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Authors: Hecker, Lee J., Bean, William T., and Marks, Sharyn B.

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Compensatory Microhabitat Selection by Northern Pacific Rattlesnakes (*Crotalus oreganus oreganus*) in a Cool and Wet Macroclimate

Lee J. Hecker,[1,2] William T. Bean,[3] and Sharyn B. Marks[1]

[1]*Department of Biological Sciences, Humboldt State University, Arcata, California, 95521, USA*
[3]*Department of Wildlife, Humboldt State University, Arcata, California, 95521, USA*

Abstract.—Northern Pacific Rattlesnakes (*Crotalus oreganus oreganus*) have a range that extends from southern California into British Columbia. This subspecies is common in relatively warm and arid regions, but also occurs in habitats that are neither warm nor arid. We hypothesized that the presence of suitable microhabitat conditions can compensate for a less suitable macroclimate, allowing *C. o. oreganus* to exist in less suitable regions. We developed environmental niche models for *C. o. oreganus* at two spatial scales: (1) northern California and western Oregon, and (2) the northern California coast. These models explored macroclimatic suitability of northern, coastal California relative to other regions within the range of *C. o. oreganus*. The models revealed that the three most northern and coastal counties of California have a significantly less suitable macroclimate relative to the rest of each study area. Next, we used paired resource selection functions to determine microhabitat differences between rocky outcrops used as hibernacula and outcrops that are unoccupied by rattlesnakes despite similarities. Our analysis indicated selection for outcrops with more deep crevices, less vegetative cover, and slopes facing due south (180° from North). Additionally, we mapped landslides near hibernacula, which revealed that hibernacula commonly occurred within the head-scarps of landslides. We suggest that because landslide triggers (e.g., heavy rainfall and earthquakes) occur frequently along California's north coast, more rocky outcrops are created that are suitable as hibernacula. The relatively high abundance of these suitable outcrops compensates for the marginal macroclimate, allowing *C. o. oreganus* to occur in the region.

Northern Pacific Rattlesnakes (*Crotalus oreganus oreganus*) have a range that expands further north and west than any other rattlesnake in North America (Ashton, 2001; Campbell and Lamar, 2004; Fig. 1). Like most rattlesnakes, this subspecies occurs in regions that are warm, arid, and receive ample amounts of solar radiation for most of the year (Campbell and Lamar, 2004). However, the range of *C. o. oreganus* includes coastal regions in northern California and southwestern Oregon that are neither warm nor arid. These snakes can occupy this expansive range by utilizing unique habitat features and adapting to their local environment (Ashton, 2001; Putman et al., 2013).

At high latitudes and elevations, *C. o. oreganus* exploit rocky outcrops as hibernacula (i.e., hibernation sites) to escape cold and/or wet winter conditions (Macartney et al., 1989). Individual *C. o. oreganus* show high levels of philopatry toward their hibernaculum and can be found denning communally in large numbers (Hirth, 1966; Brown and Parker, 1976). They select particular rocky outcrops as hibernacula while leaving nearby outcrops unoccupied (Gienger and Beck, 2011). Rattlesnakes that do not find suitable hibernacula are likely to perish (Reinert and Rupert, 1999). Emergence begins when mean maximum daily temperatures reach 16°C (Wallace and Diller, 2001). During that time, snakes can be found basking on the rocks near hibernaculum entrances. As temperatures continue to rise, males and nonbreeding females will disperse to forage, and males will seek mating opportunities (Wallace and Diller, 2001). Breeding females remain near the hibernaculum during pregnancy (Diller and Wallace, 2002). In autumn, as mean maximum daily temperatures drop to 17°C, nearly all individuals return to the same hibernaculum from which they emerged (Wallace and Diller, 2001; Gienger and Beck, 2011). The existence of philopatry, communal denning, and selectivity have led many to hypothesize that rocky outcrops used as hibernacula share unique features that make them suitable for hibernation (Burger et al., 1988; Reinert and Rupert, 1999; Gienger and Beck, 2011). Previous studies exploring hibernaculum selection have revealed that snakes select outcrops on steep, south-facing slopes with a greater density of low-lying vegetation and more deep crevices that are further from roads (Burger et al., 1988; Fortney et al., 2011; Gienger and Beck, 2011). Additionally, suitable rocky outcrops frequently occur high on open hillsides where they receive more solar radiation (Hamilton and Nowak, 2009). The presence of outcrops suitable as hibernacula allows *C. o. oreganus* to occupy a range that includes a diversity of macroclimates.

An accurate understanding of a species' ecological requirements is critical for predicting its spatial distribution (Peterson, 2006). Environmental niche models (ENMs) are commonly used to estimate the varying levels of climatic suitability for a species within a given region (Elith et al., 2011). However, ENMs can overlook the significance of habitat characteristics that only exist at finer spatial scales (Guisan and Thuiller, 2005). For a species like *C. oreganus* that is nearly ubiquitous throughout hot, arid regions of the American West, but has subspecies that also occur in cooler, wetter macroclimates, ENMs may fall short when describing the species' climatic niche.

We hypothesized that the north coast of California would contain marginal macroclimate for *C. o. oreganus* because of higher levels of precipitation and moderate temperatures, but that an abundance of rocky outcrops suitable as hibernacula compensates for the marginal macroclimate. Therefore, we examined how macrohabitat and microhabitat features influence the distribution of these rattlesnakes. First, we developed ENMs at two spatial scales in northern California and western Oregon. We compared the climatic suitability of the three most northern and coastal counties (i.e., Mendocino, Humboldt, and Del Norte) to the rest of each study area. Next, we compared the microhabitat features of hibernacula to those of nearby rocky outcrops that remain unoccupied despite having characteristics known to encourage rattlesnake presence.

[2]Corresponding Author. E-mail: leejhecker@gmail.com
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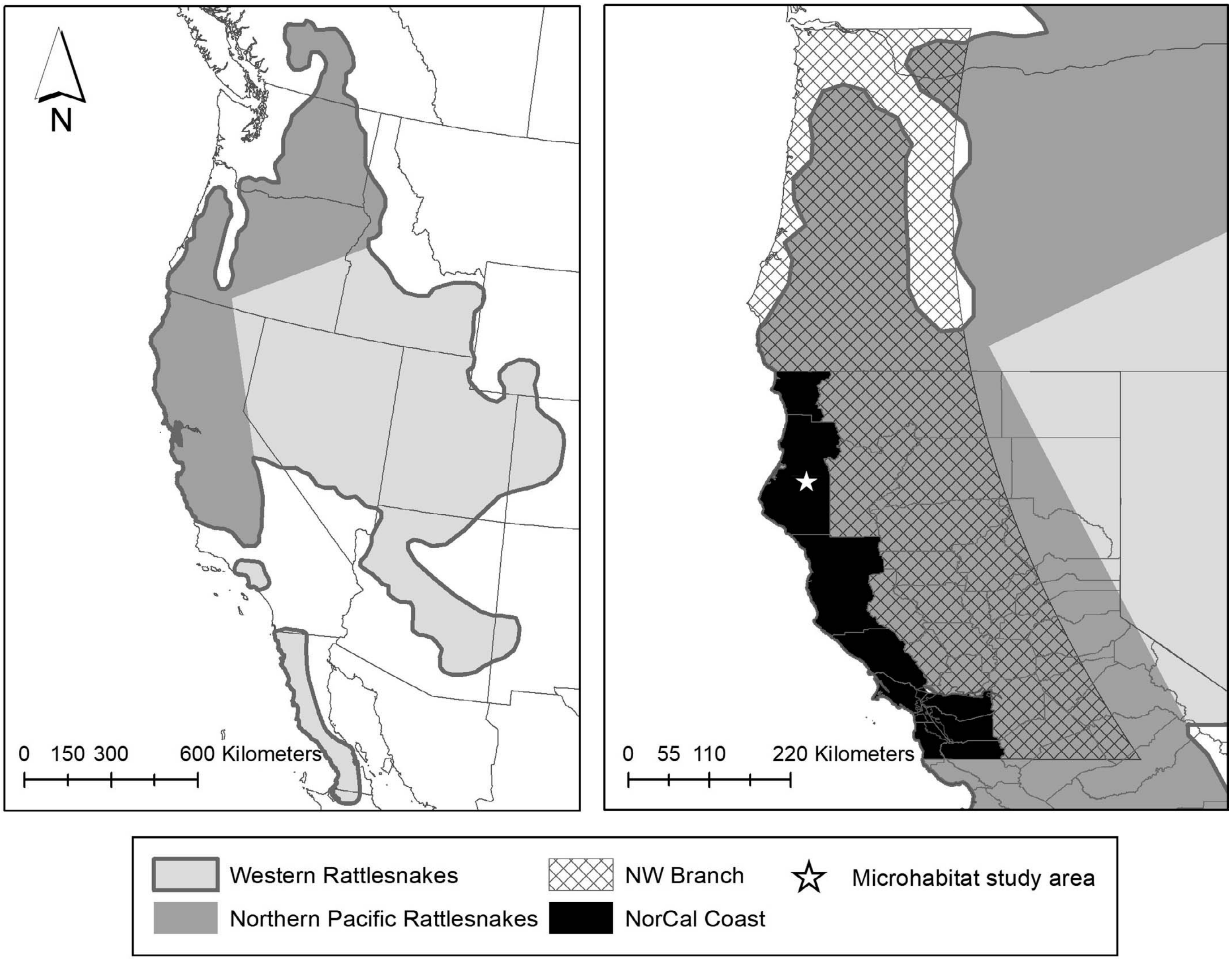

FIG. 1. (A) The range of Northern Pacific Rattlesnakes (*C. o. oreganus*) relative to Western Rattlesnakes (*C. oreganus*) and (B) the location of the two study areas within the range of Northern Pacific Rattlesnakes. The Northwest Branch (NW Branch) study area encompasses all of the different environments occupied by *C. o. oreganus* in northern California and western Oregon. The Northern California Coast (NorCal Coast) study area includes California counties that fall within the EPA's "Coastal" eco-region north of the San Francisco Bay (Omernik and Griffith, 2014). We acquired the polygon for the range of the *C. oreganus* from Natural Earth (http://www.naturalearthdata.com/) and used an estimated range as a guide to clip out the range of *C. o. oreganus* (Ashton, 2001). The microhabitat study area is where the analysis of rocky outcrops used as hibernaculum occurred.

MATERIALS AND METHODS

Regional Analysis.—We used maximum entropy (MaxEnt) modeling to generate ENMs for *C. o. oreganus* at two spatial scales. MaxEnt is widely used for creating ENMs because it consistently performs well when compared to other modeling methods (Phillips et al., 2005; Elith et al., 2011). The interpretation of MaxEnt outputs is an ongoing debate (e.g., Merow and Silander, 2014), but the outputs are understood to be a measure of relative climatic suitability for a species (Peterson et al., 2011). MaxEnt calculates climatic suitability values (CSVs) using occurrence locations for a species and a suite of environmental predictors (Elith et al., 2011). Like all ENM methods, MaxEnt is affected by the extent of the study area, number of presence locations, and environmental predictors used when modeling (Phillips et al., 2005; VanDerWal et al., 2009; Elith et al., 2011).

The study extent selected should incorporate all environmental conditions accessible by the species of interest (Barve et al., 2011). However, small study extents can produce overly fit models, and large study areas can oversimplify models, falsely increasing accuracy statistics (VanDerWal et al., 2009). Therefore, we selected two study extents to investigate suitability within the most northwestern region of the range of *C. o. oreganus* (Fig. 1). We restricted both study areas to north of the San Francisco Bay because rattlesnakes further south remain active during the winter (Putman et al., 2013). The Northwest Branch (NW Branch) study area incorporates a sample of all habitats available to the species in northern California and western Oregon. We used range data from Ashton (2001) as a guide, delimiting an area from the south shore of the San Francisco Bay north through western Oregon, with the Sierra Nevada mountain range as the eastern boundary (Fig. 1). The second study area (NorCal Coast) focused on California counties that fall within the "Coast Range" level III ecoregion from the San Francisco Bay north (Omernik and Griffith, 2014).

We acquired 1,552 occurrence locations for generating ENMs: 1,527 historical records of *C. o. oreganus* made available through Global Biodiversity Information Facility (GBIF.org, 2014) and 25 personal observations. This subspecies is the only rattlesnake within the study areas, so we included all occurrence records using modern and historical taxonomic nomenclature (Ashton, 2001). The dates of occurrences ranged from 1892–2015. Therefore, we only used abiotic predictors to create ENMs because biotic predictors (e.g., vegetative cover) would have undergone drastic changes over 123 yr.

We selected temperature, precipitation, elevation, slope, and aspect as the environmental predictors because these factors have been shown to influence rattlesnake habitat selection elsewhere (Campbell and Lamar, 2004; Hamilton and Nowak, 2009; Gienger and Beck, 2011). We acquired maximum, mean, and minimum temperatures (degrees Celsius) and mean precipitation (millimeters) data for March from the WorldClim database (Hijmans et al., 2005). We selected March as the focal period because this is the month when maximum daily temperatures consistently reach 16°C on California's north coast. For topographical data, we obtained digital elevation models from the National Elevation Dataset (NED) (U. S. Geological Service [USGS], 2015). Then, using ArcMap's 'Aspect' and 'Slope' tools, we created data sets for aspect and slope. We downsampled all the NED data layers to 1-km pixels, to match the resolution of the WorldClim data by calculating the mean of the NED's 30-m pixels within a 1-km pixel.

We designed each ENM to answer a specific biological question related to rattlesnakes' ability to thermoregulate within the macroclimate. As we generated ENMs, we calculated area under the curve (AUC) values, which we used to determine goodness of fit for each ENM; higher AUC values indicate a better-fitting model (Handley and McNeil, 1982). We compared ENMs with the use of Akaike Information Criterion (AIC) values; lower AIC values indicate a more parsimonious model (Burnham and Anderson, 2002). Using AIC has been shown to select models that estimate climatic suitability better than models selected using only AUC (Warren et al., 2014). We used a jackknife approach to assess the impact of each environmental predictor on the ENM (Phillips et al. 2005). Additionally, we cross-validated the most parsimonious ENMs using 70% training, 30% testing data for 1,000 iterations. A robust model would consistently predict climatic suitability throughout all iterations (Plant, 2012). We analyzed the macroclimate suitability for *C. o. oreganus* within California's three most northern and coastal counties by comparing the CSVs at presence locations within those counties to those at the remaining presence locations within each study area.

Microhabitat Analysis.—We used paired use-availability resource selection functions (pRSF, i.e., conditional logistic regression) to investigate the selection of rocky outcrops as hibernacula. Resources selection functions model the probability of occupancy in a binomial response variable using explanatory covariates (Hosmer et al., 2013). However, when using a pRSF each success (i.e., hibernaculum) is paired with a failure (i.e., "suitable" but unoccupied outcrop). This pairing allows for direct comparison of the resource unit (Lele et al., 2013). Paired studies tend to have greater power because of their ability to reduce spatial autocorrelation within groups (Hosmer et al., 2013).

The microhabitat study area was located on the north bank of the Mad River in northern California, approximately 32 km from the coast (Fig. 1). The vegetative structure consisted of coastal prairies and mixed-oak woodlands. The study area was situated within the central belt of the Franciscan geological complex, a lithic composition that contains a mixed graywacke, greenstone, and argillite lithic composition, leading to brittle rocky outcrops (Aalto, 1980).

We surveyed all the rocky outcrops in the study area and categorized each as "unsuitable," "suitable," or "hibernaculum." We defined a rocky outcrop as the entire outcrop and any outcrops within 5 m of the edge of the central outcrop. We based these categories on characteristics known to influence hibernaculum selection by snakes (Burger et al., 1988; Campbell and Lamar, 2004; Hamilton and Nowak, 2009; Gienger and Beck, 2011). "Unsuitable" outcrops consisted of solid rock with no deep, penetrating crevices, whereas "suitable" outcrops contained deep crevices but were not occupied by rattlesnakes. To be categorized as a "hibernaculum" the outcrop must have met one of three criteria: 1) during consecutive emergence seasons, rattlesnakes were observed at the same crevice(s); 2) within a single emergence season, a rattlesnake was observed basking within 1 m of the same crevice on consecutive surveys; or 3) within a single emergence season, multiple rattlesnakes were observed basking on consecutive surveys within the same outcrop. From February through April 2014 and 2015, we repeatedly surveyed all outcrops every 4–7 d for rattlesnakes. In total, we surveyed 160 outcrops, designating 22 "hibernacula," 64 "suitable," and 74 "unsuitable" (Fig. 2). Then, we paired each hibernaculum with the nearest suitable outcrop (hereafter referred to as "paired sites").

At each hibernaculum and paired site ($n = 44$), we measured a suite of microhabitat covariates (Table 1). These covariates included those reported to influence snake hibernaculum selection, as well as several not investigated or not found significant in previous studies (hereafter referred to as "unreported covariates"): canopy cover, area, distance to nearest water source, distance to nearest hibernaculum; and an estimated percentage of six habitat characteristics: bare soil, bare rock, grass, and small ($<$7,000 cm^3), medium (7,000–15,000 cm^3), and large talus ($>$15,000 cm^3; Gienger and Beck, 2011). To obtain estimates of canopy cover, crevice density, and cover object density, we laid 5×5 m grids across each hibernaculum and paired site. At the center of each grid, we measured canopy cover; within each grid, we counted the number of crevices deeper than 10 cm (Gienger and Beck, 2011) and the number of cover objects. Then, we calculated the mean for each of these covariates. We estimated percent cover for each habitat characteristic across the entire hibernaculum/paired site and used these estimates to calculate a Shannon index as a measure of diversity (Gotelli, 1998). The habitat characteristics were estimated to the nearest 5%. When developing pRSFs, the Shannon index and individual percent cover estimates for each habitat characteristic were used as covariates.

To start generating pRSFs, we selected the six covariates known to encourage snake presence at hibernacula: density of cover objects (e.g., woody debris or dense vegetation), canopy cover, distance to roads, slope, aspect, and crevice density (Burger et al., 1988; Campbell and Lamar, 2004; Fortney et al., 2011; Gienger and Beck, 2011). We used a backward step-selection to determine the most parsimonious literature-based model. Then, we attempted to improve this model by adding each unreported covariate to that model individually. We calculated the ΔAICc (AIC adjusted for small sample size) values and the weight of each model to select the most parsimonious model (Burnham and Anderson, 2002).

After collecting the field data, we noticed a correlation between landslide activity and hibernaculum presence. Rotational slumps were the most common type of landslide

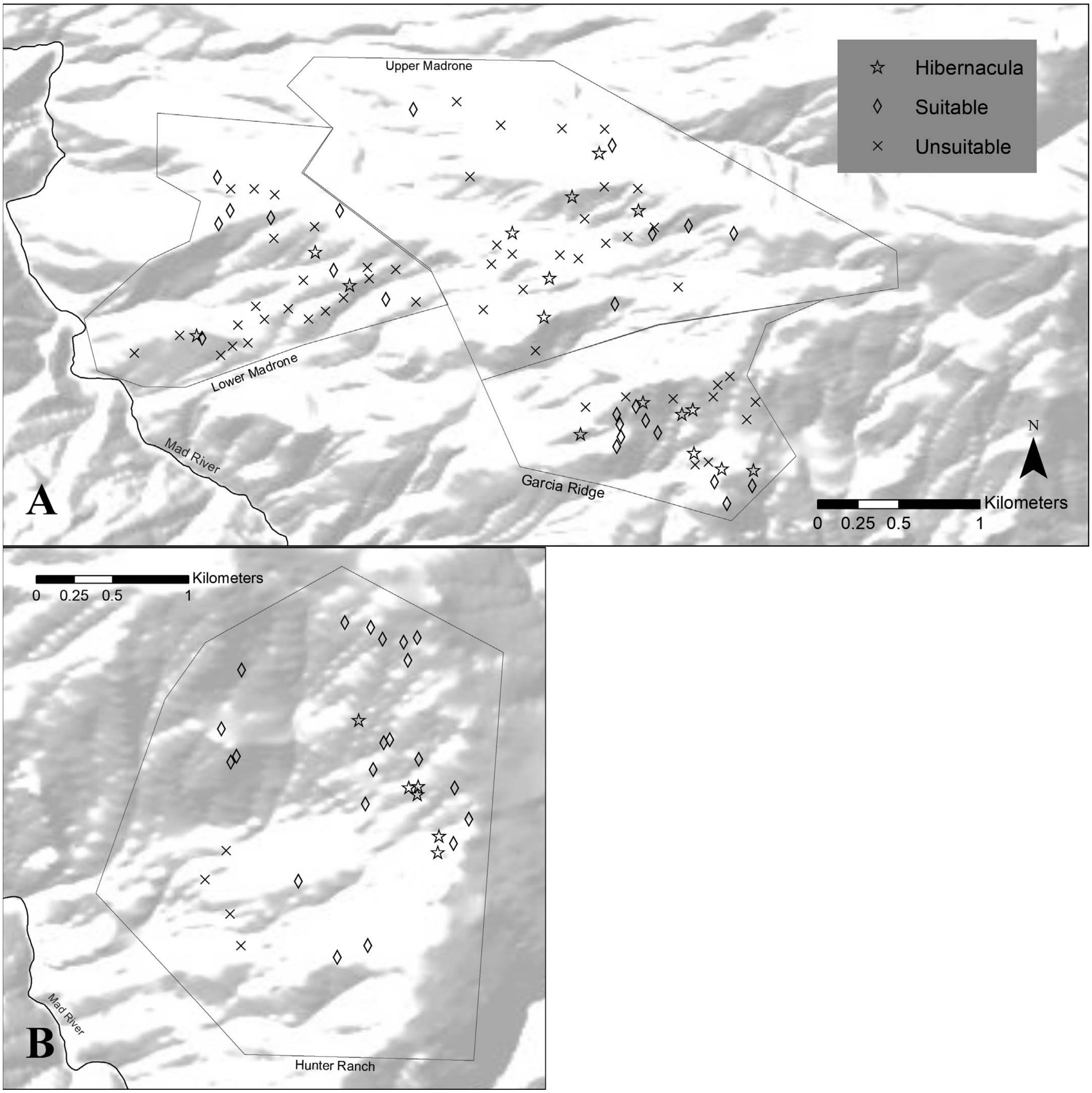

FIG. 2. Map showing all 160 outcrops that were surveyed for presence of *C. o. oreganus* and suitability as a hibernaculum near Maple Creek, California. We located 22 hibernacula, 64 suitable but unoccupied rocky outcrops, and 74 unsuitable rocky outcrops. Each polygon represents a subregion: (A) Lower Madrone, Upper Madrone, Garcia Ridge; and (B) Hunter Ranch. Subregions were designed so that all the rocky outcrops in each could be surveyed in 1 day. Note that the Hunter Ranch subregion (B) was separated from the others by approximately 9 km.

observed. These landslides are failures of a cohesive block that leaves U-shaped head-scarps (Bierman and Montgomery, 2014). We mapped landslides by exaggerating the topography and identifying these U-shaped features (following Mihir and Malamud, 2014). Head-scarps were digitized as polylines in ArcGIS using standard symbology for viewing landslide features (Lee, 2001). We used a binomial test to determine if the presence of a rotational slump increased the probability of a rocky outcrop being a hibernaculum or suitable outcrop.

RESULTS

Regional Analysis.—We generated 20 ENMs for each of the two study areas. In both cases, rattlesnake habitat suitability was associated with hotter, drier areas. The selected ENM for each study area identified suitable regions where rattlesnakes were known to occur based on data from the literature (Klauber and McClung, 1982; Campbell and Lamar, 2004) and museum collections that were not included in our models because they lacked precise locations (i.e., latitude/longitude).

TABLE 1. Summary of the covariates measured at each hibernaculum of *C. o. oreganus* and unoccupied rocky outcrops (i.e., paired sites) near Maple Creek, California. The table describes the covariate measured (Measurement), method of measurement (Tool), and the units of measurement (Units). The habitat cover types were estimated to the nearest 5%. Large, medium, and small talus were determined using the rock volumes described by Gienger and Beck (2011).

Measurement	Tool	Units
Slope	Clinometer	Percentage
Aspect	Compass	Degrees
Area	ArcGIS: 'Calculate Geometry' tool	Meters squared
Canopy cover	Spherical densiometer	Mean percentage
Crevice density	Count	Mean number
Cover object density	Count	Mean number
Distance to road	ArcGIS: 'Distance' tool	Meters
Distance to water	ArcGIS: 'Distance' tool	Meters
Distance to nearest hibernaculum	ArcGIS: 'Distance' tool	Meters
Shannon index (Gotelli, 1998)	$\sum_{i=1}^{S} p_i \mathbf{ln}(p_i)$ (where S is the number of distinct objects and p_i is the proportion of objects in that category)	Unit of habitat diversity
Bare rock	Visual estimate	Percentage of rock surface not covered by moss or lichen
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

The selected NW Branch ENM accounted for 99.96% of the AIC weight (Table 2). This model included four environmental predictors: minimum and maximum temperatures in March, elevation, and mean precipitation in March (Table 2; Fig. 3). The jackknife test indicated that maximum temperature was the most influential in the model, followed by minimum temperature, precipitation, and elevation, respectively (Fig. 3). Highly suitable regions were associated with mean maximum daily temperatures of at least 13°C, mean minimum daily temperatures of at least 4°C, mean precipitation of 14 mm or less, and elevations over 500 m. The selected NorCal Coast ENM accounted for 99.60% of the weight in the AIC table (Table 2). This model contained the same environmental predictors as the selected NW Branch ENM: minimum and maximum temperatures in March, elevation, and mean precipitation in March (Table 2; Fig. 4). However, mean precipitation in March was the most influential predictor in this model, followed by maximum, then minimum temperature in March, and then elevation (Fig. 4). Highly suitable habitat was characterized by mean precipitation of 12 mm or less, mean maximum daily temperatures of at least 16°C, mean minimum daily temperatures of at least 4°C, and elevations over 20 m.

The receiver operating characteristic (ROC) curves for the selected models had consistently high AUC values and low omission error, indicating good predictive performance. The cross validation of the selected ENM from the NW Branch study area showed a mean AUC value of 0.854 (SD = 0.008) and a mean omission error of 0.093. The cross-validation results for

TABLE 2. The seven most parsimonious environmental niche models describing the habitats selected by *C. o. oreganus* at two spatial scales: northern California and western Oregon (NW Branch) and the northern California coast (NorCal Coast). Model selection criteria included Akaike Information Criteria (AIC), difference in AIC and the most parsimonious model (ΔAIC), and model weight (weight). The number of parameters does not match number of predictors because of the use of multiple "features" in MaxEnt for each predictor. The "Weight" column does not sum to 1 because of rounding. Predictor codes: minimum (T_{min}), mean (T_{mean}), and maximum (T_{max}) temperatures (°C) for March; mean precipitation (precip, mm) for March; slope (%); aspect (°); elevation (m).

Model	AIC	ΔAIC	Weight	AUC	No. of parameters
NW Branch					
T_{min} + T_{max} + elevation + precip	10,616.8	0.0	0.996	0.854	54
T_{min} + T_{max} + precip	10,644.2	27.4	0.000	0.853	53
T_{mean} + precip	10,650.8	34.0	0.000	0.846	54
T_{mean}	10,650.8	34.0	0.000	0.846	54
T_{mean} + precip + elevation	10,650.8	34.0	0.000	0.846	54
T_{mean} + elevation + aspect + slope + precip	10,656.2	39.4	0.000	0.846	56
T_{min} + elevation + aspect + slope + precip	10,659.5	42.7	0.000	0.843	61
NorCal Coast					
T_{min} + T_{max} + elevation + precip	4,958.7	0.0	0.996	0.782	50
T_{min} + T_{max} + elevation + aspect + slope + precip	4,969.8	11.0	0.004	0.790	56
T_{mean} + precip	4,983.5	24.8	0.000	0.786	60
T_{mean}	4,983.5	24.8	0.000	0.786	60
T_{mean} + precip + elevation	4,983.5	24.8	0.000	0.786	64
T_{max} + precip	4,986.5	27.8	0.000	0.778	60
T_{max}	4,986.5	27.8	0.000	0.778	60

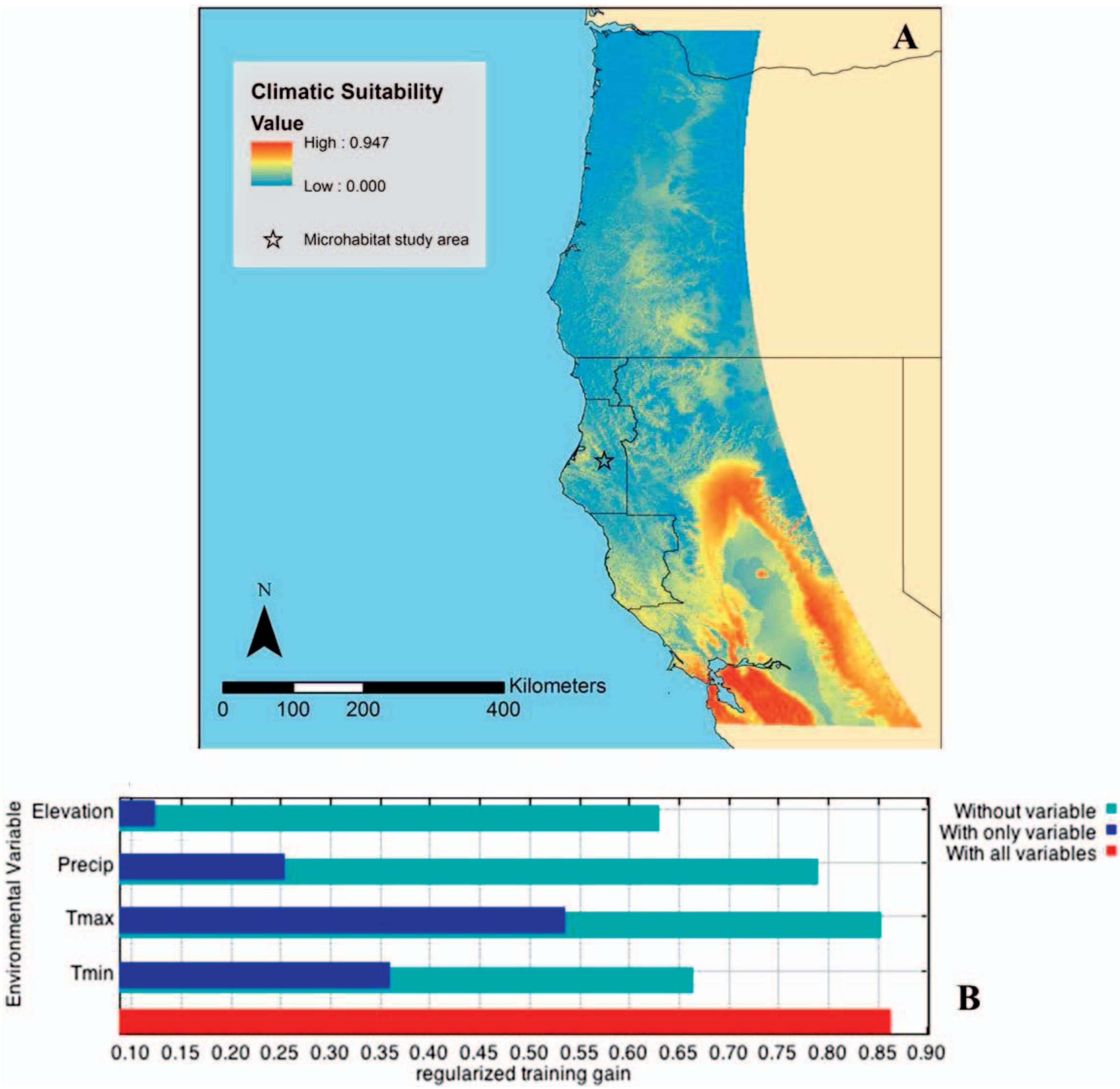

FIG. 3. The climatic suitability map (A) for *C. o. oreganus* in northern California and western Oregon (NW Branch) produced by the selected environmental niche model (ENM). The outlined California counties are (south to north) Mendocino, Humboldt, and Del Norte. The selected ENM for the NW Branch contained the environmental variables elevation, mean precipitation in March (Precip), maximum temperature in March (T_{max}), and minimum temperature in March (T_{min}). Results of the jackknife test (B) indicate that the temperature variables had the greatest influence of climactic suitability.

the selected NorCal Coast ENM showed a mean AUC of 0.782 (SD = 0.012) and a mean omission rate of 0.109.

Rattlesnake presence locations within Mendocino, Humboldt, and Del Norte counties had significantly lower CSVs relative to those for the rattlesnake localities within the rest of the NW Branch and NorCal Coast (Fig. 5). This indicates that these counties contain less suitable macroclimates for rattlesnakes than the rest of both study areas.

Microhabitat Analysis.—We created 15 pRSF models. The top models all included aspect, crevice density, and cover object density. Each of the top four models also incorporated one additional covariate: percentage of large talus, percentage of bare soil, diversity of habitats, or hibernaculum area. The two most parsimonious models accounted for 61% of the weight (Table 3). These two models indicated that rattlesnakes selected rocky outcrops as hibernacula on slopes facing due south, with more crevices, fewer cover objects, and either more large talus or more bare soil (Table 4).

Our landslide maps revealed that 38 of the 44 rocky outcrops (86%) examined were located within the head-scarps of landslides (e.g., Fig. 6). The probability of suitable outcrops and hibernacula being created by landslides was 80.23% and

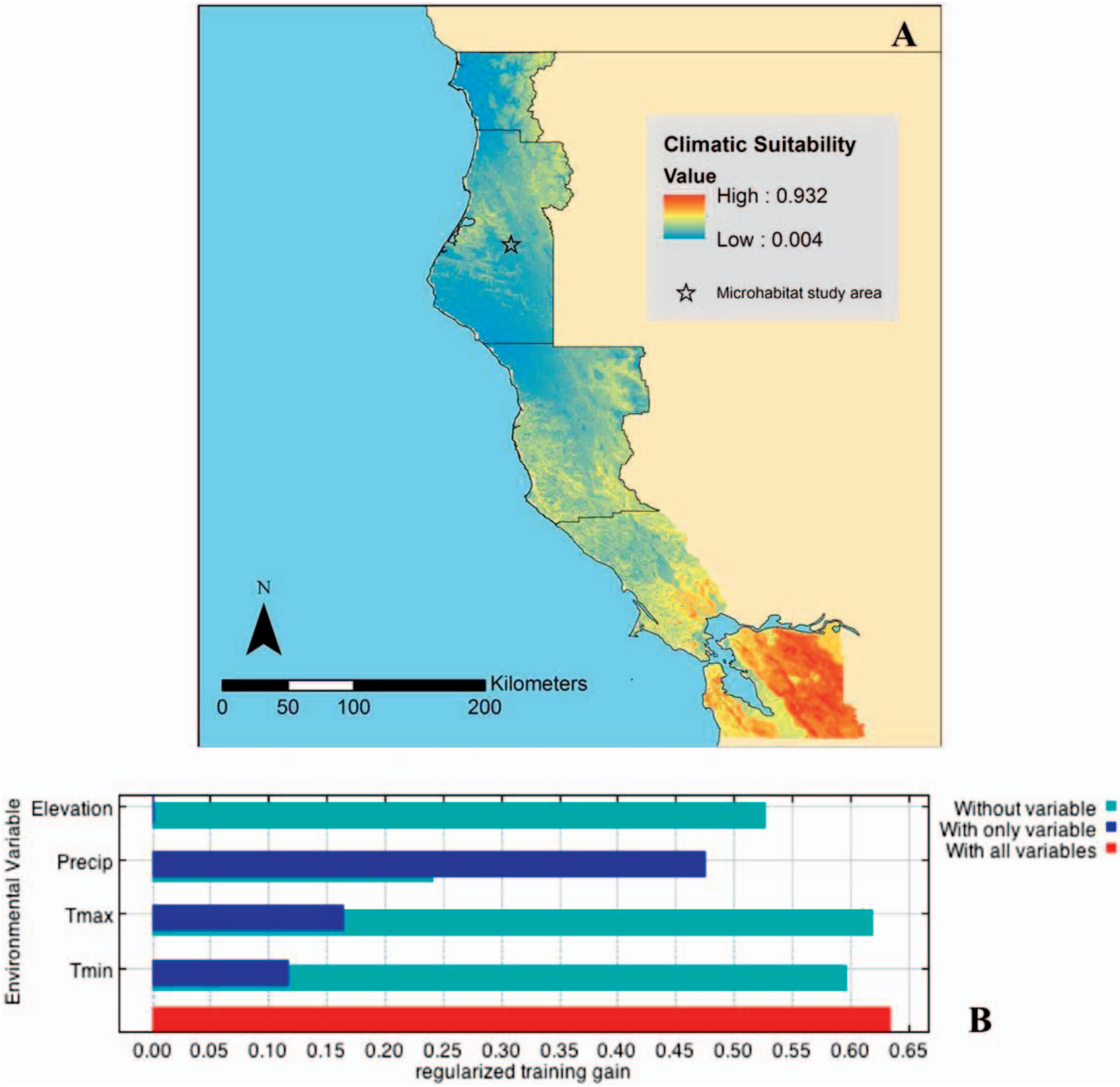

FIG. 4. The climatic suitability map (A) for *C. o. oreganus* within coastal, northern California counties (NorCal Coast) produced by the selected environmental niche model (ENM). The outlined California counties are (south to north) Mendocino, Humboldt, and Del Norte. The selected ENM for the NorCal Coast contained the environmental variables elevation, mean precipitation in March (Precip), maximum temperature in March (T_{max}), and minimum temperature in March (T_{min}). Results of the jackknife test (B) indicate that the mean precipitation had the greatest influence of climactic suitability.

significantly greater than random chance ($P < 0.001$). However, the probability of landslides creating unsuitable outcrops was 39.19% and not significantly greater than random chance ($P = 0.976$).

DISCUSSION

Our models described the habitat of Northern Pacific Rattlesnakes at multiple spatial scales, providing a detailed account of habitat preference in northern California and western Oregon. We posit that an abundance of rocky outcrops in open-canopy microhabitats allows rattlesnakes to live along the relatively cool and wet north coast of California, which is characterized by a relatively marginal macroclimate where rattlesnakes might not otherwise occur. This species utilizes highly suitable, but patchily distributed, microhabitats to compensate for a less suitable macroclimate.

Regional Analysis.—The selected ENMs for each study area included the same environmental predictors (mean precipitation in March, minimum and maximum temperature in March, and elevation), but the models differed with respect to which environmental predictors were most influential. Precipitation was the most influential environmental predictor in the selected

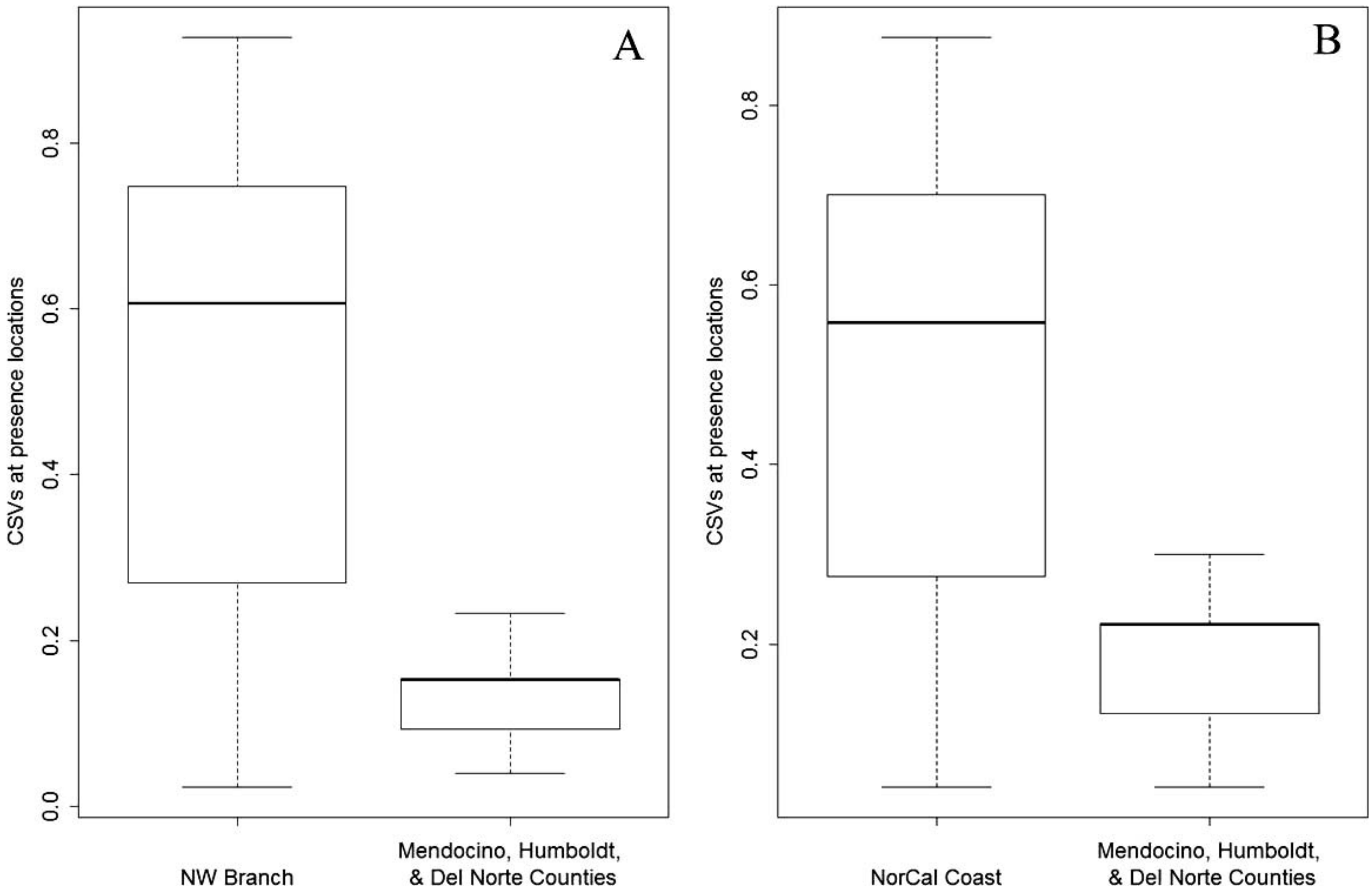

FIG. 5. The climatic suitability values (CSVs) for *C. o. oreganus* presence locations within Mendocino, Humboldt, and Del Norte counties compared to all other *C. o. oreganus* presence locations within each study area used for generating environmental niche models: northern California and western Oregon (NW Branch) and northern, coastal California counties (NorCal Coast).

NorCal Coast ENM, whereas the two temperature predictors were more influential in the selected NW Branch ENM. This discrepancy emphasizes the importance of selecting appropriate study extents when modeling a species' environmental niche. Although certain aspects of the macroclimate may be limiting at broad scales, different aspects can influence species presence at finer scales (Barve et al., 2011). Within the NorCal Coast region, temperatures remain relatively consistent and moderate throughout the year, whereas there is on average 22 mm more precipitation in March compared to the rest of the NW Branch. Consequently, suitable regions for rattlesnakes in the NorCal Coast region are constrained to areas with less precipitation. For species that occupy a diversity of habitats, populations adapt to their macroclimate behaviorally or by selecting microhabitat features (Barve et al., 2011). For example, *C. o. oreganus* in northern regions remain dormant in hibernacula during the winter months, but in southern parts of their range they remain active during the winter, adapting their behavior to local conditions (Gienger and Beck, 2011; Putman et al., 2013). In the present situation, rattlesnakes along the northern California coast appear to be selecting drier habitats over warmer ones, unlike rattlesnakes in interior regions.

The correlation between higher elevations and greater habitat suitability likely relates to the insolation of the hillsides. Insolation increases with elevation, because of higher levels of solar radiation warming soils. Also, south-facing slopes receive more sunlight throughout the day and have better insolation (Browning et al., 2005; Hamilton and Nowak, 2009). Therefore,

TABLE 3. Model selection results for the seven most parsimonious paired resources selection functions derived to predict the use of a rocky outcrop as a hibernaculum by *C. o. oreganus* near Maple Creek, California. The difference between each model's Akaike Information Criteria (corrected for small sample sizes; AICc) value and the lowest AICc is reported as the ΔAICc. Weight refers to the Akaike weight for each model. The model preceded by an asterisk (*) is derived solely from covariates previously cited as influencing snake hibernaculum selection.

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

TABLE 4. The estimated coefficients for the two most parsimonious paired resource selection function (pRSF) models describing selection of hibernacula by *C. o. oreganus* near Maple Creek, California. These two pRSF models account for 61% of the weight in their AICc table (Table 3). The covariates from the selected pRSF model are listed in the column labeled "Selected model." The column labeled "Second model" lists the covariates found in the second most parsimonious pRSF model.

Selected model	Estimated coefficient	Second 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 suitable habitat for these rattlesnakes also contains key characteristics for suitable hibernacula (Browning et al., 2005; Gienger and Beck, 2011). Unfortunately, neither model shows an upper elevation limit. Although insolation increases continuously, this species does not occur above the tree line in any part of its range, because of the decrease in mean temperature and fluctuating climatic conditions at these elevations (Campbell and Lamar, 2004; Hamilton and Nowak, 2009).

Models for both study areas identify regions that are densely populated by humans as highly suitable. This trend may be a relic of using historical presence records and relatively modern environmental predictors, or a result of presence locations being biased toward areas of high human population densities (i.e., southern portions of the study areas), which can lead to type II error in the form of spatial autocorrelation in the response variable (Veloz, 2009). Much of the developed San Francisco Bay area, California may contain suitable climatic characteristics, but human persecution and alteration of habitat prevents rattlesnakes from occupying these areas today (Campbell and Lamar, 2004). Therefore, our ENMs should be considered an estimate of the "potential distribution" because they ignore the influence of human activity (Peterson, 2006).

Microhabitat Analysis.—Our results indicated that *C. o. oreganus* select rocky outcrops that have more crevices, fewer cover objects, and occur on slopes facing due south. Further, our most parsimonious model indicated that the presence of a higher percentage of large talus encourages use of rocky outcrops as hibernacula. This analysis is the first multivariate approach to distinguish hibernacula from suitable outcrops located nearby (i.e., paired sites). Other studies have been able to distinguish hibernacula from random sites but not from paired sites (Burger et al., 1988; Prior and Weatherhead, 1996; Harvey and Weatherhead, 2006; Gienger and Beck, 2011).

Our results suggest that rattlesnakes select rocky outcrops as hibernacula based on features that aid them with thermoregulation, particularly during emergence. A higher density of crevices provides more surface area for snakes to thermoregulate throughout the day and could provide more access points to subterranean chambers. A lack of vegetation and woody debris on the surface of hibernacula allows for greater potential basking area and, coupled with south-facing slopes, the rocky outcrops receive more sunlight, leading to higher surface temperatures (Huey et al., 1989). In contrast to our results, studies on Eastern Pine Snakes (*Pituophis melanoleucus*) and Massasaugas (*Sistrurus catenatus*) found a positive association between the number of cover objects and hibernaculum suitability. However, unlike *C. o. oreganus*, these species use openings in the forest floor as hibernacula; under these circumstances, more cover objects abate daily fluctuations in temperature (Burger et al., 1988; Harvey and Weatherhead, 2006). Additionally, our results showed that rattlesnakes selected rocky outcrops dominated by large talus; this contrasts with those from a study of *C. o. oreganus* in Washington, which found that rattlesnakes selected outcrops dominated by medium talus (Gienger and Beck, 2011). The authors proposed that medium talus creates the ideal interstitial space, large enough for snakes to penetrate subterranean chambers but small enough to keep cold air out during winters (Gienger and Beck, 2011). However, in coastal Northern California winters are less intense than those in Washington, so having the correct amount of interstitial space may not be as crucial for snake survival. Larger talus creates larger interstitial spaces, leading to more subterranean volume that is accessible to the snakes, providing the potential for more snakes to use a single outcrop as a hibernaculum.

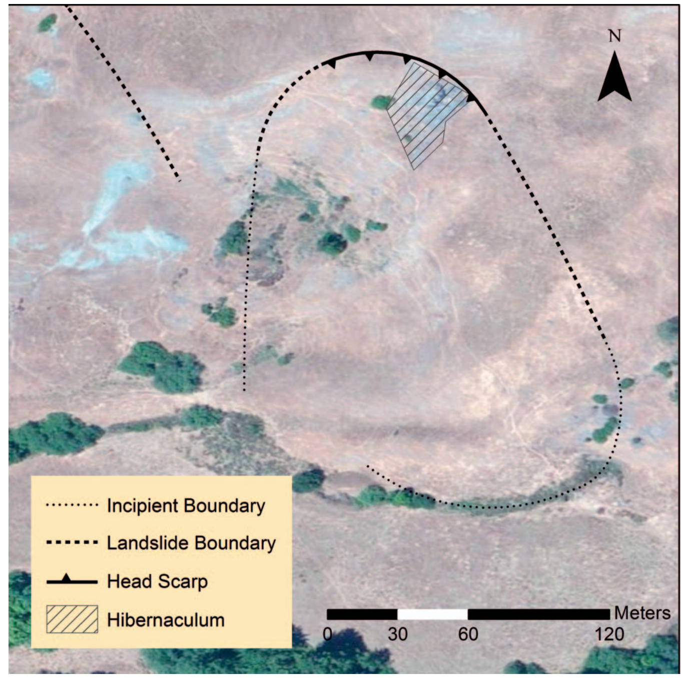

FIG. 6. Map of a landslide at a *C. o. oreganus* hibernaculum near Maple Creek, California overlaid on an aerial image provided by ArcGIS v 10.3.1. The long U-shaped line represents the landslide boundary. The incipient boundary is what we assume to be the landslide boundary (but we cannot be certain based on the local topography). Notice that the hibernaculum is located within the head scarp of this landslide.

Nearly all the covariates influencing hibernaculum selection are also associated with landslides. When a landslide occurs, the vegetative structure of the hillside is removed, exposing bedrock, and leaving an open canopy (Werner and Friedman, 2010). The removal of pressure above the bedrock can lead to jointing (i.e., crevice formation) within the now-exposed rock. Over time, weathering leads to the formation of joint-bound blocks in the outcrop, which eventually fall at the base of the outcrop, forming a talus apron around it. Landscapes with frequent landslide activity tend to have less canopy cover, less vegetation, and more bare soil, especially after recent landslides (Werner and Friedman, 2010). Landslides may create the rocky outcrops that are suitable as hibernacula.

Along the north coast of California, events that trigger landslides are common and the physical makeup of the landscape makes the region more susceptible to landslides. Heavy rainfall is the most common trigger, but earthquakes and anthropogenic activities (e.g., timber harvesting, road building, grazing, etc.) can also trigger landslides (Walker and Shiels, 2013). Steep slopes, such as those along river valleys, make landscapes more susceptible to landslides (Werner and Friedman, 2010). Additionally, the strength of the underlying bedrock can influence a hillside's susceptibility to landslides (Walker and Shiels, 2013). We found that 85% of the rattlesnake presence data used to generate the ENMs were associated with bedrocks of sandstone or slate, which have low strength values (Duvall et al., 2004; Lin et al., 2008). The relatively high frequency of landslides in the region has led to an abundance of suitable microhabitats, which has allowed the range of *C. o. oreganus* to extend further up the west coast of North America than any other rattlesnake. A more comprehensive model of habitat suitability for the region would include data on landslide occurrences. Unfortunately, meaningful data do not exist at our modeling scale. However, because landslides can cause tremendous damage to human property, they have been well documented throughout history (Walker and Shiels, 2013). Locations of landslides could serve as a starting point for locating novel rattlesnake populations or identifying locations of potential human–rattlesnake interactions.

Although no previous studies have explicitly examined the relationship between snake hibernacula and landslides, there is evidence to support the idea that this phenomenon also occurs in other regions. For example, hibernacula of Common Gartersnakes (*Thamnophis sirtalis*) were located in sinkholes created by slumps (Gregory, 1977). Furthermore, several studies on high-latitude snakes noted that populations or hibernacula occurred throughout rugged landscapes within the watersheds of large rivers where landslides are more common (e.g., Diller and Wallace, 1996; Parker and Anderson, 2007; Palis, 2010; Fortney et al., 2011).

Conclusions.—Our selected ENMs, pRSF models, and landslide maps together provide unique insight into why *C. o. oreganus* occur in cool and wet macroclimates, such as those found along California's north coast. The high density of landslides in the region likely creates more suitable rocky outcrops for hibernation, which helps compensate for the marginal macroclimatic conditions. We encourage the consideration of compensatory microhabitat selection when modeling the suitable habitat for a given species. These considerations are particularly important when the species of interest has an expansive range that includes a diversity of macroclimates. We acknowledge that other factors besides the physical environment may help explain the existence of a widespread species in a marginal macroclimate. Species can physiologically adapt to macroclimatic conditions to promote their fitness (e.g., Du et al., 2010), and marginal macroclimates may be refuges from human persecution or habitat degradation. The factors are not mutually exclusive, and all potential factors should be considered to understand how a species persists in a marginal macroclimate.

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