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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 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. Marmots preferred shallow slopes and southern aspects, similar to findings from other studies on hoary marmots 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. Hoary marmots may be selecting areas with shrubs because shrubs can accumulate deeper snow and the additional insulation can increase subnivian temperatures. Other studies suggest that marmot survival is influenced by snowpack, indicating that marmot distribution may be more closely tied to winter conditions rather than summer conditions. This highlights the difficulty of working on marmots and other alpine obligates, as most studies occur only during the short growing season. Given the current and projected increases in temperature and reduction in snowpack in Montana, areas that provide the winter conditions hoary marmots require may become more limited. 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.

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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 present 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 entering hibernation (Barash 1973). As a result, areas where marmots occur generally 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 (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). There is a lack of basic information about the distribution and abundance of hoary marmots, which is why they are a potential species of concern in Montana (Meny 2012). Thus, understanding what characterizes the places where marmots occur will be essential to their conservation. Managers want to ensure persistence of hoary marmot populations (Hammond 2010), and identifying areas that may be more susceptible to the influences of climate change will be crucial should future management action be required.

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 occurrence and important habitat characteristics (MacKenzie 2006). We used available information on hoary or other marmot species to guide the selection of a subset of covariates we considered to explain variation in detection probability and occupancy.

METHODS

Study areas

We studied five major mountain ranges throughout the distribution of hoary marmots in Montana that we grouped into three study areas: 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

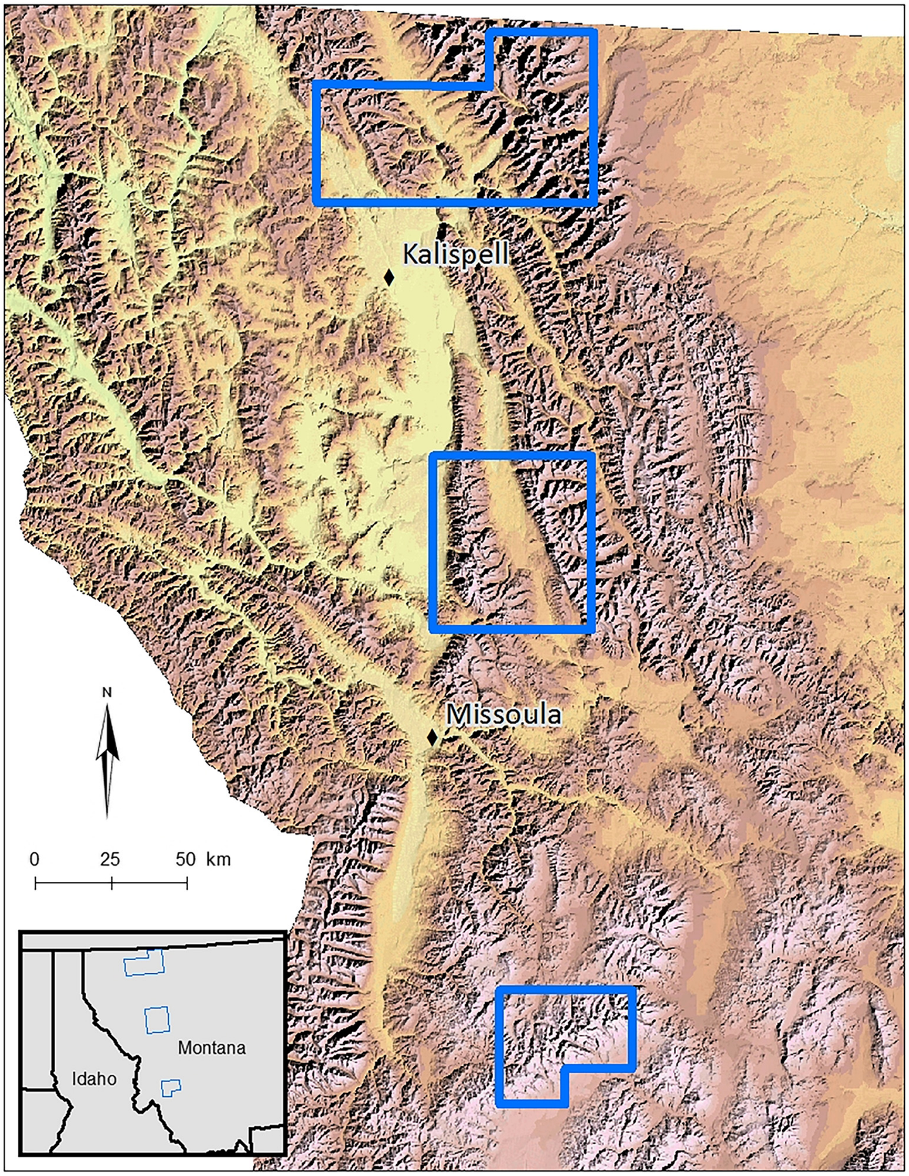

Fig. 1. The three study areas (outlined in blue), including the northern latitude study area encompassing the Whitefish and Lewis Ranges, the middle latitude study area comprised of the Mission and Swan Ranges, and the southern latitude study area of the Anaconda-Pintler Range, northwestern Montana, summers 2014 and 2015.

(Fig. 1). The Anaconda-Pintler Range receives 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-Pintler Range and has the lowest elevation (Table 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

Table 1. Characteristics of the sites included in the study by mountain range: range of average annual precipitation based on the 30-yr normal (1981–2010, PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu), range of elevations, and study area.

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

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. We refined other criteria for site placement 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 land 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 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 included ≥5% boulder field to increase the possibility that marmots might occur there; most sites were comprised of 20–80% boulders and slab rock (Appendix S1: Fig. 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 adjacent vegetation. For smaller boulder fields, we completely encompassed the area surrounding the boulder field. 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 from the third week in June to the middle of September based on methods modified from Witczuk et al. (2008) for surveying Olympic marmots (*Marmota olympus*). False negatives can bias presence–absence data, but multiple surveys can reduce the potential for estimates of occupancy to be biased (MacKenzie et al. 2006). At each site, we conducted up to five surveys using up to two 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. Timing of visual surveys was haphazard, but conducted to match when hoary marmots are most active, typically before 11 a.m. or after 4 p.m. (Gray 1967, Barash 1989). 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 observers sat within 50 m of each other but positioned so they could not see the other observer. The observers simultaneously surveyed the site with 10× binoculars for ≥20 min. 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 0.56–0.76 s (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 marmots observed. Observers used the Mesa computers and aerial imagery to accurately record the location of each uniquely identified marmot observation. 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, they 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 (two total surveys). If neither observer detected marmots, they either changed their vantage point and completed a second set of surveys later the same day or returned the next day to complete a second set of surveys (four total surveys). By using this hybrid removal survey design, we surveyed more sites while reducing 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 walkthrough 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 consolidated into four groups of covariates (land cover, water, boulder size, and topography) that we anticipated could be important characteristics of marmot habitat and promote occupancy (Table 2). We used available research on hoary or other marmot species to inform and hone this list of variables; we provide our justification for consideration below. Some of these variables were recorded in the field, but most were remotely sensed using ArcGIS 10.2.2 (ESRI, Redlands, California, USA).

*Land cover.—*Hoary marmots are tied to boulder fields, but they also require nearby vegetation for forage (Holmes 1984, Karels et al. 2004). We included these characteristics to investigate the relationship between marmot occupancy and the composition of land cover types within a site. We characterized each site based on six land cover categories (rock, grass, trees, shrubs, snow, and other, in 5% increments) in the field after completing the first pair 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.

Table 2. Site-specific characteristics considered to explain variation in occupancy 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 four 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	Presence/absence of slab rock
Small boulders	Proportion of boulders with surface area ≤4 m^2
Medium boulders	Proportion 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

*Water.—*We considered several characteristics to investigate the relationship between hoary marmots and available water. Hoary marmots glean most of their moisture from the plants that they consume, but they also use standing water sources (Barash 1989). In an alpine environment, areas with more water sources may provide forage throughout the entire growing season, facilitating increased foraging at the end of the summer for adults and juveniles. Much of a hoary marmot's diet is composed of plants associated with wetter areas (Gray 1967, Holmes 1984, Barash 1989); therefore, we predicted that water sources may be important for persistence of marmots on the landscape. We determined the availability of water using the distance to and type of the closest water source for each site with ArcGIS (Turnock 2016). 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 to add water sources that were absent from the master layer.

We calculated the average annual precipitation for all sites using GIS data for the most recent three decades (1981–2010, PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu). 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.

*Topography.—*Slope and aspect are important influences for several species of marmots (Van Vuren and Armitage 1991, Bryant 1996, Harrower 2001). 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.

*Boulder size.—*We hypothesized that boulder size might be important habitat characteristics because hoary marmots in Glacier National Park, Montana, USA, used boulders (diameter ≥2.0 m) for sunning and lookout locations (Tyser 1980). Using Google Earth's 1-m resolution aerial imagery, we measured the length and width of each boulder and grouped them into four categories: small (surface area ≤4 m^2), medium (5–15 m^2), large (≥16 m^2), and slab rock/other (Turnock 2016). We then calculated the proportion of the site comprised by each size class of boulders.

Analysis

We used single-season single-species occupancy models to estimate detection probability and occupancy (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) were recorded with a Kestrel weather meter (models 2000 and 3000, Nielsen-Kellerman, Boothwyn, Pennsylvania, USA). We estimated detection probability separately for visual and walkthrough surveys using a categorical variable. We predicted that survey-specific factors and survey method (visual survey or walkthrough) might influence the probability of detecting a marmot (Table 3). Precipitation during the survey was converted to a binary variable (rain/no rain) because it rained during only 19 of 822 surveys. We calculated the 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 prepared the characteristics of each site within the four categories: land cover, water, boulder size, and topography. 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 we observed few non-zero values over the range of proportions observed (0–0.6). We excluded the "other" 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); however, 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, and we converted data from continuous to binary (Appendix S1: Fig. 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 S1). Initially, we were interested in explicitly modeling differences among mountain ranges, but we did not have sufficient 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.

Table 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, midday, 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

Detection probability.—Within the context of occupancy modeling, 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 site (MacKenzie et al. 2002). We used several survey-specific variables to investigate what factors might influence our ability to detect hoary marmots when hoary marmots are available for detection and, in turn, to provide an unbiased estimate of occupancy (MacKenzie et al. 2006). We estimated a null model of detection probability, but also considered 10 variables we thought would influence detection probability at survey sites (Table 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. We considered a quadratic term for temperature because marmots are active at different times of day as summer progresses (Barash 1973); we hypothesized that they may be out of their burrows and most active over an intermediate range of temperatures. 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. There were a subset of detection variables that likely would influence detection probability for visual and walkthrough surveys differently. We show the effect of the covariate on detection probability by survey method where appropriate.

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. We used this reduced model as our baseline model to account for imperfect detection.

Occupancy.—We examined pairwise plots to assess correlation among continuous variables and boxplots of pairwise comparisons for continuous, categorical, and binary variables (Zuur et al. 2007); continuous covariates were not highly correlated ($|r| \leq 0.65$, Appendix S1: Table S1). 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 <40°, so we also investigated evidence for a threshold with a quadratic term for slope. We considered interactions between elevation and the three major study areas (northern, middle, and southern) and between precipitation and study areas because elevation of treeline and the range of precipitation values differed among the mountain ranges we sampled (Appendix S1: Figs. S2, S3). We also included year as an explanatory variable to understand differences in occupancy across sampling years. We began with our reduced model for detection probability and then assessed evidence for the occupancy covariates with likelihood-ratio tests to compare nested models by examining χ^2 statistics 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. We assessed model fit and evidence of over-dispersion using our global model and the parametric bootstrap approach as suggested by MacKenzie and Bailey (2004). 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). We did not find any evidence that our global model did not adequately fit the data ($\chi^2 = 269.4$, $P = 0.772$). We estimated over-dispersion of our global model as 0.72 and did not inflate variances and confidence intervals.

Table 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).

Detection probability

Cloud cover (%), proportion of medium boulders, and survey method explained the most variation in detection probability (Table 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 in detection probability (Table 4).

*Cloud cover.—*Detection probability during visual surveys increased with cloud cover (Fig. 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 (Fig. 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 5). These explanatory variables were not highly correlated (range = 0.07–0.16). Land cover covariates (except

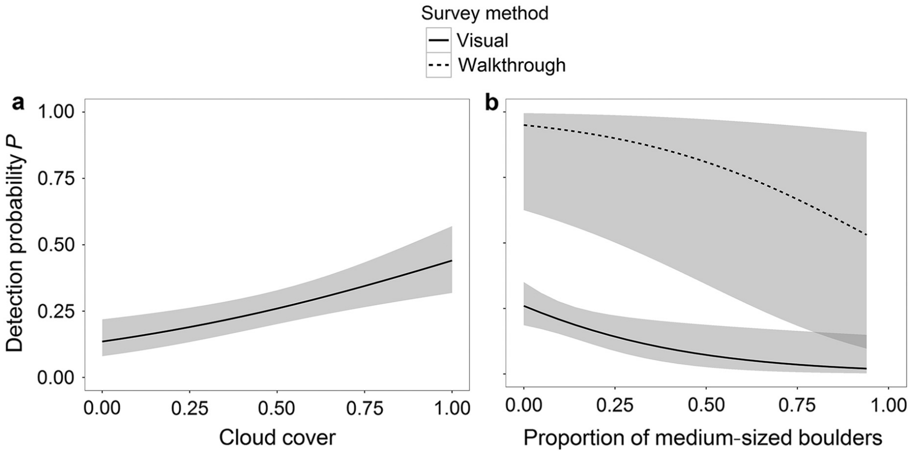

Fig. 2. Changes in detection probability (and 95% CI) during hoary marmot occupancy surveys, northwestern Montana, summers 2014 and 2015. (a) Detection probability during visual surveys over the observed range of overhead cloud cover. (b) Detection probabilities by survey method over the observed range of medium-sized boulders.

Table 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

presence of shrubs), water covariates, boulder size covariates, elevation, study area, and higher-order relationships did not explain sufficient variation in occupancy (Table 5).

*Slope.—*Occupancy by marmots decreased precipitously as average slope increased (Fig. 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 (Fig. 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 (Fig. 3c). On northern aspect sites, 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 provide hypotheses regarding the environmental and physiographic conditions that marmots seek. We suggest that the preference for shallow slopes and southern aspects we detected represents a compromise between different habitat requirements during summer and winter. Shallow slopes typically accumulate deeper snow (Smithson et al. 2008) 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 because marmots 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).

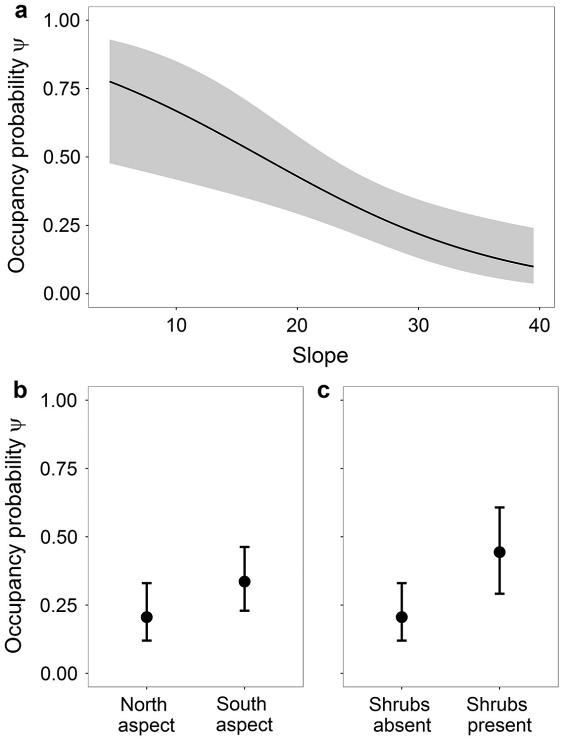

Fig. 3. Changes in occupancy (and 95% CI) with (a) slope, (b) aspect categorized as north or south, and (c) presence or absence of shrub cover, northwestern Montana, summers 2014 and 2015.

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 of where marmots occur, which may have several explanations. Marmots are generalist herbivores and 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, similar to another colonial squirrel, the Arctic ground squirrel (Wheeler et al. 2015). Anecdotally, we observed hoary marmots foraging in and around shrubs. This behavior also has been observed in North Cascades National Park, Washington, where hoary marmots foraged in areas of mixed shrubs and meadows (Christophersen 2012). Preferences for areas with shrub cover could also relate to unmeasured conditions that shrubs can create in winter. Shrubs have been associated with accumulating deeper snow by depositing windblown snow that is more insulating, yet melts earlier in the spring and summer (Sturm et al. 2001). An interaction between shrub cover and snow depth may increase the winter insulation for hibernating hoary marmots and provide early season forage for marmots upon emergence from hibernation.

We expected that summer environmental conditions would be important to understand where marmots occur on the landscape. However, given that land cover, boulder size, and water characteristics did not explain sufficient variation in occupancy, we instead 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 (*Marmota flaviventris*) (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. In the Yukon Territory, Canada, survival of hoary marmots was 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. Average January temperature within our study area is −5.7°C compared to −26.25°C found in the Yukon (Patil et al. 2013); this could indicate that hoary marmots in Montana may not rely as heavily on deep winter snowpack. This relationship could be investigated by collecting demographic data for hoary marmot populations in Montana to assess their sensitivity to winter conditions. Areas that provide the winter conditions hoary marmots require may become more limited, especially at the southern extent of their distribution; demographic data would enhance predictions about their future distribution given the impacts of climate change. 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 yr (Mote 2006). Declines in snowpack depth are projected to continue over the next 100 yr, such that many of Montana's mountain ranges will be in the transient snow zone where snow will accumulate and melt, as opposed to 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 winter snow depth at the northern extent of their range (Patil et al. 2013), investigating their relationship with snowpack at the southern extent of their distribution would provide a deeper understanding of habitat selection. Hoary marmots already occur at the maximum elevation within each mountain range in western Montana; if winter snowpack can persist only at higher elevations with climate change, the connectivity of populations within and among mountain ranges could be seriously impacted (Armitage 2013). We suggest that a comprehensive GIS layer of snow depth could improve our understanding about the influence of snowpack. Given that much of marmot life history centers around boulder fields (Barash 1974), more closely examining detailed features of boulder fields 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, more detailed 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 for burrows and lookouts may provide additional insights.

Identifying the 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, yet 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.

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LITERATURE CITED

Armitage, K. B. 2013. Climate change and the conservation of marmots. Natural Science 5:36–43.

Armitage, K. B. 2014. Marmot biology: sociality, individual fitness, and population dynamics. First edition. Cambridge University Press, Cambridge, United Kingdom.

Armitage, K. B., J. F. Downhower, and G. E. Svendsen. 1976. Seasonal changes in weights of marmots. American Midland Naturalist 96:36–51.

Barash, D. P. 1973. Habitat utilization in three species of subalpine mammals. Journal of Mammalogy 54:247–250.

Barash, D. P. 1974. The social behavior of the hoary marmot (*Marmota caligata*). Animal Behavior 22:256–261.

Barash, D. P. 1989. Marmots social behavior and biology. Stanford University Press, Stanford, California, USA.

Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone. Ecoscience 10:421–431.

Braun, J. K., T. S. Eaton, and M. A. Mares. 2011. *Marmota caligata* (Rodentia: Sciuridae). Mammalian Species 43:155–171.

Brodie, J. F., and E. Post. 2010. Nonlinear responses of wolverine populations to declining winter snowpack. Population Ecology 52:279–287.

Bryant, A. A. 1996. Reproduction and persistence of Vancouver Island marmots (*Marmota vancouverensis*) in natural and logged habitats. Canadian Journal of Zoology 74:678–687.

Bryant, A. A., and D. W. Janz. 1996. Distribution and abundance of Vancouver Island marmots (*Marmota vancouverensis*). Canadian Journal of Zoology-Revue Canadienne De Zoologie 74:667–677.

Christophersen, R. G. 2012. Distribution and abundance of hoary marmots in North Cascades National Park complex, Washington, 2007–2008. National Park Service, Sedro-Woolley, Washington, USA.

Copeland, J. P., et al. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): Do climatic constraints limit its geographic distribution? Canadian Journal of Zoology 88:233–246.

DeVoe, J. D., R. A. Garrott, J. J. Rotella, S. R. Challender, P. J. White, M. O'Reilly, and C. J. Butler. 2015. Summer range occupancy modeling of non-native mountain goats in the greater Yellowstone area. Ecosphere 6:1–20.

Elbroch, M. 2003. Mammal tracks and sign. First edition. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

ESRI. 2011. ArcGIS Desktop: release 10. Environmental Systems Research Institute, Redlands, California, USA.

Fiske, I., and R. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Foresman, K. 2012. Mammals of Montana. Second edition. Mountain Press Publishing Company, Missoula, Montana, USA.

Frase, B. A., and K. B. Armitage. 1989. Yellow-bellied marmots are generalist herbivores. Ethology, Ecology & Evolution 1:353–366.

Froidevaux, J. S. P., F. Zellweger, K. Bollmann, G. Jones, and M. K. Obrist. 2016. From field surveys to LiDAR: shining a light on how bats respond to forest structure. Remote Sensing of Environment 175:242–250.

Gaudry, W., S. Saïd, J.-M. Gaillard, T. Chevrier, A. Loison, D. Maillard, and C. Bonenfant. 2015. Partial migration or just habitat selection? Seasonal movements of roe deer in an alpine population. Journal of Mammalogy 96:502–510.

Gray, D. R. 1967. Behaviour and activity in a colony of hoary marmots (*Marmota caligata*) in Manning Park, B.C. and a comparison of behaviour with other marmot species. University of Victoria, Victoria, British Columbia, Canada.

Griffin, S. C., M. L. Taper, R. Hoffman, and L. S. Mills. 2008. The case of the missing marmots: Are metapopulation dynamics or range-wide declines responsible? Biological Conservation 141:1293–1309.

Griffin, S. C., M. L. Taper, R. Hoffman, and L. S. Mills. 2010. Ranking mahalanobis distance models for predictions of occupancy from presence-only data. Journal of Wildlife Management 74:1112.

Hammond, C. 2010. FWP northwest Montana terrestrial climate change species monitoring and conservation plan. Montana Fish, Wildlife and Parks, Kalispell, Montana, USA.

Harrower, W. L. 2001. Using wildlife-habitat models to estimate hoary marmot (*Marmota caligata*) abundances at regional scales. Bachelors Thesis. University of British Columbia, Vancouver, British Columbia, Canada.

Hock, R. J., and V. Cottini. 1966. Mammals of the Little Susitna valley, Alaska. American Midland Naturalist 76:325–339.

Holmes, W. G. 1979. Social behavior and foraging strategies of hoary marmots (*Marmota caligata*). Dissertation. University of Washington, Seattle, Washington.

Holmes, W. G. 1984. Predation risk and foraging behavior of the hoary marmot in Alaska. Behavioral Ecology and Sociobiology 15:293–301.

Hutto, R. L. 1985. Seasonal-changes in the habitat distribution of transient insectivorous birds in southeastern Arizona: Competition mediated? Auk 102: 120–132.

Inman, R. M., et al. 2012. Spatial ecology of wolverines at the southern periphery of distribution. Journal of Wildlife Management 76:778–792.

Karels, T. J., L. Koppel, and D. S. Hik. 2004. Fecal pellet counts as a technique for monitoring an alpine-dwelling social rodent, the hoary marmot (*Marmota caligata*). Arctic, Antarctic, and Alpine Research 36:490–494.

Lugina, K. M., P. Y. Groisman, K. Y. Vinnikov, V. V. Koknaeva, and N. A. Speranskaya. 2006. Monthly surface air temperature time series area-averaged over the 30-degree latitudinal belts of the globe, 1881–2005. In trends: a compendium of data on global change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, USA.

MacKenzie, D. I. 2006. Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. Journal of Wildlife Management 70:367–374.

MacKenzie, D. I., and L. L. Bailey. 2004. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9:300–318.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling. Academic Press, Burlington, Massachusetts, USA.

MacKenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42:1105–1114.

Maxell, B., and J. Ritter. 2013. Hoary marmot distribution modeling. Montana Natural Heritage Program, Helena, Montana, USA.

McKnight, T. L., and H. Darrel. 2000. Climate zones and types: the Köppen System. Pages 235–237 *in* Physical geography: a landscape appreciation. Prentice Hall, Upper Saddle River, New Jersey, USA.

Meny, C. M. 2012. The hoary marmot (*Marmota caligata*) in Montana: potential climate change vulnerability, distribution and gene flow. University of Montana, Missoula, Montana, USA.

Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science 322:261–264.

Morrison, S. F., and D. S. Hik. 2007. Demographic analysis of a declining pika (*Ochotona collaris*) population: linking survival to broad-scale climate patterns via spring snowmelt patterns. Journal of Animal Ecology 76:899–907.

Morrison, S. F., G. Pelchat, A. Donahue, and D. S. Hik. 2009. Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. Oecologia 159:107–116.

Mote, P. W. 2006. Climate driven variability and trends in mountain snowpack in western North America. Journal of Climate 19:6209–6220.

Murray, D. L., and S. Boutin. 1991. The influence of snow on lynx and coyote movements: Does morphology affect behavior? Oecologia 88:463–469.

Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. Coupled dynamics of body mass and population growth in response to environmental change. Nature 466:482–485.

Patil, V. P., S. F. Morrison, T. J. Karels, and D. S. Hik. 2013. Winter weather versus group thermoregulation: What determines survival in hibernating mammals? Oecologia 173:139–149.

Pederson, G. T., L. J. Graumlich, D. B. Fagre, T. Kipfer, and C. C. Muhlfeld. 2009. A century of climate and ecosystem change in western Montana: What do temperature trends portend? Climatic Change 98: 133–154.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reid, D. G., F. Bilodeau, C. J. Krebs, G. Gauthier, A. J. Kenney, B. S. Gilbert, M. C. Y. Leung, D. Duchesne, and E. Hofer. 2012. Lemming winter habitat choice: a snow-fencing experiment. Oecologia 168: 935–946.

Rézouki, C., M. Tafani, A. Cohas, A. Loison, J. M. Gaillard, D. Allainé, and C. Bonenfant. 2016. Socially mediated effects of climate change decrease survival of hibernating Alpine marmots. Journal of Animal Ecology 85:761–773.

Smithson, P., K. Addison, and K. Atkinson. 2008. Fundamentals of the physical environment. Fourth edition. Routledge, New York, New York, USA.

Sturm, M., J. P. McFadden, G. E. Liston, F. S. Chapin III, C. H. Racine, and J. Holmgren. 2001. Snow–shrub interactions in Arctic tundra: a hypothesis with climatic implications. Journal of Climate 14:336–345.

Tafani, M., A. Cohas, C. Bonenfant, J. M. Gaillard, and D. Allainé. 2013. Decreasing litter size of marmots over time: A life history response to climate change? Ecology 94:580–586.

Taulman, J. F.. 1975. An ethological study of the hoary marmot, *Marmota caligata cascadensis*. Central Washington State College, Ellensburg, Washington, USA.

Taulman, J. F. 1977. Vocalizations of the hoary marmot (*Marmota caligata*). Journal of Mammalogy 58:681–683.

Turnock, B. Y. 2016. Characterizing habitat relationships and establishing monitoring strategies for an alpine obligate. Thesis. Montana State University, Bozeman, Montana, USA.

Tyser, R. W. 1980. Use of substrate for surveillance behaviors in a community of talus slope mammals. American Midland Naturalist 104:32–38.

Van Vuren, D., and K. B. Armitage. 1991. Duration of snow cover and its influence on life-history variation in yellow-bellied marmots. Canadian Journal of Zoology 69:1755–1758.

Wheeler, H. C., J. D. Chipperfield, C. Roland, and J. C. Svenning. 2015. How will the greening of the Arctic affect an important prey species and disturbance agent? Vegetation effects on arctic ground squirrels. Oecologia 178:915–929.

Witczuk, J., S. Pagacz, and L. S. Mills. 2008. Optimising methods for monitoring programs: olympic marmots as a case study. Wildlife Research 35:788–797.

Zuur, A. F., E. N. Ieno, and G. M. Smith. 2007. Analysing ecological data. Springer, New York, New York, New York, USA.

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