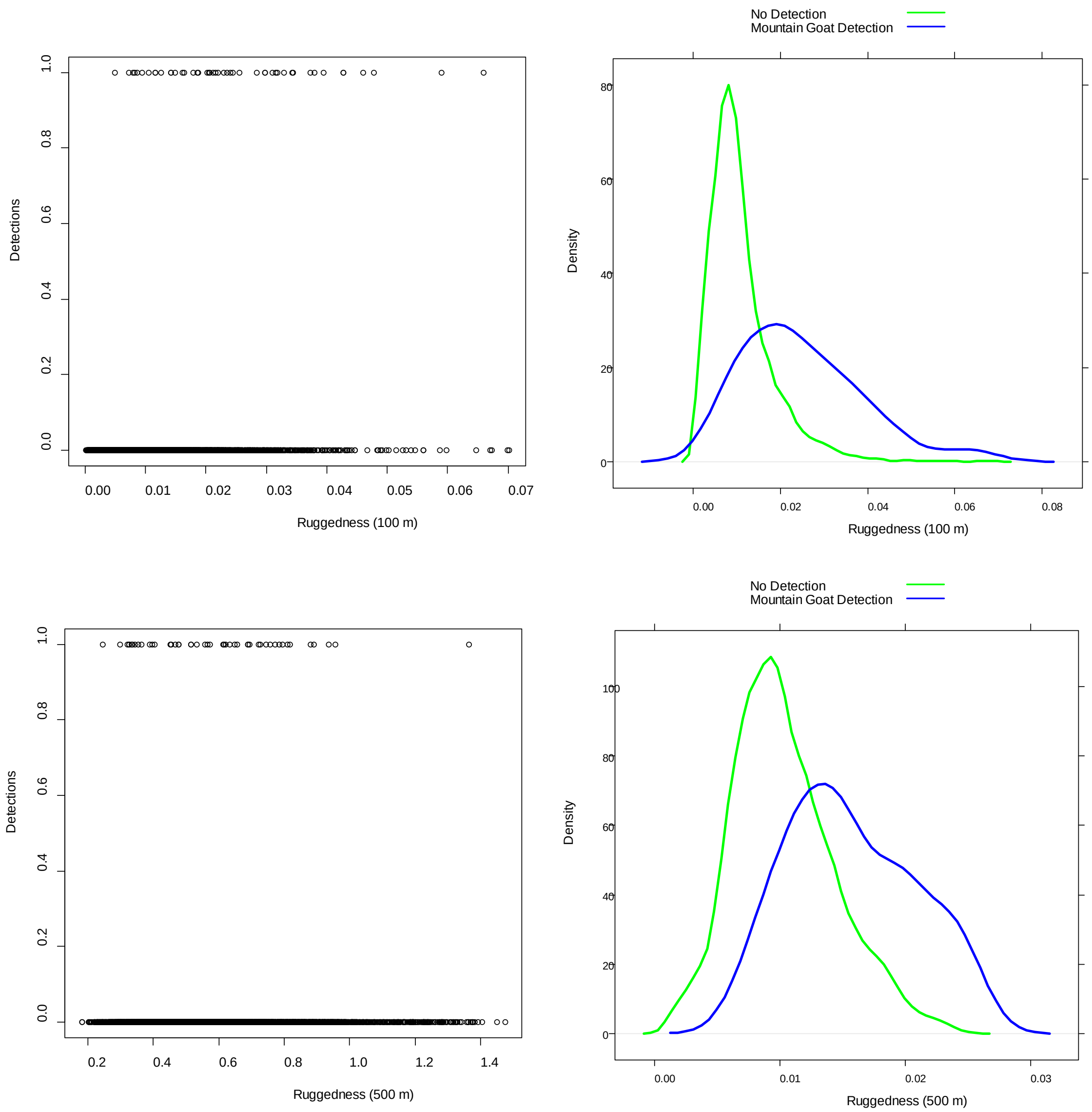


Figure 2C: Frequency plots and detection versus non-detection plots for all covariates at both the 100 meter and 500 meter scales.

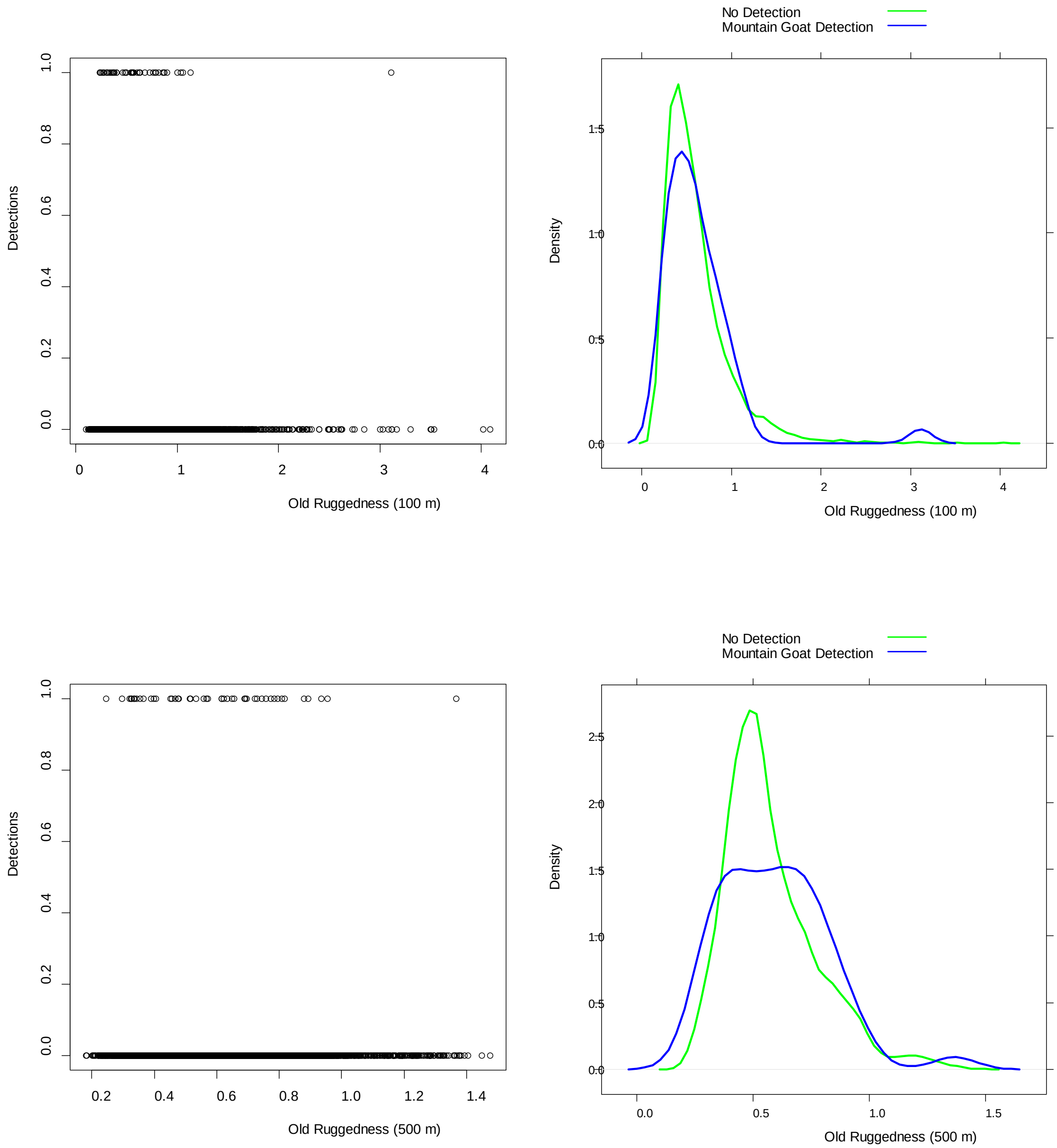


Figure 2C: Frequency plots and detection versus non-detection plots for all covariates at both the 100 meter and 500 meter scales (continued).

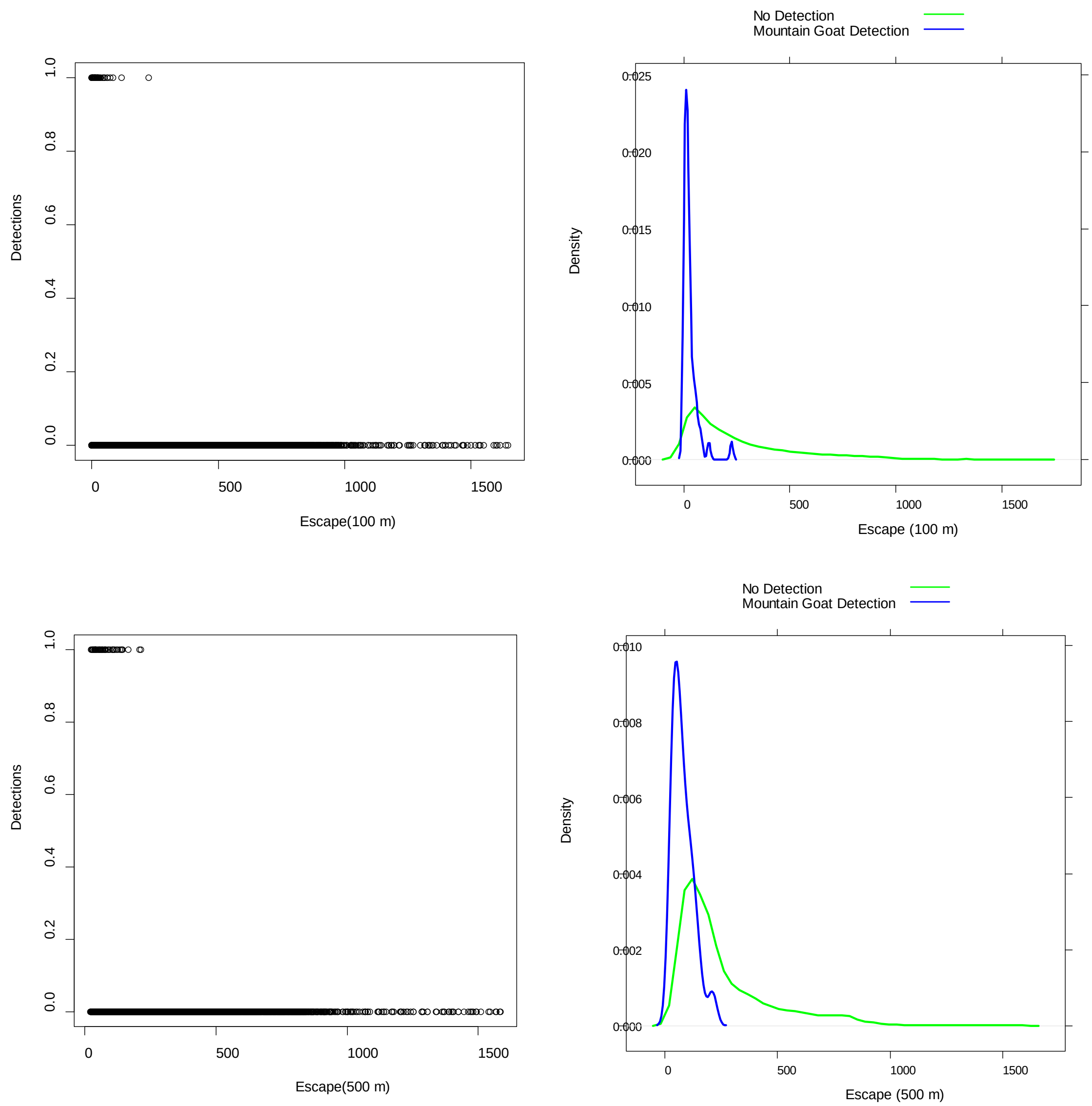


Figure 2C: Frequency plots and detection versus non-detection plots for all covariates at both the 100 meter and 500 meter scales (continued).

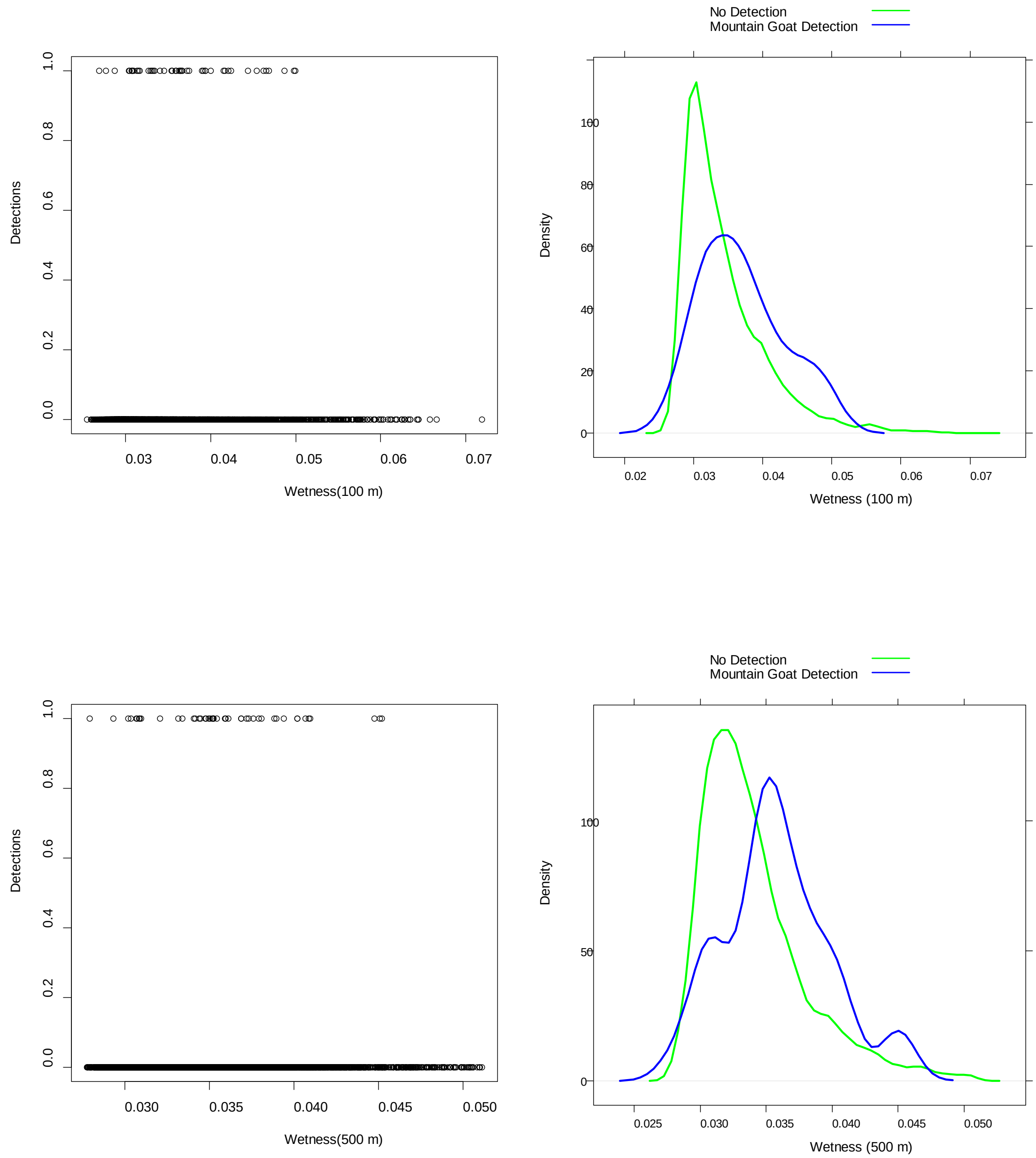


Figure 2C: Frequency plots and detection versus non-detection plots for all covariates at both the 100 meter and 500 meter scales (continued).

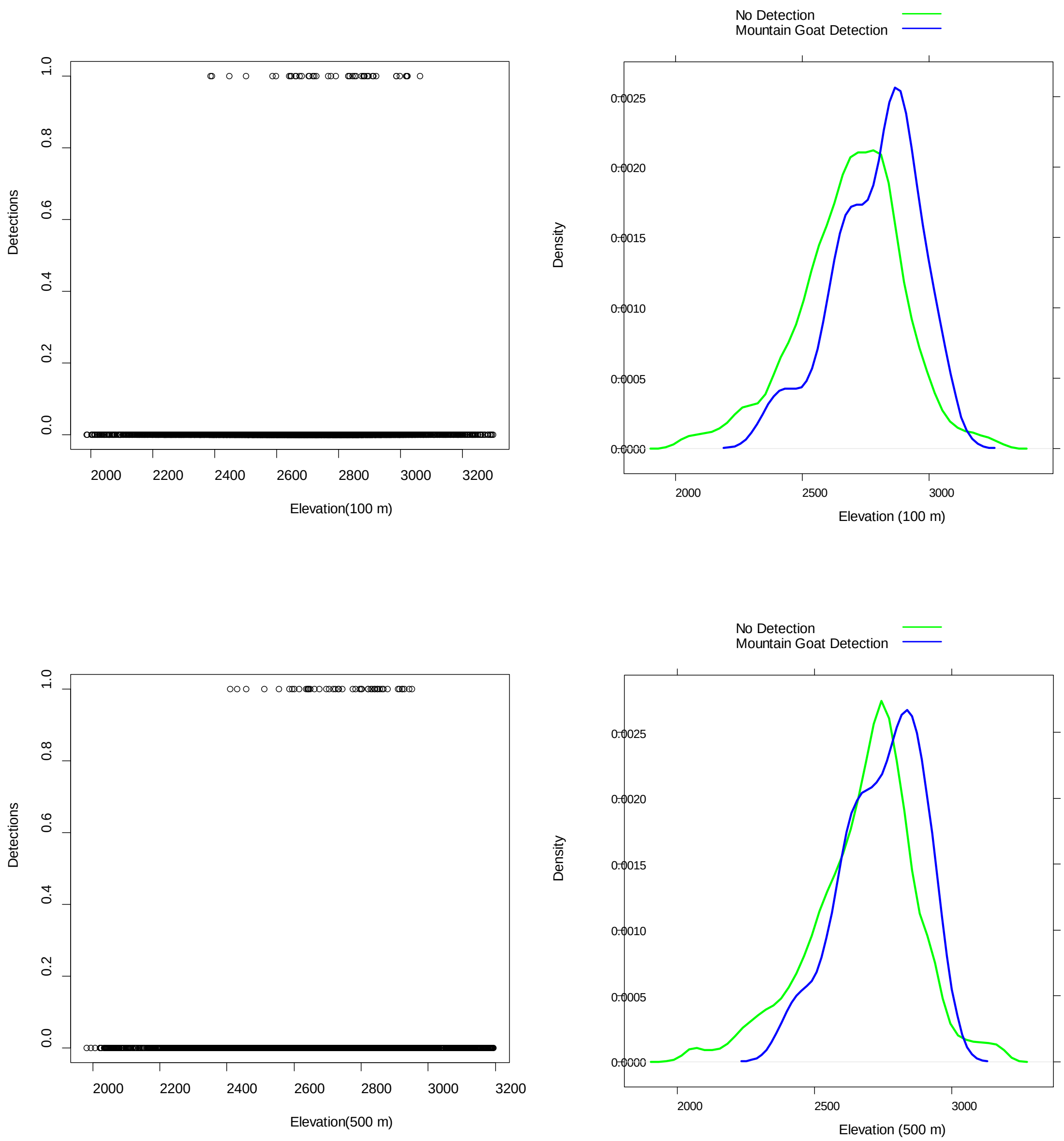


Figure 2C: Frequency plots and detection versus non-detection plots for all covariates at both the 100 meter and 500 meter scales (continued).

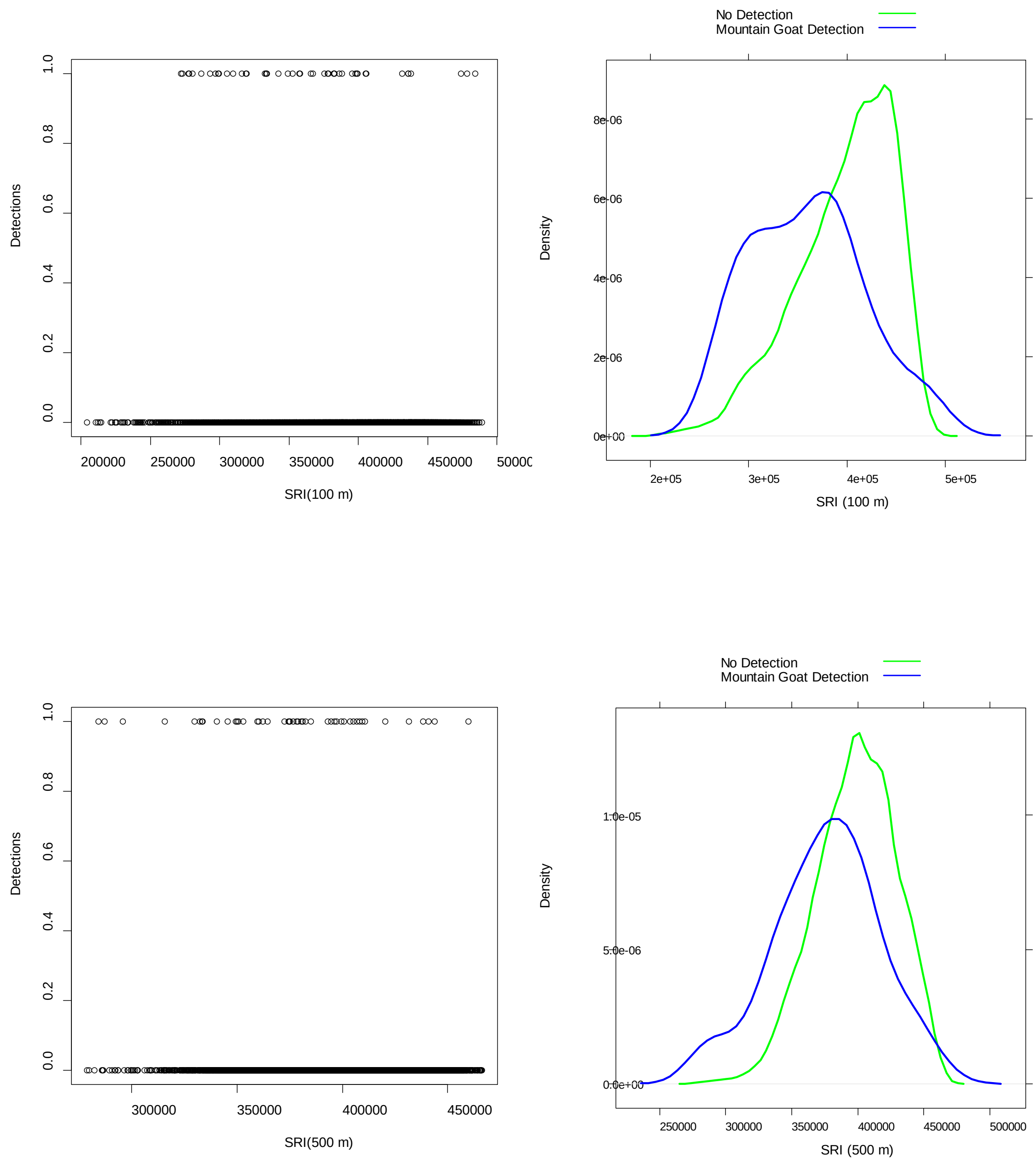


Figure 2C: Frequency plots and detection versus non-detection plots for all covariates at both the 100 meter and 500 meter scales (continued).

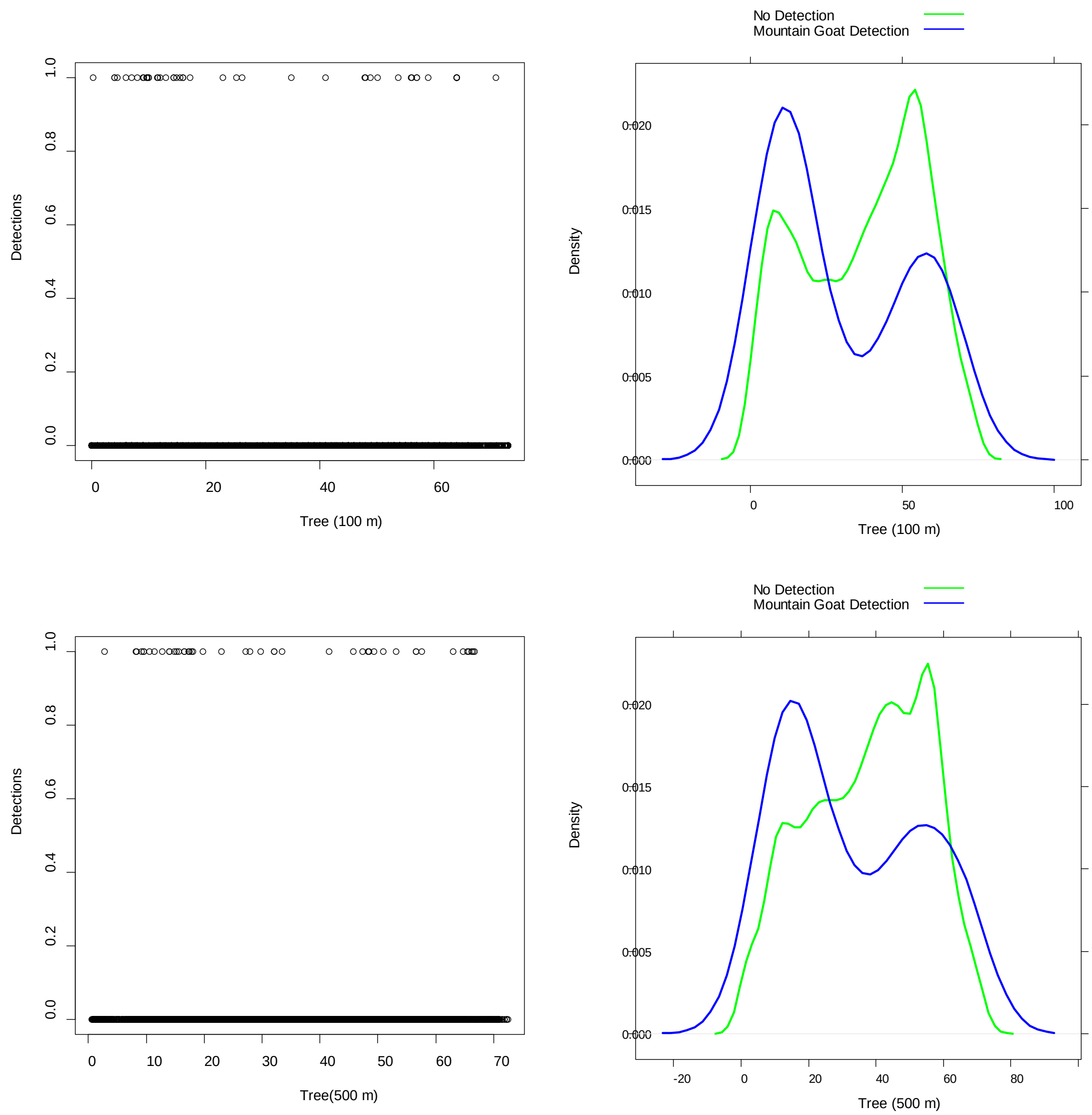


Figure 2C: Frequency plots and detection versus non-detection plots for all covariates at both the 100 meter and 500 meter scales (continued).

APPENDIX D

FULL MODEL SELECTION RESULTS

Table 1D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of six landscape covariates on mountain goat summer occupancy and detection probability at the 100 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
42	$\psi(Escape_1+Rug_1+Tree_1+Escape_1*Tree_1)p(.)$	6	507.02	0.00	0.18
142	$\psi(Escape_1+Rug_1+SRI_1+Tree_1+Tree_1*Escape_1)$ $p(Rug_1)$	8	508.72	1.70	0.08
75	$\psi(Escape_1+Rug_1+Tree_1+Tree_1*Escape_1)p(Tree_1)$	7	508.93	1.91	0.07
143	$\psi(Escape_1+Rug_1+SRI_1+Tree_1+Tree_1*Escape_1+$ $Escape_1*Rug_1)p(Rug_1)$	9	509.31	2.29	0.06
128	$\psi(Escape_1+Rug_1+Wet_1+Tree_1+Tree_1*Escape_1)p(Tree_1)$	8	509.51	2.49	0.05
131	$\psi(Escape_1+Rug_1+SRI_1+Tree_1+Tree_1*Escape_1)p(Tree_1)$	8	509.54	2.52	0.05
77	$\psi(Escape_1+Rug_1+Tree_1+Escape_1*Rug_1+$ $Tree_1*Escape_1)p(Tree_1)$	8	509.55	2.53	0.05
9	$\psi(Rug_1+Escape_1+Rug_1*Escape_1)p(.)$	5	510.09	3.07	0.04
121	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1+Tree_1*Escape_1)$ $p(Rug_1)$	9	510.12	3.10	0.04
59	$\psi(Escape_1+Rug_1+Escape_1*Rug_1)p(Rug_1)$	6	510.42	3.40	0.03
189	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1+Tree_1*Escape_1)$ $p(Tree_1+Rug_1)$	10	510.96	3.94	0.03
8	$\psi(Rug_1+Escape_1)p(.)$	4	511.07	4.05	0.02
190	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1+Tree_1*Escape_1+$ $Escape_1*Rug_1)$ $p(Tree_1+Rug_1)$	11	511.12	4.10	0.02

Table 1D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of six landscape covariates on mountain goat summer occupancy and detection probability at the 100 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i) (continued).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
156	ψ(Escape$_1$+Rug$_1$+Wet$_1$+SRI$_1$+Tree$_1$+Tree$_1$*Escape$_1$) p(Tree$_1$)	9	511.14	4.12	0.02
163	ψ(Escape$_1$+Rug$_1$+Tree$_1$+Escape$_1$*Rug$_1$ p(Tree$_1$+Rug$_1$)	8	511.61	4.59	0.02
90	ψ(Escape$_1$+Rug$_1$+Wet$_1$+Escape$_1$*Rug$_1$)p(Rug$_1$)	7	511.82	4.8	0.02
97	ψ(Escape$_1$+Rug$_1$+SRI$_1$+Escape$_1$*Rug$_1$)p(Rug$_1$)	7	511.90	4.89	0.02
100	ψ(Escape$_1$+Tree$_1$+Rug$_1$+Escape$_1$*Rug$_1$)p(Rug$_1$)	7	511.93	4.91	0.02
159	ψ(Escape$_1$+Rug$_1$+Wet$_1$+SRI$_1$+Tree$_1$+Tree$_1$*Escape$_1$+ Escape$_1$*Rug$_1$)p(Tree$_1$)	10	511.97	4.95	0.02
58	ψ(Escape$_1$+Rug$_1$)p(Rug$_1$)	5	512.15	5.13	0.01
40	ψ(Escape$_1$+Rug$_1$+Tree$_1$)p(.)	5	512.71	5.69	0.01
127	ψ(Escape$_1$+Rug$_1$+Wet$_1$+Tree$_1$+Escape$_1$*Rug$_1$)p(Tree$_1$)	8	512.84	5.83	0.01
141	ψ(Escape$_1$+Rug$_1$+SRI$_1$+Tree$_1$+Escape$_1$*Rug$_1$)p(Rug$_1$)	8	512.99	5.97	0.01
73	ψ(Escape$_1$+Rug$_1$)p(Tree$_1$)	5	513.00	5.98	0.01
43	ψ(Escape$_1$+Rug$_1$+Elev$_1$)p(.)	5	513.01	5.99	0.01
99	ψ(Escape$_1$+Tree$_1$+Rug$_1$)p(Rug$_1$)	6	513.63	6.61	0.01
89	ψ(Escape$_1$+Rug$_1$+Wet$_1$)p(Rug$_1$)	6	513.63	6.61	0.01
138	ψ(Escape$_1$+Rug$_1$+SRI$_1$+Elev$_1$+Escape$_1$*Rug$_1$)p(Rug$_1$)	8	513.72	6.7	0.01

Table 1D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of six landscape covariates on mountain goat summer occupancy and detection probability at the 100 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i) (continued).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
160	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1+Tree_1*Escape_1+Escape_1*Rug_1+Tree_1*SRI_1)p(Tree_1)$	11	513.84	6.82	0.01
162	$\psi(Escape_1+Rug_1+Tree_1)p(Tree_1+Rug_1)$	7	513.89	6.87	0.01
140	$\psi(Escape_1+Rug_1+SRI_1+Tree_1)p(Rug_1)$	7	514.01	6.99	0.01
120	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1+Escape_1*Rug_1)p(Rug_1)$	9	514.13	7.11	0.01
164	$\psi(Escape_1+Rug_1)p(Tree_1+Rug_1)$	6	514.15	7.13	0.01
179	$\psi(Escape_1+Rug_1+SRI_1+Tree_1)p(Tree_1+Rug_1)$	8	514.21	7.19	0.01
74	$\psi(Escape_1+Rug_1+Tree_1)p(Tree_1)$	6	514.41	7.39	0.01
130	$\psi(Escape_1+Rug_1+SRI_1+Tree_1)p(Tree_1)$	7	514.53	7.51	0
44	$\psi(Escape_1+Rug_1+Elev_1+Escape_1*Rug_1)p(.)$	6	514.59	7.58	0
157	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1+Escape_1*Rug_1)p(Tree_1)$	9	514.81	7.79	0
153	$\psi(Escape_1+Rug_1+Wet_1+Tree_1)p(Tree_1)$	7	514.88	7.86	0
137	$\psi(Escape_1+Rug_1+SRI_1+Elev_1)p(Rug_1)$	7	514.90	7.88	0
180	$\psi(Escape_1+Rug_1+SRI_1)p(Tree_1+Rug_1)$	7	515.08	8.06	0
144	$\psi(Escape_1+Rug_1+SRI_1+Tree_1+Tree_1*SRI_1)p(Rug_1)$	8	515.08	8.06	0

Table 1D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of six landscape covariates on mountain goat summer occupancy and detection probability at the 100 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i) (continued).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
177	$\psi(Escape_1+Wet_1+Tree_1+Tree_1*Escape_1)$ $p(Tree_1+Rug_1)$	8	515.53	8.51	0
188	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1)$ $p(Tree_1+Rug_1)$	9	515.65	8.64	0
155	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1)p(Tree_1)$	8	516.23	9.21	0
125	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Elev_1)p(Rug_1)$	8	516.85	9.84	0
192	$\psi(Escape_1+Rug_1+Wet_1+SRI_1)p(Tree_1+Rug_1)$	8	517.03	10.01	0
57	$\psi(Escape_1)p(Rug_1)$	4	517.07	10.05	0
178	$\psi(Escape_1+SRI_1)p(Tree_1+Rug_1)$	6	517.89	10.87	0
161	$\psi(Escape_1)p(Tree_1+Rug_1)$	5	518.52	11.50	0
98	$\psi(Escape_1+Tree_1)p(Rug_1)$	5	518.84	11.82	0
136	$\psi(Escape_1+SRI_1+Elev_1)p(Rug_1)$	6	518.97	11.96	0
101	$\psi(Escape_1+Elev_1)p(Rug_1)$	5	519.04	12.02	0
132	$\psi(Escape_1+Wet_1+SRI_1)p(Rug_1)$	6	519.07	12.06	0
174	$\psi(Escape_1+Wet_1)p(Tree_1+Rug_1)$	6	519.46	12.44	0
181	$\psi(Escape_1+SRI_1+Tree_1)p(Tree_1+Rug_1)$	7	519.85	12.83	0
187	$\psi(Escape_1+Wet_1+SRI_1)p(Tree_1+Rug_1)$	7	519.88	12.86	0
118	$\psi(Escape_1+Wet_1+SRI_1+Tree_1)p(Rug_1)$	7	520.31	13.29	0
165	$\psi(Escape_1+Tree_1)p(Tree_1+Rug_1)$	6	520.33	13.32	0

Table 1D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of six landscape covariates on mountain goat summer occupancy and detection probability at the 100 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i) (continued).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
124	$\psi(Escape_1+Wet_1+SRI_1+Elev_1)p(Rug_1)$	7	520.93	13.91	0
176	$\psi(Escape_1+Wet_1+Tree_1)p(Tree_1+Rug_1)$	7	521.41	14.39	0
17	$\psi(Escape_1+Tree_1+Escape_1*Tree_1)p(.)$	5	524.64	17.62	0
48	$\psi(Escape_1+SRI_1+Tree_1+Escape_1*Tree_1)p(.)$	6	524.95	17.93	0
94	$\psi(Escape_1+SRI_1+Tree_1+Tree_1*Escape_1)p(Tree_1)$	7	526.95	19.94	0
88	$\psi(Escape_1+Wet_1)p(Rug_1)$	5	527.85	20.83	0
87	$\psi(Escape_1+Wet_1+Tree_1+Tree_1*Escape_1)p(Tree_1)$	7	527.88	20.86	0
3	$\psi(Escape_1)p(.)$	3	528.43	21.41	0
15	$\psi(Escape_1+SRI_1)p(.)$	4	529.21	22.19	0
47	$\psi(Escape_1+SRI_1+Tree_1)p(.)$	5	529.60	22.58	0
16	$\psi(Escape_1+Tree_1)p(.)$	4	529.61	22.59	0
56	$\psi(Escape_1)p(Tree_1)$	4	529.88	22.86	0
18	$\psi(Escape_1+Elev_1)p(.)$	4	529.93	22.91	0
123	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1+Tree_1*SRI_1+$ $Tree_1*Escape_1+Escape_1*Rug_1)p(Rug_1)$	11	530.05	23.03	0
91	$\psi(Escape_1+SRI_1)p(Tree_1)$	5	530.10	23.08	0
14	$\psi(Escape_1+Wet_1)p(.)$	4	530.35	23.33	0
46	$\psi(Escape_1+SRI_1+Elev_1)p(.)$	5	530.42	23.40	0
122	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1+Tree_1*SRI_1)p(Rug_1)$	9	531.24	24.22	0

Table 1D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of six landscape covariates on mountain goat summer occupancy and detection probability at the 100 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i) (continued).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
85	$\psi(Escape_1+Wet_1)p(Tree_1)$	5	531.36	24.34	0
92	$\psi(Escape_1+SRI_1+Tree_1)p(Tree_1)$	6	531.56	24.54	0
133	$\psi(Escape_1+Rug_1+Wet_1+SRI_1)p(Rug_1)$	7	532.43	25.41	0
175	$\psi(Escape_1+Rug_1+Wet_1+Tree_1)p(Tree_1+Rug_1)$	8	532.64	25.62	0
93	$\psi(Escape_1+SRI_1+Tree_1+Tree_1*SRI_1)p(Tree_1)$	7	532.76	25.74	0
119	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1)p(Rug_1)$	8	532.92	25.90	0
134	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Escape_1*Rug_1)p(Rug_1)$	8	533.05	26.03	0
191	$\psi(Escape_1+Wet_1+SRI_1+Tree_1)p(Tree_1+Rug_1)$	8	533.23	26.21	0
116	$\psi(Rug_1+SRI_1+Tree_1)p(Rug_1)$	6	539.41	32.39	0
183	$\psi(Rug_1+Wet_1+SRI_1+Tree_1)p(Tree_1+Rug_1)$	8	539.99	32.97	0
49	$\psi(Rug_1+Wet_1+SRI_1)p(.)$	5	540.02	33.00	0
105	$\psi(Rug_1+Wet_1+SRI_1)p(Rug_1)$	6	540.10	33.08	0
149	$\psi(Rug_1+Wet_1+SRI_1+Tree_1)p(Rug_1)$	7	540.60	33.58	0
152	$\psi(Rug_1+Wet_1+SRI_1+Elev_1)p(Rug_1)$	7	540.83	33.81	0
11	$\psi(Rug_1+SRI_1)p(.)$	4	541.04	34.02	0
145	$\psi(Rug_1+Wet_1+SRI_1)p(Tree_1)$	6	541.93	34.91	0
81	$\psi(Rug_1+SRI_1)p(Tree_1)$	5	542.16	35.15	0
139	$\psi(Escape_1+SRI_1+Tree_1)p(Rug_1)$	6	545.97	38.95	0
104	$\psi(Wet_1+SRI_1)p(Rug_1)$	5	546.38	39.36	0

Table 1D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of six landscape covariates on mountain goat summer occupancy and detection probability at the 100 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i) (continued).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
186	$\psi(Rug_1+Wet_1+SRI_1)p(Tree_1+Rug_1)$	7	546.52	39.50	0
148	$\psi(Wet_1+SRI_1+Tree_1)p(Rug_1)$	6	547.78	40.77	0
2	$\psi(Rug_1)p(.)$	3	547.86	40.85	0
70	$\psi(Rug_1+Elev_1)p(Rug_1)$	5	547.92	40.90	0
72	$\psi(Rug_1+Tree_1)p(Rug_1)$	5	547.99	40.97	0
169	$\psi(SRI_1)p(Tree_1+Rug_1)$	5	548.40	41.38	0
173	$\psi(SRI_1+Tree_1+Tree_1*SRI_1)p(Tree_1+Rug_1)$	7	548.65	41.63	0
167	$\psi(Rug_1+Wet_1+Tree_1)p(Tree_1+Rug_1)$	7	548.68	41.66	0
84	$\psi(Rug_1+Elev_1+Tree_1)p(Tree_1)$	6	548.87	41.85	0
12	$\psi(Rug_1+Elev_1)p(.)$	4	548.99	41.97	0
115	$\psi(SRI_1+Tree_1)p(Rug_1)$	5	549.01	42.00	0
13	$\psi(Rug_1+Tree_1)p(.)$	4	549.05	42.03	0
117	$\psi(Rug_1+SRI_1+Tree_1+Tree_1*SRI_1)p(Rug_1)$	7	549.12	42.10	0
80	$\psi(Escape_1+Wet_1+Tree_{1+})p(Tree_1)$	6	549.31	42.29	0
112	$\psi(Rug_1+Wet_1+Tree_1+)p(Rug_1)$	6	549.42	42.40	0
27	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1+Rug_1*Escape_1+ SRI_1*Tree_1)p(.)$	9	549.44	42.42	0
67	$\psi(SRI_1)p(Rug_1)$	4	549.68	42.66	0
55	$\psi(Rug_1)p(Tree_1)$	4	549.81	42.79	0

Table 1D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of six landscape covariates on mountain goat summer occupancy and detection probability at the 100 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i) (continued).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
10	$\psi(Rug_1+Wet_1)p(.)$	4	549.85	42.83	0
172	$\psi(SRI_1+Tree_1)p(Tree_1+Rug_1)$	6	550.40	43.38	0
50	$\psi(Rug_1+Wet_1+Tree_1)p(.)$	5	550.58	43.56	0
83	$\psi(Rug_1+Elev_1)p(Tree_1)$	5	550.76	43.74	0
51	$\psi(Rug_1+Wet_1+Elev_1)p(.)$	5	550.84	43.82	0
168	$\psi(Rug_1+Wet_1)p(Tree_1+Rug_1)$	6	551.05	44.03	0
79	$\psi(Rug_1+Wet_1)p(Tree_1)$	5	551.76	44.74	0
114	$\psi(Rug_1+SRI_1+Elev_1)p(Rug_1)$	6	551.89	44.87	0
37	$\psi(Escape_1+Rug_1+Wet_1)p(.)$	5	552.65	45.63	0
171	$\psi(Rug_1+SRI_1)p(Tree_1+Rug_1)$	6	552.84	45.82	0
36	$\psi(Escape_1+Rug_1+Wet_1+Escape_1*Rug_1)p(.)$	6	552.89	45.87	0
103	$\psi(Escape_1+Rug_1+Elev_1+Escape_1*Rug_1)p(Rug_1)$	7	553.18	46.16	0
95	$\psi(Escape_1+SRI_1)p(Rug_1)$	5	553.58	46.57	0
68	$\psi(Rug_1+SRI_1)p(Rug_1)$	5	553.60	46.58	0
126	$\psi(Escape_1+Rug_1+Wet_1)p(Tree_1)$	6	553.64	46.62	0
45	$\psi(Escape_1+Wet_1+SRI_1)p(.)$	5	553.71	46.69	0
150	$\psi(Rug_1+Wet_1+SRI_1+Tree_1+Tree_1*SRI_1)p(Rug_1)$	8	554.31	47.29	0
86	$\psi(Escape_1+Wet_1+Tree_1)p(Tree_1)$	6	554.82	47.80	0

Table 1D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of six landscape covariates on mountain goat summer occupancy and detection probability at the 100 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i) (continued).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
158	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1+Tree_1*SRI_1)p(Tree_1)$	9	555.21	48.19	0
135	$\psi(Escape_1+Wet_1+SRI_1+Tree_1)p(Tree_1)$	6	555.29	48.27	0
32	$\psi(Escape_1+Wet_1+SRI_1+Elev_1)p(.)$	6	555.38	48.36	0
28	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Elev_1)p(.)$	7	555.46	48.44	0
96	$\psi(Escape_1+Rug_1+SRI_1)p(Rug_1)$	6	555.90	48.89	0
30	$\psi(Escape_1+Wet_1+SRI_1+Tree_1)p(.)$	6	556.03	49.01	0
184	$\psi(Rug_1+Wet_1+SRI_1+Tree_1+Tree_1*SRI_1)p(Tree_1+Rug_1)$	9	556.08	49.06	0
26	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Tree_1)p(.)$	7	556.13	49.11	0
29	$\psi(Escape_1+Rug_1+Wet_1+SRI_1+Elev_1+Escape_1*Rug_1)p(.)$	8	556.17	49.15	0
154	$\psi(Escape_1+Rug_1+Wet_1+SRI_1)p(Tree_1)$	7	556.24	49.22	0
31	$\psi(Escape_1+Wet_1+SRI_1+Tree_1+Escape_1*Tree_1)p(.)$	7	556.36	49.34	0
151	$\psi(Wet_1+SRI_1+Elev_1)p(Rug_1)$	6	557.04	50.02	0
78	$\psi(Escape_1+Rug_1)p(Rug_1)$	5	558.77	51.75	0
110	$\psi(Rug_1+Wet_1+Elev_1+)p(Rug_1)$	6	560.10	53.08	0
170	$\psi(Rug_1+Tree_1+SRI_1)p(Tree_1+Rug_1)$	7	560.50	53.48	0
194	$\psi(.)p(Rug_1)$	3	561.24	54.22	0
71	$\psi(Tree_1)p(Rug_1)$	4	562.99	55.97	0

Table 1D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of six landscape covariates on mountain goat summer occupancy and detection probability at the 100 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i) (continued).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
62	$\psi(Wet_1)p(Rug_1)$	4	563.21	56.19	0
166	$\psi(Wet_1)p(Tree_1+Rug_1)$	5	564.28	57.26	0
109	$\psi(Wet_1+Elev_1)p(Rug_1)$	5	564.82	57.80	0
63	$\psi(Rug_1+Wet_1)p(Rug_1)$	5	570.51	63.49	0
182	$\psi(Wet_1+SRI_1)p(Tree_1+Rug_1)$	6	570.63	63.61	0
113	$\psi(SRI_1+Elev_1)p(Rug_1)$	5	571.00	63.98	0
76	$\psi(Escape_1+Rug_1+Tree_1+Escape_1*Rug_1)p(Tree_1)$	7	571.06	64.04	0
102	$\psi(Escape_1+Rug_1+Elev_1)p(Rug_1)$	6	572.62	65.60	0
111	$\psi(Wet_1+Tree_1)p(Rug_1)$	5	573.54	66.53	0
69	$\psi(Elev_1)p(Rug_1)$	4	575.04	68.02	0
41	$\psi(Escape_1+Rug_1+Tree_1+Escape_1*Rug_1)p(.)$	6	577.09	70.07	0
185	$\psi(Wet_1+SRI_1+Tree_1)p(Tree_1+Rug_1)$	7	579.14	72.12	0
20	$\psi(Wet_1+SRI_1+Wet_1*SRI_1)p(.)$	5	580.81	73.79	0
34	$\psi(Rug_1+Wet_1+SRI_1+Tree_1+SRI_1*Tree_1)p(.)$	7	586.19	79.17	0
19	$\psi(Wet_1+SRI_1)p(.)$	4	587.00	79.98	0

Table 1D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of six landscape covariates on mountain goat summer occupancy and detection probability at the 100 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i) (continued).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
147	$\psi(Rug_1+Wet_1+SRI_1+Tree_1+Tree_1*SRI_1)p(Tree_1)$	8	587.47	80.46	0
106	$\psi(Wet_1+SRI_1)p(Tree_1)$	5	588.93	81.91	0
107	$\psi(Wet_1+SRI_1+Tree_1)p(Tree_1)$	6	590.57	83.55	0
35	$\psi(Rug_1+Wet_1+SRI_1+Elev_1)p(.)$	6	591.46	84.44	0
39	$\psi(Escape_1+Rug_1+SRI_1)p(.)$	5	591.67	84.66	0
129	$\psi(Escape_1+Rug_1+SRI_1)p(Tree_1)$	6	592.24	85.23	0
38	$\psi(Escape_1+Rug_1+SRI_1+Escape_1*Rug_1)p(.)$	6	593.31	86.29	0
23	$\psi(SRI_1+Elev_1)p(.)$	4	599.94	92.92	0
82	$\psi(Rug_1+SRI_1+Tree_1)p(Tree_1)$	6	602.16	95.14	0
64	$\psi(SRI_1)p(Tree_1)$	4	602.95	95.94	0
65	$\psi(SRI_1+Tree_1)p(Tree_1)$	5	603.35	96.33	0
146	$\psi(Rug_1+Wet_1+SRI_1+Tree_1)p(Tree_1)$	7	604.62	97.6	0
33	$\psi(Rug_1+Wet_1+SRI_1+Tree_1)p(.)$	6	605.19	98.17	0
54	$\psi(Wet_1+SRI_1+Elev_1)p(.)$	5	605.25	98.23	0
5	$\psi(SRI_1)p(.)$	3	605.89	98.88	0

Table 1D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of six landscape covariates on mountain goat summer occupancy and detection probability at the 100 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i) (continued).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
66	$\psi(SRI_1+Tree_1+SRI_1*Tree_1)p(Tree_1)$	6	609.25	102.23	0
108	$\psi(Wet_1+SRI_1+Tree_1+Tree_1*SRI_1)p(Tree_1)$	7	609.97	102.95	0
53	$\psi(Wet_1+SRI_1+Tree_1+Tree_1*SRI_1)p(.)$	6	610.93	103.91	0
25	$\psi(SRI_1+Tree_1+SRI_1*Tree_1)p(.)$	5	612.47	105.45	0
6	$\psi(Elev_1)p(.)$	3	626.12	119.1	0
4	$\psi(Wet_1)p(.)$	3	626.77	119.75	0
60	$\psi(Wet_1)p(Tree_1)$	4	628.71	121.69	0
7	$\psi(Tree_1)p(.)$	3	630.08	123.06	0
1	$\psi(.)p(.)$	2	630.44	123.43	0
61	$\psi(Wet_1+Tree_1)p(Tree_1)$	5	630.60	123.58	0
193	$\psi(.)p(Tree_1)$	3	630.76	123.74	0
24	$\psi(SRI_1+Tree_1)p(.)$	4	633.23	126.21	0
21	$\psi(Wet_1+Elev_1)p(.)$	4	646.61	139.59	0
22	$\psi(Wet_1+Tree_1)p(.)$	4	648.09	141.07	0
52	$\psi(Wet_1+SRI_1+Tree_1)p(.)$	5	654.75	147.73	0

Table 2D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of five landscape covariates on mountain goat summer occupancy and detection probability at the 500 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
8	$\psi(Escape_5)p(.)$	3	536.66	0	0.379
15	$\psi(Escape_5+Wet_5)p(.)$	4	538.50	1.84	0.151
17	$\psi(Escape_5+Elev_5)p(.)$	4	538.60	1.94	0.144
16	$\psi(Escape_5+SRI_5)p(.)$	4	538.65	1.99	0.14
26	$\psi(Escape_5+Wet_5+SRI_5)p(.)$	5	540.47	3.81	0.06
27	$\psi(Escape_5+Wet_5+Elev_5)p(.)$	5	540.50	3.84	0.06
28	$\psi(Escape_5+SRI_5+Elev_5)p(.)$	5	540.60	3.94	0.05
21	$\psi(Escape_5+Wet_5+SRI_5+Elev_5)p(.)$	6	542.48	5.81	0.02
23	$\psi(Rug_5+Wet_5+SRI_5)p(.)$	5	563.90	27.23	0
7	$\psi(Rug_5)p(.)$	3	565.53	28.87	0
12	$\psi(Rug_5+Wet_5)p(.)$	4	566.49	29.83	0
14	$\psi(Rug_5+Elev_5)p(.)$	4	566.81	30.15	0
34	$\psi(SRI_5+Elev_5)p(Rug_5)$	5	578.72	42.06	0
35	$\psi(.)p(Rug_5)$	3	579.02	42.36	0
1	$\psi(SRI_5+Elev_5+Rug_5)p(Rug_5)$	6	579.09	42.42	0
33	$\psi(Wet_5+Elev_5)p(Rug_5)$	5	579.83	43.17	0
4	$\psi(Elev_5+Rug_5)p(Rug_5)$	5	580.79	44.13	0
31	$\psi(Elev_5)p(Rug_5)$	4	580.80	44.14	0

Table 2D: Model selection results from an *a priori* model list for a single-season occupancy analysis examining the effects of five landscape covariates on mountain goat summer occupancy and detection probability at the 500 meter scale. All models are presented along with the number of parameters (k), ΔAIC_c value and Akaike weight (ω_i) (continued).

Model ID	Model Structure	k	AIC_c	ΔAIC_c	ω_i
2	$\psi(Wet_5+Elev_5+Rug_5)p(Rug_5)$	6	581.96	45.30	0
29	$\psi(Wet_5)p(Rug_5)$	4	584.02	47.36	0
3	$\psi(Wet_5+SRI_5+Rug_5)p(Rug_5)$	6	584.95	48.29	0
5	$\psi(Wet_5+Rug_5)p(Rug_5)$	5	586.32	49.65	0
32	$\psi(Wet_5+SRI_5)p(Rug_5)$	5	587.75	51.09	0
30	$\psi(SRI_5)p(Rug_5)$	4	589.25	52.58	0
18	$\psi(Wet_5+SRI_5)p(.)$	4	590.16	53.50	0
25	$\psi(Rug_5+SRI_5+Elev_5)p(.)$	5	614.86	78.20	0
24	$\psi(Rug_5+Wet_5+Elev_5)p(.)$	5	615.30	78.64	0
22	$\psi(Rug_5+Wet_5+SRI_5+Elev_5)p(.)$	6	615.97	79.30	0
13	$\psi(Rug_5+SRI_5)p(.)$	4	623.13	86.47	0
19	$\psi(Wet_5+Elev_5)p(.)$	4	628.93	92.27	0
6	$\psi(.)p(.)$	2	630.44	93.78	0
11	$\psi(Tree_5)p(.)$	3	631.73	95.07	0
20	$\psi(SRI_5+Elev_5)p(.)$	4	633.65	96.99	0
9	$\psi(Wet_5)p(.)$	3	651.57	114.91	0
10	$\psi(SRI_5)p(.)$	3	651.57	114.91	0