Journal of Mammalogy, 96(2):380–393, 2015
DOI:10.1093/jmammal/gyv039

A range-wide occupancy estimate and habitat model for the endangered Point Arena mountain beaver (*Aplodontia rufa nigra*)

William J. Zielinski,* Fredrick V. Schlexer, Jeffrey R. Dunk, Matthew J. Lau, and James J. Graham

USDA Forest Service, Pacific Southwest Research Station, Redwood Sciences Laboratory, 1700 Bayview Dr., Arcata, CA 95521, USA (WJZ, FVS)
Department of Environmental Science and Management, Humboldt State University, 1 Harpst Street, Arcata, CA 95521, USA (JRD, JJG)
Department of Wildlife, Humboldt State University, 1 Harpst Street, Arcata, CA 95521, USA (MJL)

* *Correspondent: bzielinski@fs.fed.us*

The mountain beaver (*Aplodontia rufa*) is notably the most primitive North American rodent with a restricted distribution in the Pacific Northwest based on its physiological limits to heat stress and water needs. The Point Arena subspecies (*A. r. nigra*) is federally listed as endangered and is 1 of 2 subspecies that have extremely small and disjunct distributions, putting the taxon at risk from habitat loss and warming global temperatures. We sought to understand their range-wide distribution, to predict the environmental features that best describe their occurrence, and to establish a foundation for monitoring their distribution. We randomly sampled the occurrence of Point Arena mountain beavers (PAMB) from the portion of their geographic range that was accessible (public lands plus private lands where permission was granted). We surveyed 127, 25-ha sample units for their distinctive burrows and estimated the probability of detecting burrows, if they were present, at > 90% per visit. Using this information, we estimated occupancy across the accessible portion of the range to be 26.2%. Range-wide estimates of occupancy, combined with strategically selected locations where abundance and survival can be estimated noninvasively, may comprise a realistic monitoring program for this taxon. We also used the detection and nondetection locations to develop a habitat suitability model by relating these locations to remotely sensed predictors. We evaluated 53 a priori candidate habitat suitability models and the best-fitting model included gentle slopes, low terrain roughness indices, and the high density of rivers and streams. Selecting the probability value that best separated the sample units into suitable and nonsuitable habitat, we estimated a total of 70.5 km^2 of suitable habit, or approximately 40.4% of the original geographic range. New detections significantly expanded the known geographic range, moderating concerns about habitat loss, including that predicted by climate change. A substantial number of suitable areas were predicted to occur outside the current range. The identification of high suitability areas allows management agencies to prioritize areas for PAMB conservation planning, evaluate human impacts on habitat, and evaluate how a changing climate may affect distribution.

Key words: *Aplodontia*, California, habitat, modeling, mountain beaver, occupancy, Point Arena

---

The mountain beaver (*Aplodontia rufa*) is the most primitive living rodent, with a distribution that is limited to the cool and moist environments in the Pacific region of North America (Feldhamer et al. 2003). Its restricted distribution has been explained by a limited ability to concentrate urine, thereby requiring abundant surface water or succulent vegetation in their diet (Nungesser and Pfeiffer 1965). The mountain beaver also lacks adequate mechanisms to avoid heat stress (Johnson 1971), which may also restrict the species to cool environments in the Pacific Northwest. It is semi-fossorial, inhabiting complex burrow systems that frequently occur in moist seeps that host a dense tangle of vegetation (Dalquest 1948). The distribution of the species is relatively limited, but 2 of the 7 subspecies have extremely limited and disjunct distributions: the Point Reyes mountain beaver (*A. r. phaea*) and the Point Arena mountain beaver (PAMB; *A. r. nigra*—Feldhamer et al. 2003). Both occupy ranges that are small (< 100 km^2) and that have probably been shrinking since the Eocene due to drying of the regional climate as well as vegetation and topographic changes (Shotwell 1958).

The PAMB is listed as endangered under the United States Endangered Species Act due to habitat loss from development and livestock grazing (Steele and Litman 1998; USFWS 2009).

Despite its endangered status, there is little known about its ecology (e.g., Camp 1918; Fitts 1996; Fitts et al. 2002; Billig and Douglas 2007; Zielinski et al. 2010). The PAMB range includes 2 very different ecosystems: forests in mountains in the eastern portion and shrub and grasslands in the coastal terraces of the western portion of the range (Fig. 1). As a result, it is of conservation interest to understand the environmental features that are associated with their occurrence in these 2 very different realms. The small size of the known range, the vulnerability of the taxon to a warming climate (USFWS 2009), and the diversity of vegetation types that the PAMB appears to occupy within its range all demand a better understanding of the features within the range that favor their occurrence.

Recovery goals for the PAMB specify minimum standards for the number and size of populations and for monitoring trends in populations and geographic range (Steele and Litman 1998; USFWS 2009), yet quantitative information about population status is limited to abundance estimates within or immediately adjacent to one of the few protected areas within the subspecies' range: Manchester State Park (Northen and Fitts 1998; Zielinski et al. 2013a). Mark-recapture methods were used to estimate population size for 2 locations within the park, and both had low but stable numbers from 2006 to 2009 (Zielinski et al. 2013a). At other historic locations throughout the subspecies' range, recent searches found no evidence of their burrows (F. V. Schlexer, pers. obs.). However, whether new sites had been colonized over the same time period is

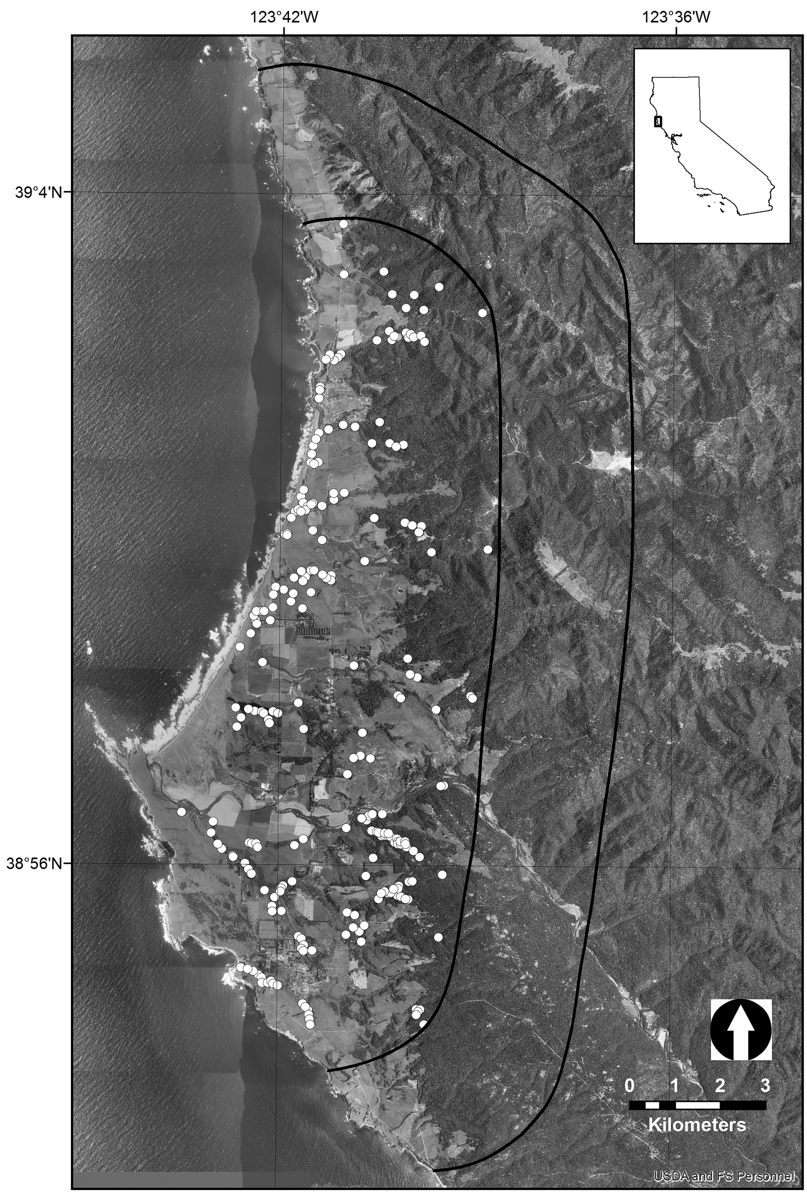

Fig. 1.—Distribution of the known sites (white dots) identified in the 5-year status review for the Point Arena mountain beaver (*Aplodontia rufa nigra*—USFWS 2009). The innermost line encircling the sites smooths the minimum convex polygon of the geographic range based on site records (~85 km^2). The outermost line represents a 3-km buffer and encompasses an area (~174 km^2) the USFWS (2009) designates as the historic distribution (USFWS 2009). The background is aerial imagery from the USDA National Agriculture Imagery Program (NAIP) illustrating the largely forested eastern portion of the range (darker areas) and the western portion that includes more grassland, agriculture, and pasture (lighter areas).

unknown. An objective and quantitative assessment of the population status of the PAMB throughout its geographic range does not exist despite it being a recovery criterion (USFWS 2009).

Monitoring an adequate number of locations intensively enough to estimate abundance directly is infeasible. An alternative, used extensively in recent wildlife studies, is occupancy estimation (MacKenzie et al. 2006). This approach samples the presence (yes ["1"] versus no ["0"]) of a species within sample units distributed randomly across the landscape and assumes that the frequency of occurrence is an index of population status. The assumption that measures of occurrence collected across the range (distribution) reflect changes in abundance has received considerable support (Brown 1984; Gaston 1996; Stanley and Royle 2005; Noon et al. 2012). Under some circumstances, such as when budget is limited or when a species is uncommonly detected, presence–absence surveys can be more effective than measures of abundance at determining population status (Joseph et al. 2006). Occupancy estimation is a well-established approach for species that are very expensive or difficult to count. The PAMB fits these characteristics and one of our objectives was to use occupancy estimation to quantitatively measure the status of the PAMB population throughout its range. Repeated sampling using the same approach can then serve as a population monitoring program, as demonstrated for other species (e.g., Karanth et al. 2011; Gould et al. 2012; Zielinski et al. 2013b).

Relating the detections and nondetections from occupancy surveys to associated environmental variables can also produce a habitat model that predicts a species' occurrence and distribution (e.g., Elith and Leathwick 2009). One of the values of species distribution modeling is that it can produce a map that identifies the location, extent, and configuration of areas where the species is likely to occur. To date, the only habitat modeling for the PAMB has been based on expert opinion (Fitts et al. 2002) or has focused on the habitat at den site locations (Zielinski et al. 2010). Both of these studies examined only a small proportion of the PAMB range, thus, our 2nd objective was to develop a range-wide map of predicted habitat suitability. This will identify likely core areas and potential corridors that can be managed to prevent their degradation. We also used our model to explore the distribution of habitat among physiographic regions where previous work (Zielinski et al. 2012) had identified genetic differentiation.

Materials and Methods

Study area.—We defined the PAMB geographic range as the potential range map in the species' 5-year status review (USFWS 2009). The United States Fish and Wildlife Service (USFWS) created it by adding a 3.2-km buffer around the perimeter of known locations (except the western boundary, which is the Pacific Ocean). Considering only the outermost points of the detection locations, the geographic range was ~85 km^2; adding the buffer expanded the range to ~174 km^2 (Fig. 1). This larger area served as the basis of our sampling frame and is henceforth referred to as the geographic range. This area includes a wide array of ecosystems, including coastal dunes and scrub, hardwood riparian forest, and coniferous forest. The western portion of the range is coastal terrace with grassland, coastal scrub, and agricultural (mostly grazing) lands dissected by largely east–west flowing streams with shrub, forb, and hardwood tree riparian areas. To the east, the coastal terrace transitions into foothills and mountains with nearly continuous forests comprised of grand fir (*Abies grandis*), redwood (*Sequoia sempervirens*), tan oak (*Notholithocarpus densiflorus*), and Douglas-fir (*Pseudotsuga menziesii*). These forests are divided by high-gradient streams bordered with conifer and hardwood (typically red alder—*Alnus rubra*) cover. The PAMB range, therefore, is characterized by low plains and hills generally lacking forest cover in the west, and mountainous and often steep forested terrain in the eastern portion (Fig. 1). The climate is Mediterranean maritime with relatively cool summers and winters that are wet with only occasional freezing temperatures. Mean annual precipitation exceeds 1,000 mm, with most falling as rain from October to April.

Occupancy surveys.—Using a geographic information system (GIS), we overlaid a rectilinear grid of 25-ha cells on the entire 174-km^2 geographic range that yielded a total of 780 complete, 25-ha cells. Twenty-five hectares was chosen because it was viewed as being small enough to survey by 2 people in one-half day and large enough for us to sample a sufficient number during our study to have a meaningful sample. Our objective was to randomly sample from this population of cells to search for sign of mountain beavers, but not all portions of the range were available for sampling. We had immediate access to 4.6% of the range because it was in state or federal public ownership; the remainder of the range was on private land and thus required seeking permission. To do so, we took advantage of a previous outreach effort to locate private landowners willing to allow surveys for either PAMB or a species of federally listed butterfly (Behren's silverspot—*Speyeria zerene behrensii*). In the spring of 2013, we contacted landowners who had responded positively to the original survey. This process resulted in permission to survey on approximately 60 km^2 of private land, or roughly 36.2% of the private land in the geographic range. We refer to this combination of public and private parcels as the accessible land base and it comprised 39.1% of the geographic range.

To evaluate whether the accessible portion of the range represented a biased subset of the entire range (i.e., sample selection bias, sensu Phillips et al. 2009) we compared the vegetation cover features of accessible and inaccessible areas. To determine if our habitat model could be extrapolated from the accessible lands to the proportion of the land base that was inaccessible, we compared the vegetation cover features of both areas. Using a dominant vegetation GIS layer (USDA Forest Service 2010), we determined that the proportions of the accessible and inaccessible land bases that were in each of 4 vegetation types were roughly equivalent (Table 1). Thus, we believe the accessible lands are representative of the inaccessible lands and that our habitat model could be applied to the entire geographic range. As further confirmation, we also compared the range of values of the variables in our final habitat model (see "Results"), for the accessible and inaccessible portions of the range, to determine whether they were similar. If so,

Table 1.—The proportion of 4 cover types, classified using the CalVeg vegetation classification system (US Forest Service 2010) and identified by accessibility within the Point Arena mountain beaver (*Aplodontia rufa nigra*) geographic range.

Vegetation type	Accessible land area (4,908 ha)	Inaccessible land area (12,110 ha)
Forest	0.60	0.60
Grass/forb/shrub	0.30	0.27
Nonhabitat	0.05	0.09
Riparian	0.05	0.04

it would suggest that the variables useful at predicting PAMB occurrence were not substantially different between the available and unavailable cells.

Not all 25-ha cells in the accessible land base were 100% accessible; those that had > 80% of their area accessible were eligible for inclusion in our sample, resulting in a total of 193 potential 25-ha sample units. Initially, we randomly selected 100 of these for inclusion in our sample. After this selection, we learned of additional private lands (36 twenty-five-ha units) that were accessible, and from these, we randomly selected 27 more units for a total of 127 sample units (Fig. 2). Each of these sample units was surveyed for the presence of at least 1 PAMB burrow. If a burrow was detected, the survey for the unit was concluded. When 1 burrow is found typically others are also present (W. J. Zielinski, pers. obs.), but we did not enumerate them for this study. PAMB burrows are distinctive; they are much wider (~20 cm) than the burrows of the most common other burrowing mammal, the pocket gopher (*Thomomys* sp.). Species of other burrowing mammals are either very rare (e.g., badger—*Taxidea taxus*) on the study area or produce very different burrow openings (e.g., California ground squirrel—*Otospermophilus beecheyi*, striped skunk—*Mephitis mephitis*). PAMB burrows that were discovered in any condition or age were used to indicate PAMB presence, but the evidence of abandoned burrows rarely persists more than a few years (F. V. Schlexer, pers. obs.). Four field technicians were trained by an experienced researcher (FVS) to search for and verify the identity of PAMB burrows. The technicians' skill at burrow identification was periodically validated by their supervisor.

Each survey visit consisted of a team of 2 technicians thoroughly searching up to 10 ha of each 25-ha unit in habitat conditions most likely to be inhabited by PAMB. This strategy allowed us to maximize the number of sample units we could search and is similar to that used for occupancy surveys for other species (e.g., Karanth et al. 2011). Previous work (e.g., Zielinski et al. 2012) suggested that we were most likely to discover PAMB burrows in areas where there was one of several conditions: (1) a mix of overhead cover and canopy openings, (2) near streams or drainages, or (3) where there were changes in topographic relief. Thus, as the technicians planned their surveys each day, these areas were prioritized for searches when they occurred within a sample unit. Using these constraints, the 2 technicians typically searched parallel paths 50–100 m apart in the sample unit. Searching 10 ha took from 1 to 4 h, depending on the terrain and access. The surveyors verified that they

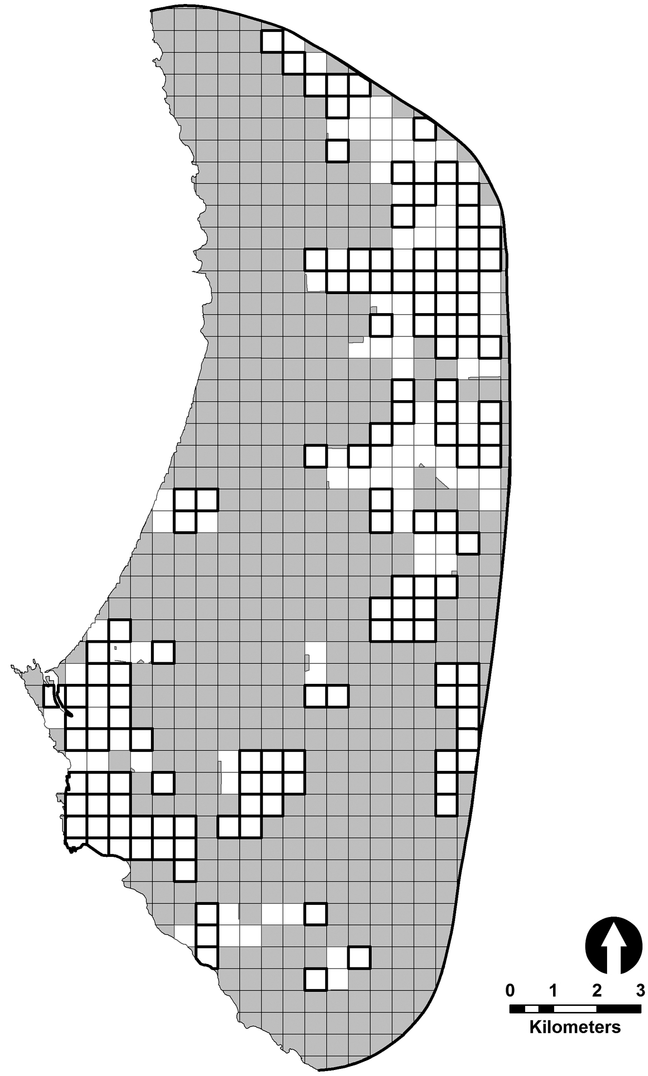

Fig. 2.—The 193, 25-ha grid cells (white squares) from which 127 sample units (squares with bold perimeters) were randomly selected to survey for Point Arena mountain beavers (*Aplodontia rufa nigra*) in the summer of 2013. Parcels accessible for sampling are in white, inaccessible parcels are in gray.

were searching within the specified sample unit by recording one of their search paths on a geographic positioning system. Cells were sampled from May to August 2013.

The pair of surveyors visited sample units only once if during the 1st visit they discovered a PAMB burrow (i.e., confirmed occupancy). If, however, they did not detect a burrow, a 2nd pair of technicians searched the unit on a subsequent day (usually within the same week). Thus, each sample unit had a "detection history" that was either: detection on the 1st occasion (notation "1"), detection on the 2nd of 2 sample occasions (notation "01"), or no detection on either occasion (notation "00"). These search replicates allowed us to estimate the probability of detection if present (MacKenzie et al. 2006), which is the proportion of sample occasions when the 1st survey resulted in no detection and the 2nd survey resulted in a detection ("01"). The information from these sample units provides an estimate of the number of occasions when surveyors overlooked a burrow and is used to adjust the naive estimates of occupancy to account for uncertainty in detection. Thus, our estimate of occupancy was the proportion of sample units where a PAMB burrow was actually detected (the naive occupancy estimate) plus the proportion of sample units where we estimated a burrow was overlooked (the adjusted occupancy estimate).

Occupancy and probability of detection were modeled using the software PRESENCE (version 6.2—Hines 2006). We tested the fit of the data to 3 models. The 1st assumed that sites were homogenous in respect to occupancy (i.e., "1 group") and had a constant probability of detection for both the 1st and the 2nd visit ("constant *p*"). The 2nd assumed 1 group but that probability of detection differed between visits ("survey-specific *p*"). The third assumed that the sample units were heterogeneous, belonging to 2 or more groups in respect to occupancy and had a constant probability of detection. The best model was determined by evaluating the relative model fit using Akaike's information criteria (AIC) and AIC weights (Burnham and Anderson 2002).

Habitat modeling.—We suspected that informative landscape-scale variables would come from 1 or more of the following categories: anthropogenic (e.g., roads), topographic, hydrologic, biotic (classified remotely sensed vegetation-related variables), and edaphic. Various pre-existing sources for variables within each category were investigated to find those that (1) had a link to the ecology of mountain beavers, (2) were available for the entire geographic range, and (3) were variable enough across the range to be useful at distinguishing detection from nondetection locations. The list of variables that remained after this filtering was reduced further by eliminating one of a pair that were highly correlated ($r > 0.80$). The final set of 10 predictor variables (Table 2) were down sampled to match the 25-ha sample unit and used to create a collection of a priori univariate and multivariate models (Appendix I) chosen to represent alternative views of environmental factors that might affect PAMB distribution (Burnham and Anderson 2002).

We used nonparametric logistic regression, a subset of generalized additive models, with loess smoothing functions (Cleveland 1985) to compare models representing the relationship between sample units with a PAMB detection and those without. We evaluated each model's fit to the data using the bias-corrected AIC (AIC_c—Akaike 1973). We calculated relative importance values for individual variables by determining the gain in AIC_c value when each variable was removed from the final model. We evaluated model discrimination by integrating the area under the receiver operating characteristic curve (area under the curve [AUC]—Fielding and Bell 1997). Random predictions result in an AUC value of 0.5, whereas a perfect prediction assumes the maximum value of 1.0. We performed cross validation of the best model to determine how robust it was to perturbations of the data used to develop it. Cross validation was done by removing a random 10% subset of the developmental data, training the model on the remaining 90% of the data, then classifying the withheld 10%. This process was repeated 10 times with replacement. The best-fitting model resulted in a prediction of habitat suitability for each sample unit that ranged from 0 to 1.

To distinguish suitable from unsuitable habitat along the continuous range of habitat suitability values, we chose a threshold value that optimized Cohen's kappa value (Cohen 1960). We evaluated kappa at 26 alternative cut-off points for classifying detection and nondetection units, at 0.01 increments, starting at predicted values of 0.20 and continuing to 0.45. The optimal cut-off was the point above which the kappa value did not increase. Sample units with values above this threshold were classified as suitable, below this value they were classified as unsuitable. We also estimated the proportion of the range that is suitable, the proportion of each of the primary watersheds (as originally identified in Zielinski et al. 2012), and the proportion of the range that is north and south of the Garcia River, a putative geographic feature that has influenced genetic substructure in the PAMB (Zielinski et al. 2012).

Results

Occupancy surveys.—A total of 127 sample units were surveyed. The detection of mountain beaver burrows at 33 of these resulted in a naive estimate of occupancy of 0.259 (Fig. 3). Thirty surveys detected evidence of burrows on the 1st visit, the balance of positive detections ($n = 3$) were confirmed on the 2nd visit after failing to detect a burrow on the 1st visit. An average (*SD*) of 1.0 (0.8) h was spent searching sample units before a detection occurred and 1.6 (0.9) h in sample units, where no burrow was detected. The "1-group, constant *p*" model best fits the data (AIC wt = 0.7311; Table 3) resulting in an adjusted estimate of occupancy of 0.262 ($SE = 0.039$; 95% confidence interval = 0.1927 – 0.3466). The per-visit probability of detection (p) was 0.90 ($SE = 0.061$). When this is compounded by the maximum number of visits possible ($n = 2$), the total probability of detection for the survey protocol was very high ($1 - [1 - 0.90]^2 = 0.99$), suggesting high confidence in detecting evidence of mountain beavers when present.

We detected PAMBs in some sample units that were within the 3-km buffer, beyond the original distribution of PAMB locations provided by the USFWS (2009). The original range of ~85 km^2 was calculated by enclosing the marginal locations in the north, east, and south and extending the range to the coastline in the west. Our new marginal locations, especially in the east and the north, expand the estimated geographic range from ~85 to ~134 km^2 (Fig. 3). Adding a 3.4-km buffer to this area, as was done with the original range (USFWS 2009), produced a new estimated geographic range of ~235 km^2.

Habitat modeling.—Of the 53 a priori models evaluated, the top-ranked model (SLOPE + TRI + RIVSTREAM) accounted for a dominant proportion of the Akaike weight (0.85; Table 4). The next 2 highest ranking models not only had weights that were far less (0.098 and 0.036, respectively; Table 4) but also included 2 or 3 of the variables included in the top model (Table 4). The variables in the top 3 models included variables from the topographic and hydrologic groups (SLOPE, ASPECT, TRI, and RIVSTREAM). The top model had an

Table 2.—Final set of predictor variables used to model range-wide Point Arena mountain beaver (*Aplodontia rufa nigra*) habitat. Definitions apply to the assessment of the variable averaged for each 25-ha sample unit.

Variable	Abbreviation	Definition
Greenness Index	GREENNESS	Calculated using a tasseled-cap transformation and 7 bands from Landsat 7 Enhanced Thematic Mapper (ETM+) (Huang et al. 2002). The greenness index produces cell values where higher numbers indicate an increased presence of chlorophyll and healthy vegetation. Values for each sample unit were extracted from the greenness raster using BlueSpray (Schooner Turtles Inc. 2014) and represent the mean value of all the pixels within each sample unit.
Wetness Index	WETNESS	Calculated using a tasseled-cap transformation and 7 bands from Landsat 7 ETM+ (Huang et al. 2002). The wetness index portrays vegetation moisture. This index is sensitive to soil and plant moisture and vegetation structure. Values for each sample unit were extracted from the wetness raster using BlueSpray (Schooner Turtles Inc. 2014) and represent the mean value of all the pixels within each sample unit.
Aspect	ASPECT	Calculated using the Aspect tool (Spatial Analyst license) in ArcGIS v.10.1 (ESRI 2013) with a 1-arc 2nd DEM downloaded from the USGS (2013), then cosine transformed to represent "northness". Values for each sample unit were extracted from the aspect raster using BlueSpray (Schooner Turtles Inc. 2014) and represent the mean "northness" value of all the pixels within each sample unit.
Slope	SLOPE	Calculated using the Slope tool (Spatial Analyst license) in ArcGIS v.10.1 with a 1-arc 2nd DEM downloaded from the USGS (2013). Values represent degree of slope. Values for each sample unit were extracted from the slope raster using BlueSpray (Schooner Turtles Inc. 2014) and represent the mean value of all the pixels within each sample unit.
Terrain Roughness Index	TRI	Calculated with the NED DEM by looking at an 8-cell neighborhood for each 30-m pixel. Specifically, it calculates the difference of the cell value and the mean of the 8-cell neighborhood. The resulting raster layer can be reclassified based on the TRI categories defined by Riley et al. (1999), ranging from flat to extremely rugged (values from 0 to 1). Values for each sample unit were extracted from the TRI raster using BlueSpray (Schooner Turtles Inc. 2014) and represent the mean value of all the pixels within each sample unit.
Relative Position Index	RPI	Calculated with the NED DEM by examining each pixel's relative position with respect to its local neighborhood (Jenness 2004). Values range from 0–1, indicating low to high ruggedness. Values for each sample unit were extracted from the RPI raster using BlueSpray (Schooner Turtles Inc. 2014) and represent the mean value of all the pixels within each sample unit.
Secondary roads	SROADS	Downloaded from USGS, The National Map Program (2013). Includes networks of local neighborhood streets as well as major roadways in the study area. Includes primarily public paved and unpaved roads (USGS 2013). Values for each sample unit represent length of secondary roads within each unit. This includes all paved and unpaved public roads. Ground-checking revealed that it also includes the majority of unpaved roads on private land.
Rivers and streams	RIVSTREAM	Downloaded from USGS, The National Map Program (2013). Values for each sample unit represent length of rivers and streams within each unit. Includes intermittent streams.
Bulk density	BD13	Downloaded from the USDA Web Soil Survey (USDA National Conservation Service 2012). Bulk density describes the oven-dry weight of soil material less than 2 mm in size per unit volume of soil at water tension of 13 bars. The ratings are measured in units of grams per cubic centimetre. Values for each sample unit were extracted from the bulk density raster using BlueSpray (Schooner Turtles Inc. 2014) and represent the mean value of all the pixels within each sample unit.
Percent clay	PERCENT CLAY	Downloaded from the USDA Web Soil Survey. This variable describes the percent of soil content containing clay particles. Values for each sample unit were extracted from the percent clay raster using BlueSpray (Schooner Turtles Inc. 2014) and represent the mean value of all the pixels within each sample unit.

AUC value of 0.837, meaning that using this model, a randomly selected detection location will have a larger predicted habitat value than a randomly selected absence location 83.7% of the time. RIVSTREAM was the most influential variable in the top model. When it was removed from the top model, the AIC_c value increased by 18.8 points, compared with removing SLOPE and TRI, which increased the AIC_c value by 4.3 and 9.0 points, respectively.

Detections occurred in sample units that, on average, were on more level slopes, with lower terrain roughness indices, and higher densities of rivers and streams (Fig. 4). This model provided good separation between the predicted values of detections and nondetections (Fig. 5A), with the maximum predicted value of 0.95 for a site with a detection. This model was also very robust to cross validation, producing equally good separation between predicted values of detections and nondetections

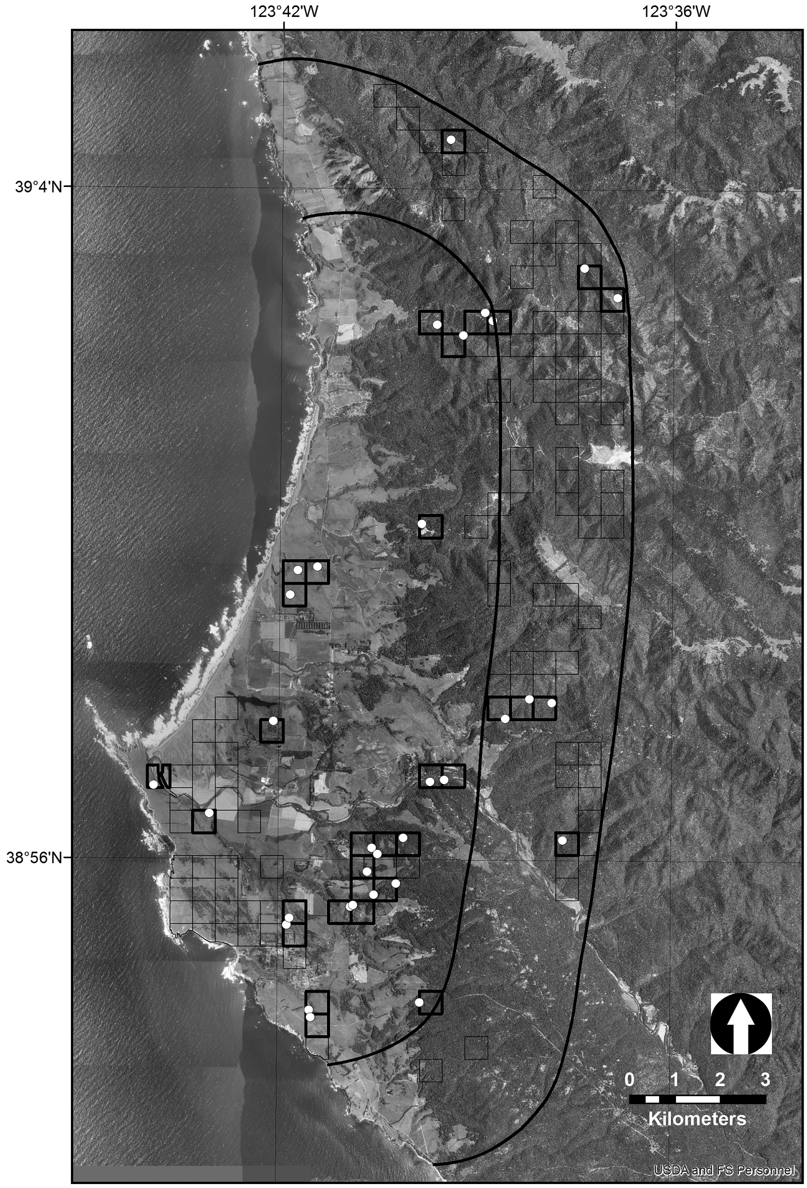

Fig. 3.—The 127 sample units used to survey for Point Arena mountain beavers (*Aplodontia rufa nigra*) during the summer of 2013. The 33 sample units with detections are noted with bold perimeters and a white dot to indicate the location of the detection.

(Fig. 5B) and an AUC value of 0.85. Cohen's Kappa for the top model achieved its maximum value at a cut-off of 0.34. This resulted in a total of 281 sample units (full plus partial) that exceeded this value (Figs. 6A and 6B). Recognizing that sample units predicted to be habitat will contain some small areas that are not suitable habitat for PAMB, while those units predicted to not contain habitat could have small areas that are habitat, we can assume that our model averages these and then predict that the total suitable habitat for the PAMB is about 70.5 km^2 or 40.4% of the USFWS (2009) originally estimated geographic range plus 3.4-km buffer (~174 km^2). Using the same approach, all watersheds in the range had at least 25% of their area in suitable habitat; the Moat Creek watershed had the highest at 47% (Table 5). The areas north and south of the Garcia River, which previous research suggested influenced historical gene flow, were 28.9% and 39.3%, respectively (Table 5).

Comparing the range of values for each of the predictors, in the accessible and inaccessible portions of the geographic range, allows us to evaluate our assumption that these 2 areas are equivalent in respect to features associated with PAMB occurrence. The percent of units in the inaccessible areas that had values that exceeded the minimum or maximum for SLOPE, TRI, and RIVSTREAM (the 3 variables in the best model) were 0.5%, 0.0%, and 0.0%, respectively. This suggests that the inaccessible portions of the range resembled the accessible portions that were sampled, in respect to the range of values for the key predictors in the model.

Discussion

Our work is an example of how surveys conducted on 1 portion of the geographic range—the accessible areas—can result

Table 3.—Top ranked models to estimate occupancy for the Point Arena mountain beaver (*Aplodontia rufa nigra*) from sampling across their geographic range in Mendocino, California. The models were derived from data collected from May to August 2013. Akaike's information criterion (AIC), change in AIC (ΔAIC), AIC weight (w_i), likelihood, and number of parameters for each model are identified.

Model	AIC_c	ΔAIC	w_i	Model likelihood	Parameters
1-group, constant *p*	169.62	0.0	0.731	1.00	2
1-group, survey-specific *p*	171.62	2.00	0.269	0.37	3
2-group, constant *p*	173.62	4.00	0.090	0.135	4

Table 4.—Top-ranked habitat models for the Point Arena mountain beaver (*Aplodontia rufa nigra*) from sampling across their geographic range in Mendocino County, California, derived from data collected from May to August, 2013. Akaike's information criterion (AIC_c), AIC weight (w_i), cumulative weight (cum. wt.), and difference in weight between top-ranked and listed model (wt_i) are presented.

Model	AIC_c	AIC wt. (w_i)	Cum. wt.	$wt./_{highest}wt_i$
SLOPE + TRI + RIVSTREAM	92.79	0.848	0.848	1.000
TRI + RIVSTREAM	99.10	0.098	0.946	8.64
ASPECT + SLOPE + TRI + RIVSTREAM	99.12	0.036	0.981	23.70

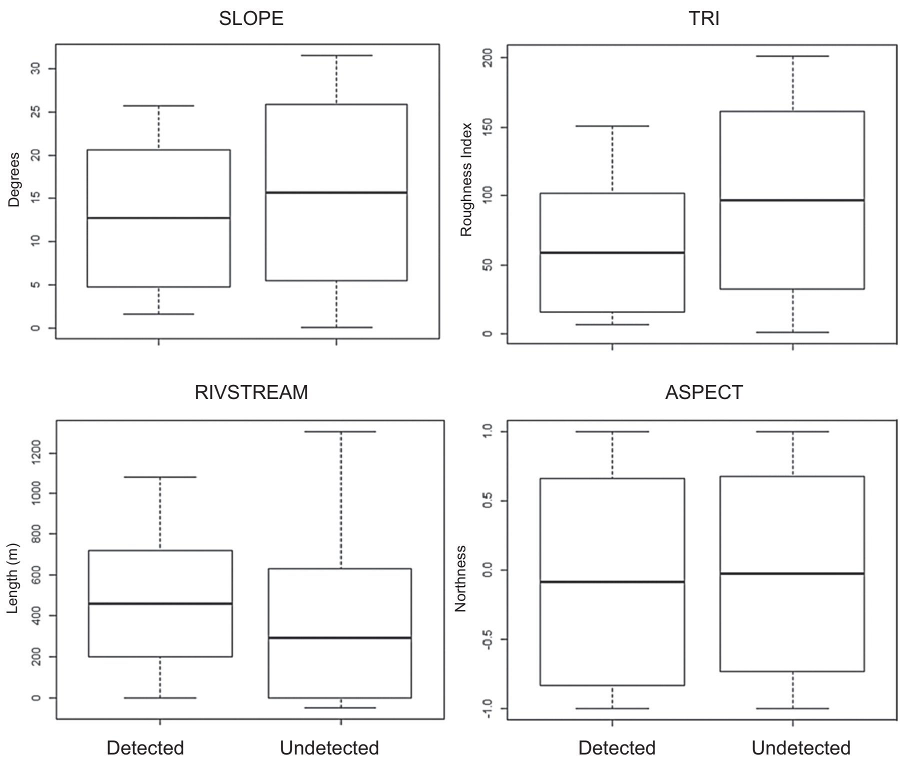

Fig. 4.—Boxplots for the 4 variables in the top 3 habitat models (SLOPE, TRI, RIVSTREAM, ASPECT). The black bar is the mean value, the box represents the *SD*, and the bars represent the range in values for the 33 sample units with detections and the 94 sample units with no detections. See Table 2 for definitions for the variables.

in predictions that can benefit the conservation of a taxon on the unsurveyed portions of the range. Endangered species often inhabit private lands where access is prohibited. Remotely sensed variables are available across all ownerships permitting the development of GIS-based models that can predict species occurrences even where surveys are not allowed. We demonstrated the conservation benefits of using remotely sensed variables for developing models for endangered species across mixed ownership landscapes (e.g., Wilson et al. 2013).

PAMB were estimated to occur at 26.2% of the sample units we surveyed. Our survey method had a high probability of detecting evidence of the PAMB when it was present (>90%), leading to confidence in the precision of our estimates of occupancy. The estimate of range-wide occupancy produced for this taxon represents a baseline for quantitatively monitoring the subspecies' distribution. This would most efficiently be accomplished by repeatedly surveying the same sample units we sampled using multiple-season occupancy models (MacKenzie et al. 2006) to estimate trends in occupancy over time. A similar program has been in place for approximately 10 years to monitor the southern Sierra fisher (*Pekania pennanti*) population (Zielinski et al. 2013b). A monitoring program of this nature would also provide opportunities to identify where sample units transition from occupied to nonoccupied ("extinction")

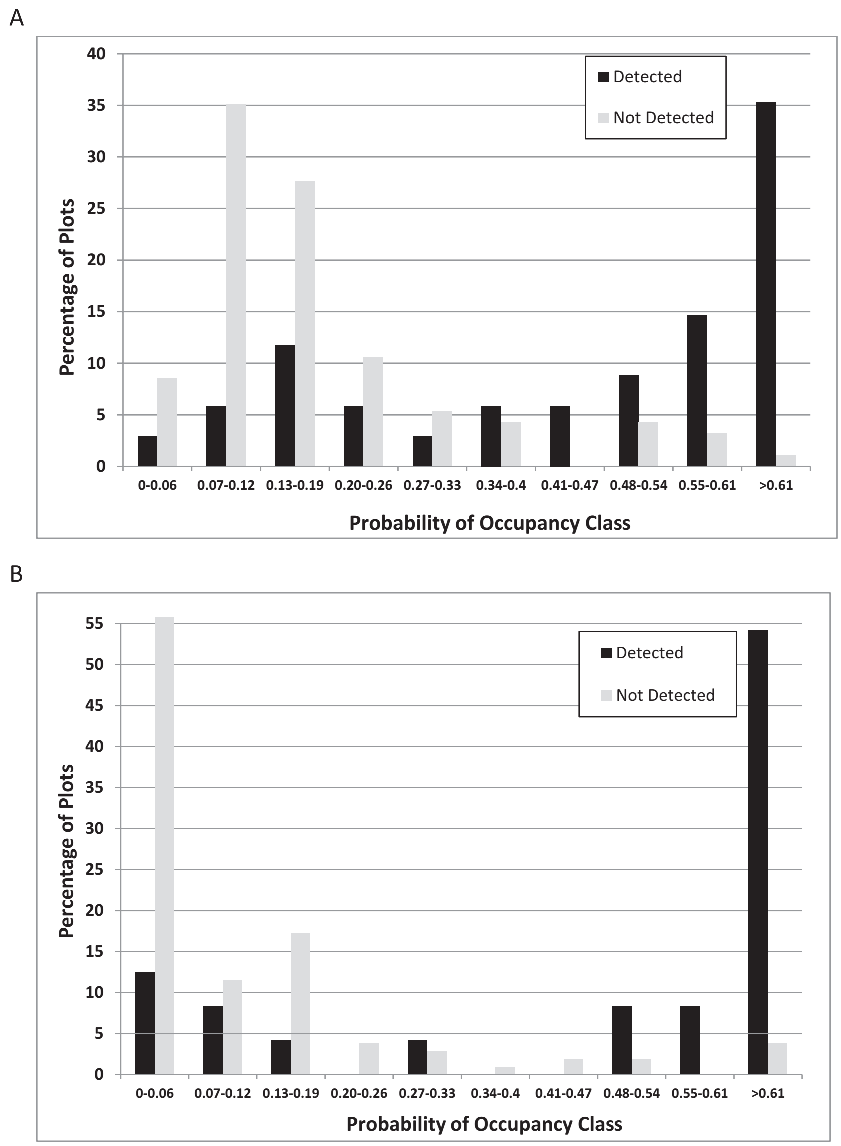

Fig. 5.—Distribution of Point Arena mountain beaver (*Aplodontia rufa nigra*) detection and nondetection sites among 10 probability of occupancy "bins" based on the best performing model (SLOPE + TRI + RIVSTREAM): A) using the full data set from all sample units and B) the distribution of 10 cross validated data sets. The final bin, > 0.61, was chosen because of the general decline in occurrences in units that exceeded this value.

and vice versa ("colonization"—MacKenzie et al. 2003), providing insights about metapopulation dynamics and turnover rates (e.g., Royle and Kéry 2007).

The best-fitting habitat model was comprised entirely of topographic and hydrologic variables: SLOPE, TRI, and RIVSTREAM. In this mountainous and highly dissected landscape, the places where PAMBs were detected had more gentle slopes, reduced terrain roughness, and higher densities of rivers and streams than the places where PAMBs were not detected. These places were influenced by the interactive forces of topography and hydrology that most likely resulted in conditions with wetter soils and well-developed, multilayered vegetation. Predictor variables related to soils or to vegetation (e.g., greenness, bulk density) were not in the best-fitting models. This does not mean that they are not important to the biology of PAMBs, which require available water and succulent vegetation to balance water demands (Nungesser and Pfeiffer 1965) and soils with appropriate composition for burrow construction (Hacker and Coblentz 1993). The topographic variables in the top model probably performed well because they are good predictors of the plants and soil conditions that are life requisites of PAMBs. Abundant and diverse vegetation occurs on gentle slopes and even terrain in locations where moisture accumulates; producing soils that are amenable for burrow construction.

It is important to note that in modeling exercises of this nature, the top-ranking model simply represents the best performing model supported by the data. The variables included in this model are not the only ones that affect the occurrence of PAMB. The best model combines predictive ability as well as parsimony (i.e., a penalty is incurred for each of the model's estimated parameters). It does provide good predictive ability, but managing only for the variables in the model would be shortsighted (see Dunk and Hawley 2009). For example, when values for 2 soil variables—soil bulk density and percent clay—are

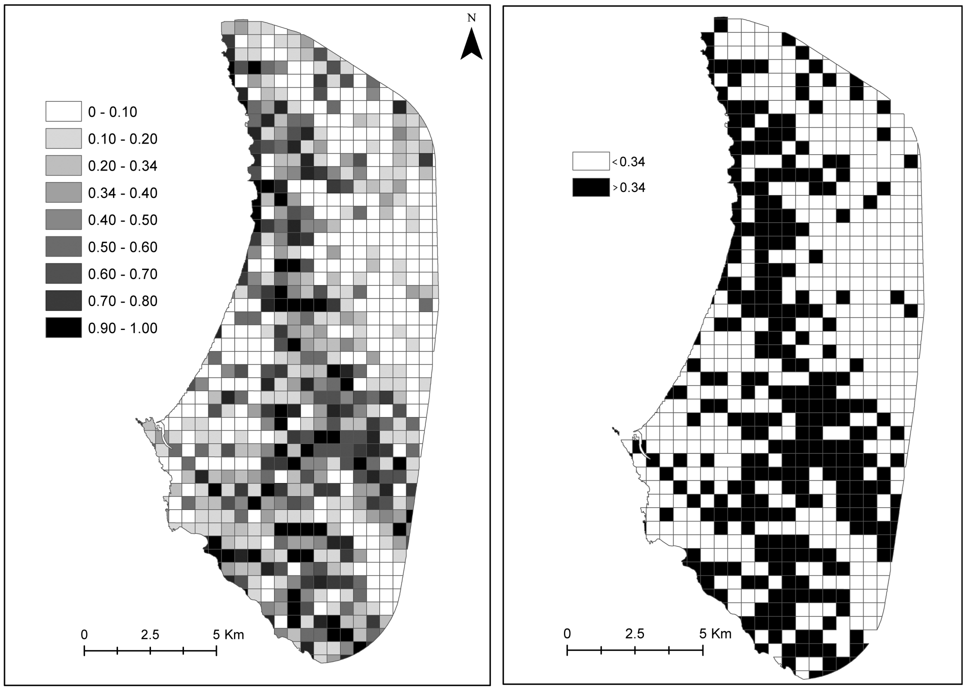

Fig. 6.—Map of the predicted values of habitat suitability for full and partial 25-ha sample units across the range of the Point Arena mountain beaver (*Aplodontia rufa nigra*) in Mendocino County, California. A) Each color shade represents a 0.10 range of predicted values from lightest (0–0.10) to darkest gray (0.91–1.00). B) The suitable cells (> 0.34 predicted value) depicted in black and the unsuitable cells (< 0.34 predicted value) in white. Simulation analysis (see text) identified an optimal "cut off," or threshold, to distinguish suitable from unsuitable predicted habitat values, of 0.34.

Table 5.—Percent suitable habitat (using the 0.34 predicted suitability cut point), and area of suitable habitat, in the 9 major watersheds identified in Zielinski et al. (2012) and north and south of the Garcia River, a feature associated with major genetic differentiation in Point Arena mountain beaver (*Aplodontia rufa nigra*—Zielinski et al. 2012).

Watershed	Percent suitable habitat	Area of suitable habitat (ha)
Mallo Pass Creek	28.9	1,597.7
Alder Owl Creek	37.5	68.4
Alder Creek	27.5	554.0
Brush Creek	31.0	898.8
Lagoon Creek	29.2	243.4
Garcia River	41.7	1,376.5
Garcia Hathaway Creek	38.4	494.7
Point Arena Creek	39.5	381.9
Moat Creek	47.0	750.6
North of Garcia River	28.9	4,075.0
South of Garcia River	39.3	2,289.0

examined at sample units that are arranged from highest to lowest probability of occurrence, the values for both variables are lowest where the probability of occurrence is highest (W. J. Zielinski, pers. obs.). This suggests that despite their exclusion from the top model, these variables may be linked to PAMB occurrence and that sample units with soils that have lower bulk densities and percent clay may be more amenable to burrowing.

We also emphasize that our model predicts only the locations where PAMB develop burrows. Mountain beavers can move surprising distances above ground (Arjo et al. 2007) and we did not model dispersal habitat because we assume that individuals do not create burrows during these movements. Previous work on landscape genetics indicates that gene flow is facilitated by forest cover (Zielinski et al. 2012), so this may be an important characteristic of dispersal habitat.

The map of predicted probabilities can serve strategic conservation planning needs by identifying areas that were not surveyed, but where predicted suitability was high and PAMB are likely. These represent areas with greater PAMB conservation interests and could help achieve conservation goals by protecting them from degradation via conservation agreement or purchase. Particularly promising areas for this purpose are in the central portion of the range (on the north–south axis), the southern half of the range, and the coastal portions of the northern half of the range (Fig. 6). Assessments of suitable habitat can also address the distribution among known genetic subdivisions in the taxon. Previous work identified the Garcia River as a significant dividing line between 2 haplotypes (Zielinski et al. 2012; see Fig. 1), suggesting distinct population subunits may be distributed above and below this river. If these subunits will be managed as separate entities in the future, our predictions indicate that they each have similar proportions of their range in suitable habitat (28.9% and 39.3%) suggesting that neither may be at greater risk of habitat limitation in the near future.

When the PAMB was listed as endangered, the primary threat to the subspecies was habitat loss. The most recent status review (USFWS 2009) notes that "the loss and modification of suitable habitat continues to be the primary threat to PAMBs, especially on private lands." Our habitat model cannot be used to monitor habitat loss related to changes in vegetation conditions. The classification schemes of available GIS vegetation layers were apparently too coarse to be useful at the scale we evaluated them. For example, some considered all the cover types in the eastern portion of the range as "forest," other layers only classified the forested lands with high resolution leaving the mixed use lands in the western portion unclassified. Most layers were incapable of identifying small patches of riparian vegetation, which may be particularly important to PAMB. Key to improving habitat mapping in the future will be the improvement in remotely sensed vegetation information. We recommend challenging our best model with higher resolution vegetation and soils data when they become available. Soils maps were also not particularly helpful. Although recently updated for Mendocino County (USDA Natural Resources Conservation Service 2012), soils maps had large unclassified areas. Promising variables that may be related to the ease of burrowing (e.g., "soil preparation—surface") did not have sufficient variation across the range to be useful in discriminating detection from nondetection locations.

Suitable and unsuitable habitat was distinguished based on a threshold predicted value. Above that value, sample units were designated as habitat, while below that value, they were designated nonhabitat. Applying this threshold resulted in 281 full or partial sample units (or ~70.5 km^2) designated as "suitable." This represents 40.4% of the range, substantially higher than a recent estimate of 10.1% (K. Wear, USFWS, cited in USFWS 2009). The difference is probably due primarily to the latter estimate being based on expert opinion about suitable vegetation types, while ours was based on predicted suitability derived from an empirical statistical model. Additionally, our estimate was based on the optimal choice of a cut point of predicted probability (i.e., 0.34); a choice above or below this value would lead to different values for the proportion of the range comprised of suitable habitat. Finally, all habitat classification systems assume assessment areas—pixels, polygons, or sample units—are categorized as either suitable or unsuitable in their entirety. As this is unlikely to be the case, our 25-ha sample units may result in higher estimates of suitability than if smaller units were considered.

Resampling the remotely sensed predictor layers can also potentially influence the habitat model results. Remotely sensed data vary in their ability to represent phenomenon on the earth based on their resolution and the complexity of the area within each cell or pixel (Cracknell 1998). We "down sampled" existing GIS layers to match the 25-ha sample unit size by taking the mean value of all the cells within each sample unit. Increasing the size of the cells for the predictors has reduced model accuracy in previous studies (Gottschalk et al. 2011). Because there are inherent inaccuracies in all spatial data, increasing the cell size has actually increased model performance in other studies because the inaccuracies have been averaged out (Guisan et al. 2007). With additional resources, data could be collected that would allow us to create habitat models with higher resolution.

Our work resulted in an expansion of the known range of the PAMB to ~134 km^2. Adding a 3-km buffer to this area, as was done to outline the previous range (USFWS 2009), increases the geographic range to ~235 km^2. We do not know if the range has actually expanded recently or if the increase is the result of expanded survey effort. Suitable areas predicted by our habitat map along the eastern margin of the current range (Fig. 6) suggest that the actual range may extend even further east, northeast, and southeast of the expanded range. Shotwell (1958) and the USFWS (2009) suggest the present range size reflects contractions that resulted from drying due to regional climate as well as vegetation and topographic changes since the Eocene. The increase in range size revealed by our sampling provides some reassurance that this pattern of contraction has not markedly progressed, at least in the past few decades. This may ameliorate some of the concern about the impacts of anthropogenic habitat loss. The larger known range may also ease concerns regarding the potential effects of climate change such as increased drought, more variable precipitation, and sea level rise (USFWS 2009).

Acknowledgments

We thank the United States Fish and Wildlife Service (USFWS) and the California Department of Fish and Wildlife (CDFW) for funding via Section 6 of the Endangered Species Act. Funding for JRD and JJG was from USDA Forest Service contract award numbers 14-JV-11272138-006 and 14-JV-11272138-007, respectively. B. Valentine of CDFW helped facilitate the funding and provided valuable input and editorial review. Funding also was provided by the Redwood Sciences Laboratory of the USDA Forest Service's Pacific Southwest Research Station. J. Brice, B. Fahey, S. Giordano, and W. Petersen served as field technicians, and D. Montoya and J. Werren provided GIS assistance. We thank A. Liebenberg and R. Pasquinelli of California State Parks, L. Morris of Redwood Coast Land Conservancy, and J. Hunter of USFWS for assistance with contacting landowners. The following provided access to private land they owned or administered: L. Bammann and P. Terzoni, F. Beidler and T. McMahon (Congaree River LLC), O. Darbro, P. and A. Dobbins, R. Douglas (Mendocino Redwood Company), D. and A. Fisher, J. and M. Hooper (Oz Farm), L. Hubbard and G. Jirak, H. Newberger and S. Kelly (The Conservation Fund, Garcia River Forest), L. Stornetta, and N. Webb and A. Levine.

Literature Cited

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pp. 267–281 in Proceedings of the second international symposium on information theory (B. N. Petrov and F. Csaki, eds.). Akademiai Kiado, Budapest, Hungary.

Arjo, W. M., R. E. Huenefeld, and D. L. Nolte. 2007. Mountain beaver home ranges, habitat use, and population dynamics in Washington. Canadian Journal of Zoology 85:328–337.

Billig, S. C., and R. B. Douglas. 2007. Habitat characteristics and spatial extent of burrow systems of Point Arena mountain beavers on managed timberlands. Pp. 491–492 in Proceedings of the redwood region forest science symposium: what does the future hold? (R. B. Standiford, G. A. Giusti, Y. Valachovic, W. J. Zielinski, and

M. J. Furniss, eds.). USDA Forest Service General Technical Report PSW-194. Pacific Southwest Research Station, Albany, California.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. American Naturalist 124:255–279.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York.

Camp, C. L. 1918. Excavations of burrows of the rodent *Aplodontia*, with observations on the habits of the animal. University of California Publications in Zoology 17:517–536.

Cleveland, W. S. 1985. The elements of graphing data. Wadsworth Publishing Company, Monterey, California.

Cohen, J. 1960. A coefficient of agreement for nominal scales. Educational and Psychological Measurement 20:37–46.

Cracknell, A. P. 1998. Synergy in remote sensing – what's in a pixel? International Journal of Remote Sensing 19:2025–2047.

Dalquest, W. W. 1948. Mammals of Washington. University of Kansas Publication of the Museum of Natural History 2:1–444.

Dunk, J. R., and J. V. G. Hawley. 2009. Red-tree vole habitat suitability modeling: implications for conservation and management. Forest Ecology and Management 256:626–634.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review Ecology and Systematics 40:677–697.

Esri. 2013. ArcGIS. Version 10.1. Environmental Systems Research Institute, Redlands, California.

Feldhamer, G. A., J. A. Rochelle, and C. D. Rushton. 2003. Mountain beaver (*Aplodontia rufa*). Pp. 179–187 in Wild mammals of North America: biology, management, and conservation (G. A. Feldhamer, B. C Thompson, and J. A. Chapman, eds.). Johns Hopkins University Press, Baltimore, Maryland.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence-absence models. Environmental Conservation 24:38–49.

Fitts, K. M. 1996. Observations on use of two non-native plants by the Point Arena mountain beaver. California Fish and Game 82:59–60.

Fitts, K., S. Flowers, D. Marshall, and P. Northen. 2002. Point Arena mountain beaver (*Aplodontia rufa nigra*) habitat protection and restoration plan for Manchester State Park. Report submitted to the California Department of Parks and Recreation, Mendocino District, Manchester State Park, Manchester, California.

Gaston, K. J. 1996. Species-range-size distributions: patterns, mechanisms, and implications. Trends in Ecology and Evolution 11:197–201.

Gottschalk, T. K., B. Aue, S. Hotes, and K. Ekschmitt. 2011. Influence of grain size on species-habitat models. Ecological Modeling 222:3403–3412.

Gould, W. R., et al. 2012. Estimating occupancy in large landscapes: evaluation of amphibian monitoring in the Greater Yellowstone ecosystem. Wetlands 32:379–389.

Guisan, A., C. H. Graham, J. Ellis, and F. Huettmann. 2007. Sensitivity of predictive species distribution models to change in grain size. Diversity and Distributions 13:332–340.

Hacker, A., and B. Coblentz. 1993. Habitat selection by mountain beavers recolonizing Oregon coast range clearcuts. Journal of Wildlife Management 57:847–853.

Hines, J. E. 2006. PRESENCE2: software to estimate patch occupancy and related parameters. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland. http://www.mbr-pwrc.usgs.gov/software/presence.html. Accessed 11 August 2014.

Huang, C., B. Wylie, L. Yang, C. Homer, and G. Zylstra. 2002. Derivation of a tasseled-cap transformation based on Landsat 7 at-satellite reflectance. International Journal of Remote Sensing 23:1741–1748.

Jenness, J. S. 2004. Calculating landscape surface area from digital elevation models. Wildlife Society Bulletin 32:829–839.

Johnson, S. R. 1971. The thermal regulation, microclimate, and distribution of the mountain beaver, *Aplodontia rufa pacifica* Merriam. Ph.D. dissertation, Oregon State University, Corvallis.

Joseph, L. N., S. A. Field, C. Wilcox, and H. P. Possingham. 2006. Presence-absence versus abundance data for monitoring threatened species. Conservation Biology 20:1679–1687.

Karanth, K. U., A. M. Gopalaswamy, N. S. Kumar, S. Vaidyanathan, J. D. Nichols, and D. I. MacKenzie. 2011. Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. Journal of Applied Ecology 48:1048–1056.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, J. E. Hines, and L. L. Bailey. 2006. Occupancy estimation and modeling: inference methods for patterns and dynamics of species occupancy. Elsevier, San Diego.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

Noon, B. R., L. L. Bailey, T. D. Sisk, and K. S. McKelvey. 2012. Efficient species-level monitoring at the landscape scale. Conservation Biology 26:432–441.

Northen, P. T., and K. M. Fitts. 1998. Monitoring of the Point Arena mountain beaver for MCI Telecommunications Corporations. Year five report. Report submitted to the U.S. Fish and Wildlife Service, Sacramento Field Office, Sacramento, California.

Nungesser, W., and E. Pfeiffer. 1965. Water balance and maximum concentrating capacity in the primitive rodent, *Aplodontia rufa*. Comparative Biochemistry and Physiology 14:289–297.

Phillips, S. J., et al. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications 19:181–197.

Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. Intermountain Journal of Sciences 5:23–27.

Royle, J. A., and M. Kéry. 2007. A Bayesian state-space formulation of dynamic occupancy models. Ecology 88:1813–1823.

Schooner Turtles Inc. 2014. BlueSpray. Version A1.2. Schooner Turtles, Inc., Arcata, California.

Shotwell, J. A. 1958. Evolution and biogeography of the aplodontid and mylagaulid rodents. Evolution 12:451–484.

Stanley, T. R., and J. A. Royle. 2005. Estimating site occupancy and abundance using indirect detection indices. Journal of Wildlife Management 69:874–883.

Steele, D. T., and L. Litman. 1998. Point Arena mountain beaver recovery plan. United States Fish and Wildlife Service, Portland, Oregon.

US Census Bureau. 2013. Geography: TIGER/Line shapefiles. http://www.census.gov/geo/maps-data/data/tiger-line.html. Accessed 16 November 2013.

USDA Natural Resources Conservation Service. 2012. Web soil survey. http://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm. Accessed 9 December 2013.

USGS. 2013. National elevation dataset. http://ned.usgs.gov/downloads.asp. Accessed 16 November 2013.

USGS. 2013. The national map program. http://nationalmap.gov/viewer.html. Accessed 16 November 2013.

US Fish and Wildlife Service. 2009. Point Arena mountain beaver (*Aplodontia rufa nigra*) 5-year review: summary and evaluation. USFWS, Arcata, California.

USDA Forest Service. 2010. Vegetation classification and mapping (CalVeg). http://www.fs.usda.gov/detail/r5/landmanagement/resourcemanagement/?cid=stelprdb5347192. Accessed December 2013.

Wilson, J. W., J. O. Sexton, R. T. Jobe, and N. M. Haddad. 2013. The relative contribution of terrain, land cover, and vegetation structure indices to species distribution models. Biological Conservation 164:170–176.

Zielinski, W. J., F. V. Schlexer, S. Parks, K. L. Pilgrim, and M. K. Schwartz. 2012. Small geographic range but not panmictic: how forests structure the endangered Point Arena mountain beaver (*Aplodontia rufa nigra*). Conservation Genetics 14:369–383. http://www.treesearch.fs.fed.us/pubs/41335. Accessed 11 August 2014.

Zielinski, W. J., F. V. Schlexer, T. L. George, K. L. Pilgrim, and M. K. Schwartz. 2013a. Estimating abundance and survival in the endangered Point Arena mountain beaver (*Aplodontia rufa nigra*) using noninvasive genetic methods. Northwest Science 87:126–139.

Zielinski, W. J., J. A. Baldwin, R. L. Truex, J. M. Tucker, and P. A. Flebbe. 2013b. Estimating trend in occupancy for the population of fishers (*Martes pennanti*) in the southern Sierra Nevada. Journal of Fish and Wildlife Management 4:3–19. http://www.treesearch.fs.fed.us/pubs/42545. Accessed 11 August 2014.

Zielinski, W. J., J. E. Hunter, R. Hamlin, K. M. Slauson, and M. J. Mazurek. 2010. Habitat characteristics at den sites of the Point Arena mountain beaver (*Aplodontia rufa nigra*). Northwest Science 84:119–130.

Submitted 15 August 2014. Accepted 7 October 2014.

Associate Editor was Harald Beck.

Appendix I

Candidate models of environmental factors used to distinguish between sample units with Point Arena mountain beaver (*Aplodontia rufa nigra*) detections and those without detections (see Table 2 for definitions of variable abbreviations).

Biological Models				
GREENNESS				
WETNESS				
GREENNESS	WETNESS			
Topographic Models				
TRI				
SLOPE				
RIVSTREAM				
ASPECT	TRI			
SLOPE	TRI			
ASPECT	RPI			
SLOPE	RPI			
ASPECT	SLOPE			
TRI	RIVSTREAM			
SLOPE	RIVSTREAM			
ASPECT	SLOPE	TRI		
ASPECT	SLOPE	RPI		
ASPECT	SLOPE	TRI	RPI	
ASPECT	SLOPE	TRI	RPI	RIVSTREAM
ASPECT	SLOPE	TRI	RPI	SROADS
ASPECT	TRI	RIVSTREAM		
SLOPE	TRI	RIVSTREAM		
ASPECT	RPI	RIVSTREAM		
SLOPE	RPI	RIVSTREAM		
ASPECT	SLOPE	RIVSTREAM		
ASPECT	SLOPE	TRI	RIVSTREAM	
ASPECT	SLOPE	RPI	RIVSTREAM	
ASPECT	SLOPE	SROADS		
ASPECT	SLOPE	SROADS	RIVSTREAM	
ASPECT	TRI	RPI	RIVSTREAM	
SLOPE	TRI	RPI	RIVSTREAM	
Soil Models				
CLAY				
CLAY	BD13			
BD13				
Multiple Class Models				
WETNESS	GREENNESS	TRI		
WETNESS	GREENNESS	TRI	RIVSTREAM	
WETNESS	GREENNESS	TRI	RIVSTREAM	SROADS
WETNESS	SLOPE	RIVSTREAM		
GREENNESS	SLOPE	RIVSTREAM		
WETNESS	ASPECT	TRI		

WETNESS	ASPECT	TRI	RIVSTREAM		
WETNESS	ASPECT	TRI	RIVSTREAM	SROADS	
WETNESS	ASPECT	RPI			
WETNESS	ASPECT	RPI	RIVSTREAM		
WETNESS	GREENNESS	TRI	BD13		
WETNESS	GREENNESS	TRI	BD13	RIVSTREAM	
WETNESS	GREENNESS	TRI	BD13	RIVSTREAM	SROADS
WETNESS	SLOPE	BD13	RIVSTREAM		
GREENNESS	SLOPE	BD13	RIVSTREAM		
WETNESS	ASPECT	TRI	BD13		
WETNESS	ASPECT	TRI	BD13	RIVSTREAM	
WETNESS	ASPECT	TRI	BD13	RIVSTREAM	SROADS
WETNESS	ASPECT	RPI	BD13		
WETNESS	ASPECT	RPI	BD13	RIVSTREAM	
WETNESS	ASPECT	RPI	BD13	RIVSTREAM	SROADS