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Habitat Characteristics at Den Sites of the Point Arena Mountain Beaver (*Aplodontia rufa nigra*)

Abstract

The Point Arena mountain beaver (*Aplodontia rufa nigra*) is a federally listed endangered species, but has been the subject of few studies. Mountain beavers use burrows that include a single subterranean den. Foremost among the information needs for this subspecies is a description of the above-ground habitat features associated with dens. Using telemetry we located dens of 23 individuals in Manchester State Park, Mendocino County, California. We measured vegetation and topographic variables directly above the dens and at two available sites within the same burrow system. Alternative resource selection functions, based on multivariate expressions of important ecological characteristics, were developed to model features associated with dens. The best model contained three variables: MEANDENS (mean vegetation density), PAMBTOP4 (cover of the four plant species most frequently used), and COSASPECT (cosine aspect). Interestingly, PAMBTOP4 was negatively associated with dens, indicating that dens were not chosen for their proximity to important plant species. Topography plays an important role in that western and northern aspects were favored and SLOPE was included in the second-highest ranked model. Cross validation indicated moderate stability for the top model suggesting that potentially important predictors that were excluded from the analysis (e.g., soil characteristics, social context) may be influential. Nonetheless, we demonstrated that dense vegetation and aspect/slope considerations are more important predictors of Point Arena mountain beaver den selection than proximity to cover of important plant species. Our results apply to Point Arena mountain beaver populations in coastal shrub communities; den selection may be different farther inland, in forests.

Introduction

The mountain beaver (*Aplodontia rufa*) is the only extant member of the monotypic genus *Aplodontia*, first described by Rafinesque in 1817 (Taylor 1918). The Point Arena mountain beaver (*Aplodontia rufa nigra*) is one of seven recognized subspecies (Hall 1981) and occurs in coastal Mendocino County, California. It occupies a small 62 km^2 geographic range and is disjunct from the three other subspecies in California (Steele and Litman 1998). This subspecies was listed by the USDI Fish and Wildlife Service in 1991 as endangered under the Endangered Species Act due to threats posed by land conversion for agriculture, urban development, construction of transportation and utility corridors, livestock grazing, human disturbance, and other factors, combined with its highly restricted distribution (USDI Fish and Wildlife Service 1991). There has been considerable interest and research on the other subspecies of mountain beaver, primarily because they can affect reforestation in areas of commercial timber production (e.g., Scheffer 1929, Beier 1989, Cafferata 1992, Feldhamer et al. 2003, Arjo and Nolte 2004, Arjo et al. 2007, Runde et al. 2008). Despite the conservation concerns regarding the Point Arena mountain beaver, however, there are very few reports in the primary literature on its ecology (i.e., Camp 1918, Fitts 1996, Billig and Douglas 2007).

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Mountain beavers are semi-fossorial and herbivorous. They utilize a wide variety of plant species (Voth 1968, Godin 1964, O'Brien 1988, Todd 1992), but it is difficult to differentiate the plants that are used as food from those used as nesting material, or both, because use is typically assessed by examining plant stems cut by mountain beavers and piled temporarily at burrow entrances (Feldhamer et al. 2003). In unpublished reports, hedge nettle (*Stachys ajugoides*), bush lupine (*Lupinus arboreus*), Douglas iris (*Iris douglasiana*) and angelica (*Angelica hendersonii*) were the most common species represented as cuttings by Point Arena mountain beavers (Fitts et al. 2002, Zielinski and Mazurek 2006).

Water balance is critical for mountain beavers because their inability to concentrate urine requires them to consume almost one-third of their body weight in water daily (Pfeiffer et al. 1960, Nungesser and Pfeiffer 1965, Cafferata 1992). Recent studies on the Point Reyes mountain beaver (*A. r. phaea*) have shown that they can likely meet their water needs through metabolic water production and water in food and do not require access to free water (Crocker et al. 2007). Thus, space use by mountain beavers should be influenced by access to plants for food and nesting material, by availability to water (either direct or from succulent plants), and by soil suitable for burrowing. This, along with their limited ability to thermoregulate, may be why mountain beavers elsewhere are typically found at mesic locations with a cool thermal regime, and well-drained, firm and friable soils (Camp 1918; Kinney 1971; Steele 1986a,b; Beier 1989; Hacker and Coblentz 1993).

Mountain beavers excavate burrow systems that include a network of tunnels along with chambers used specifically for denning, feeding, and storage of food, fecal pellets and refuse (Voth 1968). Dens are in the "home burrow" area (Hubbard 1922) and are roughly circular chambers filled with dry vegetation formed into a nest (Camp 1918, Martin 1971). One Point Arena mountain beaver den chamber that was excavated included a nest constructed primarily of Douglas iris leaves (Zielinski and Mazurek 2006). Mountain beaver dens are occupied, and defended, by a single individual (Martin 1971, Lovejoy and Black 1979, Nolte et al. 1993). Once an individual establishes a den site, they use it for long periods and rarely move to a new site (Martin 1971). Mountain beavers may spend as much as 75% of their time in the den chamber (Ingles 1959, Kinney 1971) and most of their movements occur in close proximity to the den (Martin 1971).

Dens are subterranean features that, in the Pacific Northwest, range from about 30 to 180 cm below the surface (Carey et al. 1989). Two excavated dens of the Point Arena mountain beaver were < 0.5 m below the surface (Zielinski and Mazurek 2006). Research conducted in the Pacific Northwest characterizes dens as occurring primarily under small mounds, logs, uprooted stumps, logging slash or thick vegetation (Scheffer 1929, Martin 1971, Gyug 2000). Point Arena mountain beavers in the western portion of their range, however, commonly occur in non-forest environments of coastal shrub and herbaceous cover types (Steele and Litman 1998) where logs and stumps are rare and thick, structurally complex vegetation is limited. Thus, we became interested in determining the above-ground features that may be associated with den sites for this endangered taxon. We understand that the selection of a den site may be primarily influenced by below-ground features, but sought to identify surface features that may be correlated with den sites. We expected that the above-ground plant community and other surface features may be influenced by, or may influence, the below-ground features (e.g., soil type, hydrology) that affect den site choice. We evaluated Point Arena mountain beaver den site selection within their burrow areas. The only other quantitative habitat selection studies on mountain beavers were conducted in the Sierra Nevada (Beier 1989) and Oregon Coast Range (Hacker and Coblentz 1993). We use a similar quantitative approach, but whereas these studies sought to describe areas with and without occupancy, we focus instead on describing the above-ground features of den sites within occupied areas.

Using an information-theoretic modeling approach, we seek to determine the factors that best describe locations within burrow systems where mountain beavers locate their dens. This research will help managers conserve this subspecies by understanding the environmental features associated with dens, preventing land management activities from negatively affecting them, and expanding and restoring habitat that is suitable for den sites.

Study Area

This study was conducted in Manchester State Park (Park), Mendocino County, California. The Park is located on an alluvial plain formed by the Garcia River. The topography is comprised of low hills formed by stabilized sand dune and coastal terraces. Vegetation in the areas where Point Arena mountain beaver were studied is comprised of a mix of northern dune scrub, northern coastal bluff scrub, and northern coastal scrub (Holland 1986) and no surface water is present. The portion of the park included in the study was represented by four soil map unit types: Crispin Loam, Dystropepts, Duneload and Cabrillo-Heeser Complex (Rittiman and Thorson 2006).

The climate at the Park is Mediterranean maritime, with relatively cool summers that are characterized by low clouds in the morning that burn off in the afternoon. Winters are wet with only occasional freezing temperatures. The average minimum temperature in winter is 3.8 °C, and the average summer maximum temperature is 19.7 °C. Mean annual precipitation is 1057 mm, with most falling from October to April.

Methods

General Approach to Habitat Selection Analysis

Habitat use by animals can be evaluated at various spatial scales, ranging from the geographic range to the home range (Johnson 1980). In this study, used resources (dens) and available resources (random sites) were identified at the "population" level (i.e., within the known burrow areas within the Park), and a random sample of each was collected (all known dens were sampled, but these were assumed to be a random sample from the population of all dens). This approach conforms best to habitat use sampling design I and sampling protocol A (Manly et al. 2002) and assumes that the probability of a site being used as a den was the same for all mountain beavers. Den site selection was evaluated by comparing the vegetation characteristics at plots centered above presumed den sites with randomly selected locations that are available within the occupied area, but also near the den sites (see below).

Locating Den Sites

We set traps throughout three areas in the Park that had been identified by Fitts et al. (2002) as occupied by mountain beavers: Alder Creek, Kinney Beach and Environmental Trail (Figure 1). Single (12.7 x 12.7 x 40.6 cm) and double-door (15.2 x 15.2 x 61.0 cm) Tomahawk live traps (Tomahawk Live Trap Company, Tomahawk, WI, USA) were placed both within active tunnels and at the openings of active burrows, and were baited with apple. Following standard measurements, most captured animals were fitted with 27-31 g radio collars and then precisely relocated many times at a central location that was assumed to be their den site (Zielinski and Mazurek 2006). This assumption was confirmed on several occasions when dead animals were recovered in their dens. A minority of animals were fitted with small, 0.52 g transmitters glued to the hair between the scapulae. Upon release these animals were tracked until they were inactive (i.e., no change or attenuation in signal), and the location was marked as the presumed den location. This was verified over the course of subsequent days (these small transmitters functioned for only a few weeks). All trapping and radio-telemetry was conducted from June 2004 to January 2005. Capture and handling methods followed the animal care and use guidelines approved by the American Society of Mammalogists (Animal Care and Use Committee 1998).

Sampling Used and Available Habitat

Habitat data were collected in 2-m diameter circular plots. One plot was located directly above each known den (i.e., "used sites"), and two additional plots were randomly located within the presumed burrow area for each den identified (i.e., "available sites"). Available sites (N = 46) were located only within burrow areas, since areas without any evidence of mountain beaver presence were not considered available as den sites. Available sites were located > 3 m from the dens sites to avoid any overlap between the two plots. Available sites were very unlikely to occur directly above known dens because we trapped thoroughly in the area and were confident that we had located the majority of the residents and their dens. These sites were also < 10 m from the den because the space used by individual Point Arena mountain beavers is relatively small (approximately 300

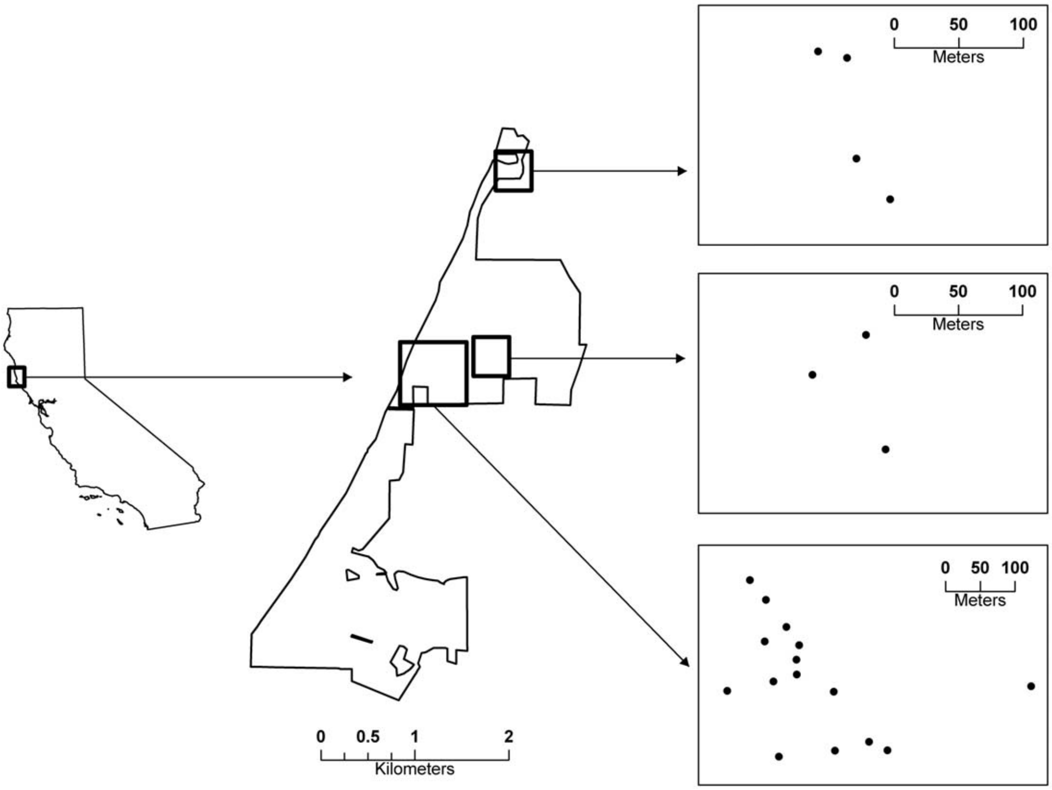

Figure 1. The three den site areas, located in Manchester State Park, that were included in the study, from north to south: Alder Creek, Environmental Trail, and Kinney Beach. Black circles indicate the locations of the dens in each area.

m^2) (Zielinski and Mazurek 2006) and locating available sites further away may sample areas that were unavailable to an animal when it selected its den site. Available sites were located by following a random compass bearing and distance ($3 < x < 10$ m) from the den site. If the bearing for the second available site was within 20 degrees of the bearing for the first, another random bearing was selected. All habitat sampling occurred from 21 through 23 June 2005. A variety of vegetation and topographic features were measured on plots (Table 1), all related to previous studies or our hypotheses about characteristics that are likely to influence Point Arena mountain beaver habitat selection (see below). To standardize the collection of field data, and to optimize the precision, one of us (JEH) conducted all the measurements and visual estimates.

Habitat Model Development

We used resource selection functions (Manly et al. 2002) as the method for determining a den site habitat selection model. The resource selection function we used conformed to standard logistic regression:

$$W_{(x)} = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_{2\ldots} + \beta_n x_n)$$

where $W_{(x)}$ is the predicted probability of resource use for the given combination of independentvariables (x_n). Slope coefficients (β_n) and intercepts (β_0) were estimated via maximum likelihood using PROC GENMOD (SAS Institute, Cary, North Carolina).

We developed a small set of alternative models, based on careful consideration of potentially biologically meaningful variables, and evaluated their fit to the data using an information-theoretic

TABLE 1. Acronyms and definitions for variables considered when developing multivariate den habitat selection models for the Point Arena mountain beaver at Manchester State Park, California.

Variable	Acronym	Measurement technique / definition
Aspect	COSASPECT	Compass bearing of the direction the slope faces; transformed to cosine-aspect to control for the circular nature of these values. Cosine transformation provides interpretation of north-south orientation; preliminary assessments suggested this was a more informative axis than west-east orientation, thus there was no sine transformation.
Percent slope	SLOPE	Mean of two clinometer readings in percent, one upslope and one downslope, along the slope axis.
Index of vegetation density	MEANDENS	Mean of two estimates of visual obstruction of a Robel pole (Robel et al. 1970), viewed from the south at a distance of 2.0 m, one with observer's eyes at 0.5 m and another at 1.0 m height.
Total vegetative cover	TOTVEGCOV	Ocular estimate of percent of total vegetation cover in 5% increments.
Total down woody material cover	TOTDWMCOV	Ocular estimate of percent of down woody material cover in 5% increments.
Tallest vegetation	TALVEG	Height of the tallest single individual plant.
Top 4 plants used by PAMB	PAMBTOP4	Ocular estimate of the percent cover of the top four species of plants known to be used by Point Arena mountain beavers at Manchester State Park, in 5% increments. Consists of the top two plants in Fitts et al. (2002; Table 2) (hedge nettle and bush lupine) and top two plants in Zielinski and Mazurek (2006; Table 8) (Douglas iris and angelica).
Top 75% of plants used by PAMB	PAMBTOP75%	Ocular estimate of the percent cover of the top 75% (11 species) of species of plants known to be used by Point Arena mountain beavers at Manchester State Park, in 5% increments. Plants chosen were based on the top 75% of all individual observations in Fitts et al. (2002; Table 2) and in Zielinski and Mazurek (2006; Table 8).
All plants known to be used by mountain beavers	MBKNOWNUSE	Ocular estimate of the percent cover of all of species of plants (33 species) known to be used by Point Arena mountain beavers at Manchester State Park, and/or any mountain beavers range-wide, as determined by published literature (15 papers), Fitts et al. (2002), and Zielinski and Mazurek (2006), in 5% increments.
Total shrub cover	TOTSHRUBCOV	Ocular estimate of the percent cover of all woody plant species (6 species) in 5% increments.
Total forb cover	TOTFORBCOV	Ocular estimate of the percent cover of all forbs (51 species) in 5% increments.
Total cover of grass species thought to have positive influence on mountain beavers	TOTGOODGRAS	Ocular estimate of the percent cover of grass species with evidence of a positive influence on mountain beaver habitat use (3 species), in 5% increments. Based on Fitts (1996) (European beachgrass), Fitts et al. (2002) (wild rye; *Leymus* sp.), and Northen and Fitts (1993) (Pacific reed grass; *Calamagrostis nutkaensis*).
Total cover of grass species thought to have negative influence on mountain beavers	TOTBADGRAS	Ocular estimate of the percent cover of grass species with evidence of a negative influence on mountain beaver habitat use (3 species), in 5% increments. Based on Zielinski and Mazurek (2006) (common velvet grass; *Holcus lanatus*), and Hacker and Coblentz's (1993) general finding that the presence of grasses was negatively related to recolonization and den site selection (seaside brome [*Bromus carinatus*] and all unidentified grass spp.).

approach (Burnham and Anderson 2002). We selected variables for inclusion in our candidate models by reviewing studies on the habitat ecology of mountain beavers, adding variables that we hypothesized had ecological importance at our study site. Each potential variable was screened for inclusion on the basis of its relevance, biological interpretability, and value as determined by previous studies of mountain beaver habitat. If two potential predictor variables were highly correlated ($r > 0.6$) the least interpretable one was excluded.

Variables that met the screening criteria were used to develop single and multivariate models representing alternative hypotheses for habitat selection. This process involved the development of conceptual models thought to represent the combination of variables that could affect den habitat choice. Conceptual models were then translated into alternative resource selection functions using the final set of variables. The resulting models represented competing hypotheses about the characteristics that may influence the selection of a den site.

We limited the total number of variables per model to four to maintain interpretability of the results. We also constrained the number of parameters per model to four, to allow a minimum of 15 observations per parameter. We ranked the fit of the alternative models using Akaike's Information Criterion for small sample sizes (AIC_c), recommended for use when the sample size divided by the total number of parameters is < 40 (Burnham and Anderson 2002). We calculated Akaike's weights (w) using ΔAIC_c values, listed models in decreasing weight, and created a 95% confidence set of models by including the fewest models that captured at least 95% of the cumulative weight (Burnham and Anderson 2002). Model averaging was not used because we were primarily interested in understanding the relationships among variables included in the top models, and what they suggest about Point Arena mountain beaver habitat selection. We were less interested in selecting one best model for the purpose of prediction, or in generating the best estimate of parameters common to all top models (Burnham and Anderson 2002).

To assess the relative importance of each variable in the selected models, we calculated their adjusted importance weights by summing the w_i for all the models the variable was included in and correcting for both the total number of models the variable was included in and the number of other variables present in each model (Anderson et al. 2001; Importance weight = (# models * w_i)/((# models with variable)* (total # variables))). We also assessed the importance of each variable by: (1) examining the magnitude and sign of coefficients in the best models, and (2) calculating odds ratios, which represents the 'odds' of an event occurring in one group (the used sites) compared to the odds of it occurring in another group (the available sites).

Model Evaluation

For the best fitting model, we evaluated the distribution of predicted probabilities and correct classification rates and compared the chance-corrected classification rates using Cohen's kappa (Manel et al. 2001) at both standard (0.5) and optimized probability cut points (Neter et al. 1989). We then conducted a 10-fold cross-validation procedure for the top model by randomly dividing the original data into 10 equal-sized subsets, estimating model coefficients using 9 subsets (training data), and classifying the remaining (10%) subset (test data) (see Boyce et al. 2002). We repeated this procedure 10 times. To evaluate the stability of each model's predictions, we evaluated the distribution of the probabilities for the test data, the correct classification rates, and compared kappa statistics for each cross-validated model.

Results

Dens from 23 individuals (13M:10F) were located in 3 general locations within the Park (Figure 1). Calculated within each location, the mean ($\pm$ SD) distance between a den and the next nearest den was 42.9 $\pm$ 18.4 m; the closest distance between any two dens was 20.9 m. A total of 69 vegetation plots were established; 23 on used sites and 46 on available sites. Screening of variables resulted in a set of 13 candidate variables (Table 1). Two of these were excluded because they had nearly identical values at all sites (TOTVEGCOV) or were extremely uncommon (TOTDWMCOV), resulting in a final set of 11 variables (Table 1). With the exception of MEANDENS and PAMBTOP4, most variables were characterized by relatively high variability and mean values for used and available sites that were quite similar (Table 2).

TABLE 2. Univariate statistics for the variables collected at used (den) and available sites at the 3 areas within Manchester State Park, Mendocino County, California. See Table 1 for variable definitions.

	Used Sites			Available Sites		
	Mean	SD	N	Mean	SD	N
COSASPECT	0.33	0.58	21	0.26	0.53	38
SLOPE	10.43	10.52	23	9.63	10.24	46
MEANDENS	7.59	2.51	23	4.88	2.86	46
TOTVEGCOV	99.35	1.72	23	99.89	0.74	46
TOTDWMCOV	0.26	1.05	23	0.07	0.25	46
TALVEG	1.30	0.29	23	1.12	0.28	46
TALLVEGCONV	13.04	2.94	23	11.20	2.80	46
PAMBTOP4	1.87	3.45	23	10.00	17.79	46
PAMBTOP75%	29.78	37.45	23	29.54	32.26	46
MBKNOWNUSE	72.04	36.65	23	73.46	32.21	46
TOTSHRUBCOV	38.65	40.80	23	31.02	37.75	46
TOTFORBCOV	29.48	30.40	23	36.76	28.12	46
TOTGOODGRAS	26.13	36.18	23	18.09	30.84	46
TOTBADGRAS	8.39	19.05	23	12.85	20.59	46

TABLE 3. The 9 den site habitat models (of 27) for the Point Arena mountain beaver at Manchester State Park, California, in the top 95% confidence set, ranked in decreasing order of model fit to the data, according to Akaike's Information Criteria (AICc). K refers to the number of parameters and *w* is the AIC weight. See Table 1 for variable definitions.

Rank	Model			K	ΔAICc	*w*	Relative Weight
1	0.2934MEANDENS	-0.0854PAMBTOP4	+0.0159COSASPECT	4	0	0.449	1
2	0.3213MEANDENS	+0.0329COSASPECT	+0.0175SLOPE	4	1.19	0.247	1.82
3	0.2852MEANDENS	-0.0843PAMBTOP4		3	3.37	0.083	5.4
4	0.2458MEANDENS	-0.081PAMBTOP4	+0.1279TALVEG	4	4.39	0.05	8.98
5	0.3354MEANDENS			2	4.9	0.039	11.51
6	0.2706MEANDENS	-0.0587PAMBTOP4	+0.1038SLOPE	4	5.32	0.031	14.49
7	0.2839MEANDENS	+0.1353TALVEG		3	5.68	0.026	17.27
8	0.3392MEANDENS	-0.0026PAMBTOP75		3	6.99	0.014	32.07
9	0.329MEANDENS	-0.0032TOTFORBCOV		3	6.99	0.014	32.07

Den Site Habitat Models

A total of 27 alternative models were developed (Appendix A). The best-fitting model, the one with the lowest ΔAIC_c value (Model 1, Table 3), contained the three variables with the highest importance weights (Table 4): MEANDENS, PAMBTOP4, and COSASPECT. This model was 1.82 times more likely than the model with the next lowest ΔAIC_c value (Table 3). MEANDENS (i.e., mean vegetation cover) was a very influential variable, included in all nine models within the 95% confidence set (Table 3). Mean vegetation density was 7.6 $\pm$ 2.5 (mean $\pm$ SD) at used sites, but was only 4.9 $\pm$ 2.9 at available sites. An increase of 1 unit in vegetation density (from, say, six to seven density units) was associated with a 72% increase in probability of den site occurrence (odds ratio = 1.72, 95% CI = 1.22 to 2.63), when holding PAMBTOP4 and COSASPECT constant.

Interestingly, an increase in PAMBTOP4 cover (cover of four most frequently cached plant species by Point Arena mountain beavers) was associated with a decrease in probability of den site occurrence. Although this relationship wasn't strong (odds = 0.988, 95% CI = 0.963 to 1.01), two other

TABLE 4. Normalized importance weights for the variables used in multivariate den site habitat selection models for Point Arena mountain beaver at Manchester State Park, California. See Table 1 for variable definitions.

Variable	Normalized Importance Weight
ASPECT	0.2835
PAMBTOP4	0.2122
MEANDENS	0.2087
TALVEG	0.1181
SLOPE	0.1173
TOTFORBCOV	0.1080
TOTBADGRAS	0.1060
PAMBTOP75%	0.0091
TOTSHRUBCOV	0.0030
TOTGOODGRAS	0.0030
MBKNOWNUSE	0.0001

variables related to species of plants potentially used as food (i.e., TOTFORBCOV and PAMPTOP75%) also had negative relationships with predicted den site value (Table 3). Topography appeared to play an important role in den site selection in that COSASPECT was an especially important predictor (Table 3, 4). Den sites were more likely to occur in western (52% of den sites) and northern (22% of den sites) aspects than any other. SLOPE was included in the second highest ranking model, but not in any other models in the 95% set (Table 3) and, thus, was of intermediate importance (Table 4). Den sites occurred at sites with slightly steeper slopes than available sites.

Model Evaluation

Cross-validation revealed that the best model was better at predicting available sites than den sites. The classification success, in general, was poor for den sites, but improved somewhat when we applied an optimal cut point (rather than the standard 0.5) (Table 5). Kappa values between 0.4 – 0.8 are considered "good" and < 0.4 considered "poor" by the standards of Landis and Koch (1977). Thus, only the evaluation of the original model, using an optimized cut-point, achieves "good" classification (Table 5).

Discussion

The choice of a den site, from within a burrow area, is presumably affected by a number of factors including topography, vegetation structure, vegetation composition, soil type, and social factors. Our research focused on the question of which above-ground vegetation and topography features are associated with den sites. In this respect, we discovered that dens sites were most likely to occur where vegetation was thick, on more westerly aspects and where common food items are *less* abundant than elsewhere within the burrow areas. Coarse woody material (logs, branches, stumps), which are often associated with den sites elsewhere (Hacker and Coblentz 1993), were too rare in our study area to affect den site choice.

Thick vegetation has consistently been associated with descriptions of mountain beaver burrow areas and den sites (Scheffer 1929, Martin 1971, Gyug 2000, Fellers et al. 2004). Whether complex vegetation structure reduces the likelihood of the den being discovered by predators, mediates temperature and precipitation, promotes soil drainage, or whether it means that there is a similar density of below-ground biomass to reinforce den chamber structure is unknown. Motobu (1978) found that coyote digging behavior increased in mountain beaver burrow areas after a fire removed the cover, suggesting that thick cover of vegetation may deter this behavior. Prior to our work we had assumed that den sites would be significantly associated with woody shrub cover because shrub roots provided potential subsurface structure to reinforce a den chamber. However, den sites were not characterized by more shrub cover than available sites. Shrubs

TABLE 5. Classification success and Kappa values for the top den site habitat selection model (0.2934MEANDENS - 0.0854PAMBTOP4 + 0.0159ASPECT) for Point Arena mountain beaver at Manchester State Park, California.

	Standard 0.5 Cut Point		Optimized 0.6 Cut Point	
Site	Original	Cross Validated	Original	Cross Validated
Den	52%	30%	65%	44%
Available	83%	91%	78%	77%
Kappa	0.36	0.26	0.44	0.21

were, however, an important contributor to mean vegetation density and, as such, may be important den site associates. The potential benefits from vegetation structure may be provided by down woody material, tree stumps, shrubs or, on the Kinney Beach portion of our study area, large perennial grasses such as European beachgrass (*Ammophila arenaria*).

Unexpectedly, plant species that are known to be used as food or nest materials were, on average, less abundant at den sites than at other locations within an animal's presumed home range. The species of plants typically found at caches at the mouth of burrow openings, represented by the variables PAMBTOP4, PAMBTOP75%, and MB-KNOWNUSE, were more common elsewhere in the home range than immediately near a den site. O'Brien (1981) also found no relationship between frequency of occurrence of plant species in cache sites and the occurrence of plants in the vicinity of these sites. If caches occur near dens sites, as some have surmised (Gyug 2000), O'Brien's work, together with our results suggest that mountain beaver den sites are not necessarily chosen to be close to foraging locations. Beier (1989) speculated that den sites are selected to be associated with one set of environmental characteristics and burrows, which lead to foraging areas, are associated with other resources, presumably food plants. Den sites are either unrelated to the distribution of food or, on the contrary, may be located to optimize access to all the food resources within a home range, consistent with central place foraging behavior (Orians and Pearson 1979). Alternatively, residents may have originally selected den sites where foods were abundant, but their subsequent foraging activities have decreased the abundance of preferred foods near the den.

That den sites were less likely to have abundant species of plants used for food or nest material suggests that other factors, such as topography and/or soil features may play a more important role in den site choice. Accordingly, the aspect of the den site was an important predictor, with den sites occurring predominately on sites with western and northern aspects. Although Beier (1989) did not find aspect as influential in distinguishing occupied from unoccupied areas, Crouch (1964) found most mountain beaver sign on northwestern aspects. These studies identified features associated with burrow areas, not dens, but our work agrees with the findings of Crouch and suggests that den sites – as well as burrow areas in general – may occur predominately in the cooler and more moist environments associated with western and northern aspects. Mountain beaver habitats, in general, are usually associated with cool, wet conditions and it may be that den sites benefit from occurring in the coolest and wettest sites within a burrow area.

Slope, or gradient, can be an important predictor of areas occupied by mountain beavers, perhaps because it allows burrows to be oriented to drain water from den and food chambers (Beier 1989). We did not, however, find slope to be an important predictor of the locations of dens, even though the slope at den sites was a bit steeper than at available sites. This is probably because there was little variation in slope within the occupied areas. Casual observation suggests, however, that the areas occupied by mountain beavers were located more commonly at transition areas, where slope breaks (W. Zielinski, pers. obs.), as also observed in the Sierra Nevada (Beier 1989). Exploring the importance of slope transition will require additional analysis that compares occupied and unoccupied burrow areas.

Den sites can presumably be influenced by factors other than those we investigated, in particular variations in soil type and social factors. The absence of these factors as potential predictors probably explains why the model did not achieve higher classification success (Table 5). Soil maps for our study area do not have sufficient resolution to help distinguish the den sites from other areas, and we did not sample soils. Given the close proximity of the den sites and their available sites, however, we do not expect much variation. We also did not account for social factors, which could be influential if den sites are chosen because of their location relative to the dens or burrow areas of other animals. This too would need to be explored in additional work which could be accomplished by examining the spatial distribution and autocorrelation of den sites, and home ranges, by gender. Finally, we advise caution when inferring these results to other areas within the range of the Point Arena mountain beaver. Not only did the top model perform rather poorly under cross validation (suggesting that factors other than those we explored here may also influence den site choice), but mountain beavers within this subspecies also occur in habitats other than those where we collected data for this report. They also occur farther inland along riparian strips within redwood forests

(Billig and Douglas 2007) and vegetation at den sites in these red alder (*Alnus rubra*) and sword fern (*Polysticum munitum*) habitats will likely be quite different structurally and floristically than in the dune and coastal scrub habitats studied here.

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APPENDIX A. Alternative den site habitat selection models for the Point Arena mountain beaver at Manchester State Park, CA. See Table 1 for variable definitions.

Model	Model name	Variables included
1	Cov_For1	MEANDENS, PAMBTOP4
2	Cov_For2	MEANDENS, PAMBTOP75
3	Cov_For3	MEANDENS, TOTPFORBCOV
4	Cov_For4	MEANDENS, TOTBADGRAS
5	Cov_For5	MEANDENS, PAMBTOP4, TALVEGCONV
6	Cov_For6	TOTSHRUBCOV, TOTGOODGRAS, PAMBTOP4
7	Cov_For7	TOTSHRUBCOV, TOTGOODGRAS, PAMBTOP75
8	Cov_For8	TOTSHRUBCOV, TOTGOODGRAS, TOTPFORBCOV
9	Cov_For9	TOTSHRUBCOV, TOTGOODGRAS, TOTBADGRAS
10	Cov_Top1	MEANDENS, COSASPECT, SLOPE
11	Cov_Top2	TOTSHRUBCOV, TOTGOODGRAS, SLOPE
12	Cov_Top3	TOTSHRUBCOV, TOTGOODGRAS, COSASPECT
13	For_Top1	PAMBTOP4, COSASPECT, SLOPE
14	For_Top2	PAMBTOP75, COSASPECT, SLOPE
15	FrCvTp_1	MEANDENS, PAMBTOP4, COSASPECT, SLOPE
16	FrCvTp_2	MEANDENS, PAMBTOP75, COSASPECT, SLOPE
17	Topo1	COSASPECT, SLOPE
18	Cover1	MEANDENS
19	Cover2	MEANDENS, TOTSHRUBCOV, TOTGOODGRAS
20	Cover3	MEANDENS, TALVEGCONV
21	Cover4	TOTSHRUBCOV, TOTGOODGRAS
22	FORAGE1	PAMBTOP4
23	FORAGE2	PAMBTOP75
24	FORAGE3	MBKNOWNUSE
25	FORAGE4	TOTPFORBCOV
26	FORAGE5	TOTBADGRAS
27	NULL	