CHARACTERIZING HABITAT RELATIONSHIPS AND ESTABLISHING MONITORING STRATEGIES FOR AN ALPINE OBLIGATE

by

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ABSTRACT

Alpine species have evolved to live in some of the harshest and most climatically diverse areas in the world, yet changes in climate are rapidly altering the areas alpine obligates call home. Warming temperatures are marching species to higher elevations and towards the poles, especially threatening species at the southern extent of their distributions. Understanding habitat requirements and monitoring abundance of species like the hoary marmot (*Marmota caligata*) at their southern extent will be crucial for tracking the magnitude of change that has begun in alpine ecosystems. We conducted double-observer occupancy surveys to collect presence-absence data and assess habitat characteristics important for the occurrence of hoary marmots; survey sites were within 5 mountain ranges in western Montana, the southern edge of this species' distribution. Marmots preferred shallow slopes, southern aspects, and areas with shrubs present. These preferences suggest that hoary marmots select habitat based on limitations they experience during both winter and summer, but winter conditions may play a stronger role in habitat selection. We then used our occupancy data to assess a broad suite of landscape variables at multiple spatial scales to create a predictive map of hoary marmot habitat throughout their distribution in Montana. We employed our predictive map to conduct a spatially-explicit power analysis and assess the ability of different monitoring strategies to detect a negative trend in abundance of marmot colonies. We were able to detect a 50% decline in colony abundance over 30 years by surveying 7-87% of sites ≥4 times every 3 years. We found that we were more likely to detect a negative trend when the abundance of colonies was higher. Based on this information, we suggest that if management objectives include assessing population trend from occupancy, monitoring plans should be implemented sooner rather than later. Habitat associations and population status information are lacking for many species. Our study has provided a way to collect valuable information to monitor and manage an alpine species. The methods we have used can be applied to monitor other species that are hard to access and our results provide information for conserving alpine species over their distribution.

CHAPTER ONE

INTRODUCTION TO THESIS

Species around the globe are shifting their distributions in response to changes in habitat, which has resulted from climate change (Parmesan and Yohe 2003). Range retractions have been occurring at a median rate of an 11 m increase in elevation and a 16.9 km increase in latitude per decade (Chen et al. 2011). Although low-elevation species may be able to maintain relatively consistent range sizes by moving up in elevation, species that occur at high elevations face a double-edged sword (Moritz et al. 2008). These species may not have the option to move up in elevation and also are losing habitat at their lower elevation threshold (Moritz et al. 2008).

Species reliant on persistent winter and spring snow cover are jeopardized by increases in temperature (Inman et al. 2012, Sultaire et al. 2016). Alpine obligates are particularly vulnerable to climate change at the southern extent of their distribution where warming trends have a more pronounced effect (Cahill et al. 2014). The edges of the distributions of alpine species are typically comprised of isolated mountain ranges rather than of continuous habitat, which increases the potential for rapid range contractions as these smaller patches are lost. Smaller areas of habitat can become isolated sky islands that are more susceptible to inbreeding, population declines, and local extinction (MacArthur and Wilson 1963, Brown 1978). These populations at the southern edge also often harbor diverse alleles that can be important for overall genetic diversity of the species (Hampe and Petit 2005). Studying alpine species at the southern extent of their distribution where climate change is already operating can demonstrate future impacts for the species over the rest of their distribution.

The hoary marmot (*Marmota caligata*) is the largest and most widely distributed marmot species in North America (Kyle et al. 2007). They live in rocky terrain and alpine meadows above tree line in mountains ranging from Alaska to Montana (Foresman 2012). They live and reproduce as family groups, known as colonies, in boulder fields that provide shelter from predators (Barash 1973). Although hoary marmots are relatively abundant throughout their range, they are a potential species of concern in Montana because we lack fundamental information on distribution, specific habitat requirements, and population sizes (MTNHP 2013). In addition, marmots occupy alpine habitats likely to be affected by climate change, especially in Montana, which represents the southern edge of their distribution (Armitage 2013). Hoary marmots are already a species of inventory focus in the Northwest Montana Climate Change plan (Hammond 2010). However, conservation and management of this species will become increasingly difficult without knowledge about habitat associations and population trend.

Areas that provide habitat for a species include all of the conditions and resources needed to promote occupancy and allow them to survive and reproduce (Hall et al. 1997). Hoary marmots live in strongly seasonal environments with distinctly different environmental conditions that are driven by temperature and precipitation, both likely to be affected by climate change (Pederson et al. 2009, Wipf et al. 2013). Hoary marmots are true hibernators that rely on snowpack for insulation from harsh winter temperatures (Patil et al. 2013). Changes in snowpack can influence hoary marmots by causing phenological mismatches and depressed demographic rates (Ozgul et al. 2010, Patil et al. 2013), potentially influencing where colonies will occur on the landscape. There are remarkably few peer-reviewed studies on hoary marmots in general and only 2 studies have documented habitat associations in Montana (Barash 1974, Tyser 1980, Patil 2010). These studies were performed at very small scales, in one basin and at a single boulder field, and did not account for imperfect detection, which can result in biased findings when assessing habitat characteristics (MacKenzie 2006). Understanding the environmental conditions important to hoary marmots can inform how temperature changes may influence habitat availability and the distribution of this species in the face of climate change (Chen et al. 2011).

Habitat characteristics also can be used to inform where to monitor animal populations and direct where future conservation action is needed. Budgets for wildlife management are limited and the cost of monitoring many species is prohibitive (Pollock et al. 2002). Compared to other methods of abundance estimation, occupancy surveys can be used for monitoring at lower cost and effort and have been used as an index of abundance for species that are hard to detect, found in low abundances, and distributed over a large area (Bailey et al. 2004, MacKenzie and Nichols 2004, Witczuk et al. 2008, Schooley et al. 2012, Fuller et al. 2016). Monitoring plans have been developed and implemented for Olympic marmots (*Marmota olympus*, Witczuk et al. 2008) and Vancouver Island marmots (*Marmota vancouverensis,* Bryant and Janz 1996) that successfully identified population declines and allowed managers to take necessary conservation actions.

We sought to address gaps in knowledge about the habitat relationships and distribution of hoary marmots and provide strategies for evaluating population trend in Montana. In Chapter 2, habitat characteristics important to hoary marmots are evaluated using occupancy methods. We examine factors that limit their current distribution and consider impacts of predicted changes in climate to discuss how their distribution may shift in the future. In Chapter 3, a predictive map of marmot habitat throughout western Montana was created using survey data. We employ our predictive map as a basis for designing a monitoring program by evaluating our ability to detect potential decreases in marmot colony abundance using occupancy. We focused on evaluating habitat and populations of hoary marmots in western Montana to observe distribution shifts and direct future management action at the southern extent of their distribution.

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CHAPTER TWO

HABITAT CHARACTERISTICS OF THE HOARY MARMOT: ASSESSING DISTRIBUTION LIMITATIONS IN MONTANA

Contributions of Authors and Co-Authors

Manuscript in Chapter 2

Author: Benjamin Y. Turnock

Contributions: Implemented the study. Collected and analyzed the data. Wrote the manuscript.

Co-Author: Andrea R. Litt

Contributions: Assisted with study design, data analysis, and preparation and review of the manuscript.

Co-Author: John M. Vore

Contributions: Conceived the initial project idea, assisted with study design and securing project funding.

Co-Author: Chris M. Hammond

Contributions: Assisted with study design and securing project funding.

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Habitat Characteristics of the Hoary Marmot: Assessing Distribution Limitations in Montana

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Abstract

Species that live in ecosystems with extremely different seasonal conditions must balance the constraints of each season to survive. Alpine species that do not migrate seasonally are especially adept at balancing the constraints created by short growing seasons and long, harsh winters. We investigated the habitat characteristics of hoary marmots in western Montana to provide a better understanding about habitat selection at the southern extent of this species' distribution. Hoary marmots are an alpine obligate of special concern in western Montana; given that climate change is impacting alpine ecosystems at a rapid rate, this species may be especially vulnerable at the southern edge of their range. We conducted occupancy surveys in Montana in three study areas along a latitudinal gradient in 2014 and 2015 to assess the importance of specific habitat characteristics to their presence on the landscape. Slope, aspect, and presence of shrubs were all important habitat characteristics for hoary marmots. Marmots in our study areas preferred shallow slopes and southern aspects, which is similar to findings from studies on other hoary marmot populations and other marmot species. Our results provide evidence that marmots may strike a balance between the environmental conditions they require during summer and winter. Shallow slopes typically accumulate deeper snow in

winter that provide the best insulating snowpack. However, a preference for southern aspects allows for more snow-free areas in spring, providing a slightly longer growing season than northern aspects. Windblown snow may collect under shrubs, providing deeper snow and more insulation that also melts earlier in the spring and summer, such that areas with shrubs result in higher occupancy by hoary marmots. Other researchers suggest that marmot survival is influenced by snowpack, therefore we propose that marmot distribution is tied to winter conditions rather than summer conditions. This idea highlights the difficulty of working on marmots and other alpine obligates, as the majority of studies only occur during the short growing season. In Montana, areas that provide the winter conditions hoary marmots require may become more limited given the current and projected increases in temperature and reduction in snowpack. Effectively conserving, monitoring, and managing alpine obligates under an uncertain climate future will require a closer look at how winter conditions drive habitat selection and distributions on the landscape.

Key words

Climate change; detection; habitat; hoary marmot; *Marmota caligata*; occupancy; selection; western Montana.

Introduction

Animals select areas based on environmental conditions and resources, and these characteristics are altered by seasonal variation (Hutto 1985). Ecosystems characterized by extreme differences among seasons can limit the distribution of species. For example, alpine areas have short growing seasons and long winters (McKnight and Darrel 2000). Some vertebrates spend only part of the year in the alpine zone and migrate to lower elevations or latitudes during winter (Murray and Boutin 1991, Boyce et al. 2003, Inman et al. 2012, Gaudry et al. 2015). Other species remain in alpine areas year-round, capitalizing on adaptations that allow them to survive and reproduce in spite of extreme seasonal variation (Barash 1989, Morrison et al. 2009, Copeland et al. 2010, Reid et al. 2012, Armitage 2014).

The hoary marmot (*Marmota caligata*) is an alpine obligate that is patchily distributed at or above treeline throughout western North America north of the 45th parallel (Braun et al. 2011). They live and reproduce as family groups, known as colonies, in boulder fields that provide shelter from predators (Barash 1973). Hoary marmots have several adaptations to accommodate the extreme seasonal differences in environmental conditions in alpine areas. They hibernate for eight months of the year to survive the long, cold winters, relying on heavy snow cover and communal burrows for protection from low temperatures (Foresman 2012, Patil et al. 2013). They emerge from hibernation in mid-May and immediately begin searching nearby snow-free areas (Armitage et al. 1976) for a variety of herbaceous plants and forbs to eat (Holmes 1979, Karels et al. 2004). During the summer, they remain in the same boulder field where they spent the winter and have only four months to regain body condition and reproduce before hibernation (Barash 1973). As a result, areas where marmots occur provide the resources they require for the entire year, although there are a few cases where entire marmot colonies moved seasonally (Hock and Cottini 1966, Barash 1974).

Understanding the habitat characteristics that influence presence of hoary marmots can inform what determines their distribution on the landscape. Climate change is projected to impact alpine ecosystems faster than other areas, which may in turn affect the phenology, demographics, and distribution of alpine-obligate species (Moritz et al. 2008, Ozgul et al. 2010). Hoary marmots are an ideal indicator of rapid environmental change in alpine areas because of their sensitivity to environmental conditions that are influenced by climate change (Meny 2012). Western Montana, the southern extent of the hoary marmot's distribution, already has experienced a 1.33˚C (1900-2006) increase in annual average temperature (Pederson et al. 2009), which is 1.87 times greater than that observed in the northern hemisphere (Lugina et al. 2006). A shift in distribution may occur because of these temperature changes, but details of such shifts will be difficult to predict reliably without understanding how environmental conditions throughout the year influence the persistence of hoary marmots. Changes in snowpack also can influence habitat for marmots by causing phenological mismatches and depressed demographic rates (Ozgul et al. 2010, Patil et al. 2013). We lack basic information about the distribution and abundance of hoary marmots, which is why they are a potential species of concern in Montana (Meny 2012). In light of these findings, understanding the specific characteristics of places where marmots occur will be essential to their conservation. Managers want to ensure persistence of hoary marmot populations (Hammond 2010), and should future management action be required, then identifying areas within the state that may be more susceptible to the influences of climate change will be crucial.

We sought to assess habitat selection of hoary marmots throughout most of their distribution in Montana. Hoary marmots are patchily distributed across the landscape, well-camouflaged within boulder fields, and not always active aboveground during daylight hours (Gray 1967, Barash 1989). To overcome these challenges, we used occupancy methods that are well-suited for rugged and remote terrain (DeVoe et al. 2015) and account for imperfect detection that could bias inferences about habitat (MacKenzie 2006).

Methods

Study areas

We studied five major mountain ranges grouped into three study areas throughout the distribution of hoary marmots in Montana: the Whitefish and Lewis Ranges in the northern study area, the Swan and Mission Ranges in the middle study area, and the Anaconda-Pintler Range in the southern study area. Each range was generally oriented in a north-south direction (Figure 2.1). The Anaconda-Pintlers receive the least precipitation and have the highest maximum elevation. Average annual precipitation generally increases with latitude, except for the Whitefish Range which receives only slightly more precipitation than the Anaconda-Pintlers and has the lowest elevation (Table 2.1).

Locations within mountain ranges

We selected two to three locations within each mountain range for data collection, based on historical observations and recent inventory surveys by Montana Fish, Wildlife and Parks. Each selected location was at or above treeline, at elevations from 1600 m in the Lewis Range to just over 2800 m in the Anaconda-Pintler Range. Straight-line distances between locations were 7-28 km within each mountain range and 25-365 km between mountain ranges.

Survey sites

To focus on and efficiently sample marmot habitat, we created polygons around boulder fields on aerial imagery of the landscape (Griffin et al. 2008). These polygons represented potential survey sites and placement of the sites was based on several criteria that remained consistent over the course of the study. We excluded areas <1600 m elevation, as these tended to be well below treeline, and boulder fields that were <0.4 ha because we thought it unlikely that marmots would inhabit such a small boulder field (Griffin et al. 2008) given their average home range size of 13.8 ha (Holmes 1979). Large boulder fields >15 ha presented logistical challenges for surveying accurately and efficiently (S. Griffin, *personal communication*). For such sites, we divided the boulder field into multiple sites that included the boulder field and some area adjacent to the edge of the boulder field. We also considered visibility from potential vantage points to delineate site boundaries. When boulder fields were large, we established site boundaries where changes in aspect or slope drastically decreased visibility; we assessed visibility at potential vantage points using ground view in Google Earth. Other criteria for site placement were refined during the initial season in 2014 to balance random sampling of the landscape and surveying sites efficiently. Initially, we selected potential survey sites based on an existing habitat suitability model, which used MaxEnt to identify nine cover types commonly associated with marmot presence (Maxell and Ritter 2013). When we surveyed sites selected based on this method, we observed only three marmots during 121 surveys of 42 sites, suggesting this method was effective for sampling the broader landscape, but less effective for identifying areas where marmots occur. We then narrowed our focus and selected potential survey sites manually, in boulder fields and bedrock using NAIP orthoimagery in ArcMap 10.2 (ESRI 2011) and Google Earth. Sites needed to include ≥5% boulder field to increase the possibility that marmots might occur there; most sites were comprised of 20-80% boulders and slab rock (Appendix A: Figure S1). We did not want to limit survey sites to boulder fields alone because hoary marmots use areas adjacent to boulder fields for foraging (Holmes 1984, Karels et al. 2004). Hoary marmots forage within 50 m of burrows on average (Karels et al. 2004) and escape burrows can be constructed within foraging areas (Holmes 1984). To capture sufficient area outside a boulder field where a marmot might forage, we allowed ≤60% of the site to be comprised of vegetation adjacent to the boulder field. For smaller boulder fields, we encompassed the area surrounding the boulder field completely. Although this manual method of site location and creation required more time, potential survey sites included other land cover types marmots may occupy (besides the nine types predicted by Maxell and Ritter 2013) and increased observer visibility during surveys.

We selected survey sites at random from all the sites created. Given the rocky nature of mountainous areas, we selected and sampled clusters of sites to balance travel time with the number of surveys that could be conducted in a single day (Witczuk et al. 2008). To create clusters, we randomly selected ≤15 sites, created a 100-m buffer around each and surveyed all sites that fell within the buffer. The number of clusters surveyed during each trip was based on the duration of the trip and the assumption that crew members could access and survey up to six sites in a day depending on the distance to sites and outcomes of surveys.

Surveys

We surveyed marmots based on methods modified from Witczuk et al. (2008) for surveying Olympic marmots (*Marmota olympus*). At each site, we conducted up to 5 surveys using up to 2 survey methods (visual and walkthrough) and a double-observer approach to account for imperfect detection of marmots (MacKenzie and Royle 2005). First, observers independently and simultaneously conducted visual surveys. We used Mesa Rugged notepad computers (Juniper Systems, Logan, Utah, USA) along with NAIP imagery to navigate to and locate each site in the field. Two observers selected a vantage point within 600 m of the site where ≥60% of the site was visible and where they were within 50 m from each other but could not see the other observer. The observers simultaneously surveyed the site with binoculars for ≥20 minutes. These surveys were independent as observers made no indication of what they saw during the survey.

Detections. Hoary marmots often are called whistle pigs because of their characteristic and easily-identifiable whistle lasting 0.56 to 0.76 seconds (Taulman 1977). When observers heard a whistle during surveys, they visually located the marmot before proceeding. They recorded the method of initial detection as sound or sight, the behavior at initial observation (resting, foraging, traveling, or fighting), the substrate where the marmot was detected (rock, trees, grass, shrubs, or snow), the time, and the number of juveniles, adults, or unknown age marmots observed. We easily distinguished young of the year and adults based on size (Barash 1974), but distinguishing between juveniles and adults from a distance was more difficult. As a result, observers typically recorded the age class as unknown, unless multiple marmots of different ages provided a size comparison during the survey. Observers used the notepad computers and aerial imagery to record the location of each uniquely identified marmot observation accurately. If the observer detected several marmots ≤50 m of each other, they were recorded as a group and assigned one location and identification number.

After completing each survey, the observers compared where they detected marmots. By corroborating observation times and locations, observers correctly recorded the number and location of marmots in the site and applied the same unique observation identification number in both field computers. If a marmot was detected by only one observer, only this observer recorded it in their field computer. Observers also noted when no marmots were detected during a survey.

If at least one observer detected a marmot during the first set of surveys, the site was not surveyed again (2 total surveys). If neither observer detected marmots, they either changed their vantage point and completed a second set of surveys later that day or returned the next day to complete a second set of surveys (4 total surveys). By using this hybrid removal survey design, we surveyed more sites and reduced potential bias in detection probability because there were always at least two surveys at each site (MacKenzie and Royle 2005).

Non-detections. If no marmots were detected after four surveys, we conducted a more intensive survey to improve our estimate of detection probability. After completing the second set of occupancy surveys from a stationary vantage point, both observers walked through the site looking for and recording any signs of marmot presence, such as scat, burrows, tracks, or sightings. Marmot scat is easily identified because it is dark green when fresh (see Elbroch 2003 for description) and does not last for more than one season (Karels et al. 2004). Active burrows often have fresh scat at the entrance and vegetation does not protrude across the opening (Taulman 1975). Inactive burrows typically have vegetation growing into the entrance (Griffin et al. 2008). We identified marmot tracks in mud, dirt, or snow using Elbroch (2003). Observers could reasonably search 1.5 m on both sides of their route (a 3 m-wide swath) and walked enough to survey 5% of the total site area. If observers detected ≥2 types of sign or saw a marmot the walkthrough ended.

Habitat characteristics

We recorded 15 site-specific features we predicted could be important characteristics of marmot habitat and promote occupancy (Table 2.2). Some of these were recorded in the field, but most were remotely sensed using ArcGIS 10.2.2 (ESRI, Redlands, California, USA).

Field measurements. We characterized each site based on six land cover categories (rock, grass, trees, shrubs, snow, and other, in 5% increments) after completing the first set of surveys. The two observers visually estimated the proportion of each land cover category present in the site independently, then compared and adjusted estimates so that values matched or were within 5%. Land cover covariates included the proportion of rock, grass, tree, shrub, and other cover, which were computed as the average between the two observers.

Remotely-sensed characteristics. We computed average slope, aspect, and elevation of each site in ArcGIS using the National Elevation Dataset 1-arc second (30 m) digital elevation model.

We determined the availability of water using the distance to and type of the closest water source for each site with ArcGIS. We compiled layers of stream and water bodies into a single shapefile. We cross-referenced this shapefile with USGS 7.5" topographic maps to include water sources not present in the source layers. We groundtruthed this master layer in the field, to assess whether water sources were still present and add water sources that were absent from the master layer (e.g., small or ephemeral water sources that may be enough to support a colony but not large enough to be mapped).

We calculated the average annual precipitation for all sites using data for the most recent three decades (1981-2010, PRISM Climate Group). We used the PRISM Climate Group's 800-m resolution precipitation layer that extrapolates precipitation measurements from weather stations and applies those values to the landscape with adjustments for slope and aspect. We hypothesized that boulder size might be important to marmot habitat selection so we characterized composition of boulder sizes at each site. Using Google Earth's 1-m resolution aerial imagery, we measured the length and width of each boulder and grouped them into 4 categories: small (surface area ≤ 4 m^2), medium (5-15 m^2), large (≥ 16 m^2), and slab rock/other. We then calculated the proportion of the area comprised by each size class of boulders.

Analysis

We used single-season single-species occupancy models to estimate detection probability (p) and occupancy (ψ) (MacKenzie et al. 2002) and used the "unmarked" package in program R version 3.2.2 to build models and generate estimates (Fiske and Chandler 2011, R Core Team 2015).

Survey variables. Before beginning a survey, observers visually estimated cloud cover (%), the occurrence and type of precipitation, how much of the site was visible from their vantage point (%), and time of day (morning [600-1100], midday [1101-1600], and evening [1601-2100]). Temperature (°C) and wind speed (m/s) was recorded with a Kestrel weather meter (models 2000 and 3000, Nielsen-Kellerman, Boothwyn, Pennsylvania, USA). We predicted that these survey-specific factors and the survey method (visual survey or walkthrough) might influence the probability of detecting a marmot (Table 2.3). Precipitation during the survey was converted to a binary variable (rain/no rain) because rain occurred during only 19 of 810 surveys. We calculated the amount of area actually surveyed during each visual survey by multiplying the area of each site by the proportion of the site visible for each observer during each visit, and used this as our measure of patch size.

Site characteristics. We considered four groups of covariates that we predicted would influence habitat for marmots: land cover, water, boulder size, and topography (Table 2.2). We converted tree cover into four categories (0, >0 to ≤ 0.1, >0.1 to ≤ 0.2, and >0.2); few sites had tree cover values >0.1. We converted shrub cover to a binary variable (present/absent) because there were few non-zero values over the range of proportions observed (0 – 0.6). We excluded the "other" land cover category because we observed few non-zero values. We also excluded snow cover as a site characteristic because values changed throughout the season, violating one of the assumptions of occupancy modeling (MacKenzie 2006); snow cover was included as a survey-specific variable for modeling detection probability. Water covariates included annual average precipitation and distance to and type of nearest water source. We broadly categorized water sources into standing, moving, and wetland. Boulder size covariates included proportions of the four size categories. There were few non-zero values for large boulders and slab rock, so we converted data from continuous to binary (Appendix A: Figure S1). Topography covariates included slope, aspect, and elevation. We categorized aspect into a binary variable (north: 271 – 90˚ or south: 91 - 270˚) to balance the large number of sites with eastern aspects; we sampled relatively few western aspects due to access and terrain ruggedness. We created frequency histograms for all covariates to examine distributions and differences among the five mountain ranges (Appendix A). Initially, we were interested in explicitly modeling differences among mountain ranges, but we did not have a sufficient number of sites within each range. Instead, we categorized mountain ranges by their respective study area: the Lewis and Whitefish Ranges as northern latitude, the Mission and Swan Ranges as middle latitude, and the Anaconda-Pintler Range as southern latitude, and included each study area in our inferential model.

Detection probability. Detection probability is defined as the probability of detecting at least one individual during a particular sampling occasion, given that individuals of the species are present in the area (MacKenzie et al. 2002). Initially, we estimated a null model of detection probability to present this definition of detection probability, but we also considered 10 variables to estimate detection probability at survey sites (Table 2.3, MacKenzie 2006). We examined pairwise plots to assess correlation among variables for detection; covariates were not highly correlated ($|r| < 0.65$). We created a general model that included all detection variables, as well as two higher-order terms. Marmots are active at different times of day as summer progresses (Barash 1973), therefore we hypothesized that they may be out of their burrows and most active over an intermediate range of temperatures and considered a quadratic term for temperature. We also considered an interaction between cloud cover and temperature, as we expected that the relationship between marmot activity and temperature may depend on cloud cover. We assessed evidence for covariates with likelihood ratio tests and rejected a more parameterized model if it was unlikely to better explain variation in detection probability ($P > 0.1$ from a likelihood-ratio test), removing higher-order terms first, followed by individual covariates. This reduced model served as our baseline to account for imperfect detection.

Occupancy. We examined pairwise plots to assess correlation among variables for occupancy; covariates were not highly correlated ($|r| < 0.65$). We created a general model for occupancy that included all site-specific variables, as well as several higher-order terms. We predicted that marmots might prefer an intermediate proportion of rock cover because they live in boulder fields, but forage in adjacent areas, and therefore considered a quadratic term for rock cover. Harrower (2001) found that hoary marmots preferred slopes less than 40˚, so we also investigated evidence for a threshold with a quadratic term for slope. Elevation of tree line and the range of precipitation values differed among the mountain ranges we sampled (Appendix A: Figure S2, Figure S3), so we considered interactions between elevation and the three major study areas (northern, middle and southern) and between precipitation and study areas. We also included year as an explanatory variable to understand differences in occupancy between sampling years. We began with our reduced model for detection probability, then assessed evidence for the occupancy covariates by examining χ^2 statistics from likelihood-ratio tests and rejected a more parameterized model if it was unlikely to better explain variation in occupancy ($P >$ 0.1). We removed higher order terms first, followed by individual covariates to reach a reduced inferential model of occupancy for hoary marmots. In the text and figures, we present estimated slopes and effect sizes for each covariate that explained sufficient variation in detection probability and occupancy.

Results

We completed 822 surveys (visual and walkthrough surveys) of 194 sites during the 2014 and 2015 sampling seasons (average = 4.25 surveys/site). At least one observer detected evidence of marmots in 63 of 194 sites (naïve occupancy = 0.32). Before accounting for covariates, we estimated detection probability for all sites as 0.25 (95% CI = 0.18 - 0.34). After accounting for detection probability, the proportion of occupied sites was 0.44 (95% CI = 0.33 - 0.56).

Detection probability

Cloud cover (%), proportion of medium boulders, and survey method explained the most variation in detection probability (Table 2.4). Small boulders, large boulders, slab rock, precipitation, snow cover, survey area, site visibility, temperature, time of survey, wind speed, and higher-order relationships did not explain sufficient variation (Table 2.4).

Cloud cover. Detection probability during visual surveys increased with cloud cover (Figure 2.2a). As cloud cover increased from 0 to 50%, detection probability increased from 0.14 (95% CI = 0.08 - 0.23) to 0.26 (0.20 - 0.33). Under complete cloud cover, detection probability increased to 0.43 (0.31 - 0.56).

Boulder size. We found some evidence that detection probability was influenced by the proportion of medium-sized boulders in a site (Figure 2.2b). During visual surveys, detection probability decreased from 0.26 (95% CI = 0.19 - 0.36) to 0.08 (0.03 - 0.19) as the proportion of medium boulders in a site increased from 0% to 50%. During walkthrough surveys, detection probability decreased from 0.95 (95% CI = 0.63 - 0.99) to 0.81 (0.35 - 0.97) over the same range of medium boulders.

Survey method. Detection probability depended on survey method and was significantly higher during walkthrough surveys. Detection probability during visual surveys was 0.22 (95% CI = 0.16 - 0.29), compared to 0.94 (0.59 - 0.99) for walkthrough surveys.

Occupancy

Slope, north/south aspect, and presence of shrub cover explained the most variation in occupancy of hoary marmots (Table 2.5). Land cover covariates (except presence of shrubs), water covariates, boulder size covariates, elevation, study area, and higher-order relationships did not explain sufficient variation (Table 2.5).

Slope. Occupancy by marmots decreased precipitously as average slope increased (Figure 2.3a). As average slope increased from 5° to 15˚, probability of occupancy decreased from 0.75 (95% CI = 0.45 - 0.92) to 0.54 (0.35 - 0.72).

Aspect. Marmot occupancy was higher on southern aspects compared to northern aspects, although uncertainty around these estimates made the distinction less clear (Figure 2.3b). Occupancy was 0.34 (95% CI = 0.23 - 0.46) for southern aspects and 0.21 (0.12 - 0.33) for northern aspects.

Shrub cover. Occupancy by marmots was higher in sites with shrubs compared to sites without (Figure 2.3c). For sites with a northern aspect, occupancy increased from 0.20 (95% CI = 0.12 - 0.33) in sites without shrubs to 0.43 (95% CI = 0.28 - 0.60) in sites where shrubs were present.

Discussion

The habitat characteristics we found to be important help define environmental and physiographic conditions that marmots seek out. We suggest that the preference for shallow slopes and southern aspects we detected represents a compromise between different habitat requirements during each season. Shallow slopes typically accumulate deeper snow in winter and hoary marmots may select these areas because they provide the most insulating snowpack. Deeper snowpack provides better thermal insulation and may increase overwinter survival (Patil et al. 2013). However, deeper snowpack may reduce reproduction and litter sizes for marmots because they also require areas that provide early-season forage (Armitage et al. 1976, Van Vuren and Armitage 1991, Patil et al. 2013, Tafani et al. 2013, Rézouki et al. 2016). We suggest that the preference for southern aspects allows for more snow-free areas in spring. This preference has been observed in Vancouver marmots (*Marmota vancouverensis*, Bryant and Janz 1996) and Olympic marmots (Griffin et al. 2010), and is commonly explained by the longer growing season that southern aspects provide (Barash 1973).

Initially, we predicted that the presence or absence of shrubs would be unlikely to influence the hoary marmot's distribution. However, the presence of shrub cover was an important characteristic for explaining occurrence of marmots; this finding has several explanations. Marmots are generalist herbivores that consume a broad diet of alpine herbaceous plants (Holmes 1984, Frase and Armitage 1989, Karels et al. 2004). In Montana, hoary marmots have been associated with alpine dwarf shrubland and they will forage in areas with shrubs (Holmes 1984, Maxell and Ritter 2013). Marmots may use shrubs as cover from predators while foraging, which has been observed in another colonial squirrel, the Arctic ground squirrel (Wheeler et al. 2015). Hoary marmots foraged in areas of mixed shrubs and meadows in North Cascades National Park, Washington (Christophersen 2012) and field personnel observed hoary marmots foraging in and around shrubs during our study.

The preference of areas with shrub cover could also relate to unmeasured conditions that shrubs can create in winter. Shrubs have been associated with creating deeper snow in adjacent areas by depositing windblown snow that provides more insulation, but also melts earlier in the spring and summer (Sturm et al. 2001). An interaction between shrub cover and snow depth may provide more winter insulation for hibernating hoary marmots as well as early season forage upon emergence from hibernation.

We expected that summer environmental conditions would be important to understand where marmots occur on the landscape. Land cover, boulder size, and water characteristics are important for hoary marmots, yet they do not seem to be the limiting factors for marmots because we did not detect differences for these characteristics in occupied and unoccupied areas. Hoary marmot survival is influenced by winter intensity rather than summer food availability (Patil et al. 2013), which may indicate that many areas supply the resources necessary for survival in the summer but not necessarily in winter. Given that land cover, boulder size, and water characteristics did not explain sufficient variation in occupancy, we further suggest that winter conditions have a greater influence on habitat selection. Decreases in overwinter survival of hoary marmots (Patil et al. 2013), litter size (Tafani et al. 2013) and juvenile survival (Rézouki et al. 2016) of alpine marmots (*Marmota marmota*), and reproduction and litter size of yellow-bellied marmots (Van Vuren and Armitage 1991) have been linked with winter conditions and provide evidence that winter severity influences where marmots can survive and reproduce on the landscape. Areas that provide the winter conditions hoary marmots require may become more limited, especially at the southern extent of their distribution. Increases in temperature in Montana (Pederson et al. 2009) have resulted in reductions in annual snowpack of 2.5 - 10 cm over the last 100 years (Mote 2006). Snowpack is projected to continue to decline over the next 100 years until many of Montana's mountain ranges will be in the transient snow zone, where snow will accumulate and melt instead of accumulating throughout winter (Mote 2006), effectively eliminating the thermal insulation hoary marmots require to survive.

We suggest further investigating specific abiotic factors, such as snow depth and boulder size, that could inform habitat selection and be useful in predicting potential shifts in distribution. We found that slope and aspect, which influence snow depth, may be important to understanding where marmots are distributed on the landscape. Given the demographic sensitivity of marmots to snow depth at the northern extent of their range (Patil et al. 2013), understanding the relationship between where marmots occur on the landscape and snowpack at the southern extent of their distribution would provide a deeper understanding of habitat selection and inform predictions about their future distribution given the impacts of climate change. Hoary marmots occur at the maximum elevation within each mountain range in western Montana; if winter snowpack persists only at higher elevations as climate changes, the connectivity of populations within and among mountain ranges could be seriously impacted (Armitage 2013). We suggest that a comprehensive GIS layer of factors that influence snow depth could improve our understanding about the influence of snowpack. Given that much of marmot life history centers around boulder fields (Barash 1974), examining detailed features of boulder fields more closely also could provide important information. Although we did not detect any influence of boulder size on occupancy, we measured surface area of boulders from aerial imagery and a different method may be required to characterize features important for marmots. For example, using LIDAR to create three-dimensional measures of boulder size (Froidevaux et al. 2016) could more accurately reflect how marmots perceive boulders, compared to our two-dimensional measurements. Further, recording detailed measurements specifically for the individual boulders that marmots use as burrows and lookouts may provide additional insights.

Identifying environmental conditions that limit the distribution and abundance of alpine species will be paramount to maintaining populations on the landscape, yet these conditions may differ seasonally. Much of the past and current research focused on alpine species occurs during summer when study areas and species are accessible and available for sampling, but winter conditions may be far more limiting to their distribution than summer conditions. Although slightly warmer conditions are predicted for Montana during winter (Pederson et al. 2009), this warming could melt the insulating layer of snowpack required by many species that live in alpine areas year-round (Van Vuren and Armitage 1991, Morrison and Hik 2007, Brodie and Post 2010). Effectively conserving, monitoring, and managing alpine obligates under an uncertain climate future will require a closer look at how winter conditions drive habitat selection and distributions on the landscape.

Tables

Table 2.1. Characteristics of the sites included in the study by mountain range: range of average annual precipitation based on the 30-year normal (1981-2010, PRISM Climate Group), range of elevations, and study area.

Mountain Range	Average annual precipitation (range, cm)	Elevation (range, m)	Study Area
Whitefish Range	127 - 177	1500 - 2465	North
Lewis Range (Glacier National Park)	203 - 254	1500 - 3184	North
Mission Range	177 - 203	1500 - 2993	Middle
Swan Range	177 - 203	1500 - 2952	Middle
Anaconda-Pintler Range	100 - 150	1540 - 3290	South

Table 2.2. Site-specific characteristics considered to explain variation in occupancy (ψ) of hoary marmots, northwestern Montana, summers 2014 and 2015.

Variable	Description
Land cover	
Rock	Proportion of rock cover
Grass	Proportion of grass cover
Trees	Proportion of tree cover converted to 4 categories (0, >0 to ≤ 0.1, >0.1 to ≤ 0.2, and >0.2)
Shrubs	Proportion of shrub cover converted to presence/absence
Water	
Precipitation	Annual average precipitation (1981 - 2010)
Distance to water	Linear distance to nearest water source
Closest water source	Standing, moving, and wetland
Boulder size	
Slab rock/other	Proportion of slab rock
Small boulders	Surface area ≤ 4 m^2
Medium boulders	Presence/absence of boulders with surface area 5 - 15 m^2
Large boulders	Presence/absence of boulders with surface area ≥ 16 m^2
Topography	
Slope	Average, degrees
Aspect	Cardinal directions converted to North or South aspect
Elevation	Meters
Study area	North (Whitefish and Lewis), Middle (Mission and Swan), South (Anaconda-Pintler)
Year	2014 or 2015

Table 2.3. Survey-specific characteristics considered to explain variation in detection probability of hoary marmots, northwestern Montana, summers 2014 and 2015.

Variable	Description
Temperature	Measured with Kestrel 2000 or 3000 (C˚)
Wind speed	Measured with Kestrel 2000 or 3000 (m/s)
Cloud cover	Overhead cloud cover, measured in 5% increments
Site visible	Percent visible by observers for each survey
Time	Morning, mid-day, and evening
Snow cover	Presence or absence
Precipitation	Overhead precipitation (Yes/No)
Survey area	Area of site multiplied by proportion of the site visible during surveys
Survey method	Visual or walkthrough
Boulder size	Small, medium, large, slab rock

Table 2.4. Likelihood-ratio tests comparing a global model for detection probability to a model without the specified variable.

Variable	χ^2†	P
Cloud cover * Temperature	1.501	0.220
Temperature^2	1.035	0.309
Snow (p/a)	0.004	0.950
Slab rock (p/a)	0.033	0.856
Survey area	0.184	0.668
Small boulders	0.238	0.626
Large boulders (p/a)	0.433	0.510
Precipitation (p/a)	1.583	0.208
Temperature	2.272	0.132
Time of day	3.668	0.160
Visibility	2.203	0.138
Wind speed	2.430	0.119
Cloud cover	12.199	<0.001
Survey method	38.179	<0.001
Medium boulders	4.663	0.030

† Likelihood ratio tests were all on 1 degree of freedom except for time of day (*df* = 2).

Table 2.5. Likelihood-ratio test comparing global occupancy model to a model without the specified variable.

Variable	χ^2	df	P
Rock^2	4.634	3	0.201
Tree cover	0.377	3	0.945
Closest water source	1.201	2	0.549
Elevation	0.197	1	0.657
Precipitation	0.003	1	0.956
Grass cover	0.038	1	0.845
Year	0.098	1	0.754
Rock cover	0.042	1	0.837
Medium boulders	0.811	1	0.368
Large boulders (p/a)	1.033	1	0.309
Distance to water	1.178	1	0.278
Small boulders	1.063	1	0.303
Slope^2	0.635	1	0.426
Study area	1.961	2	0.375
Slab rock (p/a)	2.053	1	0.152
Slope	11.537	1	<0.001
Aspect (N/S)	3.404	1	0.065
Shrub cover (p/a)	10.092	1	0.001

Figures

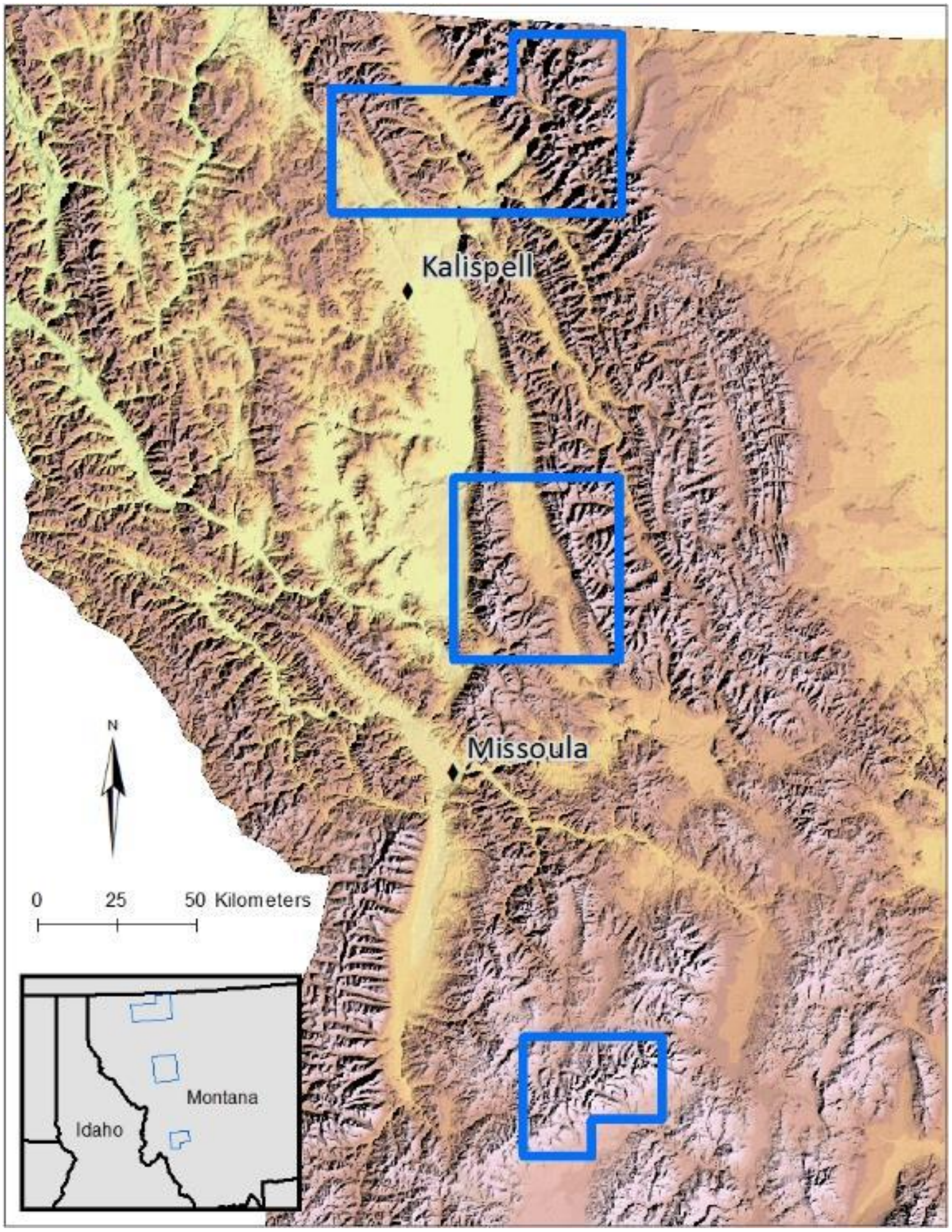

Figure 2.1. The three study areas (outlined in blue) over a latitudinal gradient, including the northern study area encompassing the Whitefish and Lewis Ranges, the middle study area comprised of the Mission and Swan Ranges, and the southern study area of the Anaconda-Pintler Range, northwestern Montana, summers 2014 and 2015.

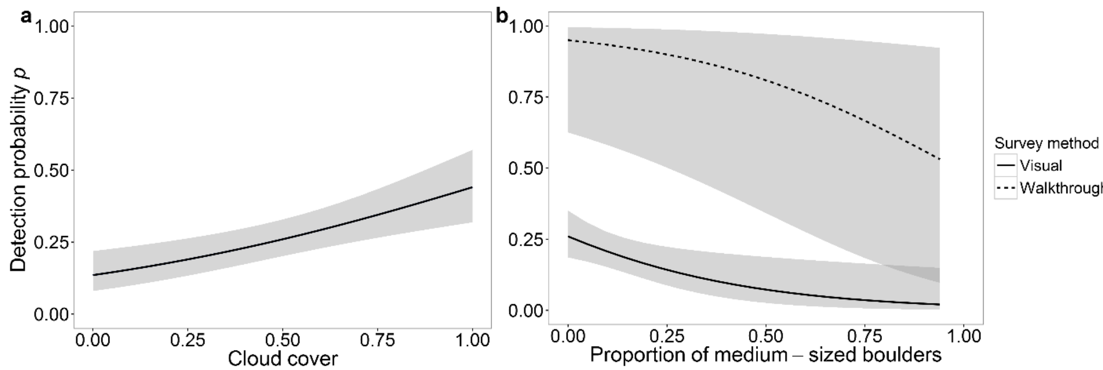

Figure 2.2. Changes in detection probability (and 95% CI) for hoary marmots during occupancy surveys, northwestern Montana, summers 2014 and 2015. (a) Detection probability during visual surveys over the observed range of overhead cloud cover. (b) Detection probabilities by survey method over the observed range of medium-sized boulders.

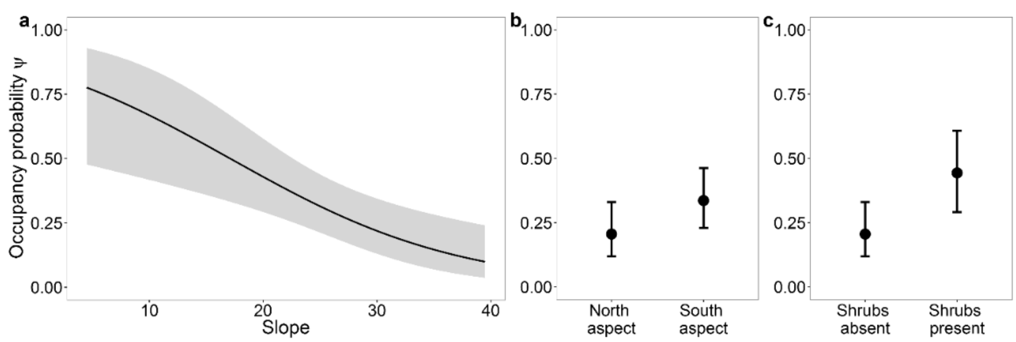

Figure 2.3. Changes in occupancy (and 95% CI) of hoary marmots with (a) slope, (b) aspect categorized as North or South, and (c) presence or absence of shrub cover, northwestern Montana, summers 2014 and 2015.

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CHAPTER THREE

MONITORING HOARY MARMOTS AT THEIR SOUTHERN EXTENT: ASSESSING DESIGN TRADEOFFS USING OCCUPANCY

Contributions of Authors and Co-Authors

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Monitoring Hoary Marmots at their Southern Extent: Assessing Design Tradeoffs Using Occupancy

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ABSTRACT Monitoring provides the necessary information for managers to make informed decisions related to the status of populations. Collecting sufficient data to reliably detect trends in abundance often is costly in time and resources. Indices of abundance are attractive because they can provide information about population trend at lower costs and effort, especially for species that are difficult to observe. We used occupancy methods to create a predictive map of hoary marmot habitat throughout their mountainous distribution in western Montana, USA. We used this predictive map and a spatially-explicit power analysis to evaluate multiple sampling designs for monitoring. We chose 2 mountain ranges in western Montana to illustrate our approach: one mountain range that is potentially isolated from other marmot habitat and another that is connected to several other mountain ranges that harbor marmot populations. We varied the number of sites, number of visits, size of sites, and sampling interval, and assessed the ability of each design to adequately detect a medium (25%) and large (50%) decline in colony abundance over 30 years. We also evaluated the effects of different estimates of colony abundance based on our estimate of occupancy. We found that detecting a 25% decline in colony abundance was either impossible with our sampling designs or often required a near census of sites within each mountain range. We were able to detect a 50% decline in colony abundance with several sampling designs. We found that sampling 7 - 87% of sites within a mountain range ≥3 times was effective for detecting the larger decline. Doubling the number of visits from 3 to 6 often cut the number of sites that had to be surveyed in half. Sampling every 3 years instead of 6 required sampling an average of 15% fewer sites. We were less likely to detect a trend when initial colony abundance was low, suggesting that initiating a monitoring program while hoary marmots still are relatively abundant will be preferable to waiting until numbers decline. Results of our power analysis provide a suite of options for Montana Fish, Wildlife and Parks to consider should they choose to implement a monitoring program for hoary marmots and other alpine species. Hoary marmots likely will be negatively impacted by climate change, especially in isolated mountain ranges at the southern extent of their distribution,

but assessing the extent of these changes will be impossible without sufficient monitoring data.

INTRODUCTION

Monitoring animal populations is paramount for effective management, but collecting reliable monitoring data can be expensive and time-consuming. Target-based objectives are required to design effective monitoring plans and trade-offs must be considered to provide the best information for the resources available (Pollock et al. 2002, MacKenzie and Royle 2005). Occupancy surveys quantify presence-absence and can be used for monitoring at lower cost and effort compared to methods of abundance estimation (Bailey et al. 2004, MacKenzie and Nichols 2004, Witczuk et al. 2008, Gaillard et al. 2010, Schooley et al. 2012, Fuller et al. 2016). Occupancy modeling is a powerful tool to learn about animal populations for species that are hard to detect, found in low abundances, and distributed over a large area (MacKenzie et al. 2003, 2006, Erb et al. 2015, Fuller et al. 2016). Recently, researchers have used occupancy as an index to track population density of bobcat (*Lynx rufus*, Clare et al. 2015), eastern box turtles (*Terrapene carolina carolina*, Erb et al. 2015), and moose (*Alces alces*, Nielsen et al. 2005). Occupancy also has become a commonly-used state variable to characterize habitat associations, species distributions, and the effects of management actions or changes in environmental conditions (Bailey et al. 2007).

Estimating occupancy requires collecting presence-absence information during repeated surveys to account for detection probabilities less than 1 (MacKenzie et al. 2002). When using occupancy for monitoring applications, the main trade-off typically is between the number of sites and the number of visits to those sites (MacKenzie and

Royle 2005, Bailey et al. 2007). Occupancy is a flexible state variable, which has led to the development of numerous methods that provide a framework for informing decisions about where and how effort should be allocated (MacKenzie and Royle 2005, MacKenzie 2006, Bailey et al. 2007, Ellis et al. 2014).

Alpine species are particularly challenging to monitor because extreme conditions in winter preclude ground survey efforts, leaving only a short time to collect data when areas become snow-free during summer. Additionally, the remote nature of mountainous areas often involves a high investment of time and effort to conduct surveys. Despite these challenges, temperature increases in North America over the last 100 years (Lugina et al. 2006) and resulting latitudinal and elevational shifts in the distribution of species (Chen et al. 2011) are strong reasons for managers to monitor alpine populations if they want to maintain the full suite of species in these systems.

One of these alpine obligates is the hoary marmot (*Marmota caligata*). Found in western North America above the 45th parallel (Foresman 2012), the range of the species spans from coastal Alaska and Canada to the North Cascades in Washington and the Rocky Mountains of Montana (Braun et al. 2011). Hoary marmots are patchily distributed in rock fields throughout mountain ranges and these patches vary in their degree of connection (Barash 1974). They are true hibernators that rely on snowpack for insulation from harsh winter temperatures (Patil et al. 2013). At the southern edge of their distribution they, like many species, may be particularly susceptible to increases in temperature that could shift their distribution (Cahill et al. 2014). Hoary marmots likely will be negatively impacted by climate change (Armitage 2013), but the extent of these changes are unknown without data on population trends.

Montana Natural Heritage Program (MTNHP) hosts a database of opportunistic observations of hoary marmots, which has been used to inform locations of recent inventory surveys. These efforts were initiated to characterize the overall distribution of the species, inventory and assess persistence of marmot colonies (Hammond 2010), and develop a MaxEnt model of commonly-used land cover types (Maxell and Ritter 2013). Although these inventory data were a crucial first step for monitoring, survey methods did not account for the possibility that marmots were present but went undetected. We sought to build on previous efforts by collecting data on marmot detections and landscape characteristics to make spatial predictions of the probability of occupancy across western Montana (MacKenzie 2006). We also considered variables at several spatial scales to improve predictions (Clare et al. 2015). We then used the predictive map to identify potential survey locations and evaluate trade-offs in designing a monitoring program.

To assess whether changes in abundance could be detected through observed changes in occupancy, we employed a method of power analysis that is spatially explicit (Ellis et al. 2014). This method has informed monitoring for wolverine (Ellis et al. 2014) and management for fisher populations (Fuller et al. 2016), but has not been applied beyond territorial carnivores. We developed a monitoring framework that can be applied over the entire distribution of hoary marmots in Montana; we assessed the effort needed to detect population trend by mountain range, which we assumed represents distinct populations. We chose to assess the necessary monitoring effort at this level because population-level responses to climate change may differ based on elevation and habitat connectivity (Gibson-Reinemer and Rahel 2015). For example, several species of small mammals in Yosemite National Park exhibited a variety of responses to similar warming trends (Moritz et al. 2008, Gibson-Reinemer and Rahel 2015). Hoary marmot populations also may respond differently to temperature increases and we believed that having the tools to detect a variety of responses might be useful for informing management action. We chose the Mission and Swan Mountains in western Montana to illustrate our approach because these ranges differ in the degree of isolation from other marmot habitat and populations. The Swan Mountains are connected to the Bob Marshall Wilderness, the largest wilderness complex in the continental United States, which provides connected alpine areas all the way into the Canadian Rockies. In contrast, the Mission Mountains are a potentially isolated mountain range, despite being relatively close to the Swan Mountains (~28 km apart, Figure 3.1). We compared the relative effectiveness of different monitoring designs for detecting population-level trends by simulating the relationship between occupancy and abundance (Ellis et al. 2015). We used the results to provide a suite of options for Montana Fish, Wildlife and Parks (FWP), the state management agency, to monitor population trends of hoary marmots across western Montana and assess responses to climate change.

STUDY AREA

We conducted occupancy surveys in five major mountain ranges throughout the distribution of hoary marmots in Montana: the Whitefish and Lewis Ranges in the north, the Swan and Mission Ranges in the middle, and the Anaconda-Pintler Range in the south; each range was generally oriented in a north-south direction (see Chapter 2 for detailed descriptions, Figure 2.1). We used these survey data to make predictions about occupancy over the entire distribution of hoary marmots in western Montana.

METHODS

Surveys

We conducted occupancy surveys throughout the five mountain ranges between June and September 2014 and 2015. We used 2 survey methods: 1) visual surveys with 10x binoculars to observe marmots within sites and 2) subsequent walkthrough surveys within a site to observe marmot sign (see Chapter 2 for details about site selection and survey methods). We conducted 822 surveys at 194 sites and detected marmots at 63 sites.

Spatial Scale

We measured predictive variables for occupancy (ψ) at 4 spatial scales to account for habitat selection processes occurring at different scales (Johnson 1980) and improve predictions of habitat selection, compared to evaluating a single scale (Holland et al. 2004, Urban and Swihart 2009). We created raster layers of predictive variables at each spatial scale using a neighborhood analysis of 30-m resolution raster layers (similar to Laforge et al. 2015). We used a minimum resolution of 150×150 m for all variables, which matches the average size of sites from our surveys in 2014 and 2015 (Chapter 2). We selected larger spatial scales based on the published range of colony sizes of hoary marmots (Braun et al. 2011). Our 4 spatial extents were 150×150 m, 240×240 m, 330×330 m, and 450×450 m, the larger extents coincided with the second and third order habitat selection criteria of Johnson (1980).

Model Variables

Previous inventory work in the state suggested that detection probability (p) for hoary marmots may be lower than that found for the Olympic marmot (*Marmota olympus*, 0.92, Witczuk et al. 2008). We measured several variables we thought would affect our ability to detect marmots including: wind speed, temperature, time of survey, overhead cloud cover, site visibility (%), survey method, and precipitation (all measured in the field during surveys, Table 2.3, see details in Chapter 2). We also estimated the proportion of 4 boulder size classes in each site using Geographic Information Systems (GIS) (Table 2.3, see details in Chapter 2).

We considered covariates related to land cover, terrain roughness, temperature, and elevation that were useful for explaining occupancy of other species of marmots and alpine obligates, and a few novel variables (Table 3.1). We quantified the proportion of 4 categories of land cover: rock, grass, shrubs, and trees, within each site based on the Montana Land Cover Framework 2013 provided by the MTNHP (2013). To quantify terrain roughness, we calculated curvature, an index of surface concavity or convexity (Evans et al. 2014a), as well as the standard deviation of slope (DeVoe et al. 2015). We considered 3 metrics of temperature – solar radiation, aspect, and heat load index. We quantified solar radiation calculated on May 21, 2015 using GIS; Griffin et al. (2010) found solar radiation values for May 21 were useful to predict occupancy of Olympic marmots in Olympic National Park, USA. We transformed aspect from degrees to radians and scaled these values between -1 and 1. This provided a different metric of temperature where -1 represented the coolest NE aspects and 1 represented the warmest SW aspects (McCune and Keon 2002). This transformation of aspect can differentiate between the temperature of a NE aspect and a SW aspect that receive the same amount of solar radiation (McCune and Keon 2002). Finally, we considered heat load index (Evans et al. 2014b), where we again transformed aspect to radians, but did not scale the values. This heat load index also incorporates steepness of slope for temperature calculations, which we found to be an important habitat characteristic (Chapter 2).

Spatial Predictions of Occupancy

We used single-season, single-species occupancy models to create spatial predictions of marmot occurrence (MacKenzie et al. 2002). First, we used a model selection approach to select covariates that best explained the observed variation in detection probability, using a null (constant) model for occupancy. Next, we used the top model for detection probability to assess covariates that best explained variation in occupancy. We developed detection and occupancy models based on all possible combinations of variables, but avoided including highly-correlated variables ($|r| > 0.6$) in the same model. We also restricted the maximum number of variables in a model to 12 to limit model complexity and because some models failed to converge with a greater number of variables. We centered and scaled all predictive variables for occupancy to improve model convergence. We investigated evidence for thresholds by including quadratic terms for all occupancy covariates.

We compared models within each spatial scale using AICc, then selected the subset of models from each spatial scale where ΔAICc ≤ 4. We then combined these subsets to create a reduced model suite, so we could compare which covariates and spatial scale best predicted marmot occupancy. We did not attempt to model average within our reduced model suite because of uncertainty associated with making spatial predictions based on models that differ in the variables included (Clare et al. 2015).

We created a continuous raster layer of predicted occupancy based on the coefficients from our top model. We limited our predictions to areas within 500 m from boulder fields and rock outcrops that were ≥1800 m of elevation, as this focused our predictions near areas where marmot colonies would occur and represented most areas above treeline. We assumed that marmots would be unlikely to occupy a small, isolated area, so we also excluded patches that were <1 km in diameter and separated from other habitat patches by ≥20 km, given that the longest recorded dispersal for a marmot species is 15.5 km (Van Vuren 1990). Based on these constraints, we created a predictive map showing the probability of marmot occupancy for 6,797 km^2 of western Montana.

Model validation.- We used two criteria to assess the predictive ability of our top model: area under the curve (AUC) and independent, presence-only observations compiled by the MTNHP. We assessed the discrimination performance of our top model by calculating AUC of the relative operating characteristic (ROC, Metz 1978) and used the Mann-Whitney technique as suggested by Pearce and Ferrier (2000). This method provides a metric of the discrimination ability of each model to accurately predict where marmots will be present. This metric ranges from 0.5 to 1, where 0.5 - 0.7 is not very different from random chance, 0.7 - 0.9 indicates a good or useful discrimination ability, and >0.9 indicates excellent discrimination (Swets 1988, Boyce et al. 2002).

We then evaluated the ability of our predictive model to accurately classify presence locations in the MTNHP database. These observations have been collected by biologists and the general public and vetted by MTNHP staff to discern false presences. We eliminated any MTNHP observations that had spatial precision >1 km as being too inaccurate. Glacier National Park had ~4 times more observations than other areas of the state because of the large number of observations around the extremely popular boardwalk to the Hidden Lake overlook that begins at the Logan Pass parking area. To eliminate this potential bias, we randomly selected 25% of the locations at Logan Pass and restricted selected locations to be >200 m apart because of the higher density of points along the boardwalk. We used the remaining MTNHP locations to determine the occupancy value that would predict 80% of these locations, similar to Griffin et al. (2010). We extracted the highest value of predicted occupancy within 100 m of each MTNHP location to account for the variability in spatial precision (0 - 1000 m). We calculated the bottom 20% quantile of extracted occupancy values to establish our 80% prediction threshold. The maximum occupancy value of that 20% became the cutoff between low and acceptable values. We considered areas with values below this cutoff to have a low probability of occupancy, whereas we classified areas with values above this cutoff as having an acceptable probability of occupancy. We used the classification of occupancy values into low and acceptable categories as a metric of predictive performance for our top model and to establish estimates of colony abundance in our power analysis.

Spatially-Explicit Power Analysis

We used the rSPACE package (Ellis et al. 2015) in R version 3.2.2 (R Core Team 2015) to conduct a spatially-explicit power analysis to assess whether we could detect changes in abundance of hoary marmot colonies using occupancy (Ellis et al. 2014). We used colonies as our population unit instead of individuals because hoary marmots rarely occur on the landscape as individuals and because colonies are the reproductive unit of marmot populations (Armitage 2014).

We needed an estimate of the number of colonies present within our monitoring area to restrict the starting estimate of colony abundance for our power analysis. For each mountain range, we assessed a range of initial colony abundances that we assumed would represent extreme values of true marmot colony abundance (N = 10 - 700). We placed these colonies throughout our predicted landscape in those grid cells that had acceptable occupancy values and then computed the proportion of the landscape that was occupied. We compared these landscape estimates of occupancy to the estimate based on our inferential model to gauge values of colony abundance that might be appropriate for our power analysis. We used the estimate and ends of the 95% confidence interval of occupancy from our inferential model to select lower, middle, and upper values for colony abundance that we used as our 3 initial estimates of colony abundance within mountain ranges for power analyses.

Within each mountain range, we used 12 scenarios to evaluate the effects of several characteristics on our ability to assess trend in colony abundance (Table 3.2). We varied the size of grid cells, estimates of colony abundance, and the size of the population trend (lambda, λ). We divided each mountain range into sampling units by overlaying a grid on the predicted area; sites were grid cells either 0.64 or 1 km^2 in size. We evaluated 3 initial estimates of colony abundance based on the computations above. We evaluated power to detect a 25% or 50% decrease in colony abundance over 30 years measured over 10 sampling occasions. We also evaluated implications of varying the number of visits (2, 3, 4, 5, or 6), the proportion of cells sampled each season (5 - 100% of predicted cells, in 3% increments), and the sampling interval (conducting surveys every 3 or 6 years). We assessed power to use occupancy to detect changes in colony abundance by computing the proportion of 100 runs that correctly identified the decrease in population (Ellis et al. 2014, Fuller et al. 2016). We present results for the Mission and Swan Mountains in the text.

RESULTS

Predictive Occupancy Model

We found that detection probability varied with cloud cover, medium-sized boulders, and survey method (top model, Table 3.3). We were better able to detect marmots as cloud cover increased and as the proportion of medium boulders decreased. Walkthrough surveys resulted in a substantially higher detection probability (mean p = 0.904, 95% CI = 0.454 - 0.991, *n* = 132 surveys) compared to visual surveys (0.213, 0.153 - 0.289, *n* =

690). We used the walkthrough detection probability for our power analysis due to the substantial increase in detection probability.

Our combined model suite for occupancy included 1,493 competing models. Model uncertainty likely was related to the large number of possible models and evaluating models with the same variables at different scales. However, the majority of models within 2 ΔAICc included variables at the 450×450 m spatial scale (Table 3.4). We chose to use the top model as our inferential model because it included similar variables as the other models within 1 ΔAICc. The top model included elevation, shrub cover, and the linear and quadratic terms for slope standard deviation. Predicted occupancy was 0.364, on average (95% CI = 0.224 - 0.517), based on our inferential model and predicted values ranged from 0.136 to 0.907 for all 194 sites.

Model validation.- The ROC value for our top model was 0.68, indicating an acceptable level of discrimination for predicting presence. We had 148 MTNHP locations across western Montana, but removed 16 because they did not overlap with the spatial extent of our predictive map. Eighty percent of the remaining 137 MTNHP locations were captured by cells with predicted values for occupancy $\geq$0.286, our minimum acceptable value where a marmot colony could be placed during our power analysis. Predicted occupancy ranged from 0.055 to 0.991 across our spatial map (Figure 3.2), resulting in 8,329 km^2 with acceptable occupancy values and 6,267 km^2 with low occupancy values. The Mission and Swan Mountains encompassed 1,965 km^2 of the total area (Figure 3.3), resulting in 702 km^2 with acceptable occupancy values and 1,263 km^2 with low occupancy values.

Spatially-Explicit Power Analysis

For the Swan Mountains, we used 60, 115, and 190 as the low, middle, and high estimates of colony abundance, respectively (Figure 3.4a). These were based on the mean and endpoints of the 95% CI for predicted occupancy from our inferential model (0.36, 0.22 - 0.51). In the Mission Mountains, our estimates of colony abundance were 20, 36, and 56 (Figure 3.4b).

Detecting population trend.- In the Mission Mountains, we found we could detect a 50% decline in colony abundance with adequate power (≥80% chance of detecting a trend) when the sampling design included ≥3 visits to each site during a season (Figure 3.5). The proportion of sites required to detect trend ranged from 25 - 92% (54 - 197 1-km^2 cells, 90 - 308 0.64-km^2 cells) of the total available sites (219 total 1-km^2 cells, 335 total 0.64-km^2 cells). We did not have adequate power to detect a 25% decline in the Mission Mountains for the majority of sampling designs (Figure 3.5). Reliably detecting a 25% decline required sampling 70 - 100% of sites (154 - 206 1-km^2 cells, 245 - 335 0.64-km^2 cells) ≥4 times per season. We had very little power (<35%) to detect trend when colony abundance was low (N = 20).

In the Swan Mountains, we could detect a 50% decline in colony abundance with adequate power when the sampling design included ≥2 visits to each site during a season (Figure 3.6). The proportion of sites required to detect trend ranged from 7 - 87% (63 - 569 1-km^2 cells, 76 - 869 0.64-km^2 cells) of the total available sites (655 total 1-km^2 cells, 1,041 total 0.64-km^2 cells). In contrast to the Missions, we were able to detect a 25% decline in colony abundance in the Swan Mountains for the majority of sampling designs

(Figure 3.6). Reliably detecting a 25% decline required sampling 37 - 100% of sites (243 - 694 1-km^2 cells, 380 - 1,041 0.64-km^2 cells) ≥4 times per season. Our ability to detect a 25% trend decreased with lower values of colony abundance.

In both mountain ranges, we could modify the sampling design in three ways to reduce the number of sites that had to be surveyed. First, sampling larger cells (i.e., 1 km^2 instead of 0.64 km^2) meant that the grid over the landscape inherently included fewer cells, thus requiring sampling fewer sites. However, there was little difference in the proportion of the landscape that had to be sampled when cell size increased from 0.64-km^2 to 1-km^2 cells. In the Missions, using 1-km^2 cells required surveying 7% less area, on average (range: -18 to 1%), but reduced the average number of sites that had to be sampled by 96 cells (34 - 146). In the Swans, using 1-km^2 cells led to an average 0.2% decrease in the area covered (range: -32 to 18%), but reduced the average number of sites that had to be sampled by 222 cells (3 - 516). Second, doubling the number of visits (e.g., 3 to 6) often reduced the number of sites that had to be surveyed by 50%. The number of visits had a strong influence on power and the necessary number of sites. Finally, sampling every 3 years instead of 6 years decreased the number of cells sampled by an average of 14% (94 1-km^2 cells, 137 0.64-km^2 cells) in the Swans and 17% (40 1-km^2 cells, 56 0.64-km^2 cells) in the Missions, holding all else constant.

DISCUSSION

Witczuk et al. (2008) detailed a process for collecting presence-absence data as an index of abundance for marmots. They concluded that, although occupancy is not as robust as direct abundance estimates for measuring population trend, it is an acceptable method for a range-wide assessment of marmot populations over time. We used spatially-explicit power analyses to explore a suite of options for monitoring hoary marmots throughout their distribution in Montana. If managers are willing to reduce their focal landscape to the level of individual mountain ranges, we found that data from occupancy surveys can detect trends in colony abundance reliably and with reasonable sampling effort. Although detecting a 25% decline in colony abundance within a mountain range typically requires extraordinary (and likely unrealistic) effort, detecting a 50% decline in colony abundance is more likely to be successful because less sampling effort is required.

Designing monitoring plans for long-term studies over large spatial scales require more than just collecting data. Three questions are key to developing effective monitoring plans: why, what, and how (Yoccoz et al. 2001). Clear objectives must be articulated to justify why the study is necessary and the desired goals (Pollock et al. 2002, MacKenzie et al. 2006, Bailey et al. 2007). What state variable will be used typically is dictated by the objectives and resources available. Finally, the answers to the first two questions inform how to collect the necessary data. Although we sought to track trends in abundance, we instead chose to use occupancy as our state variable based on the resources likely to be available. We evaluated multiple scenarios to determine how to effectively monitor over a large landscape, considering the strengths and weaknesses of different sampling designs. Our approach integrated management objectives and used relatively new methods to evaluate appropriate designs for long-term monitoring of an alpine obligate that is patchily distributed over a large landscape.

We were able to detect trends in colony abundance in the Swan and Mission Mountains by visiting sites at least 2 and 3 times within a season, respectively. Visiting sites 5 or 6 times within a season provided marginal increases in power, but reduced the number of sites to be surveyed nearly in half, demonstrating the typical tradeoff between visits and sites (MacKenzie et al. 2005). Visiting fewer sites reduces the spatial coverage of the monitoring plan, but also reduces the logistics required to access sites. Sampling fewer sites could provide two potential benefits: 1) surveyors will spend less time planning trips because they will become familiar with how to access sites and 2) they will spend less time locating sites in the field because they will visit the same locations at least 3 times during a season. In mountain ranges where points of access are limited, visiting fewer sites more frequently during the sampling season may be more prudent than spending the extra time needed to hike to more sites. We caution that sampling fewer sites does reduce the spatial coverage of the monitoring plan. This potential limitation may be required given that the total predicted area covered by our monitoring plan is at least 4 and 10 times larger than that of other monitoring projects for marmots (Griffin et al. 2010, Christophersen 2012).

We recommend surveying 1-km^2 cells within mountain ranges as the site size and the number of cells that need to be surveyed to detect a trend are reasonable. There was little difference in the proportion of sampled area between the 2 cell sizes, however the decreased number of 1-km^2 cells led to a substantially more efficient survey design. Sampling 1-km^2 cells not only reduced the number of sites, but also reduced the number of surveys. Given the average difference in the number of sites and 4 visits per site, using

1-km^2 grid cells would require 384 and 888 fewer surveys per sample interval in the Missions and Swans respectively.

We recommend using a 6-year sampling interval based on the slight increase in the number of cells required to detect trend. With a 3-year interval, we were able to detect a 25% and 50% trend with more study designs, but using a 6-year interval may be warranted based on the resources available. For either interval, we propose allocating some sampling effort each summer, completing surveys of all sites over the entire sampling interval. Sampling a proportion of the sites every summer over 3 or 6 years seems much more reasonable than sampling all sites in a single summer at either 3- or 6-year intervals.

We found that our estimate of detection probability ($p = 0.904$) was remarkably similar to Olympic marmots (0.920, Witczuk et al. 2008) when we used a very similar walkthrough survey method. We recommend using walkthrough surveys instead of visual surveys in the future because of the substantial increase in detection probability. Although visual surveys provided more actual observations of marmots, surveying for sign of marmots as an indicator of presence is still a robust method for quantifying occupancy (Noon et al. 2012).

Managers will need to select sites to apply our monitoring design. Selecting a simple random sample of cells with acceptable values of occupancy would be the most robust choice to make inferences about other marmot populations that were not sampled. However, Witczuk et al. (2008) found that this strategy maximized the effort required to reach survey sites and reduced the total number of sites that could be surveyed in a season. Instead, they outlined a cluster sampling design that accounts for the effort required to reach sample sites. We employed this design in our surveys in 2014 and 2015 and are confident that it can be applied to efficiently monitor hoary marmots in the future. Establishing the protocol for selecting sites where marmots might be present was one of our biggest initial challenges. Based on our experiences, we do not recommend selecting clusters of sites within each mountain range at random, but instead focusing on sites with historical observations. MacKenzie et al. (2006) cautioned against only choosing sites with historical observations because these sites could have a higher probability of occupancy than the larger landscape, leading to biased assessments of trend. However, they suggested minimizing this error by including a second sample of sites in the sampling frame where occupancy is unknown (MacKenzie et al. 2006). Therefore, we propose selecting sites with and without historical observations to increase efficiency of survey time and detect declines in colony abundance.

Based on a sampling scheme of visiting clusters of 1-km^2 sites ≥4 times over a 6-year sampling interval, collecting adequate data on occupancy at the level of the mountain range may require biologists to complete several multi-day trips each summer. In some mountain ranges, the time needed to adequately survey 17 - 53 sites per summer may be prohibitive. However, citizen scientists have proven to be quite effective for monitoring marmots (Witczuk et al. 2008, Christophersen 2012); combining these survey efforts with biologists' surveys could make completing sufficient sampling more reasonable.

We evaluated our approach using the Swan and Mission Mountains because these ranges occur at a similar latitude, but potentially represent different points along a spectrum of population connectivity that hoary marmots encounter in Montana. However, an assessment of habitat connectivity across mountain ranges, potentially based on genetic data, would be useful for prioritizing which marmot populations to monitor.

Although we were unable to explore the relationship between occupancy and actual colony abundance, we have shown that we can predict colony abundance on a large landscape based on informed population parameters and habitat associations. Combining actual abundance estimates with presence-absence data from occupancy would improve the overall effectiveness of monitoring (Noon et al. 2012). Resolving the relationship between occupancy and abundance of marmots also would require exploring the size of the grid cells used for sampling (MacKenzie and Nichols 2004). We used cell sizes that were slightly larger than published home ranges for marmot colonies elsewhere (Braun et al. 2011), but quantifying home range sizes specifically for marmots in Montana would be beneficial. Short of actual abundance data, observing reproduction within colonies could provide information about multiple occupancy states. Estimating the proportion of marmot colonies that are reproductively active would provide information about potential population growth, as has been done with northern spotted owls (i.e., by denoting the difference between reproductive and non-reproductive pairs, Franklin et al. 2004).

Hoary marmots are a species of greater inventory need and a potential species of concern in Montana (MTNHP 2013). But they represent only one such species and available monitoring effort in the state will be divided among numerous other species. The options we provide to detect population trends were a concerted effort to provide reliable information, while limiting effort required when working in remote areas. In addition, our survey method allows time for surveys of other alpine species to be conducted simultaneously and perhaps even in the same sites. Over several days in the backcountry, biologists could collect data for other alpine species of inventory need or concern that have similar habitat associations, such as American pika (*Ochotona princeps*), Black or Gray-crowned rosy finch (*Leucosticte atrata*, *L. tephrocotis*), White-tailed ptarmigan (*Lagopus leucura*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), grizzly and black bears (*Ursus arctos horribilis, U. americanus*), and wolverine (*Gulo gulo*) (Foresman 2012, MTNHP 2013). The approach we used to assess necessary sampling effort for hoary marmots also could be applied to improve monitoring strategies for some of these alpine species. Monitoring plans that can detect changes in population trend effectively will be imperative for successful management and conservation of alpine species in the face of an uncertain climate future.

MANAGEMENT IMPLICATIONS

Monitoring plans that balance budget constraints with the need for reliable data are extremely valuable for assessing responses to climate change. Focusing monitoring efforts on indicator species still represents the most cost-efficient way to measure the broader impacts of changes in environmental conditions (Noon et al. 2012) and populations at the edge of a species' distribution can act as indicators of future impacts

(Cahill et al. 2014, Sultaire et al. 2016). Populations of hoary marmot may be robust to climate change where they have large tracts of connected habitat, but this species likely is more vulnerable in isolated mountain ranges; without monitoring, assessing trends will be impossible. Although hoary marmots currently are relatively common, the extraordinary decline of the Vancouver Island marmot (Bryant and Page 2005) and observed declines in Olympic marmots (Griffin et al. 2008) further illustrate the importance of long-term monitoring efforts. Given that we were less likely to detect trends with smaller values for colony abundance, we recommend that a monitoring program be initiated now while hoary marmots are relatively common.

Tables

Table 3.1. Variables considered to predict occupancy of hoary marmots throughout their distribution in Montana, based on surveys in 2014 and 2015. We also explored the potential for threshold responses by including quadratic terms for all variables. Each variable was measured over 4 spatial scales (150×150, 240×240, 300×300, 450×450 m).

Variable	Description	Reference
Land cover		
Rock	Proportion of rock cover	
Grass	Proportion of grass cover	
Trees	Proportion of tree cover	
Shrubs	Proportion of shrub cover	
Temperature		
Aspect	Aspect scaled between -1 and 1	McCune and Keon 2002
Solar radiation	Calculated for May 21, 2015	Griffin et al. 2010
Heat load	Aspect by temperature, incorporating steepness of slope	Evans et al. 2014
Terrain		
Elevation	Elevation (m)	
Slope	Average slope	
Slope standard deviation	Standard deviation of slope	DeVoe et al. 2015
Curvature	Index of surface concavity or convexity	Evans et al. 2014

Table 3.2. Characteristics we varied to assess effects on power to detect a trend in colony abundance of hoary marmots based on occupancy surveys in western Montana. Characteristics with multiple values represent those used to create different study designs.

Characteristic	**Description**	**Values**
N	Initial population size based on available habitat	60, 115, 290 | 20, 36, 56[a]
Lambda	25% and 50% decline in colony abundance over 30 years	0.977, 0.933[b]
Grid cell size	Size of the cells (km^2) used for sampling	0.64, 1
Occupancy cutoff	Value above which grid cells were considered acceptable	0.283
Detection probability	Based on walkthrough surveys	0.904
Sampling interval	Timeframe when surveys of all sites must be completed	Every 3 or 6 years
Visits	Number of times each cell is surveyed during a season	2, 3, 4, 5, 6
Sampling effort	Proportion of cells visited during a single season	5-100%

[a] Values used for the Swan Mountains | Values used for the Mission Mountains

[b] Lambda values represent a decline of 2.3% and 6.7% every 3 years, respectively.

Table 3.3. Competing models (≤2 ΔAICc) for detection probability (p) of hoary marmots during 822 surveys in western Montana, summers 2014-2015. We used a null model for occupancy (ψ) and included wind speed, temperature, time of survey, overhead cloud cover, site visibility (%), survey method, and precipitation as potential covariates for detection probability. *K* = number of model parameters.

Model	***K***	**AICc**	**ΔAICc**	**AICc weight**	**LogLik**
ψ(.), p(cloud cover + medium boulder + survey type)	5	472.21	0.00	0.126	-231.10
ψ(.), p(cloud cover + medium boulder + survey type + wind)	6	472.23	0.03	0.124	-230.12
ψ(.), p(cloud cover + medium boulder + survey type + temp + wind)	7	472.51	0.31	0.108	-229.26
ψ(.), p(cloud cover + medium boulder + survey type + visibility + wind)	7	472.68	0.48	0.099	-229.34
ψ(.), p(cloud cover + medium boulder + survey type + temp)	6	472.79	0.58	0.094	-230.40
ψ(.), p(cloud cover + medium boulder + survey type + visibility)	6	473.11	0.90	0.080	-230.55
ψ(.), p(cloud cover + medium boulder + survey type + temp + visibility + wind)	8	473.14	0.93	0.079	-228.57
ψ(.), p(cloud cover + medium boulder + survey type + temp + visibility)	7	473.85	1.65	0.055	-229.93

Table 3.4. Competing models (≤2 ΔAICc) for occupancy (ψ) of hoary marmots based on surveys of 194 sites, western Montana, summers 2014-2015. We used the top model for detection probability (Table 3.3) and considered land cover, temperature, and terrain variables (Table 3.1) measured over 4 spatial scales (150×150, 240×240, 300×300, 450×450 m) to model variation in occupancy. Models without a superscript were measured at 450 m. *K* = number of model parameters.

Model	***K***	**AICc**	**ΔAICc**	**AICc weight**	**LogLik**
ψ(elev + shrub + slope sd + slope sd^2)	9	459.00	0.00	0.005	-220.01
ψ(shrub + slope sd)	7	459.03	0.03	0.005	-222.21
ψ(elev + rock + shrub + slope sd + slope sd^2)	10	459.06	0.06	0.005	-218.93
ψ(shrub + slope sd + slope sd^2)	8	459.21	0.21	0.005	-221.22
ψ(heat + shrub + slope sd + slope sd^2)	9	459.31	0.31	0.005	-220.16
ψ(heat + shrub + slope sd)	8	459.34	0.34	0.005	-221.28
ψ(elev + shrub + slope sd)	8	459.35	0.35	0.005	-221.28
ψ(elev + heat + shrub + slope + slope sd^2)	10	459.48	0.48	0.004	-219.14
ψ(elev + rock + rock2 + shrub + slope^2)	10	459.5	0.50	0.004	-219.15
ψ(elev + shrub + slope sd + slope sd^2 + tree)	10	459.51	0.51	0.004	-219.15
ψ(aspect + elev + shrub + slope + slope sd^2)	10	459.73	0.73	0.004	-219.26
ψ(elev + rock + rock^2 + shrub + slope sd + slope sd^2)	11	459.73	0.73	0.004	-218.14
ψ(curve + shrub + slope sd)	8	459.79	0.79	0.004	-221.50
ψ(aspect + shrub + slope sd + slope sd^2)	9	459.88	0.88	0.003	-220.45
ψ(elev + heat + rock + rock^2 + shrub + slope sd)	11	459.90	0.90	0.003	-218.22
ψ(curve + shrub + slope sd + slope sd^2)	9	459.96	0.97	0.003	-220.49
ψ(elev + heat + shrub + slope sd)	9	459.99	0.99	0.003	-220.51
ψ(heat + heat^2 + shrub + shrub^2+ slope sd)$_{330}$	10	460.02	1.02	0.003	-219.41
ψ(curve + heat + slope sd + slope sd^2)	9	460.04	1.04	0.003	-219.42
ψ(elev + heat + rock + shrub + slope sd + slope sd^2)	11	460.07	1.07	0.003	-218.31
ψ(aspect + shrub + slope sd)	8	460.07	1.07	0.003	-221.64

ψ(curve + heat + shrub + slope sd)	9	460.07	1.08	0.003	-220.55
ψ(aspect + aspect^2 + shrub + slope sd + slope sd^2 + tree)$_{240}$	11	460.09	1.09	0.003	-218.32
ψ(elev + rock + shrub + slope sd)	9	460.11	1.11	0.003	-220.56
ψ(heat + shrub + shrub^2 + slope sd)$_{330}$	9	460.13	1.14	0.003	-219.46
ψ(elev + heat + shrub + slope sd + slope sd^2 + tree)	11	460.15	1.15	0.003	-218.35
ψ(elev + shrub + slope sd + tree)	9	460.15	1.15	0.003	-220.59
ψ(aspect + aspect^2 + shrub + shrub^2 + slope sd)$_{330}$	10	460.18	1.18	0.003	-219.49
ψ(shrub + slope sd + slope sd^2)	8	460.19	1.19	0.003	-220.61
ψ(elev + heat + rock + rock^2 + shrub + slope sd + slope sd^2)	12	460.23	1.23	0.003	-217.25
ψ(elev + shrub + slope sd + slope sd^2 + tree + tree^2)	11	460.29	1.29	0.003	-218.42
ψ(aspect + aspect^2 + grass + shrub + slope sd + slope sd^2)$_{240}$	11	460.30	1.30	0.003	-218.42
ψ(curve + shrub)	7	460.32	1.32	0.003	-222.86
ψ(heat + shrub + shrub^2 + slope sd)$_{330}$	9	460.32	1.32	0.003	-220.67
ψ(heat + rock + rock^2 + shrub + slope sd + tree + tree^2)	12	460.34	1.35	0.003	-217.31
ψ(elev + solar radiation + rock + shrub + slope sd + slope sd^2)	11	460.37	1.37	0.003	-218.46
ψ(rock + shrub + slope sd)	8	460.37	1.37	0.003	-221.80
ψ(curve + elev + shrub + slope sd + slope sd^2)	10	460.41	1.42	0.003	-219.61
ψ(rock + rock^2 + shrub + slope sd + tree + tree^2)	11	460.41	1.42	0.003	-218.48
ψ(aspect + elev + rock + shrub + slope sd + slope sd^2)	11	460.45	1.45	0.003	-218.50
ψ(elev + shrub + slope + slope sd + slope sd^2)	10	460.47	1.47	0.003	-219.63
ψ(Aspect + elev + shrub + slope sd)	9	460.50	1.50	0.003	-220.76
ψ(Aspect + curve + shrub + slope sd + slope sd^2)	10	460.53	1.53	0.002	-219.66
ψ(curve + elev + rock + shrub + slope sd + slope sd^2)	11	460.56	1.57	0.002	-218.56
ψ(aspect + aspect^2 + rock + shrub + slope sd + slope sd^2 + tree)$_{240}$	12	460.59	1.60	0.002	-217.43
ψ(shrub + slope + slope^2 + slope sd + slope sd^2)	10	460.60	1.60	0.002	-219.70
ψ(elev + shrub + slope sd + tree + tree^2)	10	460.66	1.67	0.002	-219.73
ψ(heat + rock + shrub + slope sd + slope sd^2)	10	460.68	1.68	0.002	-219.74
ψ(curve + elev + shrub + slope sd)	9	460.69	1.69	0.002	-220.85
ψ(heat + rock + rock^2 + shrub + slope sd)	10	460.69	1.69	0.002	-219.74

ψ(elev + grass + rock + shrub + slope sd + slope sd^2)	11	460.71	1.72	0.002	-218.63
ψ(curve + elev + shrub + slope sd + slope sd^2 + tree)	11	460.74	1.74	0.002	-218.64
ψ(curve + heat + shrub + shrub^2 + slope sd + slope sd^2)$_{330}$	11	460.74	1.75	0.002	-218.65
ψ(elev + solar radiation + rock + rock^2 + shrub + slope sd)	11	460.75	1.75	0.002	-218.65
ψ(aspect + curve + shrub + slope sd)	9	460.76	1.76	0.002	-220.89
ψ(heat + heat^2 + shrub + shrub^2 + slope sd + slope sd^2)	11	460.77	1.77	0.002	-218.66
ψ(rock + rock^2 + shrub + slope sd)	9	460.79	1.80	0.002	-220.91
ψ(curve + curve^2 + shrub)	8	460.80	1.81	0.002	-222.01
ψ(elev + grass + shrub + slope sd + slope sd^2)	10	460.83	1.84	0.002	-219.82
ψ(heat + shrub + shrub^2 + slope sd)	9	460.83	1.84	0.002	-220.93
ψ(curve + elev + heat + shrub)	9	460.84	1.84	0.002	-218.69
ψ(elev + solar radiation + rock + rock^2 + shrub + slope sd + slope sd^2)	12	460.86	1.86	0.002	-217.57
ψ(curve + curve^2 + heat + shrub + slope sd + slope sd^2)	11	460.86	1.87	0.002	-218.71
ψ(elev + rock + rock^2 + shrub + slope sd + tree + tree^2)	12	460.87	1.88	0.002	-217.57
ψ(curve + curve^2 + shrub + slope sd)	9	460.87	1.88	0.002	-220.95
ψ(curve + rock + shrub + slope sd + slope sd^2)	10	460.90	1.91	0.002	-219.85
ψ(shrub + slope + slope sd)	8	460.93	1.93	0.002	-222.07
ψ(curve + elev + rock + rock^2 + shrub + slope sd)	11	460.94	1.94	0.002	-218.74
ψ(elev + heat + shrub + slope sd + slope sd^2 + tree + tree^2)	12	460.94	1.94	0.002	-217.61
ψ(elev + rock + shrub + slope sd + slope sd^2 + tree)	11	460.94	1.94	0.002	-218.75
ψ(elev + grass + heat + shrub + slope sd + slope sd^2)	11	460.94	1.95	0.002	-218.75
ψ(elev + shrub + slope + slope sd)	9	460.95	1.95	0.002	-220.98
ψ(shrub + shrub^2 + slope sd)	8	460.95	1.96	0.002	-222.09
ψ(elev + solar radiation + shrub + slope sd + slope sd^2)	10	460.96	1.96	0.002	-219.88
ψ(aspect + elev + rock + rock^2 + shrub + slope sd)	11	460.96	1.96	0.002	-218.75
ψ(curve + curve^2 + heat + shrub + slope sd)	10	460.96	1.96	0.002	-219.88
ψ(elev + heat + shrub + slope sd + tree)	10	460.97	1.98	0.002	-219.89
ψ(solar radiation + shrub + shrub^2 + slope sd)$_{330}$	9	460.98	1.98	0.002	-221.00
ψ(shrub + shrub^2 + slope sd)$_{330}$	8	460.98	1.98	0.002	-222.10

ψ(curve + heat + heat^2 + shrub + shrub^2 + slope sd)$_{330}$	11	460.98	1.98	0.002	-218.76
ψ(aspect + aspect^2 + curve + shrub + shrub^2 + slope sd)$_{330}$	11	460.99	1.99	0.002	-218.77
ψ(curve + shrub + tree + tree^2)	9	460.99	2.00	0.002	-221.01

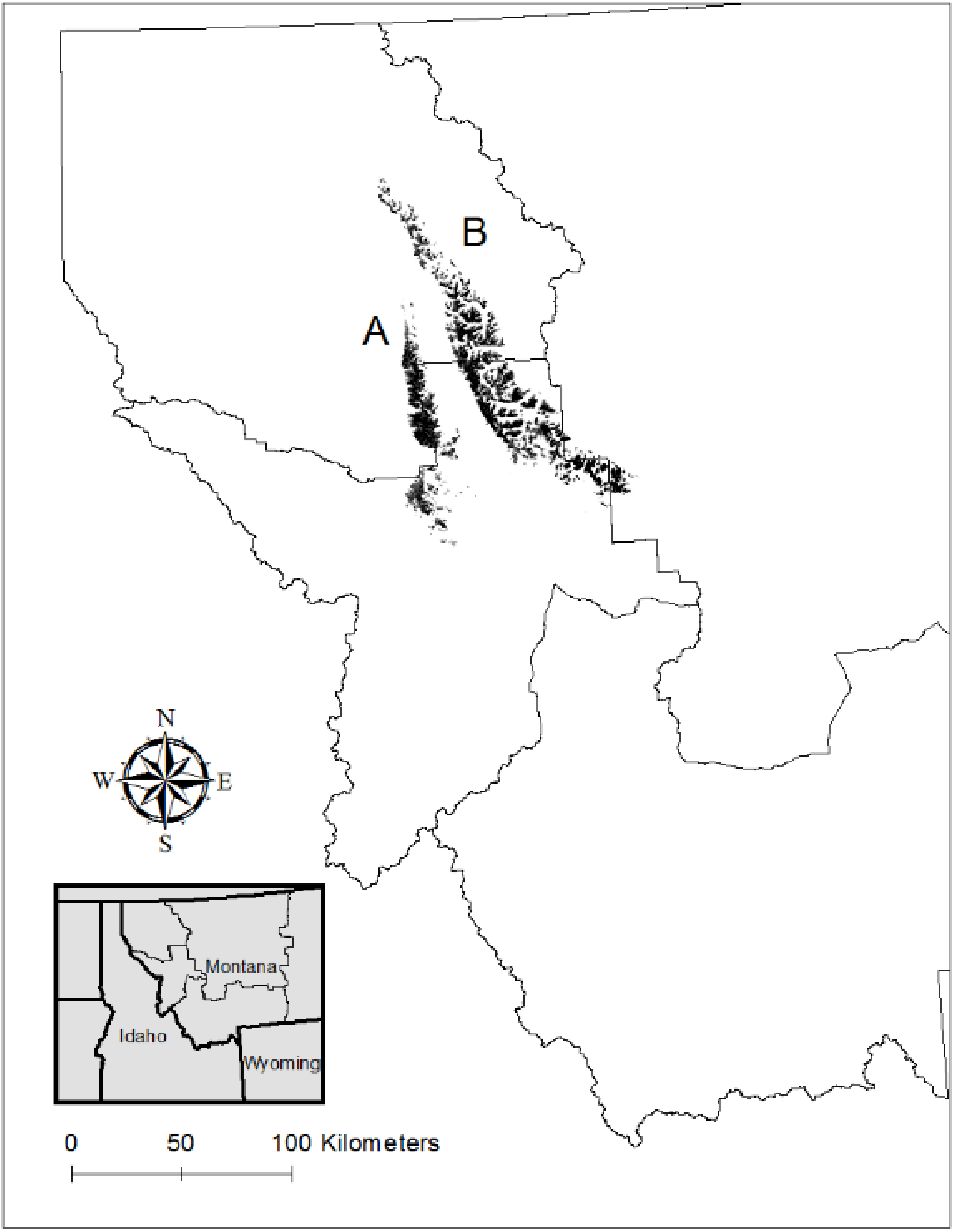

Figure 3.1. The (A) Mission and (B) Swan Mountains, Montana, USA, which we used to evaluate sampling effort needed to detect a decline in colony abundance of hoary marmots based on occupancy methods. The boundary lines denote Montana FWP administrative regions 1-4.

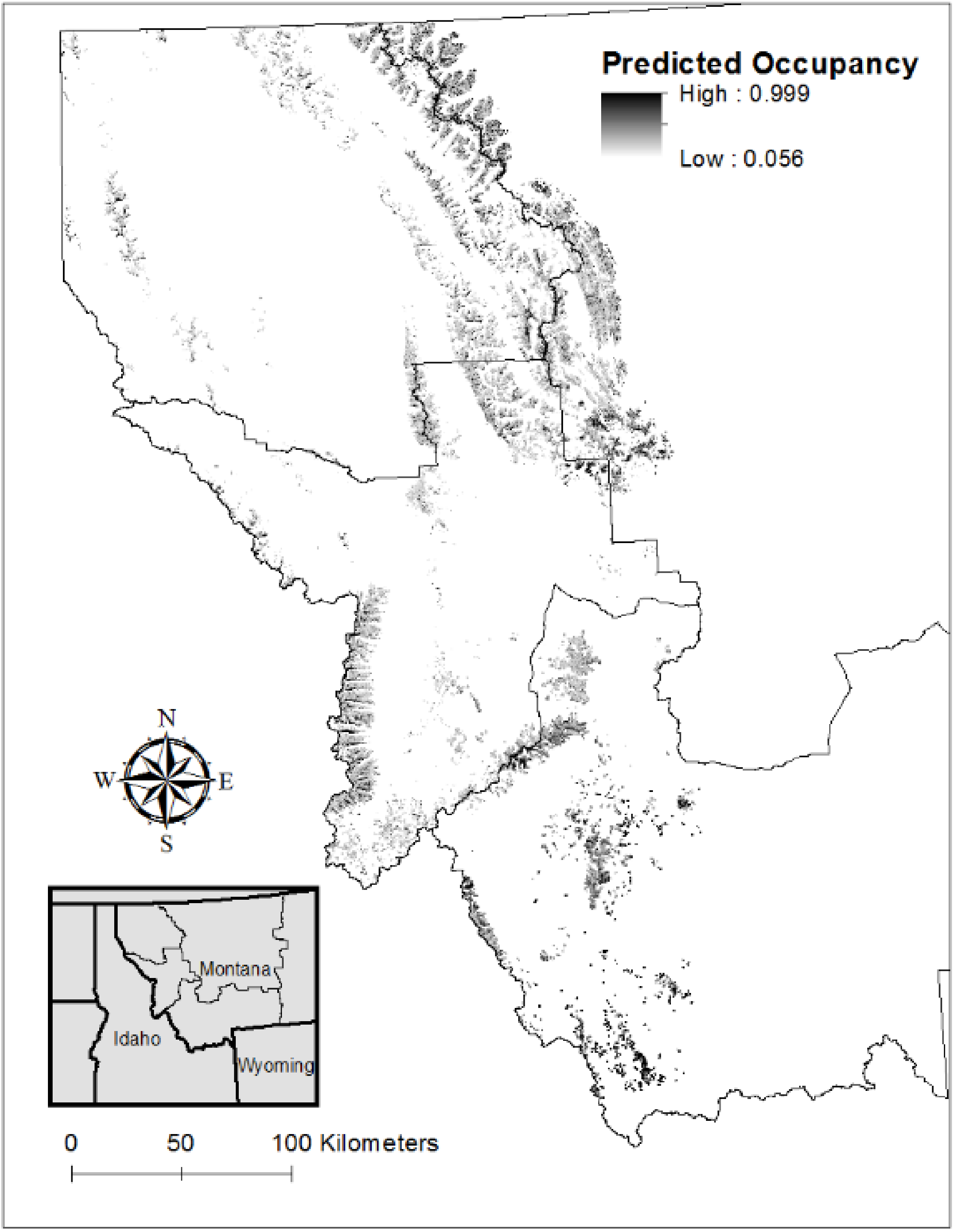

Figure 3.2. Map of predicted occupancy of hoary marmots in western Montana, USA used to evaluate tradeoffs in designing a monitoring program. The boundary lines denote Montana FWP administrative regions 1-4.

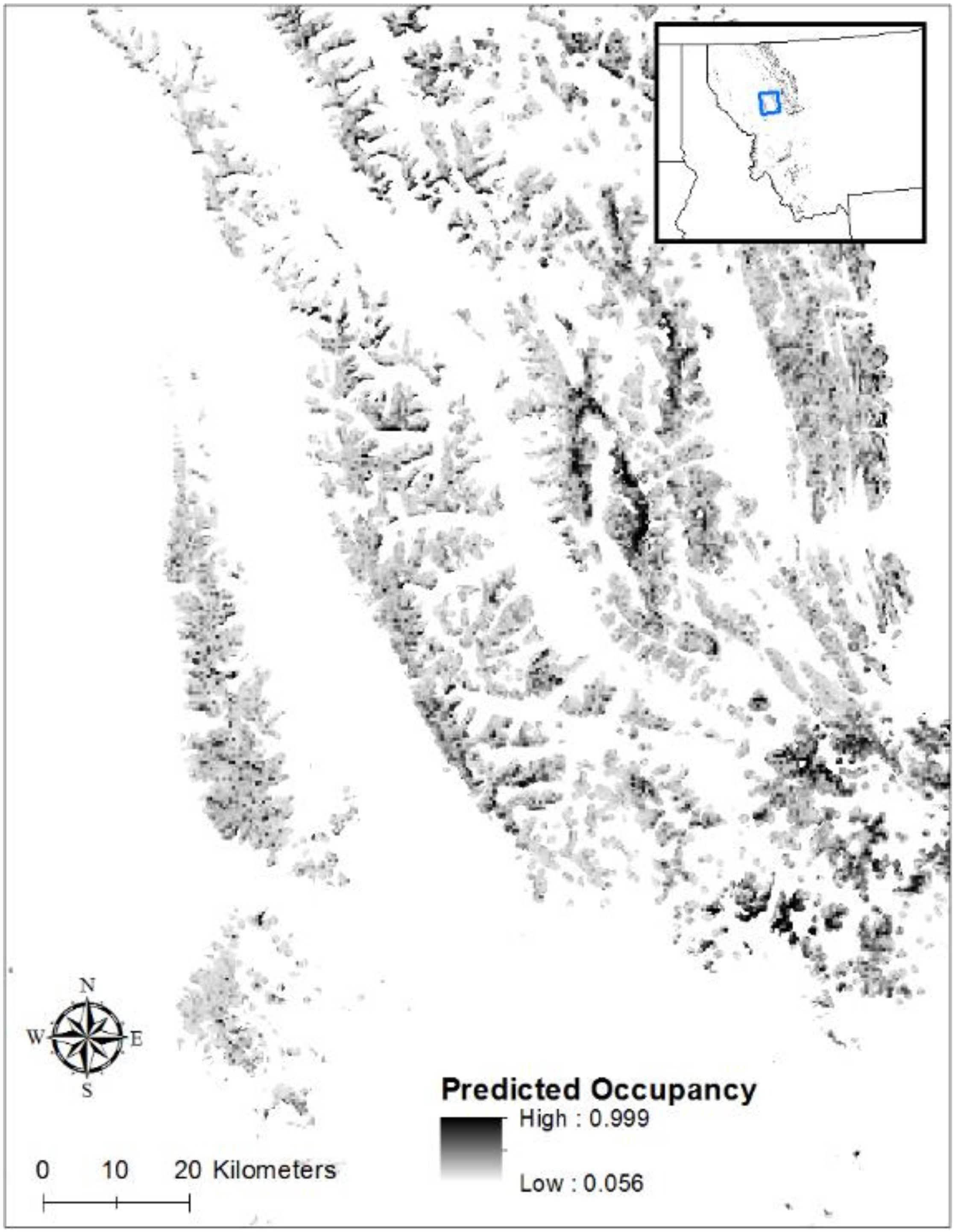

Figure 3.3. Map of predicted occupancy of hoary marmots in the Mission and Swan Mountains, USA, which we used to evaluate tradeoffs in designing a monitoring program.

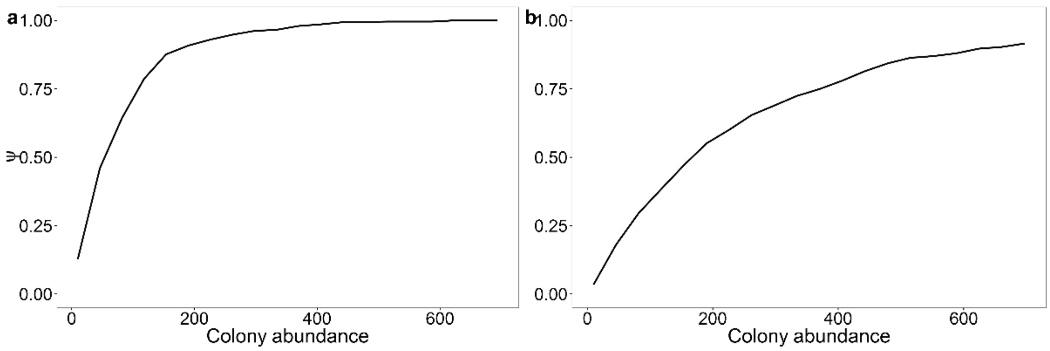

Figure 3.4. Estimates of colony abundance for hoary marmots in the (a) Mission and (b) Swan Mountains of northwest Montana, USA. Possible values of colony abundance ranged from 10-700 in each mountain range. We used these values to place colonies in cells that had acceptable values for occupancy ($\psi_{pred} \geq 0.286$) within each mountain range. We computed landscape occupancy (ψ) based on the proportion of occupied cells.

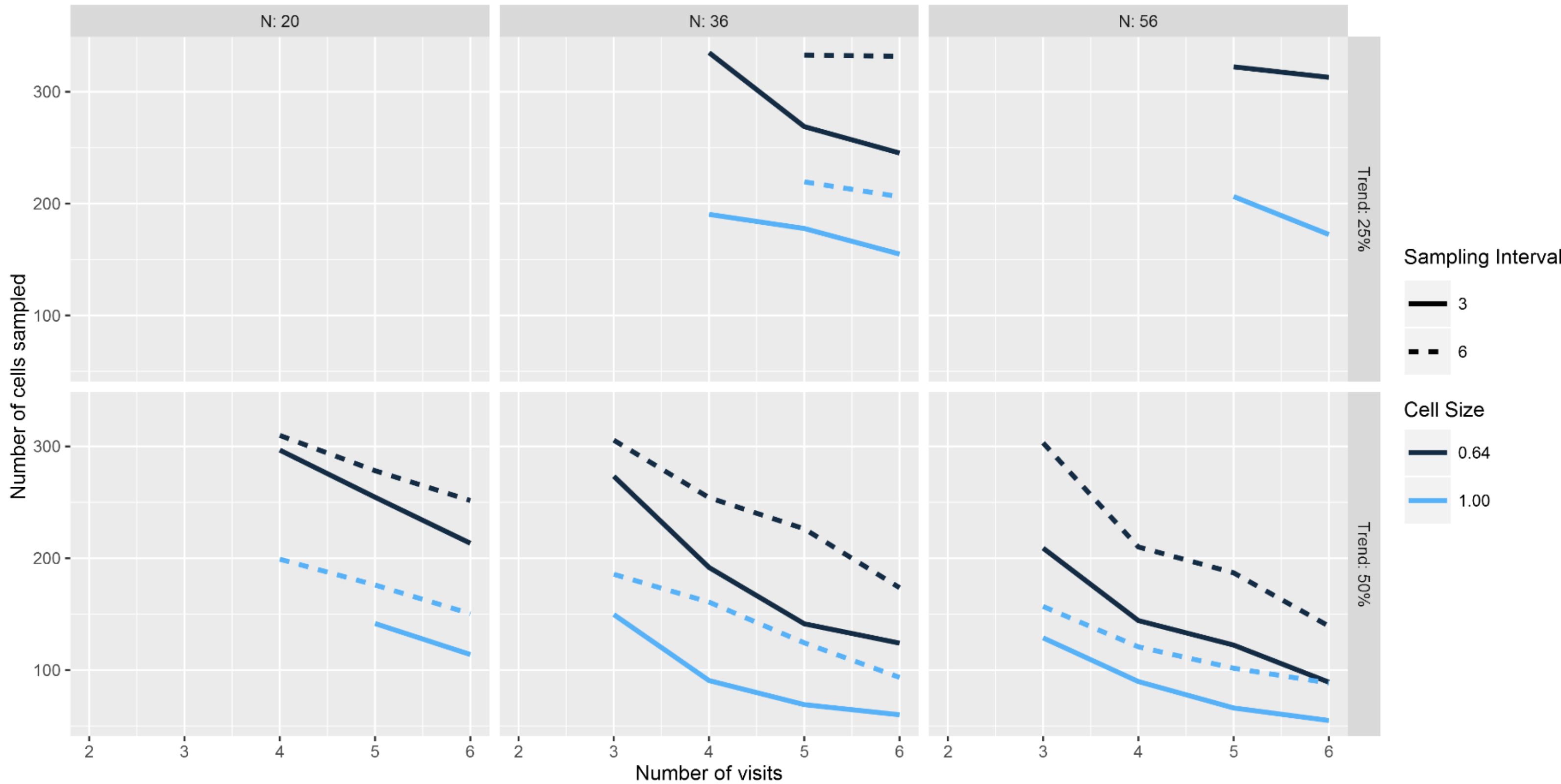

Figure 3.5. Sampling effort (number of cells, number of visits, sampling interval, cell size [km^2]) required to adequately detect a 50% (top graphs) or 25% decline (bottom graphs) in colony abundance over 30 years for hoary marmots in the Mission Mountains, Montana, USA. Solid lines represent sampling every 3 years, dashed lines every 6 years. Each column of graphs illustrates the sampling effort required under low, medium, and high values of colony abundance (Table 3.2).

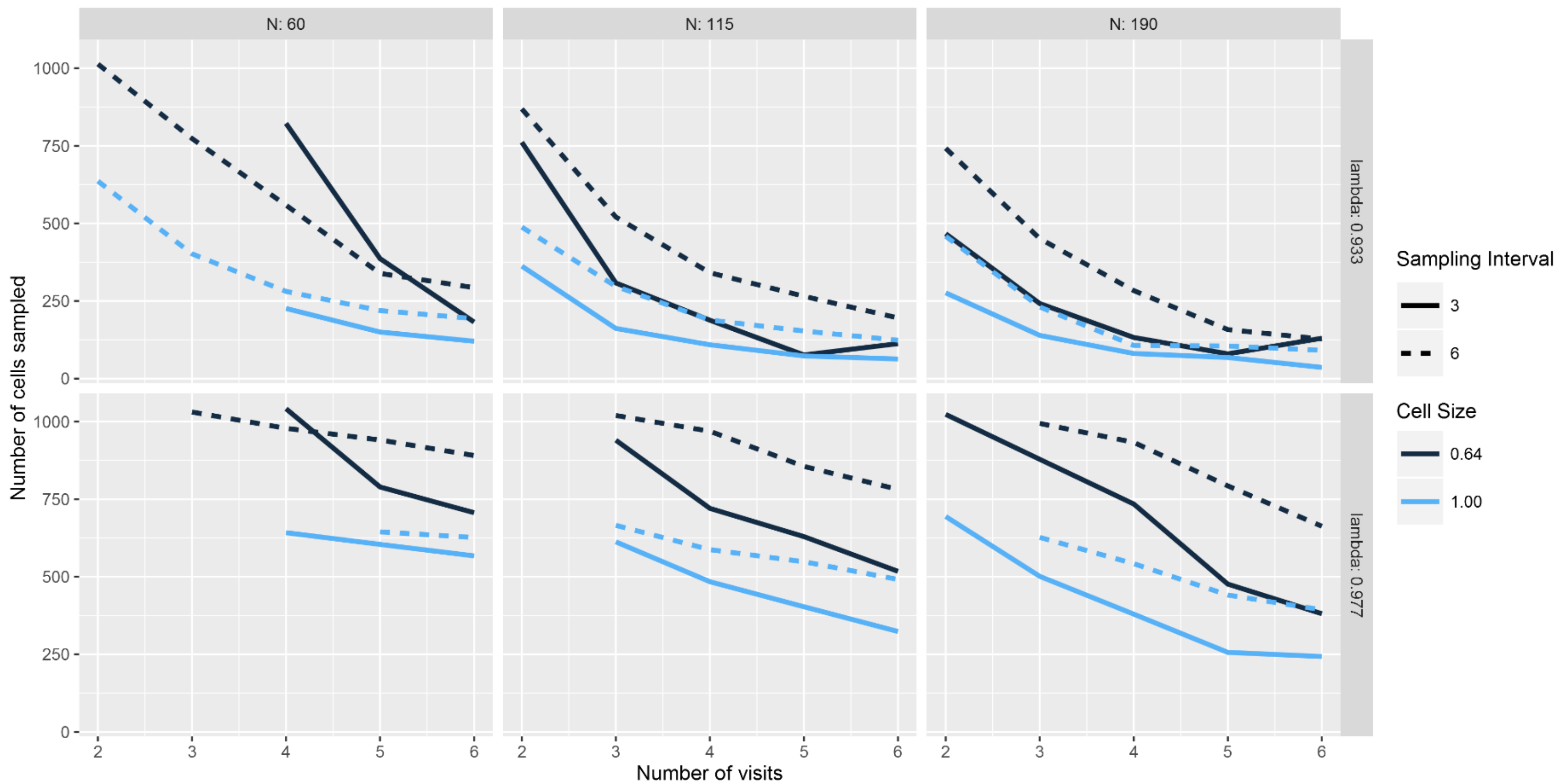

Figure 3.6. Sampling effort (number of cells, number of visits, sampling interval, cell size [km^2]) required to adequately detect a 50% (top graphs) or 25% decline (bottom graphs) in colony abundance for hoary marmots in the Swan Mountains, Montana, USA. Solid lines represent sampling every 3 years, dashed lines every 6 years. Each column of graphs illustrates the sampling effort required under low, medium, and high values of colony abundance (Table 3.2).

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CHAPTER FOUR

CONCLUSIONS

Species already are responding to climate change with broad shifts in their distributions (Chen et al. 2011), yet for many species, we lack the information needed to evaluate such responses. Populations at the southern edge of species' distributions are more vulnerable because warming is occurring at a faster rate (Cahill et al. 2014). Therefore, these populations may serve as bellwethers, revealing where distribution shifts and habitat loss will occur (Inman et al. 2012, Sultaire et al. 2016). Monitoring will be necessary to evaluate species responses to climate change and to direct where management action may be necessary to preserve the full suite of species on the landscape.

We found that hoary marmots select shallow slopes, southern aspects, and areas with shrubs present, likely representing a balance between deep snowpack and early season forage (Armitage et al. 1976, Patil et al. 2013). Although hoary marmots may balance constraints between conditions in winter and early summer we did not find evidence that summer conditions influence habitat selection. Similarly, vital rates in marmots may be influenced more by winter than summer (Van Vuren and Armitage 1991, Patil et al. 2013, Rézouki et al. 2016). We propose based on previous studies and our results that winter conditions drive habitat selection of hoary marmots at the southern extent of their distribution. Winter conditions also may limit the distribution of wolverine and snowshoe hare (*Lepus americanus*) at their southern extent (Inman et al. 2012, Sultaire et al. 2016). Therefore, hoary marmots may be one of many species that could experience range retractions as temperature and precipitation change.

We found that a decline in colony abundance within a mountain range can be detected using occupancy. We weighed trade-offs to inform how sampling effort can be allocated to create a robust monitoring plan. Sampling designs that incorporated 4 - 6 visits to sites over a 6-year time interval resulted in sufficient power to detect a 50% decline in colony abundance. However, when colony abundance was small, detecting a trend required much higher effort. Populations with lower abundance require more effort to monitor adequately (Ellis et al. 2014), therefore initiating monitoring early will help ensure that declines are observed should they occur.

Future work to characterize fine-scale habitat associations will inform local impacts of climate change on hoary marmots (Aryal et al. 2015). Investigating winter conditions such as depth of snowpack may further clarify habitat selection of hoary marmots. Differences between ambient temperatures and conditions in the hibernation burrow also could be important for our understanding. Further assessing the limitations to the distribution of hoary marmots will require continued surveys throughout the southern extent of their range. Implementing a monitoring plan based on our recommendations can provide the necessary data to continue evaluating habitat associations (MacKenzie 2006, Fuller et al. 2016), ensure that population declines are detected, and provide information about metapopulation dynamics of the hoary marmot at the southern extent of their distribution (MacKenzie et al. 2003, Ozgul et al. 2006).

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APPENDIX A

SUPPORTING INFORMATION FOR CHAPTER 2

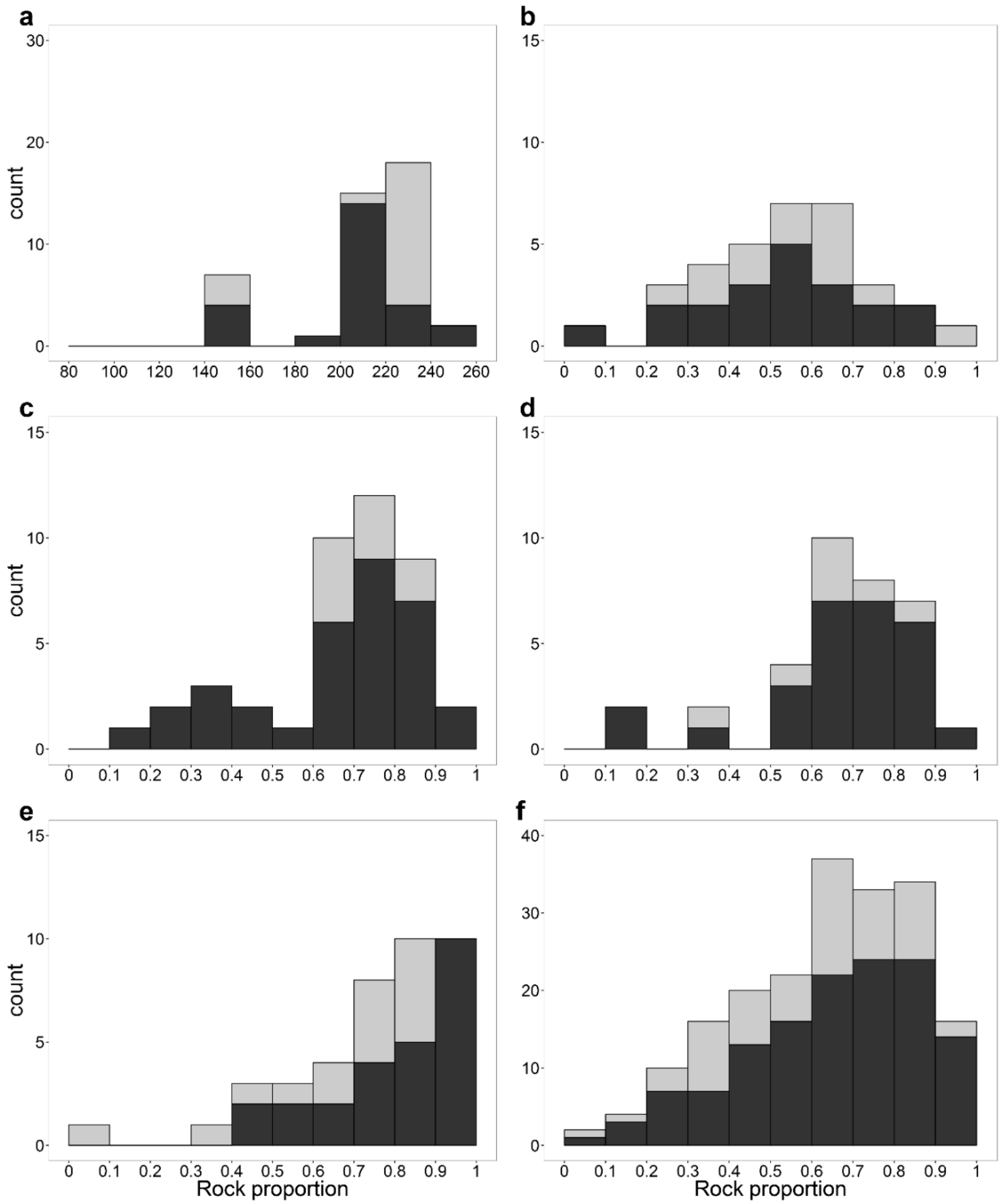

Figure S1. Proportion of rock cover in survey sites (n = 194) by mountain range (a) Lewis, (b) Whitefish, (c) Swan, (d) Missions, (e) Anaconda-Pintler, and (f) for all sites combined in western Montana, 2014-2015. Occupied sites are in light gray and unoccupied sites are in dark gray.

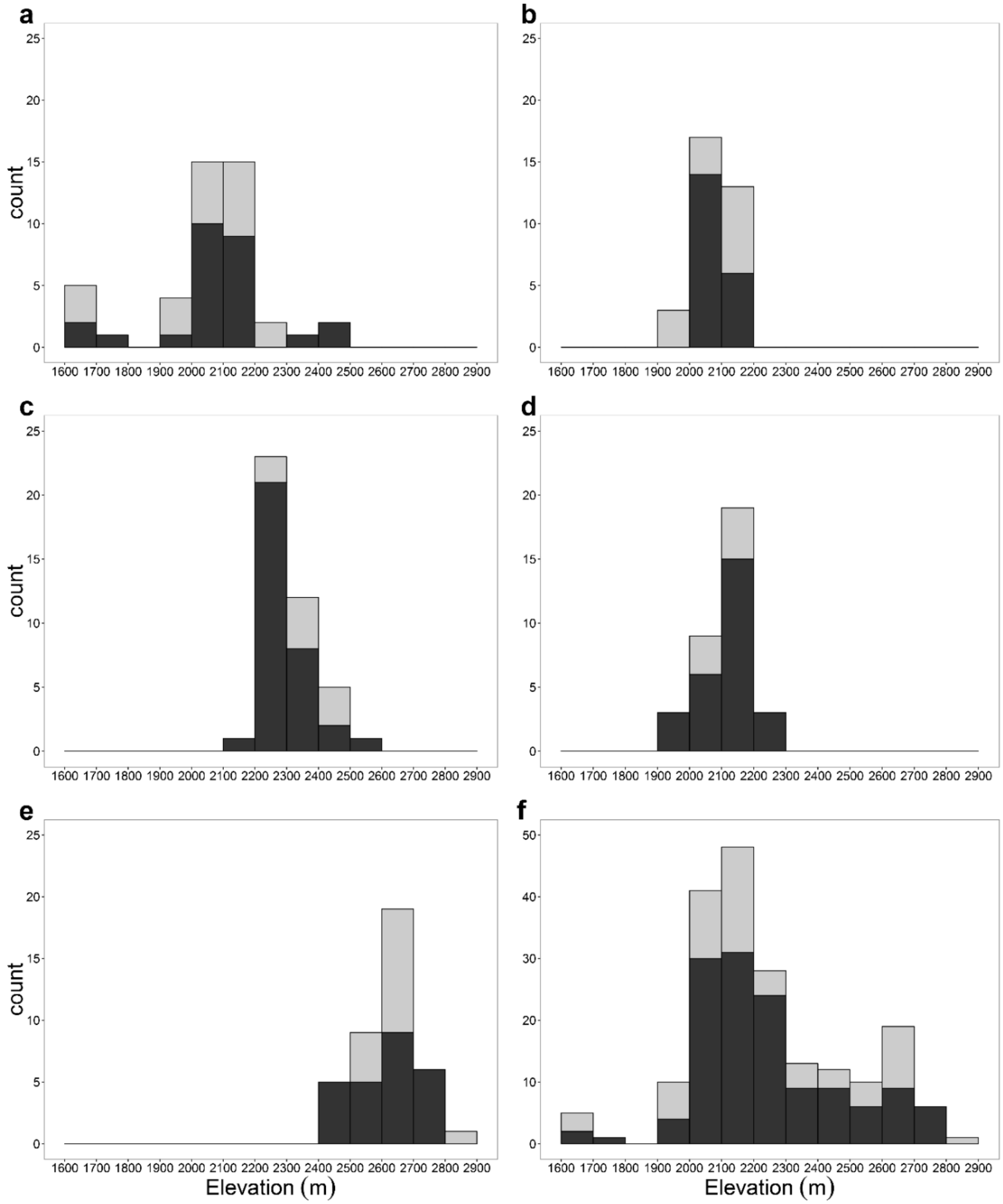

Figure S2. Elevation in survey sites (*n* = 194) by mountain range (a) Lewis, (b) Whitefish, (c) Swan, (d) Missions, (e) Anaconda-Pintler, and (f) for all sites combined in western Montana, 2014-2015. Occupied sites are in light gray and unoccupied sites are in dark gray.

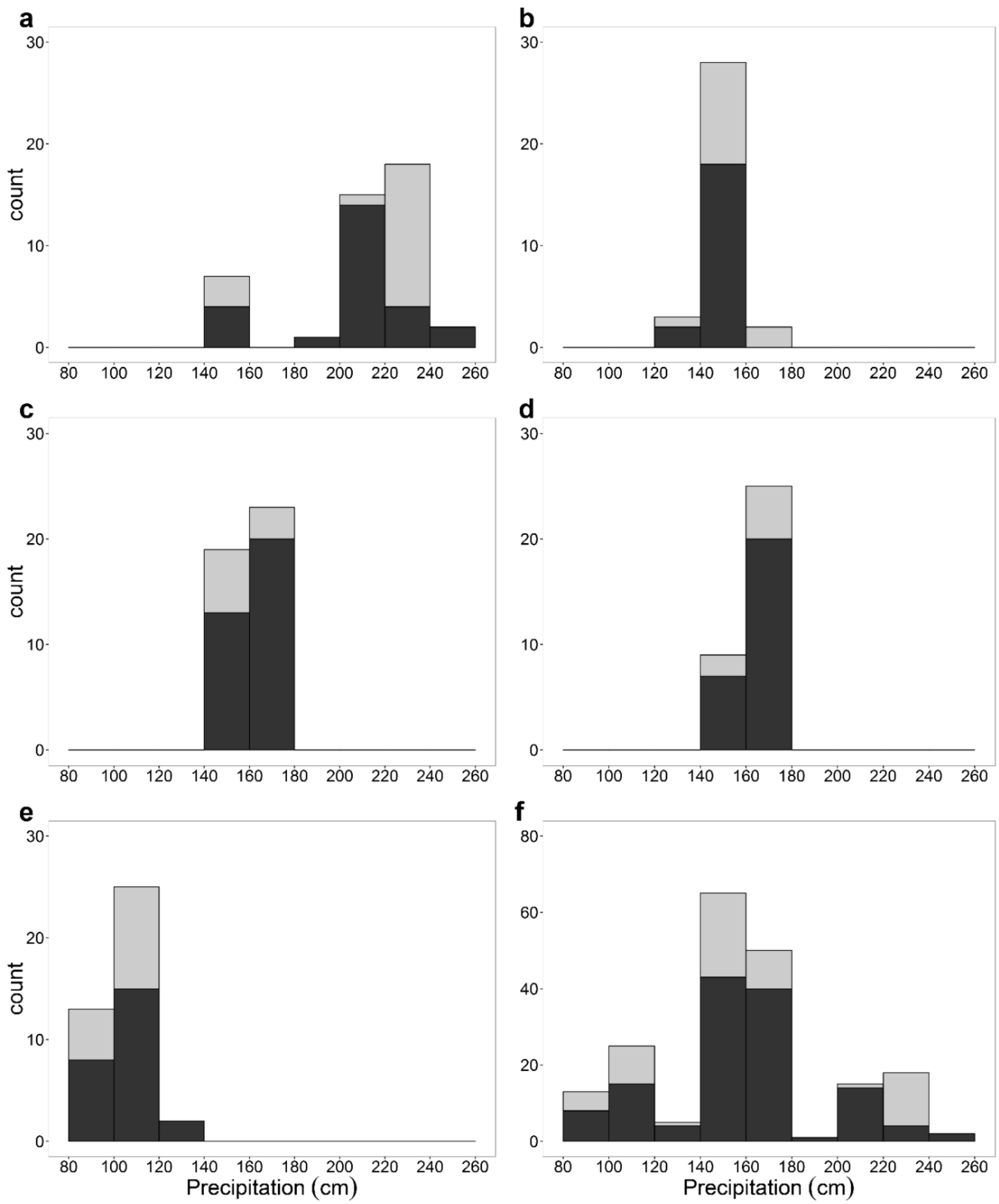

Figure S3. Precipitation (cm) in survey sites (*n* = 194) by mountain range (a) Lewis, (b) Whitefish, (c) Swan, (d) Missions, (e) Anaconda-Pintler, and (f) for all sites combined in western Montana, 2014-2015. Occupied sites are in light gray and unoccupied sites are in dark gray.