HABITAT SUITABILITY AND SELECTION OF NORTHERN PACIFIC RATTLESNAKES (*CROTALUS OREGANUS OREGANUS*) AT MULTIPLE SPATIAL SCALES

By

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ABSTRACT

HABITAT SUITABILITY AND SELECTION OF NORTHERN PACIFIC RATTLESNAKES (*CROTALUS OREGANUS OREGANUS*) AT MULTIPLE SPATIAL SCALES

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Habitat modeling techniques are widely used to determine where species occur on the landscape and what habitat or environmental factors influence their presence. These techniques are particularly useful for rattlesnakes, which have life history traits that make them difficult to study in the field. Additionally, rattlesnakes like the northern Pacific rattlesnake (*Crotalus oreganus oreganus*) occupy a widespread and diverse range, making their environmental constraints difficult to determine. I used MaxEnt to create an environmental niche model (ENM) at two spatial scales to estimate where the suitable habitat for this species occurs in the Pacific Northwest and, more specifically, in coastal northern California. My results indicate selection for warmer habitats throughout the Pacific Northwest and drier environments within coastal northern California. I also examined the selection of a key aspect of the habitat of *C. o. oreganus*, the hibernaculum. I used a paired resource selection function to determine microhabitat differences between rocky outcrops used as hibernacula and outcrops that are visually similar, but unoccupied by the rattlesnakes. My top models reveal selection for outcrops with more crevices, fewer cover objects, and slopes facing due south (180° from North) for use as hibernacula. Additionally, temperatures loggers deployed at the hibernacula and their paired sites revealed that hibernacula are consistently warmer, particularly when rattlesnakes emerge in the spring. Lastly, I mapped the landslide activity within the vicinity of the hibernacula, which revealed a positive correlation between landslide presence and hibernacula. Combining these observations with the results of my models paint a comprehensive picture of where the suitable habitat for *C. o. oreganus* occurs in the Pacific Northwest.

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INTRODUCTION

Accurate knowledge of a species' habitat is critical to understanding how it is distributed across the landscape. Modeling the habitat or environmental niche of a species reveals correlations between that species' presence and certain habitat characteristics (Barrows 2011). These correlations shed light on where historical, present, and future populations of the species may occur (Barrows et al. 2008). Habitat modeling has been successfully used to locate unknown populations (Groff et al. 2014; Yousefi et al. 2015), identify potential areas of species invasions (Pyron et al. 2008), and predict the effects of climate change on species distributions (Barrows 2011). This knowledge is vital to wildlife researchers, managers, and conservationists, who often require reliable information about a species' habitat to make informed research or management decisions, particularly those managing endangered, threatened, or at-risk species (Lyet et al. 2013).

While research tends to focus on species that are already listed as threatened or endangered, many more species are at "high risk for extinction" but are not listed as threatened or endangered (Santos et al. 2006). Certain life history traits make a species susceptible to extinction including low reproductive rates, low population densities, and high degrees of habitat and/or diet specialization (Reed and Shine 2002; Lyet et al. 2013). Snakes nearly universally share these traits (Reading et al. 2010). Amongst snakes, rattlesnakes commonly have additional life history traits that make them even more susceptible to extinction, such as large body size, low dispersal, and, in high latitudes, belated maturation (Waldron et al. 2013). These traits limit the ability of rattlesnakes to adapt to a changing environment. The timber rattlesnake (*C. horridus*) once occupied all of the northeastern United States, Quebec and maritime Canada, but now has been extirpated from Maine, New Hampshire and Rhode Island, and is a species at risk in Canada (Bushar et al. 2015). Similarly, in the western United States, populations of the western rattlesnake (*Crotalus oreganus*) are thought to be in decline throughout its range (St. John 2002; Campbell and Lamar 2004). Gaining a comprehensive understanding of habitat constraints can help prevent populations falling to threatened or endangered levels.

In this study I will examine the environmental constraints of the northern Pacific rattlesnake, *Crotalus oreganus oreganus* (Ashton and de Queiroz 2001), at multiple spatial scales. Populations of this subspecies are also thought to be in decline throughout the range due to habitat loss and human persecution (St. John 2002). These rattlesnakes range from central California to southern British Columbia (Figure 1), where they occupy a diversity of habitats from the high Sierras to northern California's coastal prairies and north through high deserts and along river valleys. Throughout its range, this subspecies presence at a particular location is influenced by temperature, precipitation, elevation, and solar radiation (Campbell and Lamar 2004; Hamilton and Nowak 2009; Gienger and Beck 2011). Most of the research on this subspecies has occurred at the northernmost (Diller and Wallace 1984; Macartney and Gregory 1988; Macartney 1989; Wallace and Diller 1990; Diller and Wallace 1996; Wallace and Diller 2001; Diller and Wallace 2002; Gienger and Beck 2011; Loughran et al. 2015) and southernmost (Hersek et al. 1992;

Putman et al. 2013) portions of its range, leaving a large gap in northern California and western Oregon where its ecology and habitat are poorly understood.

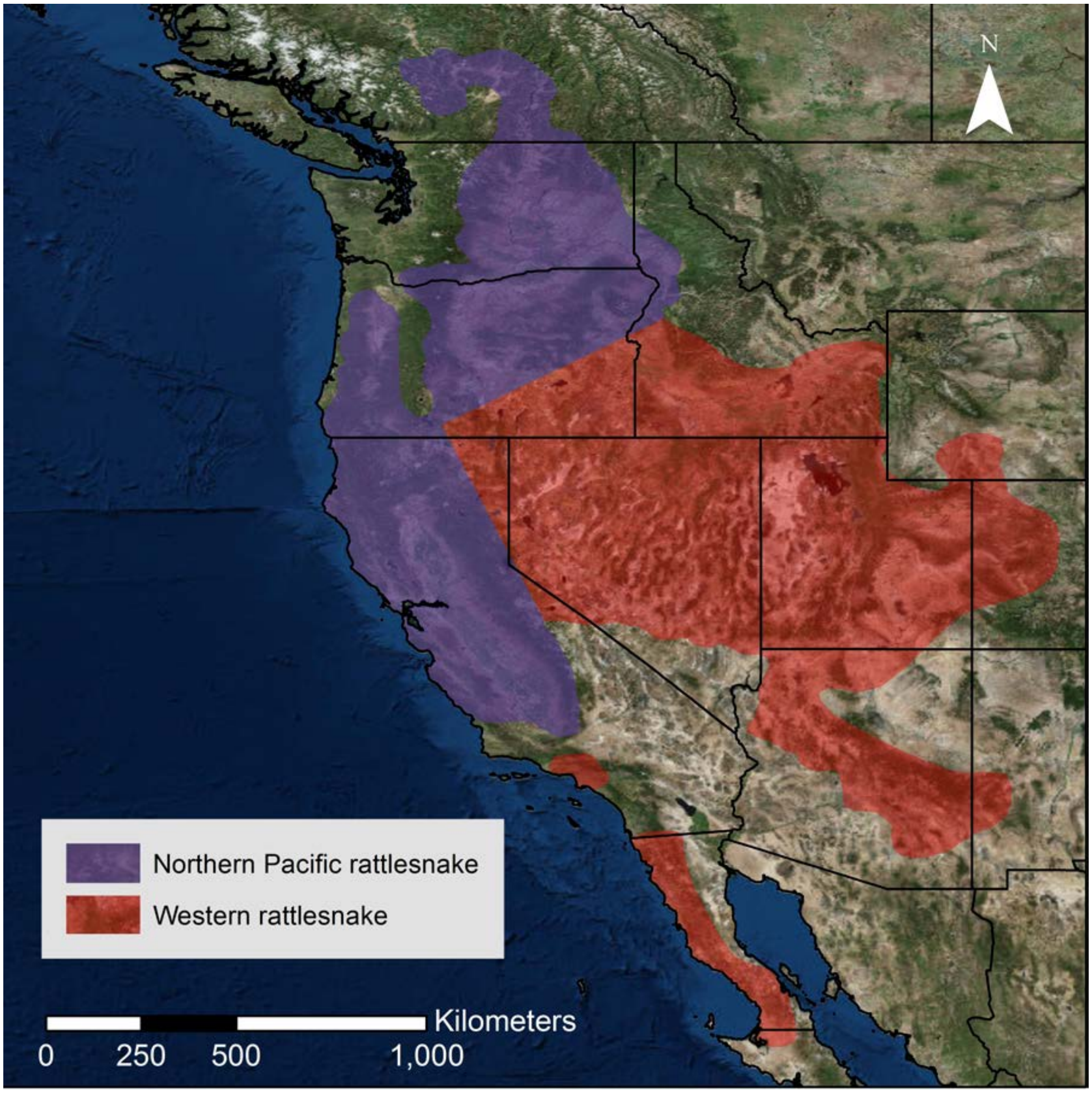

Figure 1: Ranges of the western rattlesnake (*Crotalus oreganus*) and its subspecies the northern Pacific rattlesnake (*Crotalus oreganus oreganus*). I acquired the polygon for the western rattlesnake's range from Natural Earth (http://www.naturalearthdata.com) and used an estimated range (Ashton 2001) as a guide to clip the northern Pacific rattlesnake's range from it.

Modeling habitat is especially important for these rattlesnakes because they are cryptic and independent creatures, making them difficult to locate and study (Gienger and Beck 2011). The coloration of these snakes tends to vary but generally matches with that of the local substrate (Nussbaum et al. 1983). Additionally, as sit-and-wait predators, these rattlesnakes tend to be sedentary in concealed locations during most day-to-day activities making them difficult to observe (Campbell and Lamar 2004; St. John 2002). Aside from spring emergence, when snakes can be found in large numbers at hibernacula (i.e., dens), rattlesnakes are commonly encountered individually (Clark 2007; Gienger and Beck 2011). Because of those features, studies on key aspects of their ecology, such as habitat suitability and population distributions, are relatively few when compared to those on other taxa (Santos et al. 2006). Modern habitat modeling techniques are allowing researchers and managers to explore these topics (Browning et al. 2005; Santos et al. 2006; Pyron et al. 2008; Lyet et al. 2013; Yousefi et al. 2015).

Environmental niche models (ENMs) estimate the distribution of suitable habitat on a given landscape. Maximum entropy (MaxEnt) modeling is currently the most widely used method for creating ENMs, because it consistently performs well when compared to other modeling methods (Phillips et al. 2005; Elith et al. 2006). MaxEnt seeks to estimate a probability of suitable habitat using occurrence locations for a given species and a suite of environmental predictors (Elith et al. 2011). One reason this technique is preferred over other ENM approaches, such as GARP (Genetic Algorithm for Ruleset Production; Stockwell 1999), is that it requires only presence locations for the species of interest. The use of presence-only datasets is important because using absence data may lead to misidentification of unsuitable habitat when species are unobserved rather than truly absent from an area (Baldwin 2009). Additionally, MaxEnt accounts for the complex relationships between environmental predictors, making it less susceptible to issues with spatial correlations than other environmental niche modeling methods (Phillips and Dudík 2008; Elith et al. 2011). This method also performs as well or better than other modeling methods when few presence locations are available, making it particularly useful for investigating cryptic species like rattlesnakes (Pearson et al. 2007; Yousefi et al. 2015). I utilized MaxEnt in the development of ENMs for the portion of the range of *C. o. oreganus* that has remained unstudied. By shedding light on the environmental constraints for *C. o. oreganus* in this westernmost part of its range, I hope to contribute to the understanding of the environmental niche of this species, within such a diverse suite of environments.

One reason that *C. o. oreganus* are able to occupy such an expansive range is their utilization of hibernacula, which are critical for survival, reproduction, and early life stages of all high latitude rattlesnakes. As ectotherms, it is necessary for rattlesnakes to find ways to maintain optimal body temperatures when ambient temperatures plummet during winter. Additionally, during breeding years, pregnant females will remain at hibernacula for better thermoregulation (Graves and Duvall 1993). Neonates are born near the hibernaculum and follow conspecific cues back to their hibernaculum of birth to withstand winter conditions (Clark et al. 2012). For *C. o. oreganus*, hibernacula are typically rocky outcrops with crevices that allow snakes to penetrate deep into the rock. Snakes retreat into a hibernaculum and remain dormant during the winter months, emerging in the spring as temperatures rise (Gienger and Beck 2011). In Idaho, rattlesnakes emerged in April when maximum daily temperatures reached about 16°C (Wallace and Diller 2001).

Two important phenomena are commonly seen in hibernating rattlesnakes: communal denning and high levels of philopatry (Gienger and Beck 2011). Communal denning may have evolved as an adaptation to survive harsh winter conditions, but has drastic effects on various aspects of the life history of overwintering rattlesnakes. Rattlesnakes often gather at hibernacula in relatively large numbers, leading some to think that hibernacula are rare on the landscape (Gienger and Beck 2011). However, not all hibernacula are occupied by large numbers of rattlesnakes, and instances of hibernacula occupied by one or two rattlesnakes have been recorded (Campbell and Lamar 2004; Browning et al. 2005; Hamilton and Nowak 2009). Philopatry, the propensity of an individual to return to its place of birth (Pearce 2007), is well documented in high latitude snakes such as redbelly snakes (*Storeria occipitomaculata*), racers (*Coluber constrictor mormon*), striped whip snakes (*Masticophis taeniatus taeniatus*), and Great Basin rattlesnakes (*C. o. lutosus*) (Hirth 1966; Brown and Parker 1976). Although philopatry has not been explicitly studied in *C. o. oreganus,* it is likely that it exhibits similar levels of philopatry (Gienger and Beck 2011). Timber rattlesnakes (*C. horridus*) that were relocated to a novel environment struggled to find suitable hibernacula (Reinert and Rupert 1999). If snakes are unable to establish novel hibernacula, it is necessary to find and protect areas where hibernacula are likely to exist. Environmental and physical microhabitat data collected at hibernacula can aid wildlife managers by providing a set of minimum habitat characteristics necessary for rattlesnakes to utilize a rocky outcrop as a hibernaculum.

Studies comparing hibernacula to random sites on the landscape have found that rattlesnakes select hibernacula with more vegetation (Burger et al. 1988; Havery and Weatherhead 2006), open canopies (Browning et al. 2005), lots of deep crevices, and steep, south-facing slopes (Prior and Weatherhead 1996; Gienger and Beck 2011). These features lead to more daylight sunlight and greater amounts of insolation. Additionally, rattlesnakes exhibit higher rates of mortality when emerging from hibernacula near roads (Fortney et al. 2011). However, most studies were unable to find differences between hibernacula and sites that appeared suitable but were unoccupied by snakes (Burger et al. 1988; Prior and Weatherhead 1996; Havery and Weatherhead 2006).

A use-available resource selection function (RSF) is a habitat modeling approach that is used to investigate a species' selection of habitat and habitat features. The design of a RSF study is dependent upon which level of habitat selection is being investigated: selection of geographic range, selection of home range for an individual or population, selection of habitat components within the home range, or selection of a vital resource (e.g., feeding or hibernation site) (Johnson 1980). The last level of selection is particularly useful for the study of habitat suitability of rattlesnakes, as they are known to gather only at hibernacula (Campbell and Lamar 2004; Gienger and Beck 2011).

In this study, I used MaxEnt to predict the environmental niche of *C. o. oreganus* in northwestern California and western Oregon. Mapping these models should reveal where suitable habitat occurs within the range of this subspecies. Additionally, I used a

RSF to conduct a multivariate comparison of hibernacula to unoccupied rocky outcrops. By examining the environmental constraints of this species on a regional scale and why individuals are selecting particular rocky outcrops as hibernacula, this study offers a comprehensive understanding of the suitable habitat for *C. o. oreganus* in the Pacific Northwest.

METHODS

Regional Analysis

Environmental niche models, niche-theory models, species distribution models, habitat suitability models and climate envelop models are a suite of habitat modeling techniques that attempt to estimate the distribution of suitable habitat for a given species (Elith et al. 2006). The suitability of habitat is a measure of how appropriate the area is for a given species (Peterson et al. 2011). These methods derive models by examining correlations between species presence and trends in environmental predictors (Elith et al. 2011). All habitat modeling methods are affected by the number of presence locations (Elith et al. 2006), the selection of environmental predictors (Elith et al. 2006), and the size of the study area (Phillips et al. 2005; VanDerWal et al. 2009; Barve et al. 2011).

A study area should be selected to incorporate all environmental conditions accessible by the species of interest (Barve et al. 2011); however, the size of the study area can have significant effects on the performance of ENMs (VanDerWal et al. 2009). Study areas too large can lead to the classification of more areas as suitable habitat than actually exist (i.e., type 1 error), while study areas that are too small often result in inconsistent ENMs (VanDerWal et al. 2009). Therefore, I selected two study areas for modeling suitable habitat for *C. o. oreganus* within its known range in the Pacific Northwest (Figure 2**)**. Both study areas were restricted to north of the San Francisco Bay because rattlesnakes remain active during the winter further south and therefore do not utilize hibernacula (Putman et al. 2013). The California/Oregon study area was created to incorporate all habitats available to the species. Using Natural Earth's range for *C. o. oreganus* as a guide, I drew a polygon around the portion of the range from the south shore of the San Francisco Bay north through western Oregon using the Sierra Nevada as my eastern boundary through California (Figure 2). The NorCal study area focuses only on California counties that fall within the Pacific "Coast Range" ecoregion (Omernik and Griffith 2008).

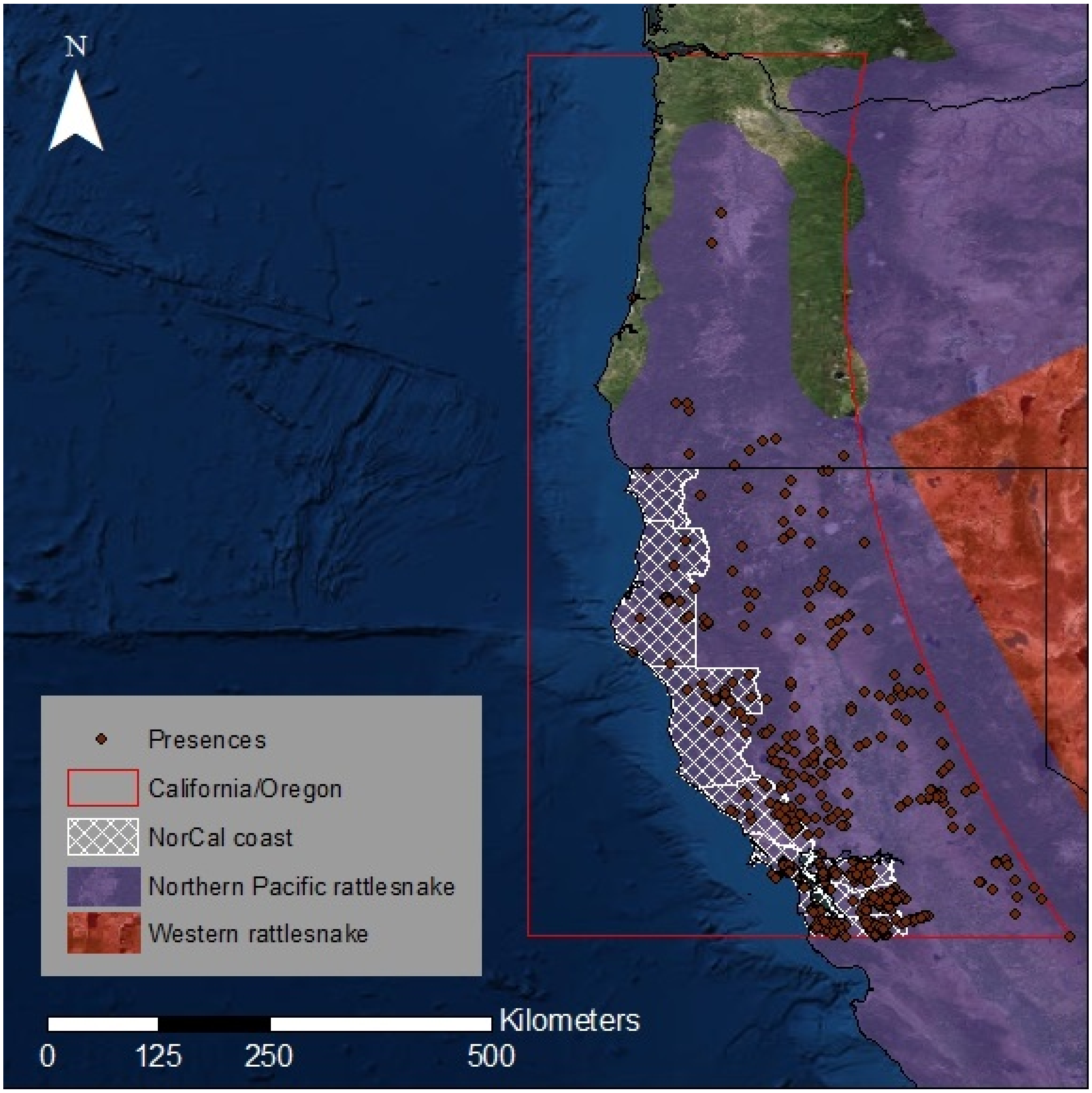

Figure 2: The California/Oregon study area was selected to encompass all the different environments *C. o. oreganus* occupies in northern California and western Oregon. The California North Coast (NorCal coast) study area includes California counties that fall within the EPA's "Coastal" eco-region (Omernik and Griffith, 2008). Notice the concentration of presence locations around the San Francisco Bay.

The environmental predictors were gathered from a variety of sources. I acquired raster data layers of maximum, mean, and minimum temperatures (˚C) for the month of

March from the WorldClim database (WorldClim 2014). March was selected because this is when mean maximum daily temperatures reach 16˚C in the coastal part of the Pacific Northwest (Wallace and Diller 2001). Therefore, March is an important month as snakes spend most of their time basking in preparation for the active season. Because slope and aspect are known to correlate with *C. o. oreganus* presence at hibernacula (Gienger and Beck 2011) these variables were also included. I gathered digital elevation models (DEMs) from the National Elevation Dataset (NED) as a measure of elevation (USGS 2015). Then, I used ArcMap's 'Aspect' and 'Slope' tools to create datasets for aspect and slope. All data layers were down-sampled to one-kilometer pixels, the size of the lowest resolution data layer. To down-sample the elevation, slope, and aspect data layers, I calculated the mean of all the data values from each of the NED's 30 meter pixels that fell within the 1 kilometer pixel.

I obtained 1,552 occurrence locations from two sources: 1,527 from the Global Biodiversity Information Facility (GBIF 2012) and 25 from personal observations (Figure 2). Due to recent taxonomic changes (Ashton and de Queiroz 2001) I used key word searches for *Crotalus oreganus oreganus, Crotalus viridis oreganus, Crotalus oreganus* and *Crotalus viridis* to gather occurrence data from GBIF. Furthermore, this subspecies is the only rattlesnake within my study areas so I felt comfortable using presence records under the species *C. oreganus* and *C. viridis* (Ashton 2001). Of the 25 data points derived from personal observations, 22 represent the hibernacula used for my microhabitat analysis while the three additional individual rattlesnakes were observed in Humboldt and Del Norte counties. The majority of presence locations were reported from the San Francisco Bay area in the southern portions of my study areas (Figure 2).

Using MaxEnt, I generated 20 ENMs from the environmental covariates for each study area. Each model was designed to answer a specific biological question relevant to *C. o. oreganus* habitat selection. As suggested, preliminary models were run using all predictors and regularization parameters of 1, 2, and 3 (Phillips 2005). Models generated using a regularization parameter of 3 were deemed to be the most biologically relevant and were used to create all the following 20 ENMs.

As models were created, a receiver operating curve (ROC) was generated and the area under the curve (AUC) values were used to determine which model was the best fit (Handley and McNeil 1982). Higher AUC values indicate a better fitting model. The number of parameters used to fit the models were also recorded. All models were compared using AIC values, which is a common model comparison statistic where lower AIC values indicate a better model (Burnham and Anderson 2002). The AIC values were used to generate ΔAIC (difference in AIC between each model and the top model) and cumulative weight (amount of weight each model contains when compared to other models in the table) statistics (Burnham and Anderson 2002; Warren and Seifert 2011). The use of AIC values has been shown to select models that are more transferable to future climate scenarios, and estimate habitat suitability better than models selected using only AUC values (Warren and Seifert 2011; Warren et al. 2014). A jack-knife approach, where each predictor was removed one at a time to generate a new set of models, was used to assess the impact of each predictor on the original model. Gains were calculated for each environmental predictor with and without the other predictors; by comparing the two I was able to determine the influence of each predictor on the model. Additionally, a cross-validation of the best model was conducted using a dataset split of 70% training, 30% testing data for 100 iterations. A robust model would have a consistent prediction of suitable habitat throughout all iterations (Plant 2012).

Microhabitat Analysis

To investigate the selection of rocky outcrops as hibernacula by *C. o. oreganus,* I utilized a special case of the RSF, a paired use-availability resource selection function (pRSF). The pRSF is a conditional (a.k.a. matched-pairs or paired) logistic regression. This special case of logistic regression is like a classic logistic regression in the sense that it seeks to model the probability of success using explanatory covariates and requires a binomial response variable (Hosmer et al. 2013). However, when using a pRSF each success (i.e., hibernacula) is paired with a failure (i.e., 'suitable' but unoccupied rocky outcrop). This pairing allows for direct comparison of the resource unit as opposed to other use-available RSF study designs that compare occupancy locations to any random location on the landscape (Thomas and Taylor 2006; Lele et al. 2013). Paired studies tend to have greater power due to their ability to reduce spatial autocorrelation within groups (Compton et al. 2002; Hosmer et al. 2013).

To collect data for my habitat selection analysis I needed to locate a number of hibernacula and suitable, but unoccupied rocky outcrops on the landscape. Fieldwork took place on south-facing slopes within the Mad River watershed near Maple Creek, California (Figure 3). Maple Creek is located approximately 20 miles from the coast. The vegetative structure of the area is a mixture of coastal prairies and mixed-oak woodlands. Maple Creek is within the central belt of the geological Franciscan complex (Aalto 1980). This location results in hillsides that are scattered with rocky outcrops that are primarily composed of graywacke, greenstone, and argillite (Dadzis 2014).

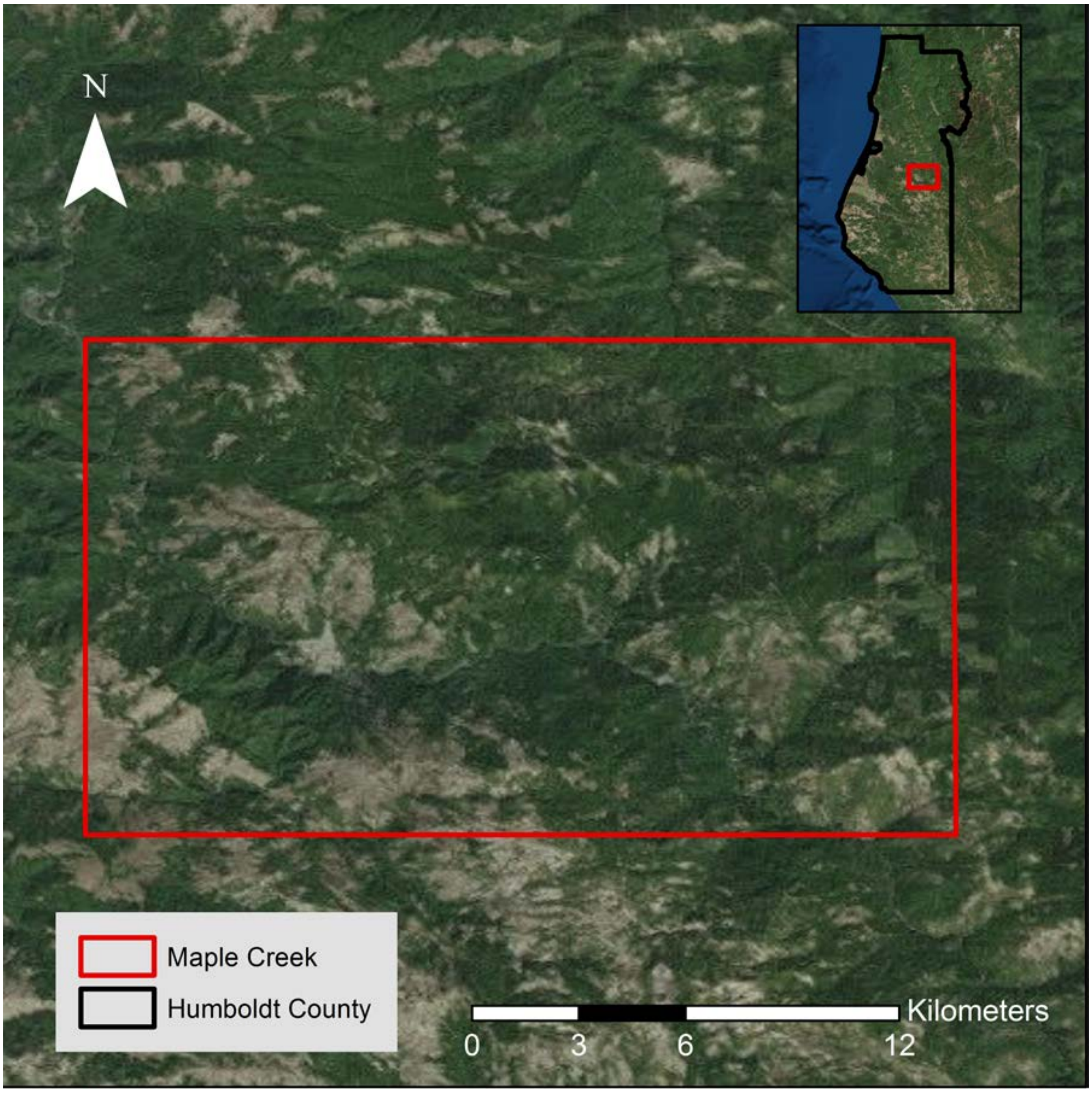

Figure 3: The study area is located near Maple Creek, CA. The locator map (top right corner) shows where Maple Creek is located in relation to the rest of Humboldt County California.

Surveys for hibernacula began on March 16, 2014, when rattlesnakes were likely to emerge (Wallace and Diller 2001). Two hibernacula were previously known to exist within the study area from surveys conducted by Dr. Sharyn Marks and Dr. Lowell Diller as part of Humboldt State University's Herpetology course (unpublished data). Green Diamond Resource Company provided aerial images of the study area (unpublished data) that served as a starting point for locating novel hibernacula. I divided the study area into five sub-regions: Graham Ridge, Upper Madrone, Lower Madrone, Garcia's Ridge, and Hunters Ranch (Figure 4). All sub-regions were restricted to areas where the majority of the habitat was open canopy. Each sub-region was established to maximize the number of rocky outcrops that could be surveyed in one day by minimizing travel distance between outcrops.

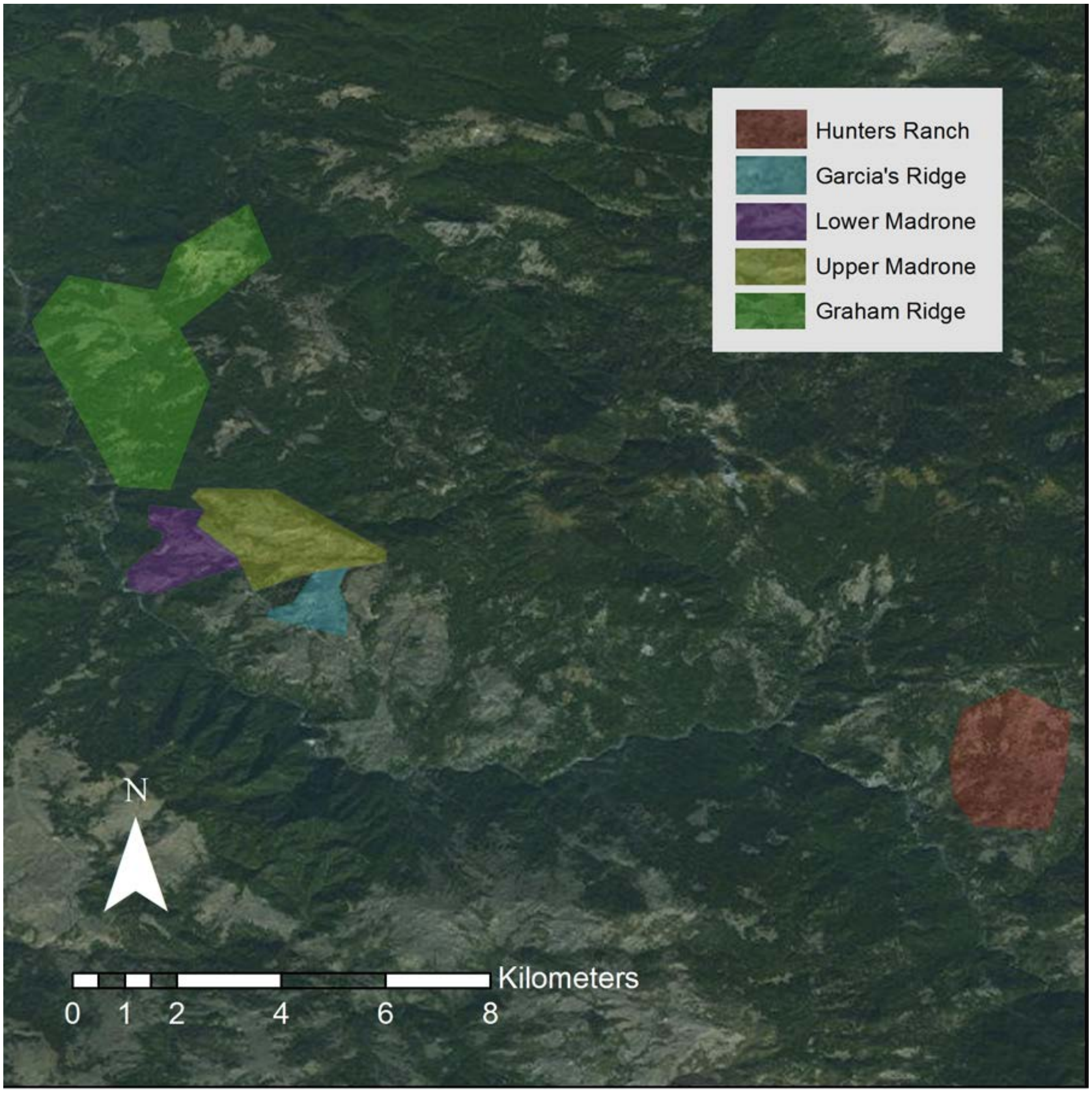

Figure 4: The five sub-regions selected for efficient surveying. Note the large separation between Hunters Ranch and the rest of the sub-regions. This gap represents private land that I lacked permission to survey.

Preliminary surveys sought to locate as many rocky outcrops as possible and assess their suitability as hibernacula. Transects were walked across each sub-region to locate rocky outcrops. Universal Transverse Mercator (UTM) coordinates were recorded on a Garmin eTrex 30 handheld GPS (Garmin Ltd., Lenexa, KS) at the most northern point of every rocky outcrop encountered. Each rocky outcrop was then ranked on a 1 to 5 scale based on an assessment of its suitability as a hibernaculum (Table 1). Outcrops would receive a rank of 5 only after being repeatedly surveyed.

Table 1: Rankings used to assign outcrop suitability as a hibernaculum. The number of outcrops breaks down the 131 outcrops by their respective ranks. Note there are no sites ranked possible (3) because they were reclassified at the end of the first field season.

Rank	**Category**	**Description**	**Number of outcrops**
1	Uninhabitable	Solid rock outcrop	37
2	Unlikely	Only shallow crevices present	44
3	Possible	Has deep crevices, but faces north or dense canopy	0
4	Likely	Has deep crevices, southern orientation, and open canopy	28
5	Hibernaculum	*C. o. oreganus* regularly observed	22

After assigning rankings and marking the locations of all the rocky outcrops in the study area, surveys were repeated to increase the chances of observing rattlesnakes. Each outcrop was surveyed every three to seven days. To determine occupancy, outcrops were searched for rattlesnakes exhibiting emergence behaviors, including basking partly emerged from crevices (i.e., gaps in the talus and/or joints in the solid rock), basking on rock surfaces near a crevice (within 1 meter), or basking while huddled with other individuals. Hibernaculum status (rank 5) was assigned to an outcrop only if it met one of these three criteria:

1. Rattlesnakes were observed at the same crevice(s) within the same rocky outcrop during emergence seasons in consecutive years.

2. Within a single emergence season, rattlesnakes were observed basking within 1 meter of the same crevice on consecutive surveys.
3. Within a single emergence season, multiple rattlesnakes were observed basking on consecutive surveys within the outcrop.

The first season of emergence surveys ended on May 20, 2014 when rattlesnakes were no longer regularly encountered at hibernacula.

Unfortunately, preliminary surveys of the Hunters Ranch were delayed because I was not granted permission to access the sites until June 2014. Surveys were conducted throughout June. Mating occurs near the female's hibernaculum shortly after males disperse, which would make it difficult to determine if a rattlesnake encountered at an outcrop emerged from that outcrop (Hayes 1986). Therefore, no conclusions about hibernaculum status of Hunters Ranch were made at that time.

At the end of the first field season 131 rocky outcrops (including 21 hibernacula) were marked and ranked (Table 1). A pool of suitable but unoccupied rocky outcrops was generated as follows. First, the 1 to 5 scale of habitat suitability was reclassified as: unsuitable, suitable, or hibernaculum. Unsuitable sites contained all outcrops ranked as 1 or 2. All rocky outcrops ranked as 3 or 4 were classified as 'suitable'. Second, the 'suitable' outcrops were separated into five pools based on their sub-region, and a random number generator was used to select suitable sites equal to the number of hibernacula within each sub-region. Each hibernaculum was then paired with the nearest selected 'suitable' outcrop. The selected 'suitable' outcrops will hereafter be referred to as paired sites.

A second season of emergence surveys began on February 28, 2015. The purpose of the second season was to confirm that outcrops classified as hibernacula were occupied by *C. o. oreganus* and that suitable pairs were not. Only hibernacula and paired sites were surveyed during these emergence surveys. However, in the event that one of the paired sites had rattlesnakes present during this season, two additional 'suitable' outcrops were surveyed within each sub-region. One paired site was found to have rattlesnakes present during the second field season bringing the total number of hibernacula to 22 (Table 2). No outcrops were surveyed within the Graham Ridge sub-region during 2015, because no hibernacula were found there during the first field season (Table 2).

Table 2: The 22 hibernaculum broken down by sub-region.

Sub-region	**Number of Hibernacula**
Graham Ridge	0
Lower Madrone	3
Upper Madrone	5
Garcia's Ridge	8
Hunters Ranch	6

Multivariate models for selection of rocky outcrops as hibernacula were created using a pRSF. The response variable was rocky outcrop occupancy: occupied (1), unoccupied (0). The initial covariates selected were based on previous studies and were known to encourage snake presence at hibernacula: increased density of cover objects (e.g., woody debris or loose vegetation) (Burger et al. 1998), less canopy (Campbell and Lamar 2004), greater distance from roads (Fortney et al. 2011), steep, south-facing slopes, and increased crevice density (Gienger and Beck 2011). Additionally, I included the following microhabitat variables that had not been previously investigated: area of the rocky outcrop, visual estimate of percentage of rock not covered by mosses or lichens, distance to nearest water source, distance to the nearest hibernaculum, and an estimate of habitat diversity (Table 3). Data for all of the covariates were gathered during July and August 2014, after *C. o. oreganus* had dispersed for the summer.

Table 3: All covariates measured at each hibernaculum including units and the measurement tool.

Measurement	**Tool**	**Units**
Slope	Clinometer	Percentage
Aspect	Compass	Degrees
Area	ArcGIS: 'Calculate Geometry' tool	Meters squared
Canopy cover	Spherical densiometer	Mean percentage for all grids
Crevice density	Count	Mean number per grid
Cover object density	Count	Mean number per grid
Distance to road	ArcGIS: 'Distance' tool	Meters
Distance to water	ArcGIS: 'Distance' tool	Meters
Distance to nearest hibernacula	ArcGIS: 'Distance' tool	Meters
Bare rock	Visual estimate	Percentage of rock surface not covered by moss or lichen
Shannon Index	Calculated from habitat estimates below	Unit of habitat diversity
Large talus	Visual estimate	Percentage of area covered
Medium talus	Visual estimate	Percentage of area covered
Small talus	Visual estimate	Percentage of area covered
Grass	Visual estimate	Percentage of area covered
Cover objects	Visual estimate	Percentage of area covered
Bare soil	Visual estimate	Percentage of area covered

For the purposes of this study, I defined the hibernaculum or paired site as the entire rocky outcrop plus any other outcrops within five meters of the edge of the original outcrop. Slope and aspect were measured using a clinometer and Brunton compass (Brunton Inc., Louisville, CO). These measurements were taken at the highest and lowest points of the perimeter (i.e., at the edge of the five meter buffer) of each site. I used my

GPS to record UTM waypoints at the extreme points of the site. Later, ArcGIS was used to connect the waypoints to create a polygon that represented the entire hibernaculum. Then, the area of that polygon was calculated using the ArcGIS 'Calculate Geometry' tool. Distance measurements to roads, water, nearest hibernaculum, and paired sites were calculated using the ArcGIS 'Distance' tool from the northernmost point of each site. All distances were measured to the nearest whole meter (Table 3).

I estimated habitat diversity using a Shannon diversity index (Shannon and Weaver 1949). This index accounts for how many different types of habitat exist within each hibernaculum, and how evenly these different habitat types are distributed across the hibernaculum (Shannon and Weaver 1949; Spellerberg and Fedor 2003). The habitat characteristics (solid rock, large talus, medium talus, small talus, grass, cover objects, and bare soil) were quantified using a percentage category (i.e., <1, 1-10, 11-25, 26-50, 51-75, 76-90, 90-99, >99) such that all the habitat characteristics within a site would sum to 100. These variables were later reduced to a single covariate, the Shannon Index.

To get an accurate measurement of the number of deep crevices (≥10cm) (Gienger and Beck 2011), the number of cover objects, and the percent canopy cover, the sites were broken down into five by five meter grids. The mean number of crevices and cover objects per grid were calculated to provide crevice and cover object density measurements. The percent canopy cover was gathered using a spherical densiometer from the center of each grid. A mean of all canopy cover measurement was used as a rough estimate of total canopy cover over the site (Table 3).

Before generating the pRSF models, all covariates were examined for covariance amongst each other and for normal distributions. I used Pearson's correlation values to identify covariance (Hauke and Kossowski 2011). The habitat estimate of cover objects was strongly correlated with cover object density (Pearson's correlation value of 0.7) and the habitat characteristic estimate of medium talus showed some correlation with crevice density (Pearson's correlation value of 0.44). Cover object density and crevice density were more accurately measured, so I removed cover objects and medium talus from the models.

Once correlated covariates were eliminated and transformations were made the pRSF models were generated. The first model included all covariates cited in the literature as influencing use of a rocky outcrop by *C. o. oreganus* as a hibernaculum: slope, aspect, crevice density (Gienger and Beck 2011), cover object density (Burger et al. 1988), canopy cover (Campbell and Lamar 2004), and distance to road (Fortney et al. 2011). Next, the least significant covariate in the model was removed and a new model was created. This process continued until only two covariates remained. Akaike Information Criteria corrected for small sample sizes (AICc) was used to compare models. The best model has the lowest AICc value (Hurvich and Tsai 1989). After the best model was determined, the novel covariates I measured were added one at a time to try to improve the best model. An AICc table was used to record and compare the AICc from each model. The difference in AICc values and the weight of each model was calculated using the same method as used for the ENMs.

To investigate potential thermal differences between hibernacula and paired sites, two Maxim DS1921Z-F5 temperature data-loggers (Embedded Data Systems LLC, Lawrenceburg, KY) were placed at all hibernacula and paired sites. I programmed each temperature logger to record a temperature every four hours daily at 1:00 AM, 5:00 AM, 9:00 AM, 1:00 PM, 5:00 PM, and 9:00 PM. Temperature loggers were deployed on November 18, 2014 and retrieved on June 24, 2015. One of each pair of temperature loggers was deployed in either a RS1 Solar Shield (Onset Computer Corp. Bourne, MA) or a homemade solar shield, which was hung off of a t-post one meter off the ground. The solar shields ensured that the temperature loggers were recording the ambient air temperature and were unaffected by solar radiation capabilities of the temperature logger. The other temperature logger was placed directly on the rock surface where rattlesnakes were likely to bask. A solar shield did not cover the surface logger because this logger was intended to get an estimate of the temperature on the basking surface. Differences between hibernacula and paired sites were analyzed using simple significance tests on summary statistics from each time group.

Geological Investigation

Since *C. o. oreganus* are selecting specific rocky outcrops, I wanted to investigate if there were differences in the geological make-up of hibernacula and paired sites. Eddy Dadzis, then a Geology undergraduate at Humboldt State University (HSU), investigated the lithology of six hibernacula and six paired sites in the Lower and Upper Madrones.

He examined thin slices from each rocky outcrop and characterized the composition of each slice by denoting percentages of different rock types within each slide (Dadzis 2014). In addition, Dr. Mark Hemphill-Haley led a group of HSU undergraduates to take strike-dip measurements (Marshak 2009) and make observations at the hibernacula and paired sites in the Lower Madrone on April 2, 2015.

While at the field sites, Dr. Hemphill-Haley observed that all of the hibernacula and paired sites appeared to be located on the head scarps of landslides. There are many types of landslides, but a combination of rotational slumps and earth flows were most commonly observed in Maple Creek. Rotational slumps are failures that occur in cohesive blocks leaving a well-defined sheer plane, whereas earth flows don't leave a prominent sheer plane (Bierman and Montgomery 2014**)**. These blocks tend to disperse into less cohesive flows as they extend downslope from their origin. From this point forward when I refer to a landslide I am discussing slumps. These landslides are easily recognized because they leave behind one or a series of well-defined head scarps, often along a curved surface (Bierman and Montgomery 2014**)**. I used Google Earth to search for the landslides in Maple Creek **(**Mihir and Malamud 2014**)**. When detected, landslides were mapped to test for correlation between landslide activity and hibernaculum presence.

RESULTS

Regional Analysis

I generated 26 ENMs for each study area. The best model for California/Oregon accounted for 99.96% of the weight in the table and contained four environmental predictors: minimum temperature for March, maximum temperature for March, mean precipitation for March, and elevation (Table 4). The habitat suitability map produced by this model does a good job of identifying areas with more open vegetative structures (e.g., prairies) while discriminating against densely forested regions (Figure 5). The results of the jack-knife test indicated that the temperature predictors had the most influence on the model, followed by precipitation, and then elevation (Figure 6). Both temperature predictors showed positive correlations with habitat suitability, whereas precipitation had a negative correlation with habitat suitability (Figure 7). More suitable habitat occurred in areas above 500 meters in elevation (Figure 7).

Table 4: AIC values of each model made for the CA/OR study area, the difference between each model's AIC and the lowest AIC (ΔAIC), and the weight of each model's AIC value. Additionally, AUC values and the number of parameters used to create each model are reported. Predictor codes: minimum (Tmin), mean (Tmean), and maximum (Tmax) temperatures (°C) for March, mean precipitation (Precip, millimeters) for March, Slope (%), Aspect (°), and Elevation (meters).

Model	**AIC**	**ΔAIC**	**Weight**	**AUC**	**# Parameters per model**
Tmin + Tmax + Elevation + Precip	10616.8	0.0	0.996	0.854	54
Tmin + Tmax + Precip	10644.2	27.4	0.000	0.853	53
Tmean + Precip	10650.8	34.0	0.000	0.846	54
Tmean	10650.8	34.0	0.000	0.846	54
Tmean + Precip + Elevation	10650.8	34.0	0.000	0.846	54
Tmean + Elevation + Aspect + Slope + Precip	10656.2	39.4	0.000	0.846	56
Tmin + Elevation + Aspect + Slope + Precip	10659.5	42.7	0.000	0.843	61
Tmin + Elevation	10660.2	43.4	0.000	0.844	61
Tmin + Precip	10660.2	43.4	0.000	0.844	61
Tmin	10660.2	43.4	0.000	0.844	61
Tmin + Tmax + Elevation + Aspect + Slope + Precip	10664.8	48.0	0.000	0.853	78
Tmin + Slope + Aspect + Elevation	10712.9	96.1	0.000	0.834	42
Tmax + Precip	10714.2	97.4	0.000	0.839	74
Tmax	10714.2	97.4	0.000	0.839	74
Tmax + Elevation + Aspect + Slope + Precip	10742.5	125.7	0.000	0.839	87
Tmin + Tmax + Aspect + Slope + Precip	10752.9	136.1	0.000	0.825	60
Tmin + Tmax + Slope + Precip	10752.9	136.1	0.000	0.825	60
Tmin + Tmax + Aspect + Precip	10786.4	169.6	0.000	0.825	78
Tmean + Precip + Aspect	10809.7	192.9	0.000	0.806	58
Tmean + Precip + Slope + Aspect	10809.7	192.9	0.000	0.806	58
Tmean + Precip + Slope	10828.3	211.4	0.000	0.806	67
Tmin + Slope	10888.0	271.2	0.000	0.786	57
Tmin + Aspect	10894.2	277.4	0.000	0.786	60
Tmin + Slope + Aspect	10999.1	382.3	0.000	0.758	60
Elevation + Slope + Aspect	11094.7	477.9	0.000	0.680	33
Slope + Aspect	11200.8	584.0	0.000	0.568	32

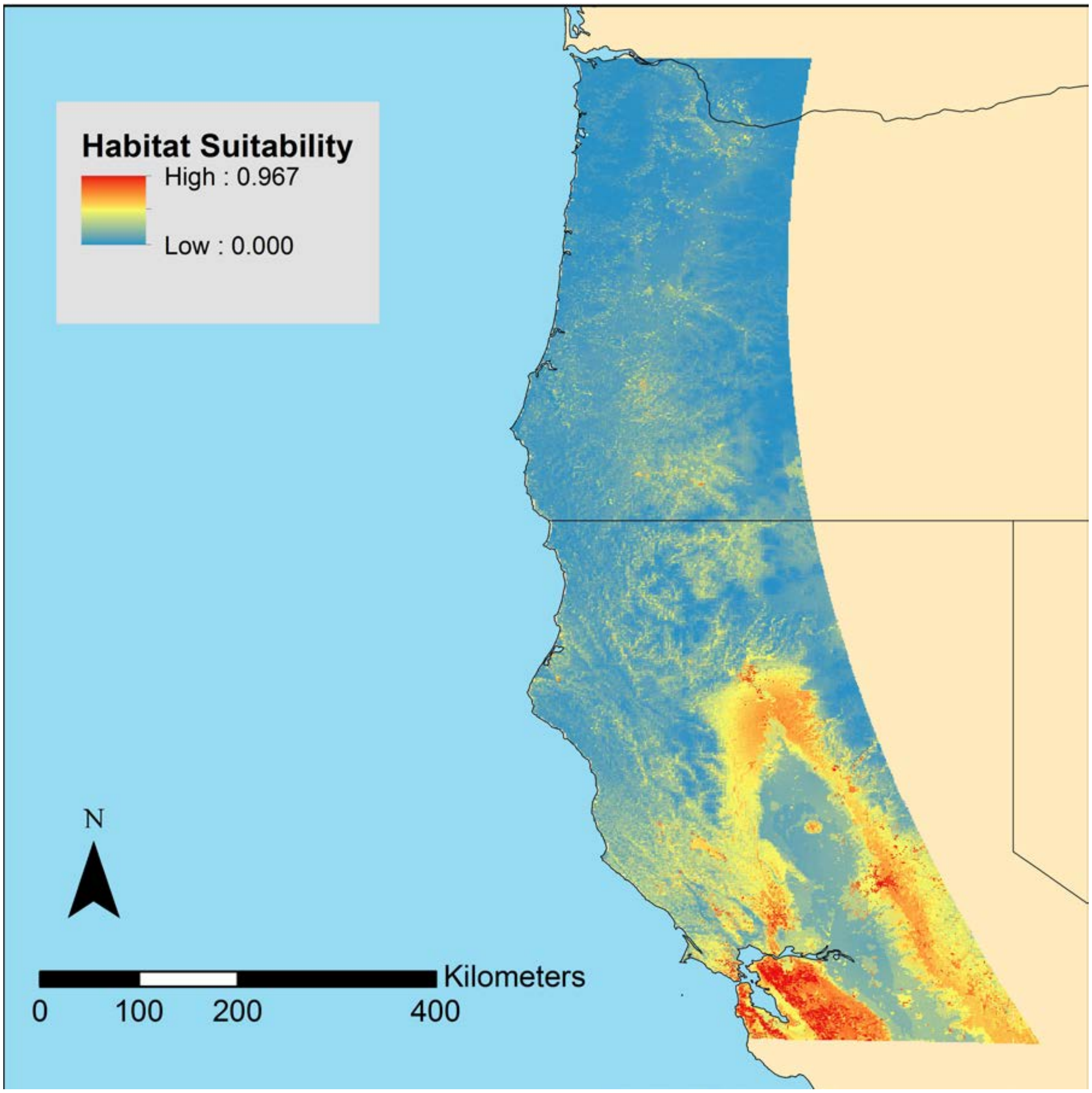

Figure 5: Habitat suitability map produced by the best model from the California/Oregon study area.

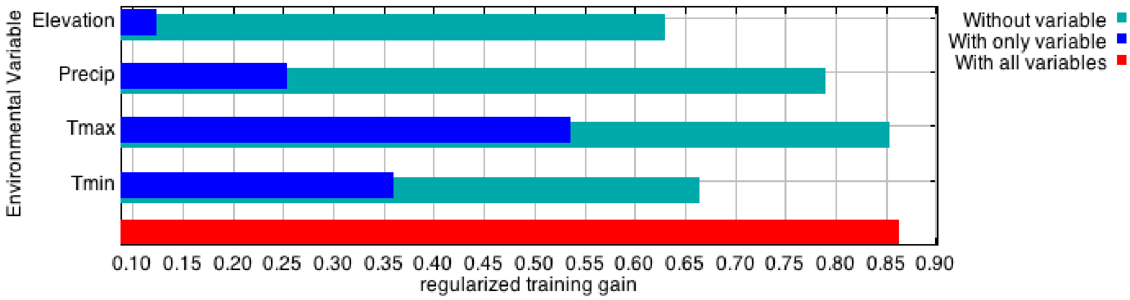

Figure 6: Results of the jackknife test performed on the training dataset. The jackknife test shows how much every predictor affects the model by removing each predictor individually and creating a new model (Burnham and Anderson 2002). Predictor codes: minimum temperature (Tmin), maximum temperature (Tmax), and mean precipitation (Precip) for March, and Elevation.

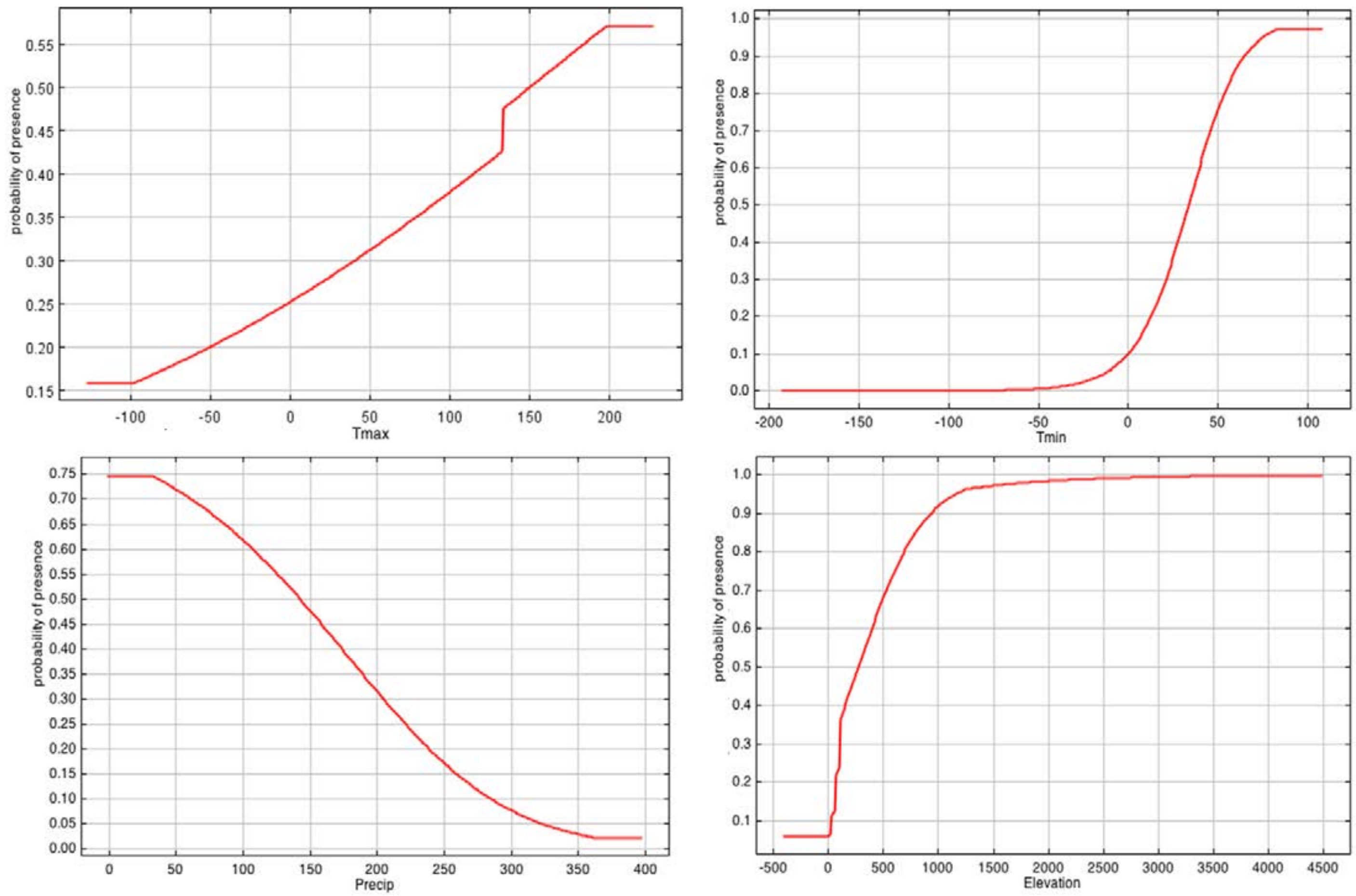

Figure 7: Response curves for all the predictors used in the best model for the California/Oregon study area. Predictor codes: minimum temperature (Tmin, °C*10), maximum temperature (Tmax, °C*10), and mean precipitation (Precip, millimeters) for March, and Elevation (meters).

Of the 26 ENMs produced for the NorCal coast study area, the best model accounted for 99.60% of the weight in the AIC table (Table 5). This model contained the same predictors as the best model for the California/Oregon study area: minimum temperature for March, maximum temperature for March, mean precipitation for March, and elevation (Table 5). Again, the model did a good job discriminating against densely forested areas and identifying that suitable habitat occurs in areas with open canopies (Figure 8). However, mean precipitation for March was the main driver of this model (Figure 9), and showed a negative correlation with habitat suitability (Figure 10). The temperature predictors had the next greatest effects (Figure 9) and showed positive correlations with habitat suitability (Figure 10). The elevation predictor had the least effect and revealed that habitat suitability steadily increased with elevation until it plateaued around 20 meters (Figure 10).

Table 5: AIC values of each model made for the CA/OR study area, the difference between each model's AIC and the lowest AIC (ΔAIC), and the weight of each model's AIC value. Additionally, AUC values and the number of parameters used to create each model are reported. Predictor codes: minimum (Tmin), mean (Tmean), and maximum (Tmax) temperatures (°C) for March, mean precipitation (Precip, millimeters) for March, Slope (%), Aspect (°), and Elevation (meters).

Model	**AIC**	**ΔAIC**	**Weight**	**AUC**	**# Parameters per model**
Tmin + Tmax + Elevation + Precip	4958.7	0.0	0.996	0.782	50
Tmin + Tmax + Elevation + Aspect + Slope + Precip	4969.8	11.0	0.004	0.790	56
Tmean + Precip	4983.5	24.8	0.000	0.786	60
Tmean	4983.5	24.8	0.000	0.786	60
Tmean + Precip + Elevation	4983.5	24.8	0.000	0.786	64
Tmax + Precip	4986.5	27.8	0.000	0.778	60
Tmax	4986.5	27.8	0.000	0.778	60
Tmin + Elevation	4986.5	27.8	0.000	0.792	64
Tmin + Precip	4986.5	27.8	0.000	0.792	64
Tmin	4986.5	27.8	0.000	0.792	64
Tmax + Elevation + Aspect + Slope + Precip	4998.6	39.9	0.000	0.779	66
Tmean + Elevation + Aspect + Slope + Precip	5001.3	42.5	0.000	0.786	69
Tmin + Tmax + Aspect + Precip	5003.6	44.9	0.000	0.765	45
Tmean + Precip + Slope	5013.6	54.8	0.000	0.769	49
Tmean + Precip + Aspect	5015.5	56.8	0.000	0.770	50
Tmean + Precip + Slope + Aspect	5015.5	56.8	0.000	0.770	50
Tmin + Elevation + Aspect + Slope + Precip	5018.6	59.9	0.000	0.792	80
Tmin + Aspect	5023.2	64.4	0.000	0.766	52
Tmin + Slope_+ Aspect	5023.2	64.4	0.000	0.766	52
Tmin + Tmax + Aspect + Slope + Precip	5028.3	69.5	0.000	0.767	57
Tmin + Tmax + Slope + Precip	5028.3	69.5	0.000	0.767	57
Tmin + Tmax + Precip	5028.3	69.5	0.000	0.767	57
Tmin + Slope	5041.1	82.4	0.000	0.765	61
Tmin + Slope + Aspect + Elevation	5130.6	171.8	0.000	0.716	51
Elevation + Slope + Aspect	5229.1	270.4	0.000	0.572	42

Model	AIC	ΔAIC	Weight	AUC	# Parameters per model
Slope + Aspect	5266.5	307.8	0.000	0.552	51

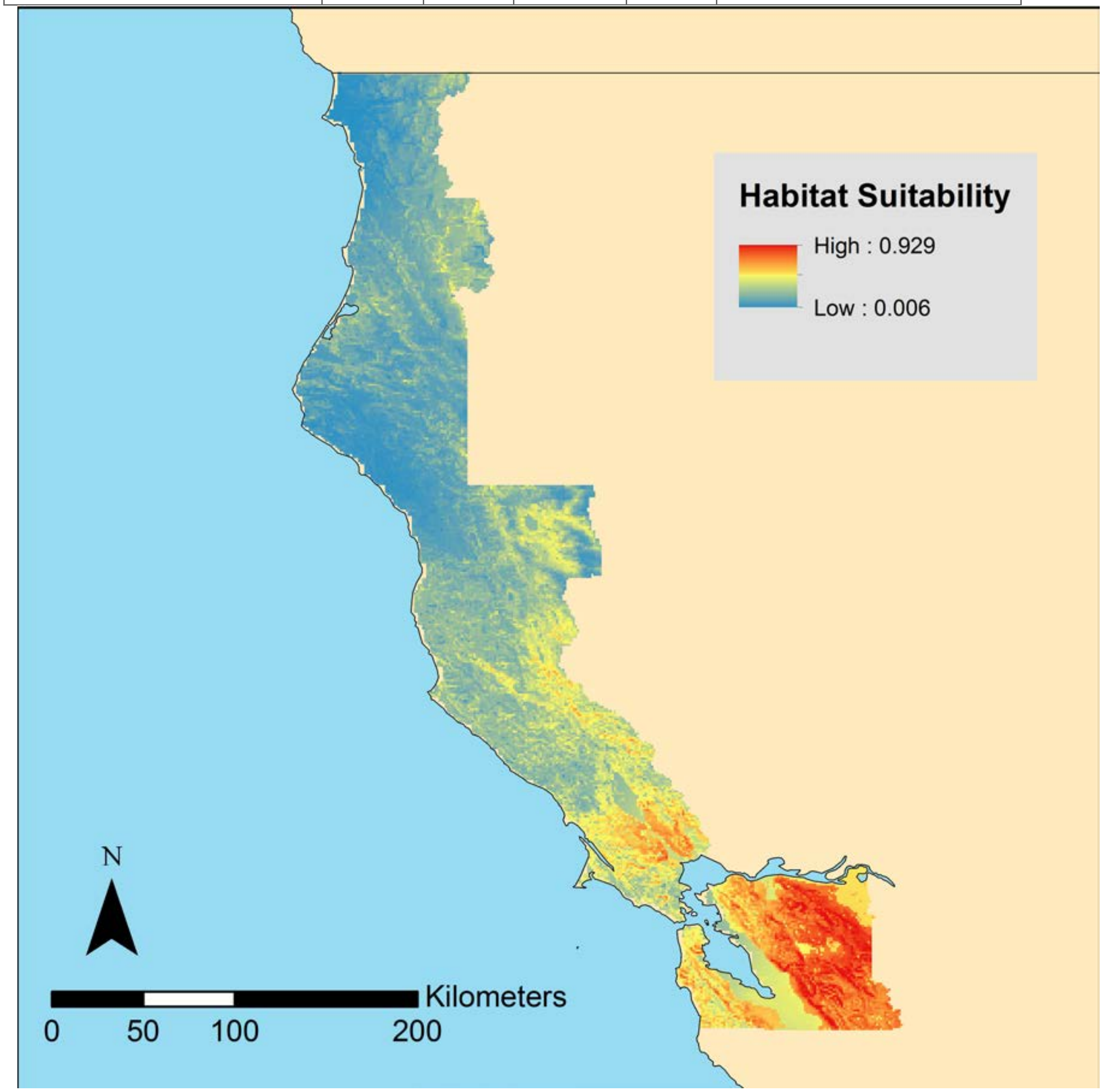

Figure 8: Habitat suitability map produced by the best model for the NorCal coast study area.

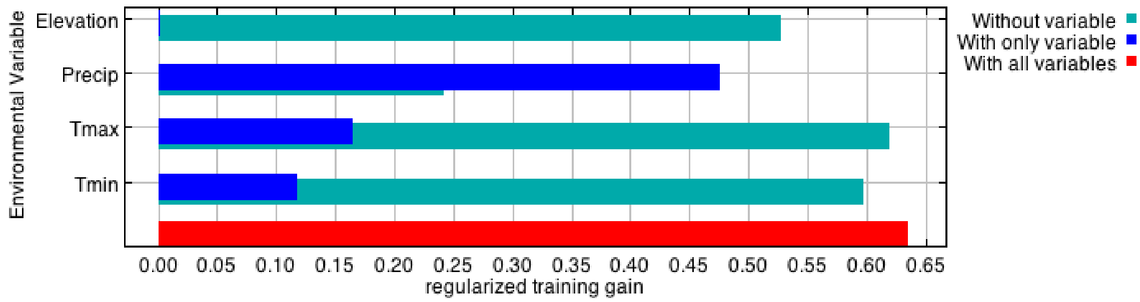

Figure 9: Results of the jackknife test performed on the training dataset. The jackknife test shows how much every predictor affects the model by removing each predictor individually and creating a new model (Burnham and Anderson 2002). Predictor codes: minimum temperature (Tmin), maximum temperature (Tmax), and mean precipitation (Precip) for March, and Elevation.

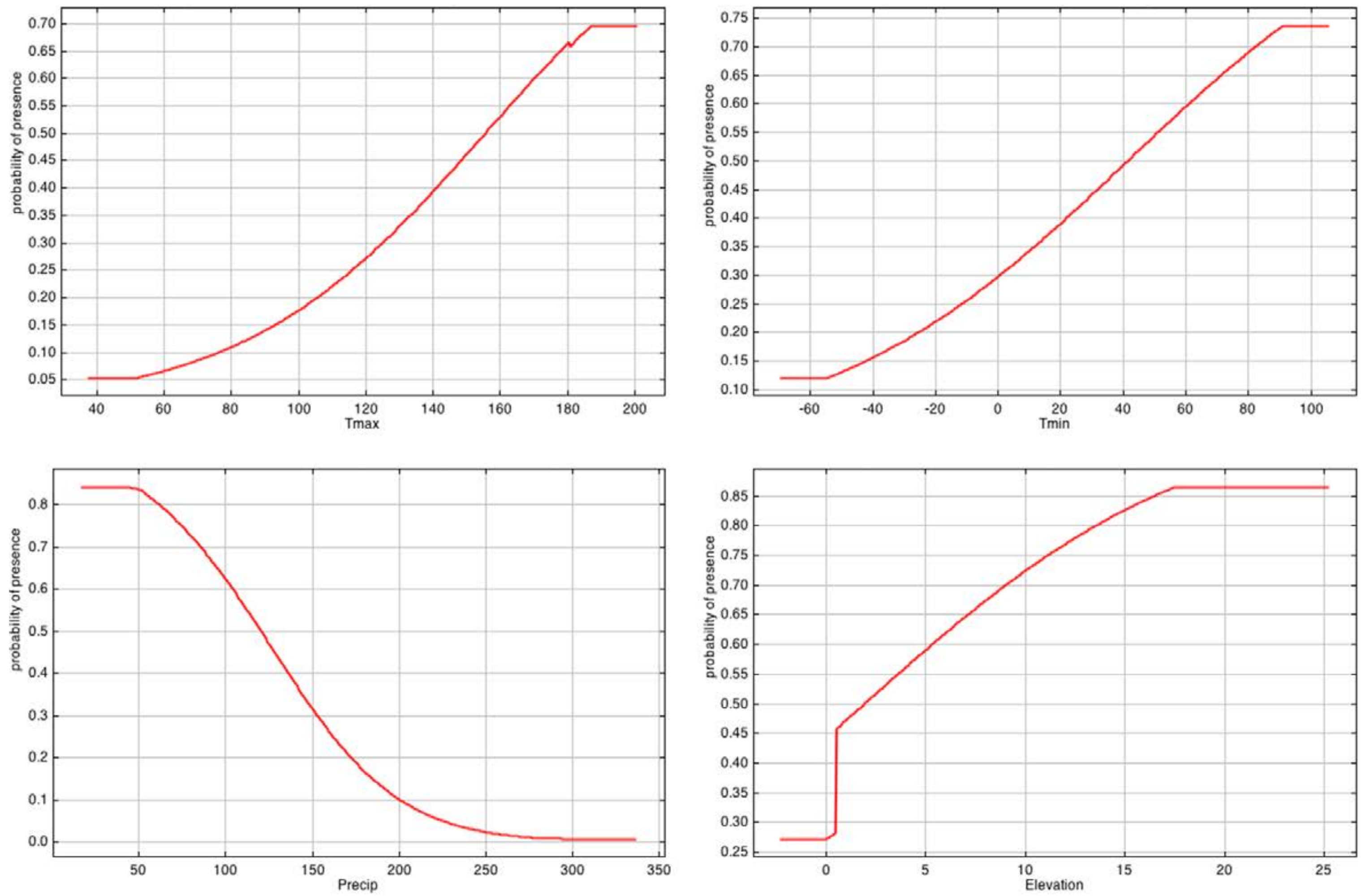

Figure 10: Response curves for all the predictors used in the best model for the NorCal coast study area. Predictor codes: minimum temperature (Tmin, °C*10), maximum temperature (Tmax, °C*10), and mean precipitation (Precip, millimeters) for March, and Elevation (meters).

The ROC plots for the top models from both study areas revealed consistently high AUC values and low omission error indicating good predictive performance. The cross validation of the best model from the California/Oregon study area had a mean AUC value of 0.847 (standard deviation=0.008) and a mean omission error of 0.093. Similarly, results of the best NorCal coast's cross validation had a mean AUC of 0.782 (standard deviation=0.012) and a mean omission rate of 0.109. The low omission error rates and standard deviations of the mean AUC values show high precision in the best models.

Microhabitat Analysis

Fifteen pRSF models were created (Table 6). Of the five models that were derived from covariates implicated by previous studies, the best (based on AICc values) included three variables: aspect, crevice density, and cover object density (Table 6). This model showed that presence of slopes facing due south (180° from North), more crevices, and fewer cover objects encourage rattlesnake use of a rocky outcrop as a hibernaculum. Four models with added novel covariates were better than the best model derived from covariates from the literature (Table 6). These models included the same three variables as the best model from the literature (aspect, crevice density, and cover object density) as well as four novel covariates (presented in order of lowest to highest AICc values): percentage of large talus, percentage of bare soil, the Shannon Index, and hibernaculum area (Table 6).

Table 6: AICc table of all 15 paired RSF models. The ΔAICc values represent the difference between each models AICc value and the lowest AICc. The Akaike weight of each model is also included. Models preceded by an asterisk (*) are derived only from covariates found in the literature.

Model	**AICc**	**ΔAICc**	**Weight**
Aspect, Crevice density, Cover object density, Percent large talus	25.32	0	0.43
Aspect, Crevice density, Cover object density, Percent bare soil	27.05	1.73	0.18
Aspect, Crevice density, Cover object density, Shannon Index	28.84	3.52	0.07
Aspect, Crevice density, Cover object density, Hibernaculum area	29.32	4.01	0.06
*Aspect, Crevice density, Cover object density	29.41	4.09	0.06
Aspect, Crevice density, Cover object density, Percent bare rock	29.48	4.17	0.05
Aspect, Crevice density, Cover object density, Percent solid rock	29.83	4.52	0.04
Aspect, Crevice density, Cover object density, Percent small talus	31.77	6.45	0.02
Aspect, Crevice density, Cover object density, Percent grass	31.80	6.49	0.02
*Aspect, Slope, Crevice density, Cover object density, Canopy cover	31.82	6.50	0.02
Aspect, Crevice density, Cover object density, Distance to nearest hibernaculum	31.82	6.50	0.02
Aspect, Crevice density, Cover object density, Distance to water	31.83	6.51	0.02
*Aspect, Crevice density	32.03	6.72	0.01
*Aspect, Crevice density, Cover object density, Canopy cover	32.87	7.56	0.01
*Aspect, Slope, Distance to nearest road, Crevice density, Cover object density, Canopy cover	36.72	11.40	0.00

The top two models accounted for the majority of the weight in the AICc table (Table 6). Both of these top models contained the covariates aspect, crevice density, and cover object density. The top model (which accounted for 43% of the weight of the AICc table) also contained percentage of large talus, and the second best model (which accounted for 18% of the weight) included percentage of bare soil. These top two models indicated that *C. o. oreganus* select as hibernacula those rocky outcrops that occur on slopes facing due south, have higher crevice density, and a lower number of cover objects (Table 7). These results concur with those from the best model based on the literature. My finding that hibernacula contain greater amounts of large talus (Table 7) contradicts with prior studies that show that medium talus is associated with hibernacula (Gienger and Beck 2011) results that medium talus is associated with hibernacula. The positive correlation between bare soil (Table 7) and hibernacula is a novel result.

Table 7: The estimated coefficients from the top two models, which account for about 61% of the weight of the AICc table. The covariates from the best pRSF model are listed in the column labeled 'Best model'. The column labeled '2nd Model' lists the covariates found in the second best pRSF model.

Best Model	**Estimated Coefficient**	**2nd Model**	**Estimated Coefficient**
Aspect	-0.039	Aspect	0.026
Crevice Density	0.469	Crevice Density	0.325
Cover Object Density	-3.274	Cover Object Density	-2.124
Percentage of Large Talus	2.482	Percentage of Bare Soil	0.116

The data from the temperature loggers revealed consistently higher temperatures at hibernacula compared to paired sites (Tables 8 & 9). Unfortunately, I was only able to retrieve temperature data from 65 of the 80 temperature loggers: 33 ambient loggers (19 from hibernacula, 14 from paired sites) and 32 surface loggers (19 from hibernacula, 13 from paired sites). The remaining 15 temperature loggers either went missing during deployment or were corrupted so the data were irretrievable. Most of the temperature loggers revealed no significant difference in temperatures (Tables 8 & 9), but I found that all the significantly different times showed warmer temperatures at hibernacula except for the minimum surface 1:00 PM temperature logger (Table 9). The greatest difference between ambient and surface loggers indicated warmer temperatures occurred at 9:00 PM for maximum temperature (Tables 8 & 9). Interestingly, plots of these temperature logger data reveal that the greatest differences between hibernacula and paired sites occurred between February and May when the snakes were emerging from hibernacula (Figures 11 & 12). However, the duration of the warmer period began earlier, in January for the surface loggers (Figures 11 & 12).

Table 8: Summary statistics and results of t-tests for ambient temperature logger data taken from October 2014 to June 2015. The Δmeans values are the absolute value of the difference between hibernacula and paired site means. P values that are less than 0.05 are considered to be significantly different (Ramsey and Schafer 2002).

Time	Measure	Hibernacula mean (°C)	Paired sites mean (°C)	Δmeans	p
1:00 AM	Min	4.934	4.805	0.129	0.686
1:00 AM	Mean	8.317	8.127	0.190	0.587
1:00 AM	Max	12.181	11.137	1.044	0.014
5:00 AM	Min	4.724	4.446	0.278	0.259
5:00 AM	Mean	8.018	7.812	0.206	0.484
5:00 AM	Max	11.030	10.572	0.458	0.242
9:00 AM	Min	6.092	5.638	0.454	0.259
9:00 AM	Mean	9.579	9.178	0.401	0.334
9:00 AM	Max	13.332	12.661	0.671	0.157
1:00 PM	Min	11.910	11.726	0.184	0.707
1:00 PM	Mean	15.215	14.732	0.483	0.307
1:00 PM	Max	22.241	20.896	1.345	0.014
5:00 PM	Min	10.768	10.805	0.037	0.936
5:00 PM	Mean	13.464	13.373	0.091	0.844
5:00 PM	Max	19.254	18.498	0.756	0.192
9:00 PM	Min	6.252	6.010	0.242	0.477
9:00 PM	Mean	8.843	8.678	0.165	0.626
9:00 PM	Max	13.547	11.467	2.080	0.000

Table 9: Summary statistics and results of t-tests for surface temperature logger data taken from October 2014 to June 2015. The Δmeans values are the absolute value of the difference between hibernacula and paired site means. P values that are less than 0.05 are considered to be significantly different (Ramsey and Schafer 2002).

Time	Measure	Hibernacula mean (°C)	Paired sites mean (°C)	Δmeans	p
1:00 AM	Min	6.056	5.294	0.762	0.031
1:00 AM	Mean	9.304	8.769	0.535	0.126
1:00 AM	Max	13.199	12.095	1.104	0.001
5:00 AM	Min	5.322	4.381	0.941	0.007
5:00 AM	Mean	8.251	7.769	0.482	0.154
5:00 AM	Max	11.785	11.013	0.772	0.017
9:00 AM	Min	6.036	5.461	0.575	0.311
9:00 AM	Mean	9.806	9.540	0.266	0.551
9:00 AM	Max	14.580	14.468	0.112	0.845
1:00 PM	Min	8.998	11.527	2.529	0.000
1:00 PM	Mean	18.305	17.928	0.377	0.470
1:00 PM	Max	22.195	22.626	0.431	0.410
5:00 PM	Min	11.272	12.183	0.911	0.055
5:00 PM	Mean	17.846	17.544	0.302	0.592
5:00 PM	Max	21.763	21.113	0.650	0.240
9:00 PM	Min	7.732	7.285	0.447	0.222
9:00 PM	Mean	11.603	10.861	0.742	0.080
9:00 PM	Max	15.929	14.053	1.876	0.000

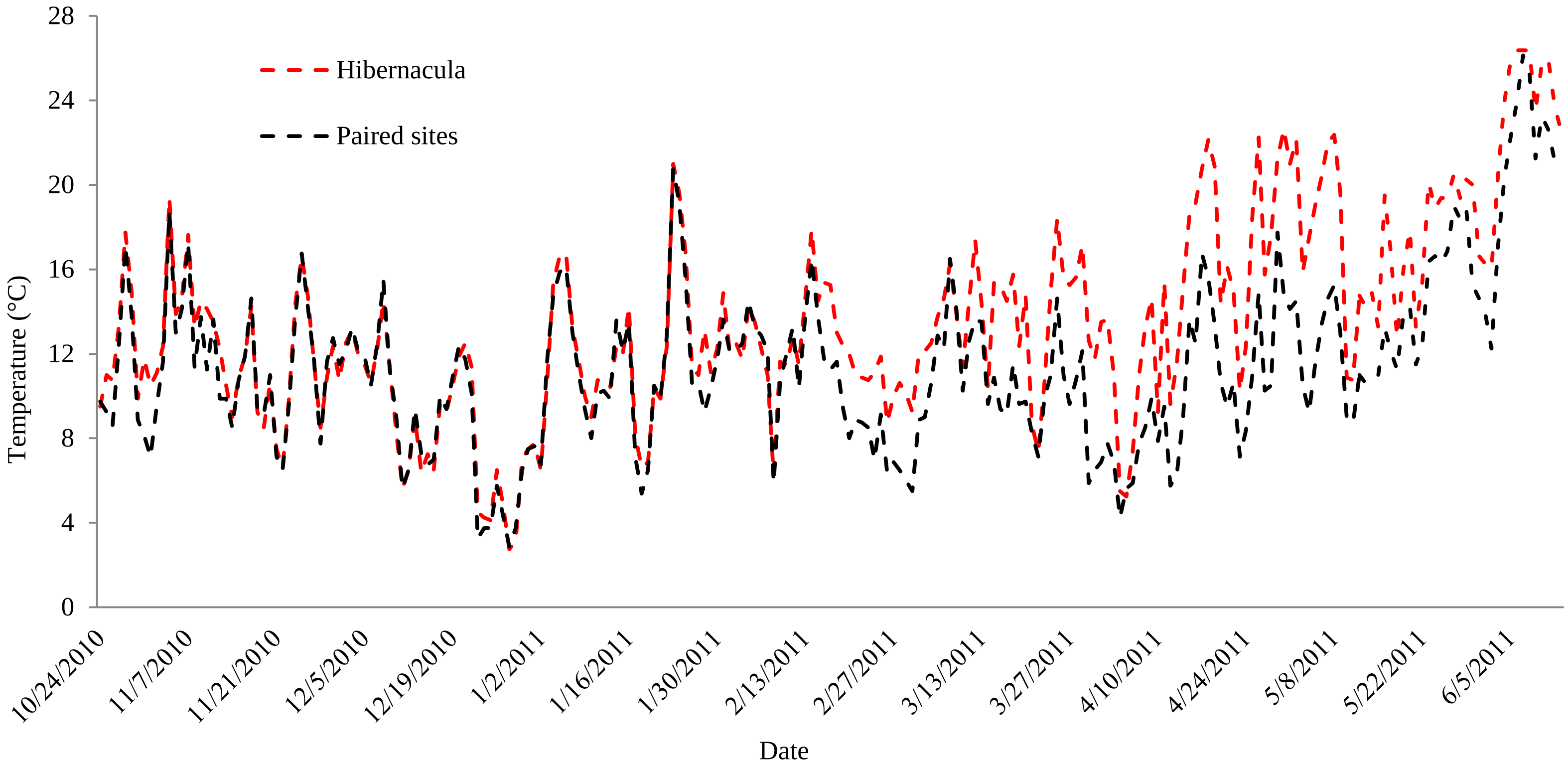

Figure 11: The graphs show the daily average of maximum temperatures at hibernacula and paired sites. Both graphs are for temperatures recorded at 9:00 pm for ambient temperature loggers. Dates (x-axis) are written MM/DD/YYYY.

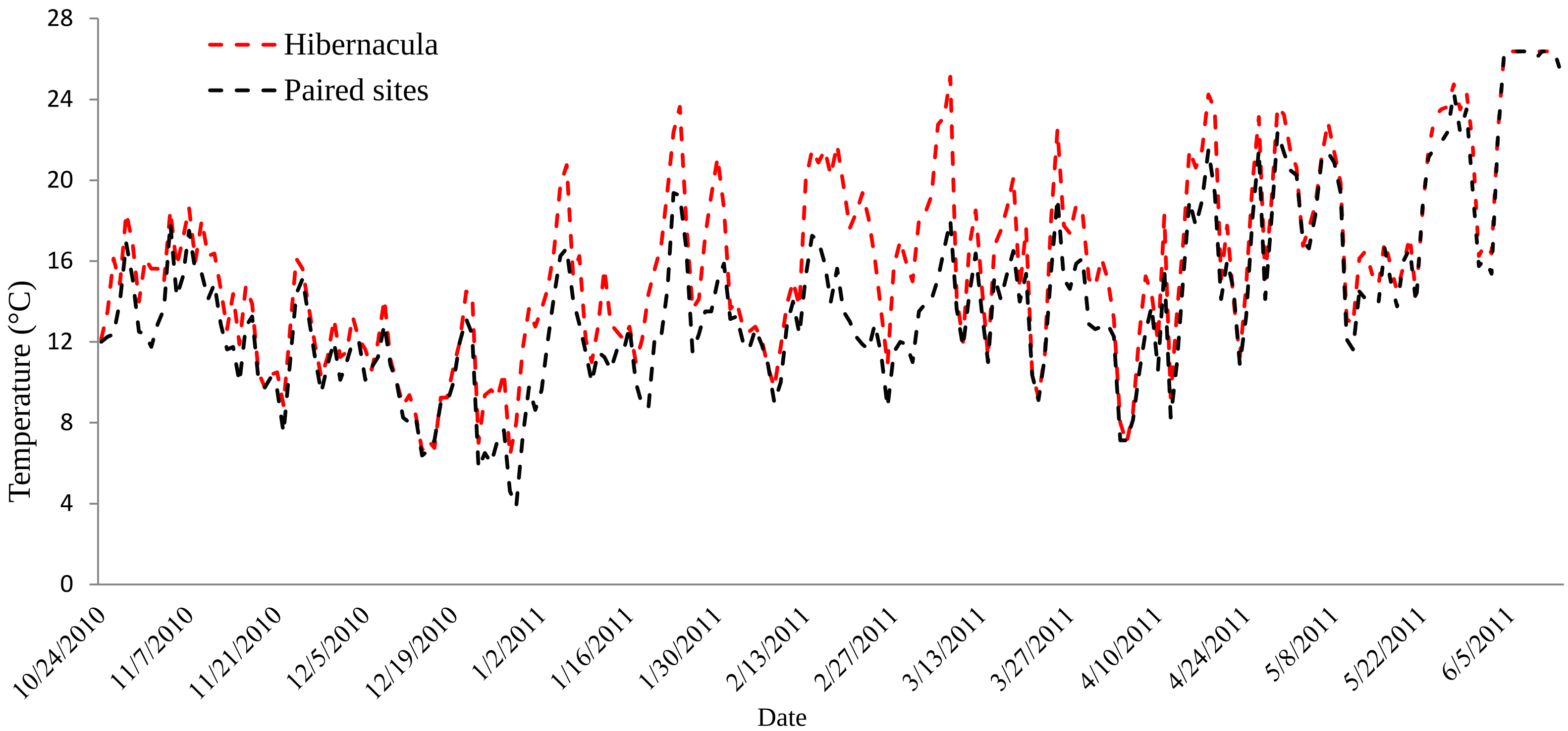

Figure 12: The graphs show the daily average of maximum temperatures at hibernacula and paired sites. Both graphs are for temperatures recorded at 9:00 pm for surface temperature loggers. Dates (x-axis) are written MM/DD/YYYY.

Geological Investigation

The examination of lithology on a subset of sites revealed that no single attribute of the outcrop was significantly distinct (Dadzis 2014). The strike-dip measurements also did not reveal any consistent differences between the joint orientation of hibernacula and paired sites. The maps revealed that 19 of the 22 hibernacula were associated with landslides (Appendices A - E). Interestingly, all of these hibernacula were located within the head scarps (i.e., slip-face) of the landslide (Figure 13).

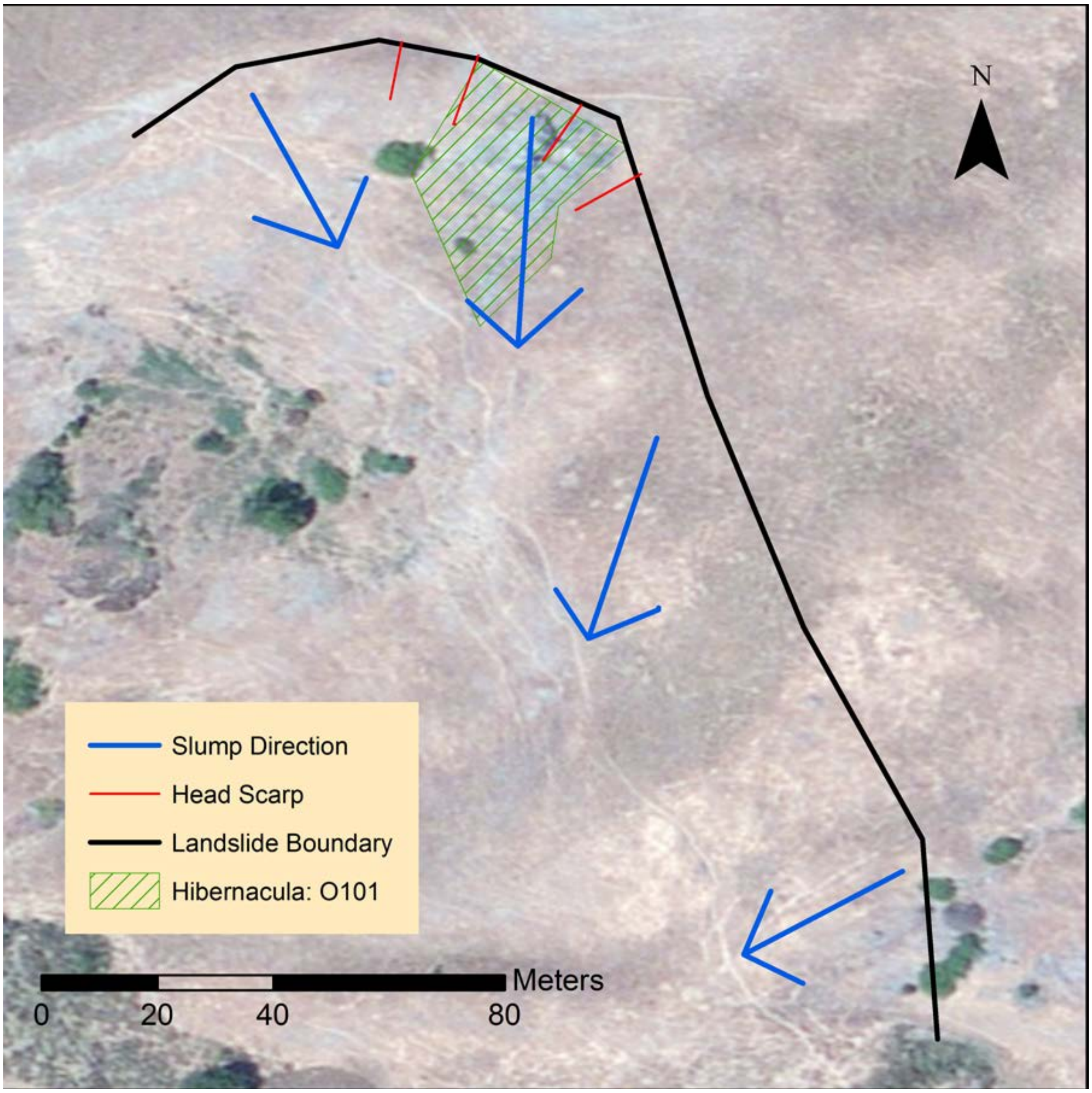

Figure 13: Map of a landslide at hibernacula O101. The long u-shaped line represents the landslide boundary. The small red lines perpendicular to the landslide boundary show the head scarp of the landslide. Notice the hibernaculum is located well within the head scarp of this landslide.

DISCUSSION

Regional Analysis

The best ENMs I created appropriately portray the suitable habitat within the historic range of *C. o. oreganus*. These models were able to identify regions where rattlesnakes are known to occur based on the literature (Klauber and McClung 1982; St. John 2002; Campbell and Lamar 2004) and data from museum collections (Oregon State Herpetological Collections at OSU), but for which no presence data (i.e., latitude/longitude) were available for modeling in that region. The results of both analyses of habitat suitability indicate that higher elevations, warmer temperatures, and less precipitation are abiotic conditions that create suitable habitat for these rattlesnakes. However, the amount of influence each predictor had on the models varied between the two study areas.

Higher temperatures and lower precipitation had positive effects on habitat suitability in both study areas. While *C. o. oreganus* can exist in wet and cool regions, my models reveal that these abiotic factors decrease habitat suitability north of the latitude of Humboldt Bay. Interestingly, precipitation was the most influential environmental predictor for the best NorCal coast model, but the two temperature predictors were more influential for the best California/Oregon model (Figures 6 & 9). Within the NorCal coast region, there is more precipitation (mean = 166 mm compared with mean = 144 mm for the rest of the California/Oregon study area) and temperatures stay mostly moderate throughout the year. With such high levels of precipitation in the NorCal coast region, suitable habitat is constrained more to areas with less precipitation, whereas in the California/Oregon study area, higher temperatures have a greater effect on habitat suitability. This difference exhibits why modeling multiple study areas is a worthwhile exercise for a species like *C. o. oreganus*, which can be considered a habitat generalist throughout its range, but a habitat specialist locally. In general, species that occupy a diversity of habitats also tend to implement a variety of life history traits that help them adapt to their microclimate (Barve et al. 2011). Rattlesnakes along the northern California coast may be selecting drier habitats over warmer ones, unlike *C. o. oreganus* in other parts of its range.

The correlation between higher elevations and habitat suitability likely relates to the insolation (i.e., thermal radiation) of the hillsides (Hamilton and Nowak 2009). Insolation increases with elevation. Consequently, higher elevations have relatively warmer soils (Hamilton and Nowak 2009). Steep slopes and a southern aspect can also increase insolation (Hamilton and Nowak 2009). Therefore, the suitable habitat for these rattlesnakes also contains key characteristics for suitable hibernacula (Geinger and Beck 2011). Unfortunately, neither model shows an upper elevation limit. While insolation increases continuously, this species is not known to occur above the tree line (Klauber and McClung 1982; St. John 2002; Campbell and Lamar 2004; Hamilton and Nowak 2009). It is likely that this result occurred due to a low number of high elevations in the dataset used to create the ENMs. A lack of extreme high elevations in the NED’s elevation data layer, due to its 1 kilometer resolution, prevented MaxEnt from being able to show selection against high elevations in the output.

Models for both study areas falsely identify areas densely populated by humans as highly suitable. This trend may be a relic of using historical presence records and relatively modern environmental predictors. Much of the developed area around Portland, OR and San Francisco, CA may contain suitable environmental characteristics, but human persecution keeps rattlesnakes from occupying these areas today (St. John 2002; Campbell and Lamar 2004). Further, the presence records are biased towards densely populated areas, parks, and roadways, because these are where people are most likely to encounter rattlesnakes. This correlation may have led to these areas being recognized as more suitable, when in reality they are less suitable now due to the inherent risks for rattlesnakes living in close proximity to humans.

Microhabitat Analysis

My results indicate that *C. o. oreganus* select rocky outcrops with fewer cover objects and more crevices on slopes facing due south. These habitat characteristics are useful for determining if a rocky outcrop is suitable as a hibernaculum. This analysis is the first multivariate approach to statistically distinguish hibernacula from suitable outcrops located nearby (i.e., paired sites). Other studies have been able to distinguish hibernacula from random sites, but not paired sites (Burger et al. 1988; Prior and Weatherhead 1996; Havery and Weatherhead 2006). Consequently, not all of the covariates in my top model agree with previous research on selection for hibernacula over random rocky outcrops.

The association of hibernacula with south-facing slopes and a higher density of crevices in my models is consistent with previous research, my result that fewer cover objects and more large talus are associated with hibernacula is not. South-facing slopes and higher crevice density are thought to aid rattlesnakes with thermoregulation, particularly during emergence (Prior and Weatherhead 1996; Gienger and Beck 2011). South-facing slopes receive more sunlight throughout the day and have better insolation than north-facing slopes (Browning et al. 2005; Hamilton and Nowak 2009). A higher density of crevices gives snakes more opportunities to regulate their body temperatures throughout the day and could provide more access points to hibernating chambers. While most high latitude rattlesnakes are thought to den in a single chamber within the hibernaculum, individuals of other snake species hibernate in their own chambers within the hibernaculum (Burger et al. 1988; Prior and Weatherhead 1996; Havery and Weatherhead 2006). More crevices could be an indication of more "chambers", encouraging more snakes to be present. A lack of vegetation and woody debris within hibernacula allows for more direct sunlight on the rocky outcrops, warming them faster (Huey et al. 1989). The previous research that found a positive association between number of cover objects and hibernaculum suitability involved pine snakes (*Pituophis melanoleucus*) and Eastern massasauga rattlesnakes (*Sistrurus catenatus*), which use holes in the ground in forested areas as hibernacula; under these circumstances, more vegetation and woody debris (i.e., cover objects) aid in insolation (Burger et al. 1988;

Harvey and Weatherhead 2006). By contrast, patchy vegetation and woody debris do not help with insolation at rocky outcrops. Additionally, Gienger and Beck (2011) found that medium talus was associated with hibernacula in Washington. They proposed that medium talus provides the right amount of interstitial space that is large enough for snakes to penetrate deep into the rock but small enough keep to cold air out. In Maple Creek, California winters are not as harsh as those in Washington, so having just the right amount of interstitial space may not be as vital for snakes in this part of their range.

My temperature logger data support the idea that hibernacula have greater insolation properties than paired sites. Previous research has found that hibernacula are consistently warmer than random sites (Gienger and Beck 2011), but no results have shown that hibernacula retain heat longer on a daily basis. The ability of rocky outcrops to retain heat later into the evening during the time of emergence could influence rattlesnake selection of hibernacula. If hibernacula retain heat longer on a daily basis, then rattlesnakes would have more opportunities for basking and hunting. These activities are especially important during the time of emergence because they can lead to earlier dispersal. For all individuals, early dispersal would offer a longer foraging season, and reproductive males would benefit even more, because mating occurs in the weeks following emergence (Macartney and Gregory 1988; Gregory 2011; Clark et al. 2012). Further investigations into temperature regimes at hibernacula should look into how temperature fluctuates throughout the day, particularly during the emergence season.

Geological Investigation

Nearly all of the covariates I found that influence hibernaculum selection in *C. o. oreganus* can be related to the idea that suitable outcrops are associated with landslides. When a landslide occurs the vegetative structure of the hillside is more-or-less removed, leaving an open canopy and potentially exposing bedrock (Werner and Friedman 2010). The removal of pressure from on top of the bedrock can lead to further jointing (formation of crevices) of the bedrock (Marshak 2009). Over time, weathering will lead to the formation of joint-bound blocks in the rocky outcrop, which fall at the base of the outcrop forming an apron of talus around it. The weathering process may be expedited in areas where freeze-thaw cycles occur (Marshak 2009). Moreover, areas with frequent landslide activity are known to have less canopy cover, less vegetation, and greater amounts of bare soil, especially after recent landslides (Werner and Friedman 2010). It appears that landslides may create the rocky outcrops that are suitable as hibernacula.

Landslides are common throughout portions of the Pacific Northwest and especially coastal northern California. Heavy rainfall is the most common trigger, but earthquakes and construction activity (e.g., timber harvesting and road building) can also influence landslide activity and location. Additionally, steep slopes, such as those along river valleys, contribute to landslide susceptibility (Werner and Friedman 2010). Taken all together, these factors lead to a relatively high frequency of landslides in the Pacific Northwest (Walker and Shiels 2013). The high frequency of landslides that create suitable habitat may be what has allowed *C. o. oreganus* to expand its range further up the west coast than any other rattlesnake.

While no previous studies have explicitly studied the relationship between snake hibernacula and landslides, there is evidence to support the idea that this phenomenon occurs outside the Pacific Northwest. For example, hibernacula of *Thamnophis sirtalis* are known to occur in sinkholes created by slumps (Gregory 1977). Furthermore, a number of studies on *C. o. oreganus* and other high latitude snakes noted that populations and in many cases hibernacula occur along rivers or within their watersheds (Diller and Wallace 1996; Prior and Weatherhead 1996; Shine et al. 2001; Wallace and Diller 2001; Browning et al. 2005; Parker and Anderson 2007; Olson 2009; Lindt et al. 2010; Palis 2010; Fortney et al. 2011) where landslides are more common (Walker and Shiels 2013). Klauber and McClung (1982) even went so far as to suggest that *C. oreganus* follows the Columbia River to northern extents of its range. While landslides are likely creating hibernacula in the Pacific Northwest, other aspects of the local geology may have greater significance in different parts this rattlesnake's range. For example, river valleys in western Idaho were created by lava flows, leaving relatively stable slopes, and rattlesnakes find talus created by other sources for hibernation (Diller, data unpublished).

An understanding of the correlation between hibernacula and landslide activity is important for the conservation of snakes and other reptiles that utilize similar hibernacula. Because landslides can cause tremendous damage to human property, they have been well documented throughout history (Walker and Shiels 2013). Occurrence locations for landslides could potentially serve as a starting point for locating rattlesnake hibernacula, especially if other climatic and habitat variables known to enhance rattlesnake habitat suitability (e.g., warmer temperatures, less precipitation, open canopies) are considered as well. Furthermore, if it is generally true that hibernacula occur within the head scarps of landslides, as my results suggest (Figure 13, Appendices A-D), maps of landslides already in existence could be used to locate hibernacula and potentially populations of rattlesnakes; of course, observations of snakes in the field would still be required to determine if the site is actually a hibernaculum. Again, this technique would be more successful when coupled with the knowledge of other habitat characteristics that create suitable hibernacula, because landslides likely also create unused outcrops with suitable appearances (i.e., paired sites).

Future research into hibernaculum selection should investigate their association with landslides. For example, there may be thermal gradients and moisture retention differences at the head scarp compared with talus at the toe of the landslide. Perhaps snakes prefer the head scarps because they are warmer and retain less water. The head scarp is at the highest elevation of the landslide and likely retains heat better. Additionally, landslides may need to be of a certain age to create suitable hibernacula. Relatively soon after a failure event, talus within a landslide headscarp is less stable (Walker and Shiels 2013). The successional process set in motion by a landslide attracts different plants and animals as it proceeds (Walker and Shiels 2013) and snakes may not be attracted to a hibernaculum until their prey (e.g., small rodent and lizards) are present.

CONCLUSIONS

My best ENMs and the best pRSF model provide valuable insight into habitat suitability and selection for *C. o. oreganus* in a largely unstudied part of its range. Considering my results together, the most suitable habitat for *C. o oreganus* in the Pacific Northwest contains south-facing hillsides with large distributions of landslides, in regions where temperatures are relatively high and precipitation is relatively low. Combining observations of landslides with micro- and macro-habitat modeling approaches brought to light different habitat constraints that would have been lost using any one approach. This comprehensive approach to studying a species' habitat suitability should be considered by all wildlife managers and researchers.

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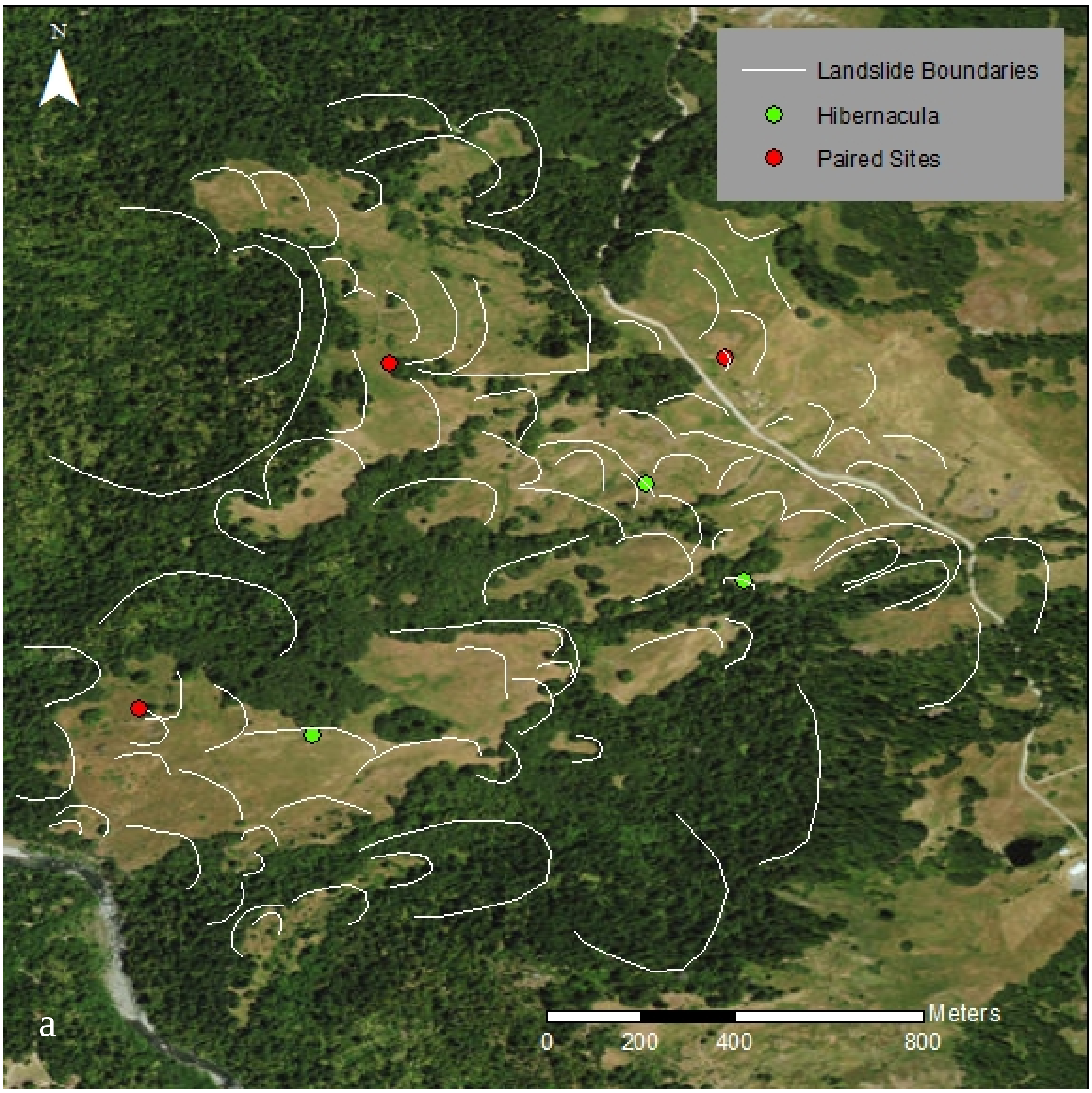
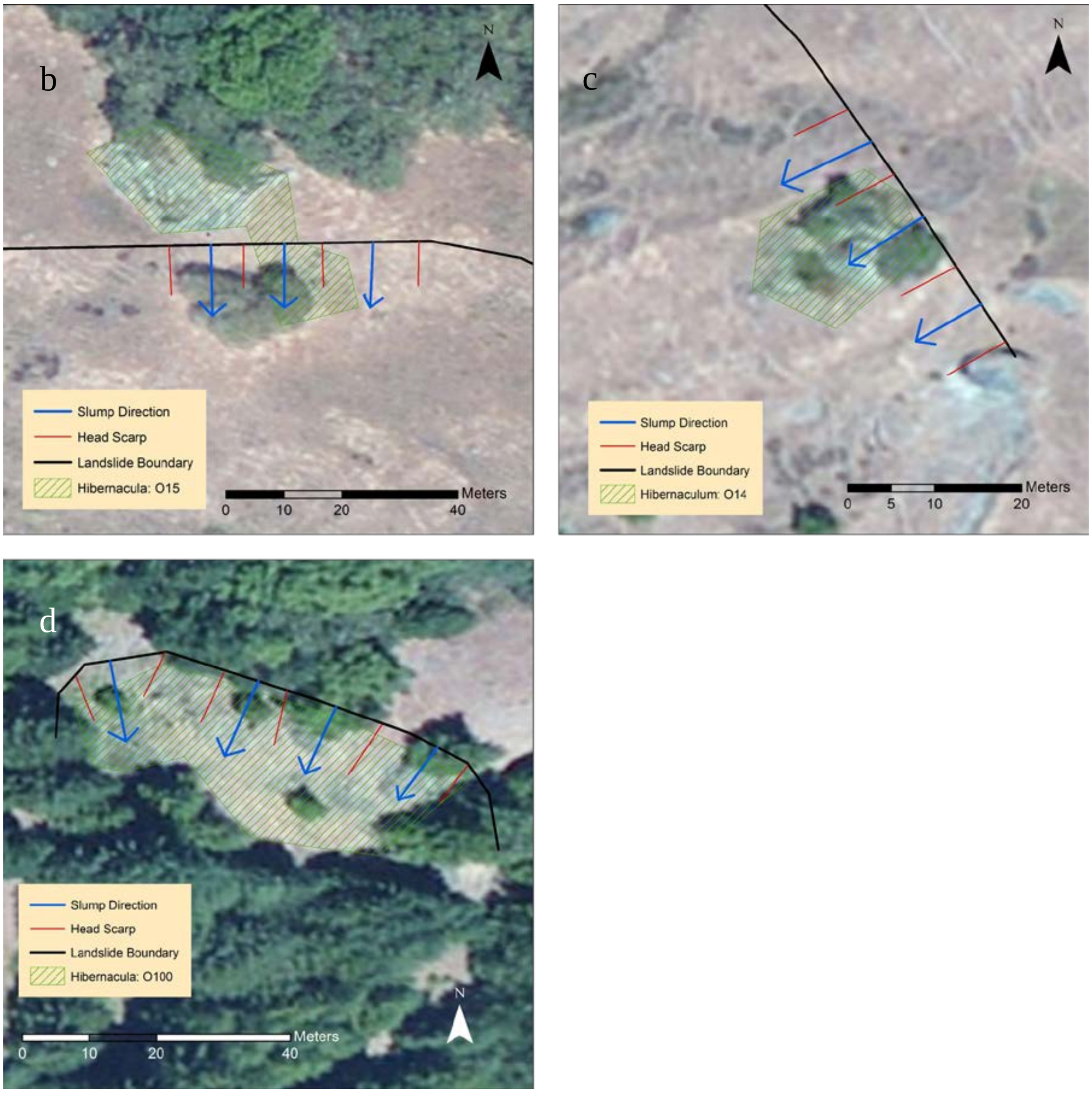
APPENDIX A

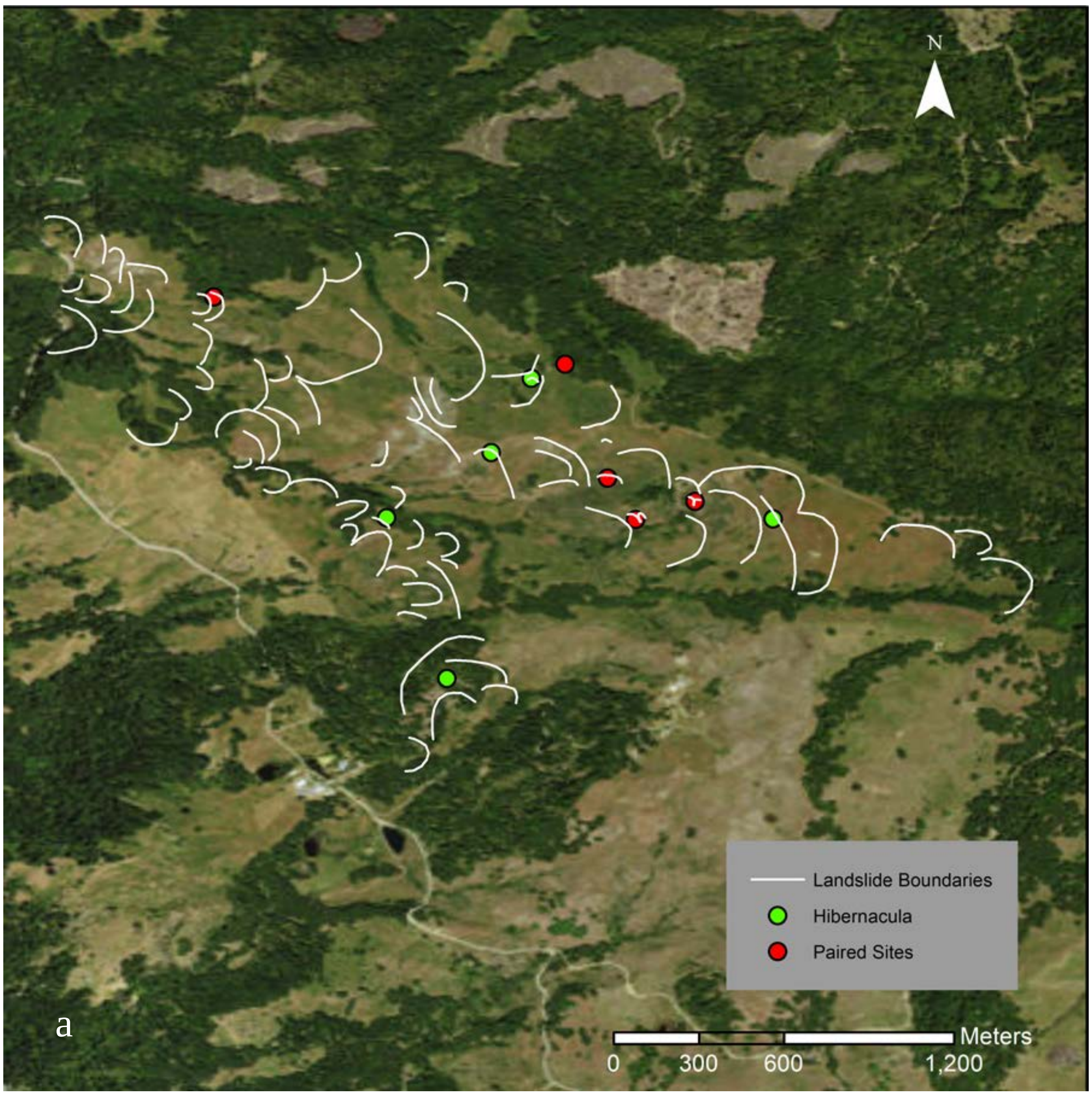
Appendix A: All of the landslides found within the Lower Madrone sub-region (a). Additionally, a closer look at the landslides associated with each hibernaculum within the Lower Madrone (b-c).

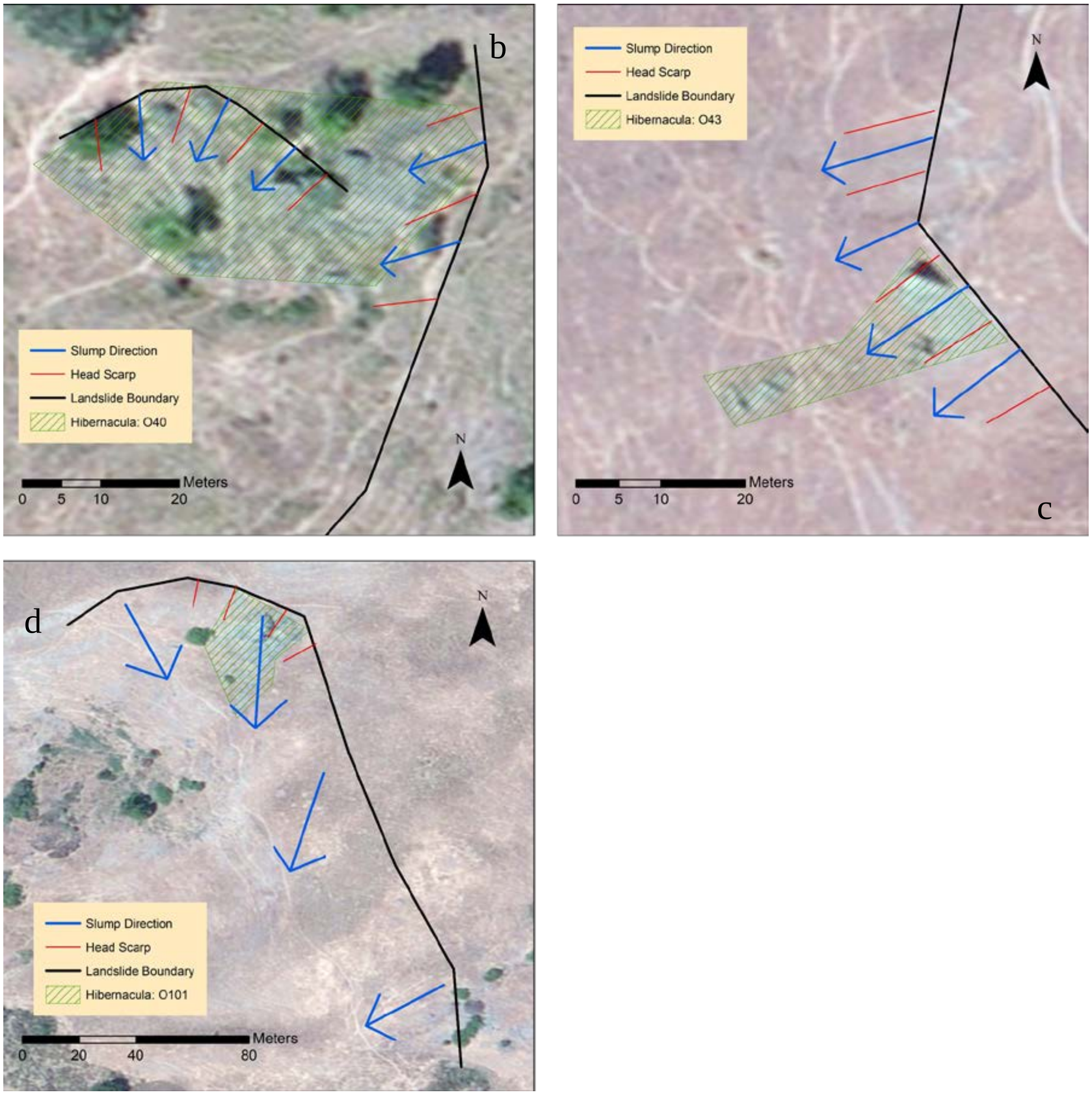



b
N
Slump Direction
Head Scarp
Landslide Boundary
Hibernacula: O15
Meters
0 10 20 40
c
N
Slump Direction
Head Scarp
Landslide Boundary
Hibernaculum: O14
Meters
0 5 10 20
d
Slump Direction
Head Scarp
Landslide Boundary
Hibernacula: O100
N
Meters
0 10 20 40

APPENDIX B

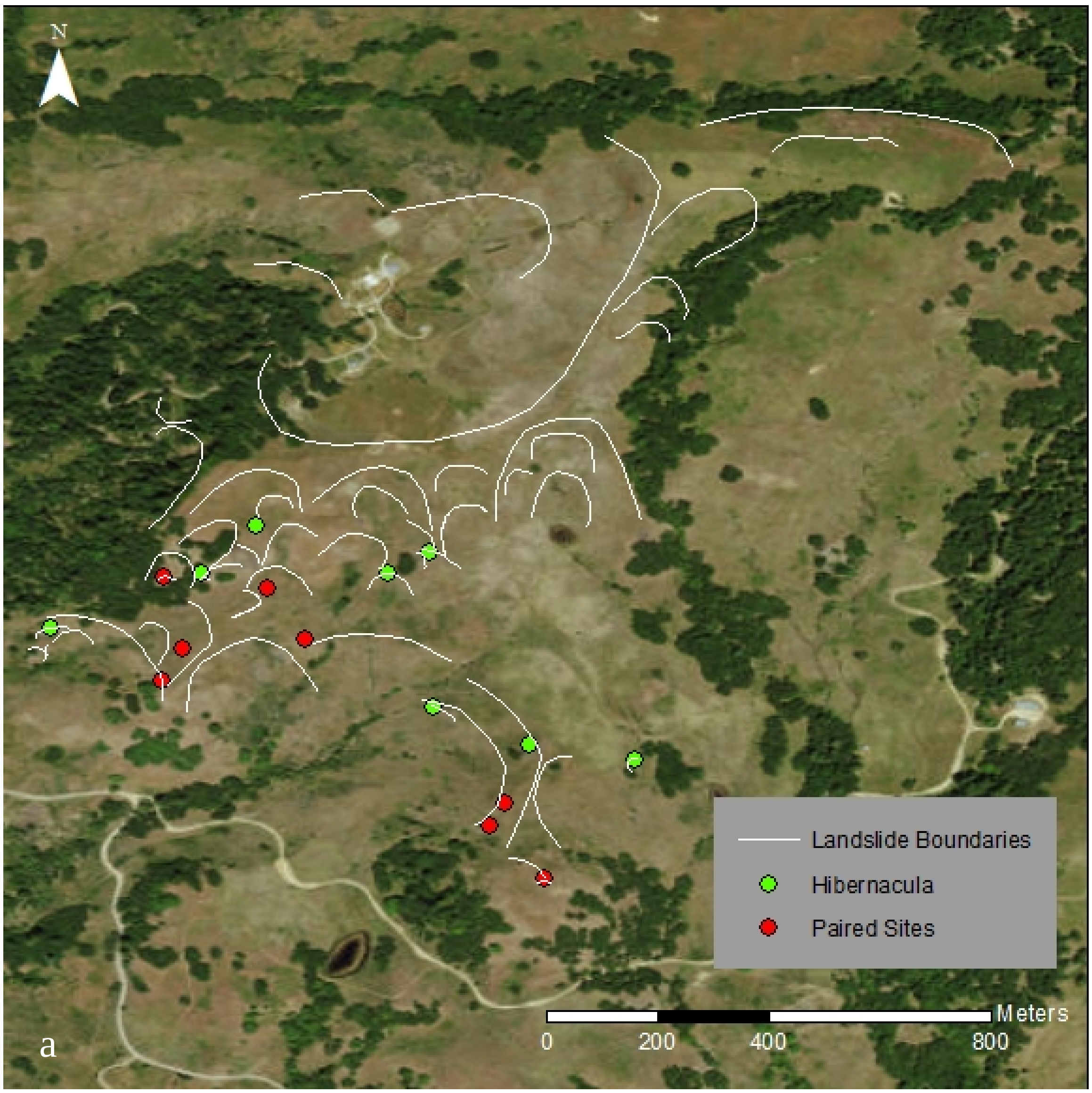
Appendix B: All of the landslides found within the Upper Madrone sub-region (a). Additionally, a closer look at the landslides associated with each hibernaculum in the Upper Madrone (b-d).

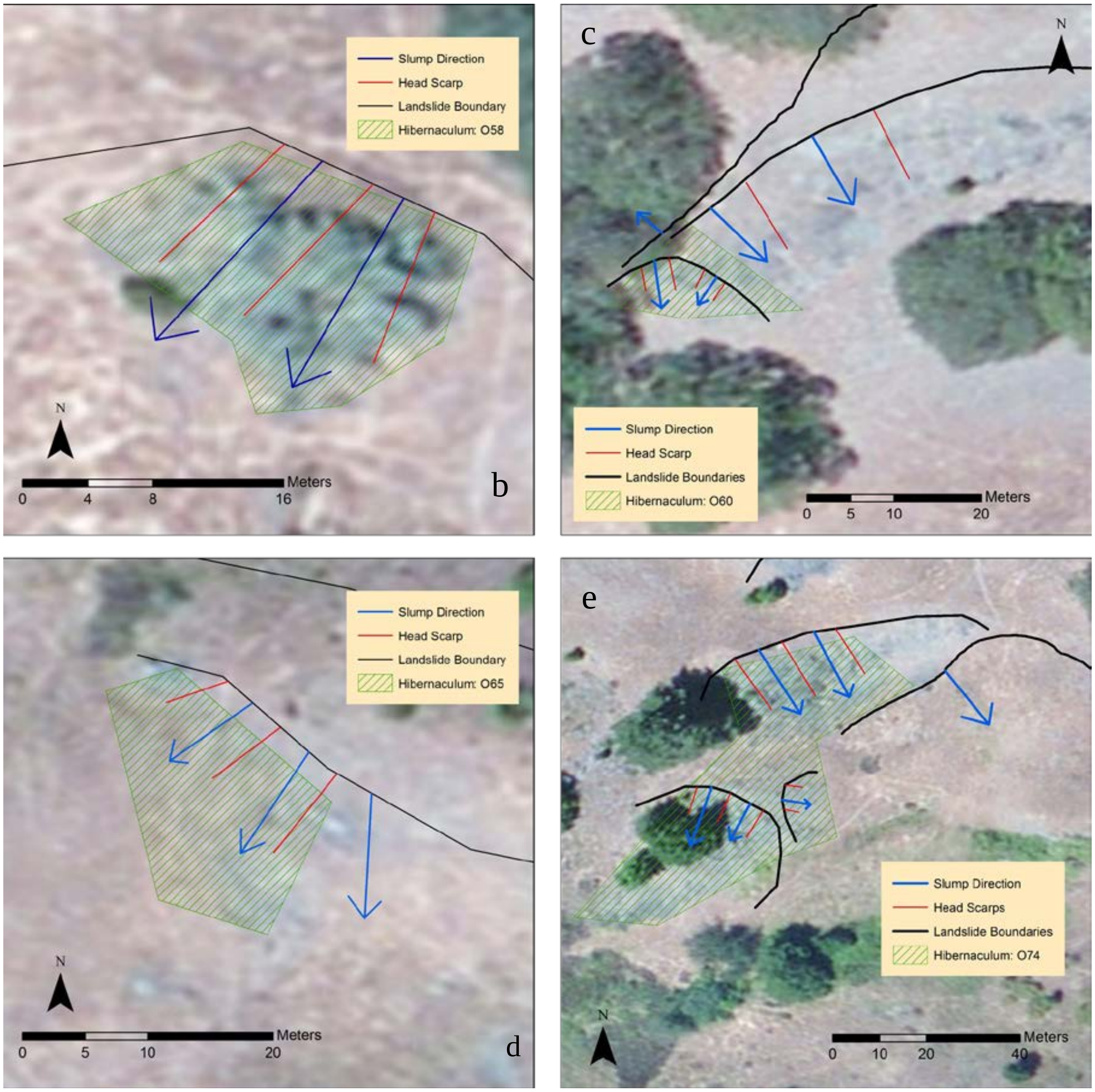


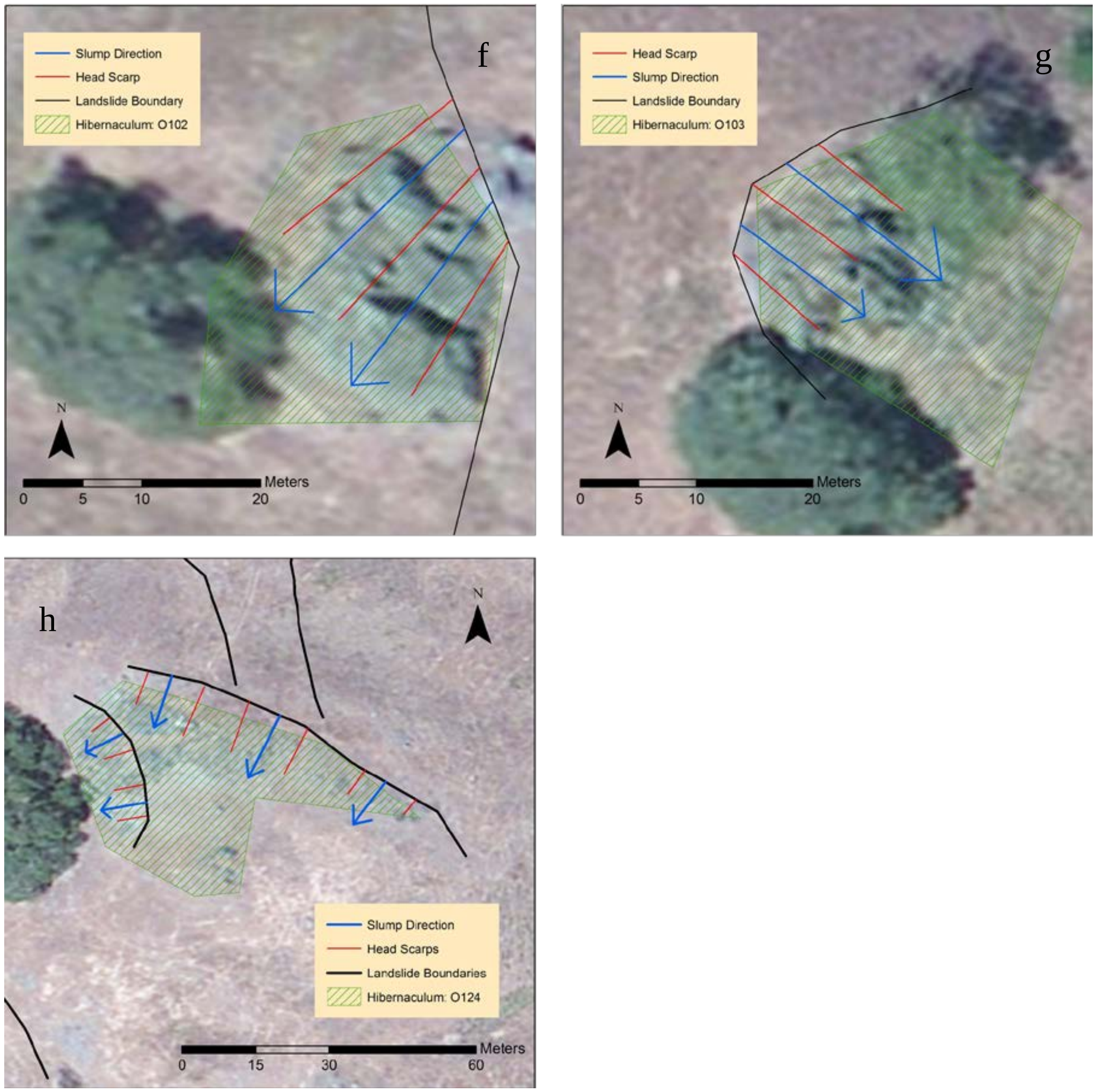

b
Slump Direction
Head Scarp
Landslide Boundary
Hibernacula: O40
N
0 5 10 20 Meters
Slump Direction
Head Scarp
Landslide Boundary
Hibernacula: O43
N
0 5 10 20 Meters
c
d
N
Slump Direction
Head Scarp
Landslide Boundary
Hibernacula: O101
0 20 40 80 Meters

APPENDIX C

Appendix C: All of the landslides found on the Garcia's Ridge sub-region (a). Additionally, a closer look at the landslides associated with each hibernaculum on the Garcia's Ridge (b-h).

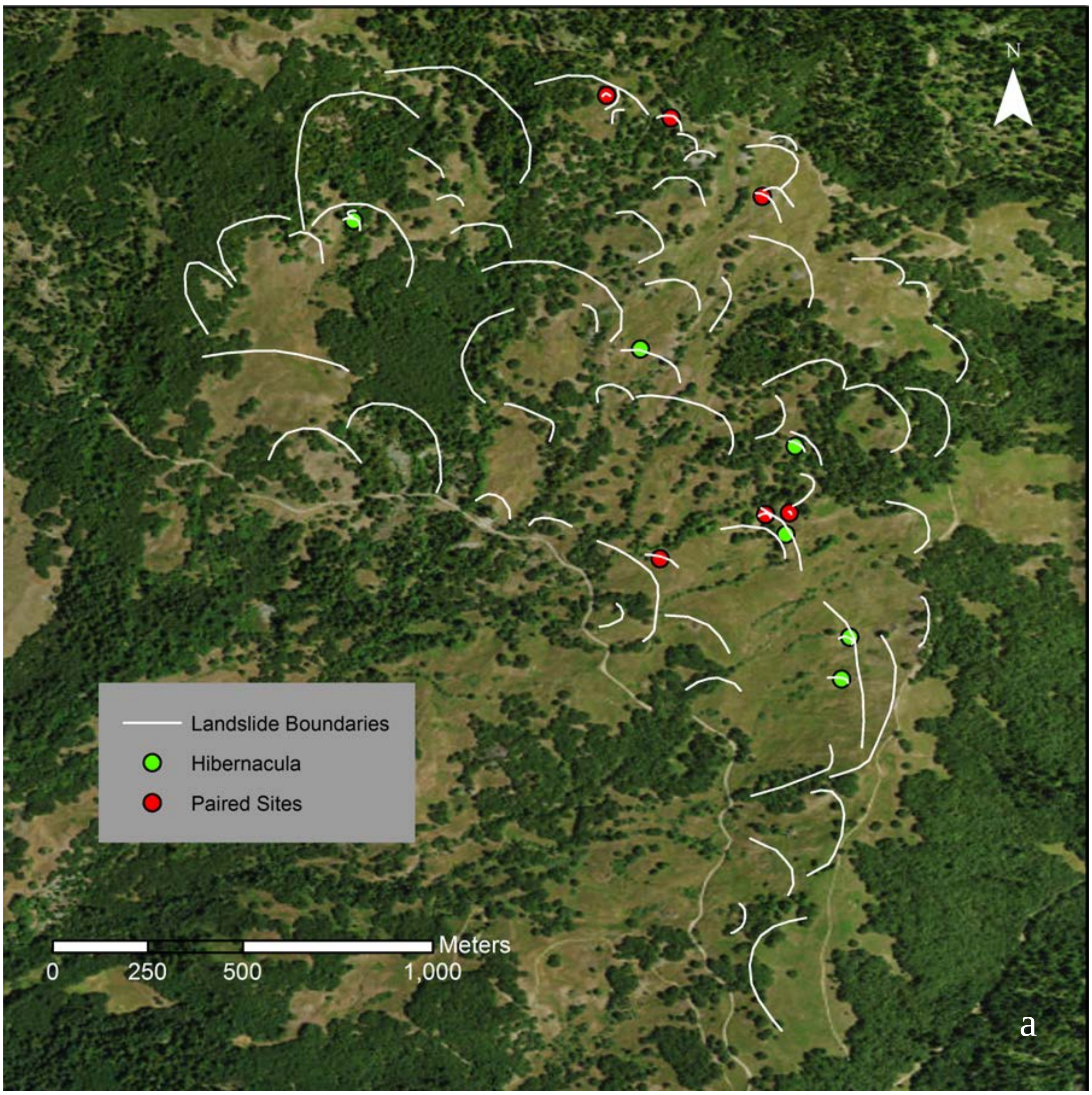


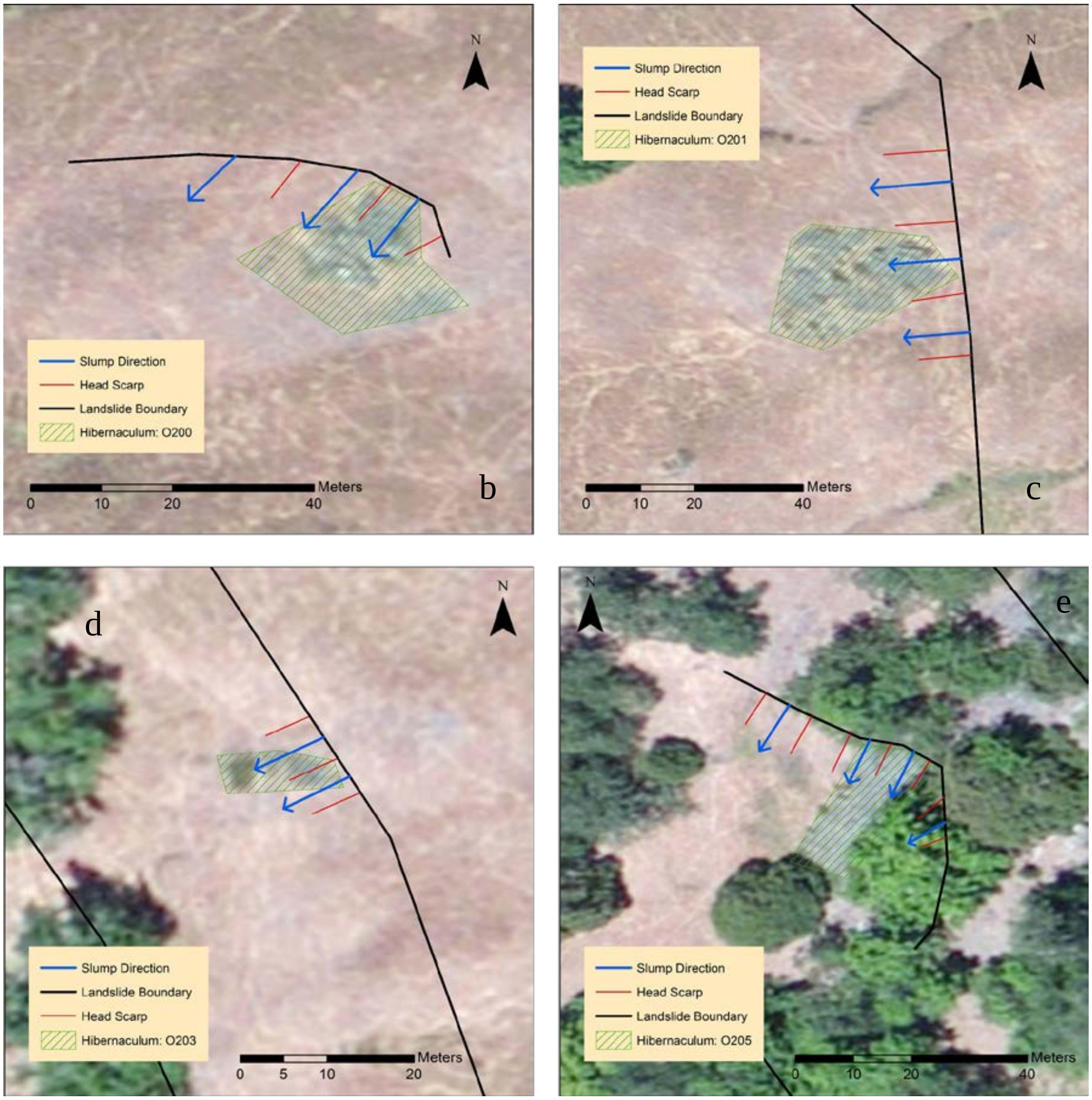

Slump Direction
Head Scarp
Landslide Boundary
Hibernaculum: O58
N
0 4 8 16 Meters
b
c
N
Slump Direction
Head Scarp
Landslide Boundaries
Hibernaculum: O60
0 5 10 20 Meters
Slump Direction
Head Scarp
Landslide Boundary
Hibernaculum: O65
N
0 5 10 20 Meters
d
e
Slump Direction
Head Scarps
Landslide Boundaries
Hibernaculum: O74
N
0 10 20 40 Meters

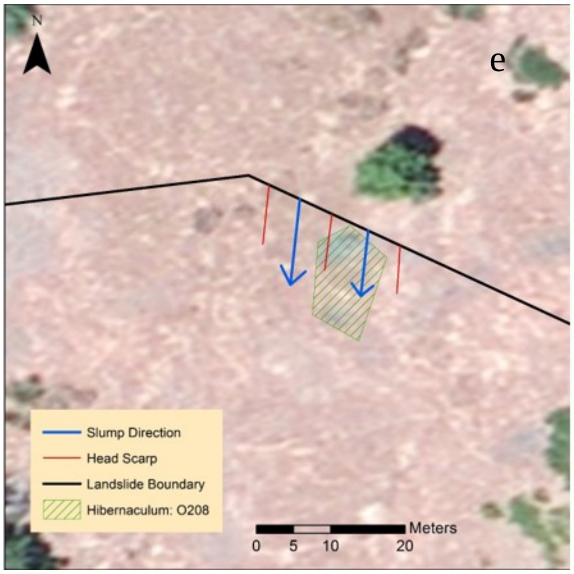

f
Slump Direction
Head Scarp
Landslide Boundary
Hibernaculum: O102
N
0 5 10 20 Meters
g
Head Scarp
Slump Direction
Landslide Boundary
Hibernaculum: O103
N
0 5 10 20 Meters
h
N
Slump Direction
Head Scarps
Landslide Boundaries
Hibernaculum: O124
0 15 30 60 Meters

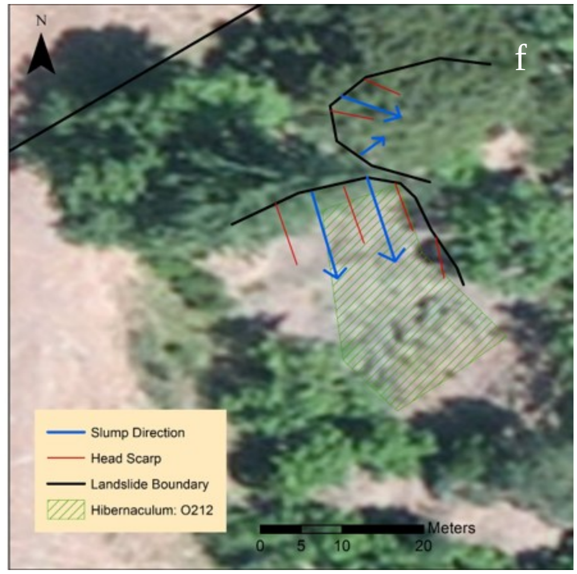
APPENDIX D

Appendix D: All of the landslides found on the Hunters Ranch sub-region (a). Additionally, a closer look at the landslides associated with each hibernaculum on the Hunters Ranch (b-g).




N
Slump Direction
Head Scarp
Landslide Boundary
Hibernaculum: O200
0 10 20 40 Meters
b
Slump Direction
Head Scarp
Landslide Boundary
Hibernaculum: O201
N
0 10 20 40 Meters
c
d
N
Slump Direction
Landslide Boundary
Head Scarp
Hibernaculum: O203
0 5 10 20 Meters
N
e
Slump Direction
Head Scarp
Landslide Boundary
Hibernaculum: O205
0 10 20 40 Meters


N
e
Slump Direction
Head Scarp
Landslide Boundary
Hibernaculum: O208
Meters
0 5 10 20


N
f
Slump Direction
Head Scarp
Landslide Boundary
Hibernaculum: O212
Meters
0 5 10 20

APPENDIX E

Appendix E: The hibernacula that are not directly associated with landslides (a-c). Hibernacula O34 (a) and O120 (b) were located within the Upper Madrone. Hibernaculum O125 (c) was located on the Garcia's Ridge.