

EVALUATING HABITAT SELECTION MODELS TO IMPROVE SITE SELECTION
IN A POPULATION MONITORING PROGRAM FOR TOWNSEND'S BIG-EARED
BATS (*CORYNORHINUS TOWNSENDII*)

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ABSTRACT

EVALUATING HABITAT SELECTION MODELS TO IMPROVE SITE SELECTION IN A POPULATION MONITORING PROGRAM FOR TOWNSEND'S BIG-EARED BATS (*CORYNORHINUS TOWNSENDII*)

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Winter roost (hibernacula) surveys offer a unique opportunity to monitor Townsend's big-eared bats (*Corynorhinus townsendii*) while the population is generally closed, using a simple count method to census the population. Existing knowledge of *C. townsendii* hibernacula facilitates long-term population trend analysis but improving the accuracy of trend estimates requires identification of additional hibernacula to increase the proportion of the population monitored. Over 800 caves are known within Lava Beds National Monument; 322 of these have never been surveyed in the winter and could potentially hold a substantial portion of the *C. townsendii* population currently missing from the annual census. Given funding limitations, the process of selection for new survey sites should be carefully evaluated to improve the probability that new sites will contain larger numbers of bats, thus increasing the proportion of the population monitored. Therefore, I proposed and validated predictions for several habitat selection models built from multiple datasets for a species of concern, Townsend's big-eared bats (*Corynorhinus townsendii*), threatened by disease (white-nose syndrome) and disturbance in an area with 30 years of survey history (Lava Beds National Monument, Siskiyou County, CA). Hibernating bat abundance in 30 caves was negatively correlated with mean winter cave temperature measured hourly over four years. However, the complexity

of monitoring over 800 caves renders intensive temperature monitoring infeasible. Instead, I explored several cave morphology metrics thought to influence airflow as proxies for cave microclimate. Principal components analysis suggested a link between cave temperature and trench length, trench depth, and constriction area, but models built from an intensive dataset (n=30) did not perform well in predicting bat abundance. Boosted regression tree models built from an extensive dataset (n=191) were validated (n=50) and show moderate predictive performance using just three cave morphology variables. These most important predictors included interactions between number of entrances, passage slope, and passage size, along with cave length and trench length. Use of this model to prioritize unsurveyed sites could lead to faster discovery of important hibernacula, given the large number of caves to be surveyed and that most of them are unlikely to be occupied. Discovery of new hibernacula would increase the monitored proportion of the *C. townsendii* population that resides within Lava Beds National Monument, potentially providing a more accurate population monitoring program. As this *C. townsendii* population monitoring program provides the most consistent data at some of the largest known hibernacula in the western U.S., continued development and implementation of this program is critical to informing decisions related to this species of special concern.

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INTRODUCTION

Wildlife population trend monitoring facilitates an understanding of both normal variability and the effects of stochastic events such as disease and human disturbance. Effective population trend monitoring programs can influence management decisions by identifying species at risk of population decline, or, alternatively, prioritizing application of protections to one population or species over another (Morrison et al. 2006, Nichols & Williams 2006). Population monitoring in bats is limited by the cryptic habitat use patterns of most species, resulting in the application of variable and inconsistent survey methods, and consequent imprecise trend estimates. Much of the published data on bat population monitoring is opportunistic and very few studies incorporate repeated site visits or consistent survey methods (O'Shea et al. 2003). Surveys at cavernicolous winter roosts (hibernacula) offer an opportunity to count bats during a period when the population is generally closed and thus provide an important opportunity to effectively monitor some populations (Tuttle 2003). This approach has been used for cave-roosting species in the eastern U.S. for decades (Langwig et al. 2015). However, a recent summary of known hibernacula in the western U.S. reports sparse records of bat abundance for most species despite increased survey effort in many types of potential hibernacula structures (Weller et al. 2018). A major exception to this pattern is for a single species, Townsend's big-eared bat (*Corynorhinus townsendii*), which hibernates primarily in caves and mines (Humphrey & Kunz 1976). This species roosts openly on

walls and ceilings rather than in crevices, making it relatively easy to observe and facilitating census counts (Pearson et al. 1952).

The National Park Service (NPS) at Lava Beds National Monument (Lava Beds NM) supports the most robust *C. townsendii* population trend monitoring program in California and presents an example of data that are vital to the accurate assessment of species extinction risk (Bonham 2016). Existing knowledge of *C. townsendii* hibernacula facilitates long-term population trend analysis but improving the accuracy of trend estimates requires identification of additional hibernacula to increase the proportion of the population monitored. Over 800 caves are known within Lava Beds NM; 322 of these have never been surveyed in the winter and could potentially hold a substantial portion of the *C. townsendii* population currently missing from the annual census. Given funding limitations, the process of selection for new survey sites should be carefully evaluated to improve the probability that new sites will contain larger numbers of bats, thus increasing the proportion of the population monitored.

Continued monitoring for this species of concern is vital to the future of their conservation. Though the NPS Inventory and Monitoring program supports annual surveys at the largest known hibernacula within Lava Beds National Monument boundaries, additional prospective surveys are limited by availability of qualified surveyors.

According to a recent statewide status review of *C. townsendii*, this is the Bonham's review (2016) suggests that microclimates in caves and mines are important factors in habitat selection by *C. townsendii*, but that a comprehensive assessment of cave

or mine morphology, especially in relation to size of passages, is lacking. Listed as a species of concern in many of the states it occupies, *C. townsendii* populations have experienced declines due to habitat loss and human disturbance of roost structures. In addition, an introduced fungal disease known as white-nose syndrome (WNS) threatens hibernating bat species including, potentially, *C. townsendii*.

First documented in New York in 2006, WNS has spread quickly across the continent with a recent jump from the Midwest to Washington state (Lorch et al. 2016). WNS is caused by the cryophilic soil fungus *Pseudogymnoascus destructans*, which invades skin tissue on the muzzle and wing membranes (Cryan et al. 2012). This disease affects bats during hibernation, increasing arousal frequency and depleting fat stores necessary to survive through the winter (Reeder et al. 2012). WNS causes additional physiological disruptions leading to dehydration and electrolyte imbalance from invasion of skin tissue by fungal hyphae (Cryan et al. 2012). Throughout the disease's short history of spread across North America, WNS has caused severe population declines in some hibernating bat species, while others have remained relatively unaffected (Frick et al. 2010). Population decline from WNS is correlated with differences among species in body size, torpor bout length, and environmental characteristics of winter roost sites (Langwig et al. 2012, Langwig et al. 2016, Hayman et al. 2016). This new threat to bat populations warrants increased efficiency and effectiveness of bat monitoring to inform species distribution models, disease surveillance, and population trend analysis (Frick et al. 2010, Langwig et al. 2014).

Though no clinical sign of WNS has yet been documented in eastern subspecies of *C. townsendii*, the fungus that causes this disease has been detected on the muzzle and forearm during hibernation (Coleman 2014, White-nose Syndrome Response Team 2018). This suggests that all subspecies of *C. townsendii* could be vectors for WNS transmission, an important consideration as *Myotis spp.* and *Eptesicus fuscus*, species more likely to be affected by WNS, roost in some of the same caves as *C. townsendii* at Lava Beds NM (NPS unpublished data). In addition, a single case of physical contact between a torpid *C. townsendii* individual and a torpid *Myotis ciliolabrum/californicus* individual (species identification unconfirmed due to disturbance risk) was documented during 2018 hibernacula surveys (NPS unpublished data). The clinical effect of WNS on western *C. townsendii* populations remains uncertain and will only be detected through disease surveillance and robust population trend monitoring programs.

Occupancy of cave and mine hibernacula by *C. townsendii* appears correlated with internal microclimate conditions and site morphology across several western states (Gilles et al. 2014, Sherwin et al. 2000). This habitat association may be explained by the physiological mechanisms of torpor, favoring selection of hibernacula with cold temperatures that allow individuals to conserve energy (Szewczak 1997, Boyles & McKechnie 2010, Rodhouse 2016). Though among-site differences in microclimate are likely the ultimate cause of habitat selection, microclimate data are more difficult to obtain than cave morphological characteristics that can be easily collected. Analysis of the relationship between microclimate, simple cave morphology metrics, and hibernating bat abundance is essential to the development of efficient site selection strategies for

discovering new *C. townsendii* hibernacula and developing effective trend-monitoring programs. The goal of this research was to improve site selection in the *C. townsendii* population monitoring program at Lava Beds National Monument through investigation of the habitat selection of hibernating bats among volcanic caves.

Study Objectives

- 1) Describe *C. townsendii* habitat associations in relation to cave microclimate and efficiently-measured cave morphology variables collected for large numbers of caves with low effort.
- 2) Create a predictive model of bat abundance with efficiently-measured cave morphology variables.
- 3) Validate model predictions of bat abundance with a novel dataset of previously unsurveyed caves within the monument.
- 4) Evaluate the feasibility of using predictive models for site selection to improve the probability of finding new *C. townsendii* hibernacula among the remaining unsurveyed caves.

METHODS

Bat Surveys in the Study Area

Located in northeastern California, Lava Beds National Monument is a 19,000-hectare NPS site protecting over 800 volcanic caves, a plethora of cliff faces and rock crevices, and high elevation mixed-conifer forests that support 14 species of bats (Figure 1). Cave inventory and bat monitoring are supported by the NPS as the protection of volcanic caves and associated wildlife are included in the monument's enabling legislation. Although historic hibernacula survey records date back to 1988, the current population monitoring program has been implemented annually since 2012. Current hibernacula survey protocols focus on *C. townsendii*, but observations of *Eptesicus fuscus* and *Myotis* spp. are also recorded. The *C. townsendii* population at known hibernacula within Lava Beds NM consists of more than 1,500 individuals and was stable from 1991-2012 (Weller et al. 2014).

Hibernacula surveys are restricted to a short mid-winter time frame (approximately one week each January) to improve population estimates, as bats are most likely to be torpid in hibernacula during in the coldest months and bats may move among hibernacula during the winter (Weller et al. 2014). To reduce disturbance to hibernating bats and ensure accurate observations, surveyors are well-experienced in moving through caves and identifying bat species during a single visit to each cave per winter. Surveyors move quietly through all cave passages, scanning walls and ceilings with lights, using

binoculars to identify bats from a distance. Binoculars and photos are used to count the number of individuals in a cluster (roosting in direct contact with other bats). The total number of caves surveyed each year varies depending on the availability of surveyors.

Current site selection for the *C. townsendii* monitoring program uses a stratified random sampling method based on estimates of bat abundance per cave from previous years' surveys (Table 1, Thomas 2014). Caves with high abundance (greater than 30 bats, n=11) in previous years are surveyed annually. As additional surveyor time allows, caves with low abundance in previous years (less than 30 bats, n=71) as well as unsurveyed caves of interest (n=322) are selected on a rotating random basis. Caves eliminated from the sampling frame include those with three consecutive counts of zero bats since 2010, considered unoccupied sites (n=19), along with surface tubes, bridges, and those considered unsafe or sensitive due to fragile geologic or cultural resources (n=343). Surface tubes and bridges were identified for elimination from the sampling frame by experienced NPS staff according to guidelines detailed in Appendix A. These sites had internal microclimates very similar to the surface microclimate and are assumed to have extremely low bat abundance. These assumptions are supported by data from 137 surveys at these site types showing mean bat abundance of 0.22 (SE=0.07) bats per surface tube or bridge (NPS unpublished data).

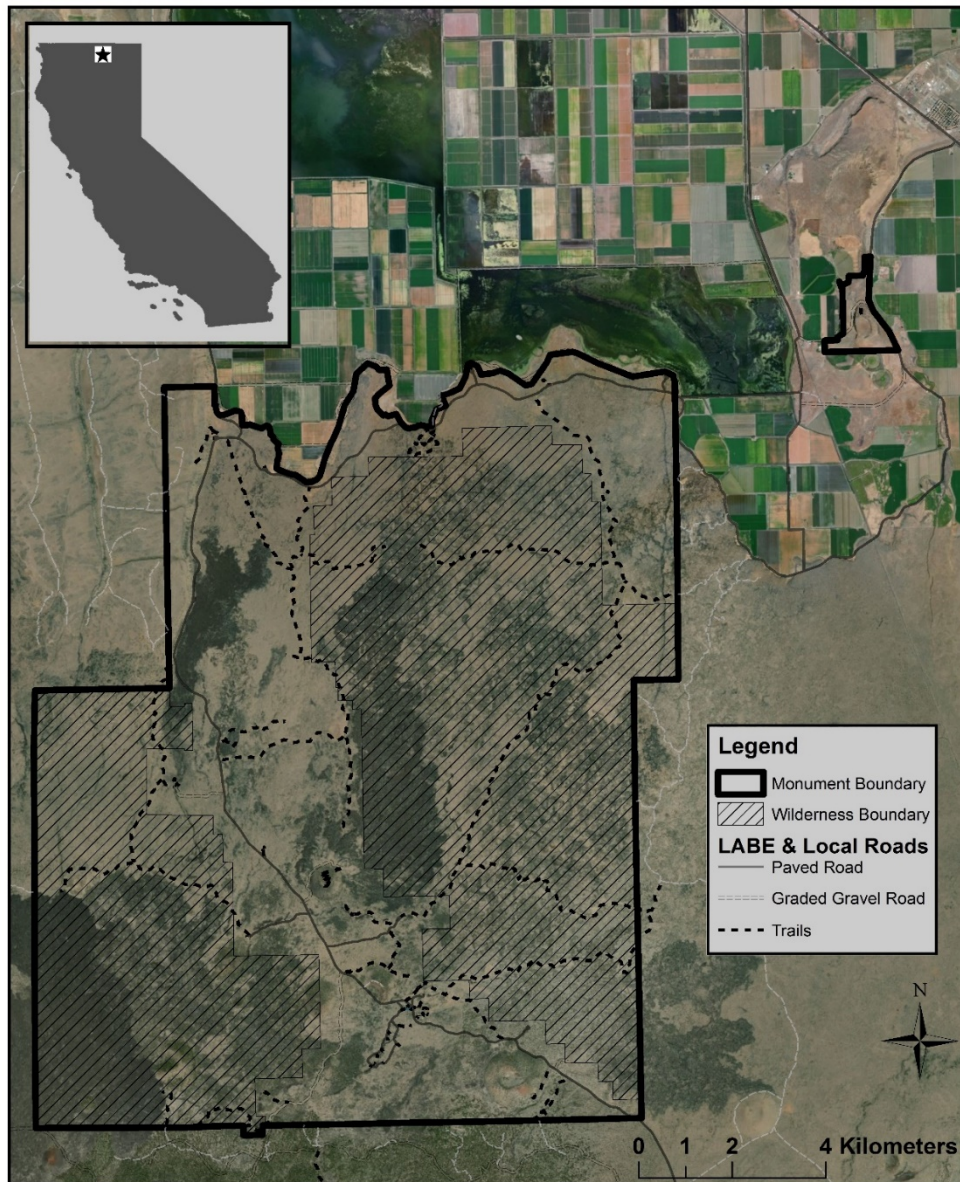


Figure 1. Aerial imagery, roads, trails, and boundaries of Lava Beds National Monument, Siskiyou County, California. Volcanic caves are dispersed across the monument except near the Petroglyph Point unit shown in the northeast. Cave locations were purposely excluded from this locator map to protect sensitive locations in compliance with the Federal Cave Resources Protection Act. Vegetation communities include sagebrush-steppe, juniper woodlands, and ponderosa pine forest, but are sparse on recent lava flows (dark areas shown on aerial imagery). Agricultural fields and remnants of Tule Lake border the north end of the monument, managed by the US Fish and Wildlife Service. A few parcels of private land border the monument to the east, but much of the monument boundary is surrounded by the Modoc National Forest (US Forest Service).

Cave Microclimate

Cave microclimate data (temperature and relative humidity) was collected hourly from HOBO Pro v2 dataloggers placed 0-2 meters above the floor in the deep zones of 30 caves. Relative humidity was excluded from this analysis due to its collinearity with temperature. Instead, temperature was used to better compare these results with other studies of bat hibernacula. These dataloggers were installed for preliminary implementation of the NPS Klamath Inventory and Monitoring Network's Integrated Monitoring Protocol for Cave Entrance Communities and Cave Environments (Krejca et al., 2017). Twenty caves were randomly selected from a sampling frame containing all known caves greater than 91 meters in length using a Generalized Random Tessellation Stratified (GRTS) sampling method. Ten additional caves were selected based on expert opinion of their resource value; these included four ice caves and six known bat hibernacula. One cave originally included in the monitoring protocol was excluded from my analysis due to access issues related to cultural significance. Though statistical inference from this sample selection method does not easily generalize to all caves in the monument, this design provided reasonable representation across the range of bat abundance categories used to define strata for the current hibernacula survey design (Table 1). Linear regression was chosen to describe the relationship between log₁₀-transformed mean bat abundance compiled from 8 years of survey data (2010-2017) and mean winter cave temperature compiled from 4 years of data collection (November 15 –

March 15, 2012-2016). Two separate analyses were used to determine patterns among only occupied caves and among all monitored caves.

Table 1. Distribution of volcanic caves in relation to known bat abundance or cave type used for site selection in the Townsend's big-eared bat (*Corynorhinus townsendii*) population monitoring program at Lava Beds National Monument. Caves selected for microclimate analysis (n=30) were compiled from pilot implementation of the Klamath Inventory and Monitoring Network's Integrated Monitoring Protocol for Cave Entrance Communities and Cave Environments.

Selection Group Number	Selection Group Qualification	Number of Caves per Selection Group	Number of Caves Selected for Microclimate Analysis
1	Mean > 30 bats	11	7
2	Last Count 6-30 bats	20	6
3	Last Count 0-5 bats	51	4
4	Last Two Counts = 0 bats	34	6
5	Three Counts = 0 bats	19	7
6	Surface Tube, Bridge, or Unsafe Access	343	0
7	Unsurveyed Caves of Interest	322	0
	TOTAL	800	30

Habitat Data Collection

Two separate datasets were used describe *C. townsendii* habitat associations in relation to cave microclimate and cave morphology variables. The first was an intensive dataset consisting of the 30 caves used in microclimate monitoring. Cave morphology variables were measured at each of these 30 sites. The second was an extensive dataset (n=191 caves) with efficiently-measured cave morphology metrics representing all caves longer than 15 meters with hibernacula survey records. The intensive dataset was expected to yield more accurate habitat association models but involved more logistical complexity and required more time to collect. The extensive dataset was used to

investigate whether models created using data that required relatively little time to collect would provide predictive power for bat abundance to adequately inform the prioritization of the 322 unsurveyed caves of interest.

Ten cave morphology metrics (Table 2) were measured or compiled for the 30 sampled caves with robust maps, microclimate data, and bat survey records. All cave morphology variables were measured by the author in the field using a laser rangefinder and compass, except direct cave length and depth, which were calculated from existing cave survey data extracted from a Lava Beds NM database.

Eight cave morphology metrics (Table 2) were compiled for 191 caves with bat survey records, excluding sites identified as surface tubes or bridges (Appendix A). This dataset built upon previous cave inventory records from the monument's cave database. All variables except trench length and cave morphology category were extracted from a Lava Beds NM cave database. Trench length was measured in ArcGIS (ESRI 2011) using the monument's 2005 aerial imagery and cave location points. Cave morphology categories were assigned using cave maps to identify whether a cave had a single or multiple entrances (S or M), sloped or flat passages (S or F), and had small, medium, or large passage size (S,M,L) based on maximum ceiling height. One combination of these categories did not exist in the dataset (MSS: multiple entrances, sloped passages, small ceiling height), therefore this category had eleven possible values with at least five caves in each possible category value (Appendix B).

Table 2. Cave morphology metrics used to predict habitat selection by Townsend's big-eared bats (*Corynorhinus townsendii*) in volcanic caves at Lava Beds National Monument. Two separate datasets were used to compare predictive ability of intensive data collected in the field specifically for this project with extensive dataset compiled from existing database records, aerial imagery, and cave maps.

Predictor Variable	Units	Definition
Trench Depth ^a	m	Distance from surface to bottom of volcanic trench at the cave entrance closest to the deepest passage
Entrance Area (single) ^a	m ²	Area of the deep entrance*
Entrance Area (total) ^a	m ²	Summed area of all cave entrances
Constriction Area ^a	m ²	Area of the first constriction (passage smaller than 50% of the entrance area) beyond the deep entrance*; if the entrance is the smallest constriction, entrance area was measured for both
Distance to Constriction ^a	m	Distance to the first constriction (passage smaller than 50% of the entrance area) beyond the deep entrance*
Slope ^a	degrees	Degree of cave slope from the deep entrance* to first area beyond the entrance where slope changes
Distance to Change in Slope ^a	m	Distance from the deep entrance* to first area beyond the entrance where slope changes
Entrance Azimuth ^a	degrees	Compass direction looking out of deep entrance*
Direct Cave Length ^a	m	Distance from the deep entrance* to the end of the deepest passage (excludes length of side passages)
Direct Cave Depth ^a	m	Depth from the deep entrance* to the deepest section of cave passage
Total Cave Length ^b	m	Total cave survey length including all side passages and multiple levels
Trench Length ^b	m	Distance from cave entrance to opposite end of volcanic trench
Trend ^b	cardinal direction	Directional trend of cave passages (e.g. NW-SE)
Morphology Category ^b	category	Three letter code describing 1) a single or multiple entrances, 2) sloped or flat passage floor, and 3) passage size based on maximum ceiling height: small (< 1.5 m), medium (1.6-6 m), or large (> 6 m)

System ^b	y/n	Subflow within the Mammoth Crater Geologic Flow
Branched ^b	y/n	Presence/absence of branched passages
Multilevel ^b	y/n	Presence/absence of multiple levels
Entrances ^b	integer	Total number of entrances to a single cave

a: Data collected in the field specifically for this project at 30 caves.

b: Data compiled from records in the existing cave database, using existing cave maps, or calculated from aerial imagery and cave locations at 191 caves.

* Deep entrance is defined as the entrance that most likely has the greatest influence on airflow into the cave. This is often the entrance with the shortest distance to the deepest cave passage, though other entrances were selected based on the researcher's field expertise for caves with multiple entrances or multiple levels.

Building Habitat Selection Models

Principal components analysis

Principal components analysis (PCA) was used to visually identify patterns among cave morphology and microclimate variables to reduce the number of variables used in linear regression. This approach reduces the problematic effect of multicollinearity on regression model outputs from the use of several ecological predictor variables (Graham 2003). PCA was also used to evaluate the within-sample predictive power of different approaches to measuring two types of cave morphology variables. First, I compared the within-sample predictive power when using the area of a single cave entrance or the total area of all cave entrances. Second, I compared the within-sample predictive power when using missing values or mean entrance aspect as a fill-in value for vertical cave entrances that have no true aspect. A probabilistic PCA with two principal components was performed in R statistical software using package “pcaMethods” (R Core Team, 2018). Multicollinearity was assessed for all variables prior to conducting the PCA and resulted in the removal of entrance area and direct cave length due to correlations greater than 0.60 with other variables. Entrance area was correlated with constriction area (0.69) and trench depth (0.75); direct cave length was correlated with total cave length (0.66) and cave depth (0.67).

Generalized linear modeling

Linear regression with a Gaussian error distribution and an identity link were used to further describe the relationship between cave microclimate and morphology. Cave

morphology variables with a strong relationship to temperature in the initial PCA were included in a linear regression candidate model set. Model selection was performed using AICc values and weights, but parameter estimates and their 95% confidence intervals were compared across the top four models. Predictions of bat abundance from the linear model best describing mean winter temperature were created for the validation dataset, but were excluded due to the model's poor predictive performance.

Boosted regression trees

Boosted regression trees were chosen for use with the extensive dataset (n=191) due to their improved predictive performance (Elith et al. 2008). This machine learning approach creates decision trees using threshold values for each predictor variable. Boosting the regression tree analysis is a sequential method where additional trees are added to improve the performance of the previous collection of trees. All trees are then combined to yield a single consensus prediction. These models do not produce AICc scores but rather provide an estimate of the relative influence of each predictor variable. Variables with higher relative influence provide a larger decrease in the residual sum of squares and are therefore weighted when building the boosted regression tree model (Elith et al. 2008). These highly weighted variables can be interpreted as the most influential predictor variables.

Due to the limited availability of morphology variables that were easy to measure for all caves in the extensive dataset (n=191), principal components analysis was not used to reduce the number of variables prior to conducting boosted regression tree analysis. No multicollinearity was found between these seven variables; all were included in the

analysis. Simplification of models by stepwise removal of predictor variables with low relative influence was assessed following methods outlined in Elith et al. (2008) but did not improve model performance and was therefore not used for further analysis.

To determine the optimal settings for the boosted regression tree analysis, I conducted a systematic assessment of values for tree complexity, learning rate, and bag fraction. The analysis yielded very similar cross-validation (CV) deviance and correlation for all value combinations considered reasonable based on guidance in Elith et al. (2008). Therefore, I set tree complexity equal to 4 for the intensive dataset, corresponding to four predictor variables. For the extensive dataset, tree complexity was set to 5, as this is a commonly used upper limit of tree complexity in the ecological application literature (Elith et al. 2008). To reduce overfitting of the model, the proportion of the data used to build each regression tree, known as bag fraction, was set to 0.75, and learning rate, used to inform sequential regression tree construction, was set to 0.001. This produced an optimal number of trees greater than 1000, as suggested by Elith et al. (2008).

Evaluating Habitat Selection Models

To validate habitat selection models, 50 caves with no prior hibernacula survey data were selected through stratified random sampling based on cave length to ensure that shorter caves (more abundant in the sample frame) were not selected more frequently than longer caves (substantially less abundant in the sample frame). Caves classified as surface tubes or bridges (Appendix A) were excluded due to previous survey data showing extremely low abundance at these sites (NPS, unpublished data). From the

remaining dataset of 322 unsurveyed caves, ten were selected from each of the five length bins (15-44m, 45-75m, 76-106m, 107-136m, greater than 137m). Important cave morphology variables as identified by the PCA (entrance area, constriction area, trench depth) and included in the extensive dataset (trench length, morphology category) were measured at all 50 caves in 2017. Bat abundance surveys at these sites were completed in conjunction with normally-scheduled hibernacula surveys in January 2018. Prior to surveys conducted for this thesis, the Institutional Animal Care and Use Committee (IACUC) from Humboldt State University approved protocol no. 15/16.W.111-A, titled “Characterizing Western Bat Hibernacula through Cave Morphology and Microclimate” on January 23, 2017.

RESULTS

Describing Cave Microclimate and Bat Abundance

Mean winter temperature (November 15 – March 15, 2012-2016) compiled for the intensive dataset (n=30 caves) showed warmer temperatures and increased variability among sites with fewer hibernating bats with direct reference to the abundance categories used for stratified random site selection in the population monitoring program (Figure 2). Closer investigation of this pattern using linear regression again suggested hibernating bat abundance was inversely related to mean winter cave temperature, but that this pattern was stronger among occupied caves (Figure 3A). When considering habitat selection among all caves in the dataset (occupied and unoccupied sites), this pattern was less strong as influenced by variability in unoccupied sites (Figure 3B). All six caves in this dataset with mean winter temperature below 0°C contained ice deposits present year-round; the two caves occupied by bats had substantially smaller ice deposits than the four unoccupied ice caves (Kern & Thomas 2014). Small ice deposits ranged from approximately 3 to 6 square meters, while large ice deposits ranged from approximately 20 to 60 square meters (NPS unpublished data).

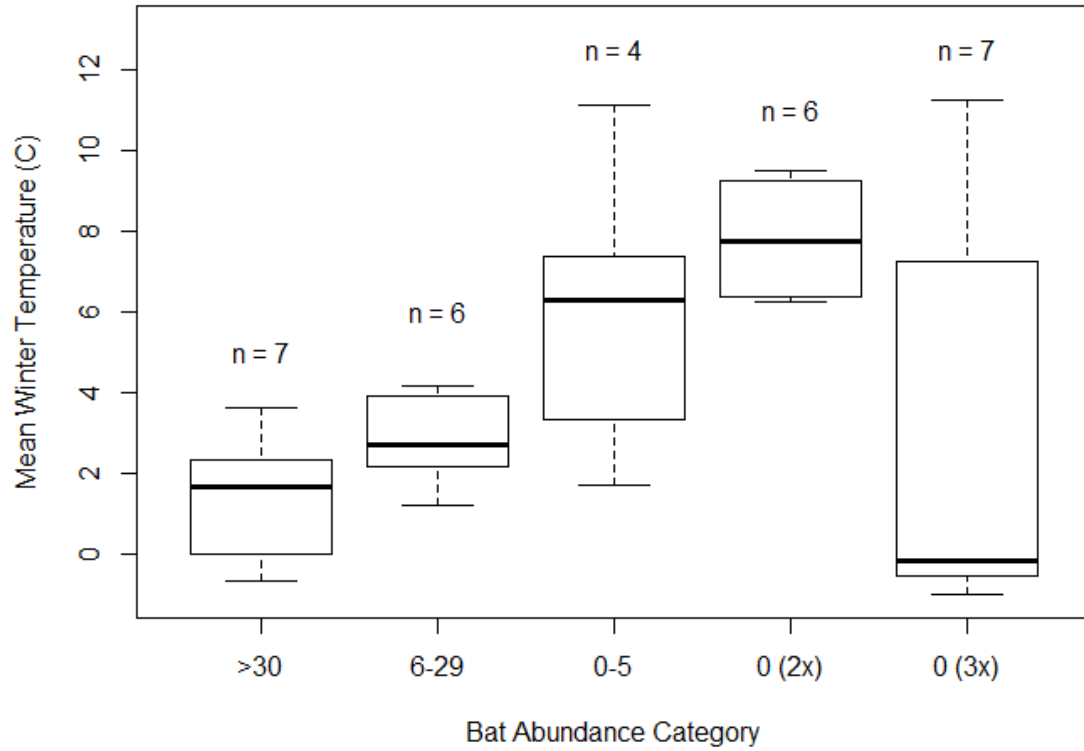


Figure 2. Variation in mean winter temperature from the deep zone of 30 volcanic caves shows warmer temperatures and increased variability among sites with fewer hibernating bats (*C. townsendii*). The bold line, box, and whiskers represent the mean, quartiles, and 95 percentiles, respectively. Data collected at Lava Beds National Monument, Tulelake, California with Onset HOBO Pro U23-001 v2 dataloggers from Nov 15- Mar 15, 2012-2016.

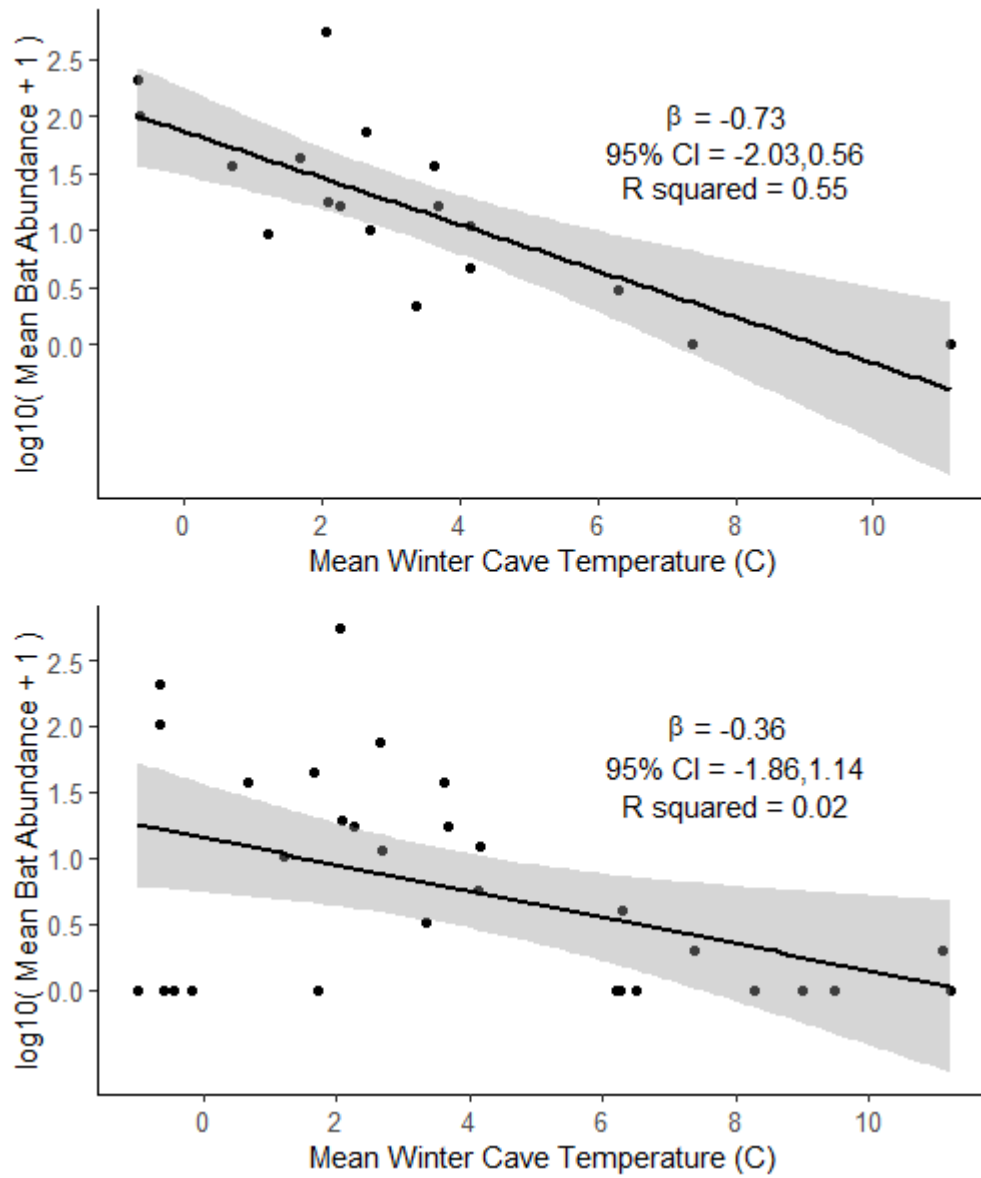


Figure 3. Negative relationships with beta values, 95% confidence intervals, and R^2 values as determined by linear regression using mean winter cave temperature to describe \log_{10} -transformed mean bat abundance for (A) occupied caves (n=18) and (B) all caves (n=30).

Patterns in Cave Microclimate and Morphology

Principal components analysis (PCA) showed cave temperature had a strong positive influence on the first principal component, while trench length, trench depth, and constriction area had strong positive influence on the second principal component (Figure 4A). Depth was highly correlated with temperature and was therefore removed to reduce multicollinearity within the candidate model set. Simplification of the predictor variables through removal of those not related to temperature increased the amount of variance explained by the two principal components from 44% to 78%. The PCA scores plot showed little to no clustering of sites based on bat abundance categories (Figure 4B).

Comparisons of PCAs showed minimal differences in percent of variance explained when using the combined area of all entrances compared to the area of a single entrance closest to the deepest passage in the cave. Similarly, for caves with vertical entrances, percent of variance explained when using missing values for entrance aspect did not differ from a PCA using the mean aspect of all cave entrances. Therefore, the simplest metrics (area of a single entrance, N/A for vertical entrances) were used in final analysis.

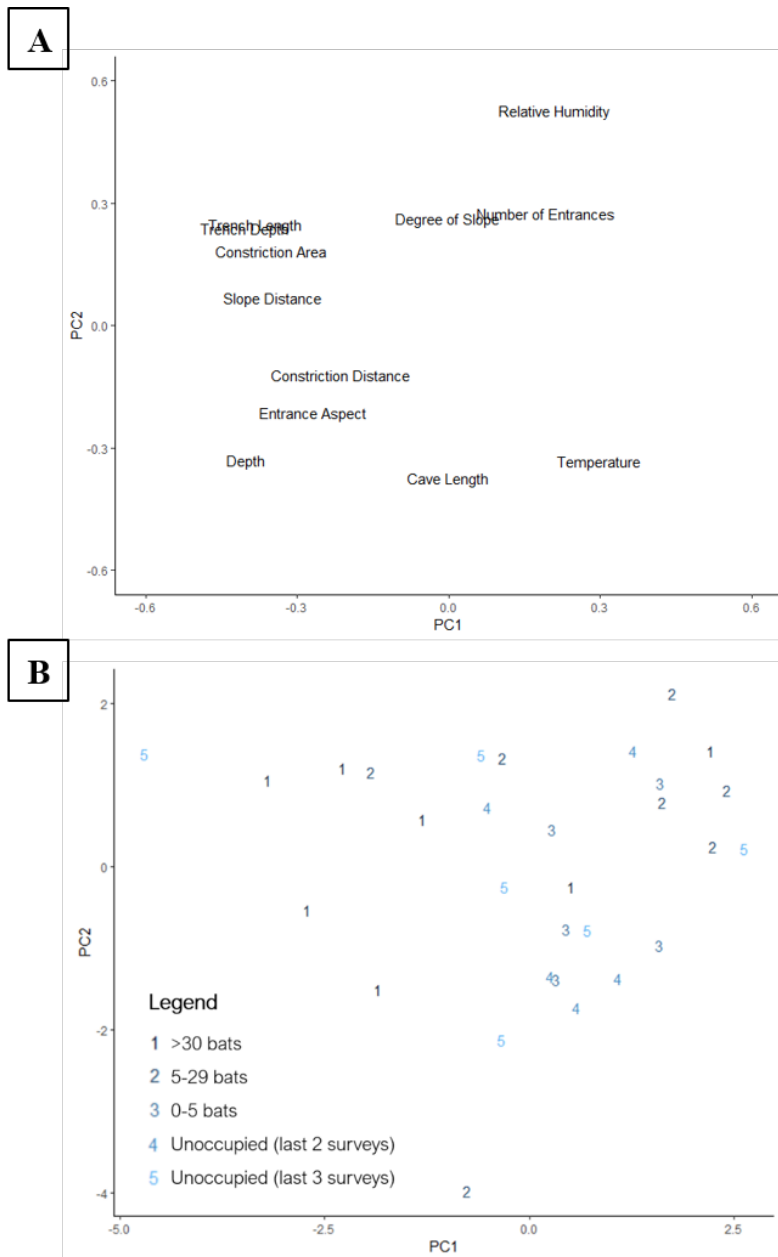


Figure 4. Principal components analysis of cave morphology and microclimate variables, and in relation to bat abundance. (A) Loadings plot showing a relationship between mean winter temperature (Nov 15-Mar 15, 2012-2016) and three cave morphology variables (trench length, trench depth, and constriction area). Percent of variance explained by two principal components improved from 44% to 78% when the remaining eight variables with weak relationships to

temperature were removed from analysis. (B) Scores plot showing little to no clustering of sites based on bat abundance categories.

Investigations of the relationships between temperature and cave morphology were explored through generalized linear models (Table 3, Figure 5). Continuous predictor variables were selected from patterns identified in PCA (trench depth, trench length, and constriction area). Categorical predictor variables (Trend, Morphology Category, System, Branched, and Multilevel) were included in the candidate model set, but none were in the top 4 models (Table 3). All models with categorical predictor variables had very low AICc weights (<1%) and delta AICc values greater than 2 when compared to the top 4 models. The top model had an R^2 value of 0.44, suggesting moderate goodness-of-fit. Parameter estimates and 95% confidence intervals were similar across all four models, suggesting negligible effects of model selection uncertainty (Figure 5).

Table 3. Model selection criteria for linear regression models describing mean winter cave temperature (Nov 15-Mar 15, 2012-2016) with three cave morphology predictor variables identified through PCA from a set of ten total cave morphology measurements (Figure 4). Data was collected at 30 caves in Lava Beds National Monument, Tulelake, California.

Temperature Models	K	AICc	Δ AICc	AICc Weight
Trench Depth + Trench Length	4	76.12	0	0.42
Trench Depth	3	76.56	0.44	0.34
Constriction Area + Trench Depth + Trench Length	5	78.57	2.45	0.12
Constriction Area + Trench Depth	4	78.95	2.83	0.1
Trench Length	3	83.01	6.89	0.01
Constriction Area + Trench Length	4	85.03	8.91	0
Constriction Area	3	89.07	12.95	0

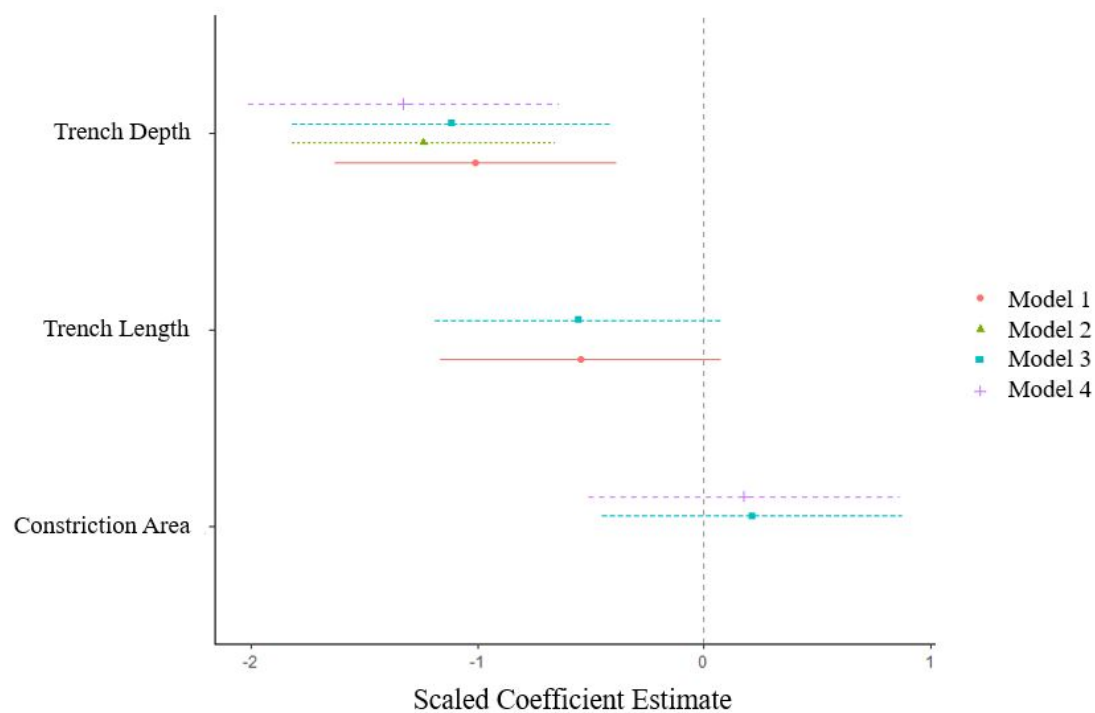


Figure 5. Scaled coefficient estimates and 95% confidence intervals for predictor variables in the top four linear regression models describing mean winter cave temperature (Nov 15-Mar 15, 2012-2016) at 30 caves in Lava Beds National Monument, Tulelake, California.

Predicting Bat Abundance with Cave Morphology Variables

The boosted regression tree model was built using the extensive dataset (n=191) with seven efficiently-measured predictor variables. Deviance and cross-validation (CV) correlation values indicated moderately poor predictive performance and possible overfitting (Table 4). However, predicted bat abundance was different from actual bat abundance by only a few individuals in most cases (Figure 6). In general, the model over-predicted bat abundance, but predictions could be improved if a few individuals were subtracted from each prediction before being considered for use in prioritizing caves for future surveys.

Three of the seven morphology variables provided 99% of the relative influence in model construction (Figure 7). When included separately in the boosted regression tree models, number of entrances, passage slope, and passage size were not identified as important variables (less than 10% of the relative influence). However, when coded as a unique categorical variable (Morphology Category), these variables had high relative influence (63%) on regression tree structure, suggesting an interaction between these three variables was critical to the prediction of bat abundance (Figure 7).

Four cave morphology category values showed increased bat abundance at caves with multiple entrances, sloped passages, and medium or large ceiling heights (Figure 8). This increase was also seen at caves with a single entrance, flat or sloped passages, and medium or large ceiling heights (Figure 8). Five cave morphology category values showed the lowest mean bat abundance at small or medium sized caves, and all but one

was assigned a flat slope, though some outliers with moderate bat abundance exist in those category values (Figure 8). Partial dependence plots showed a positive relationship between bat abundance and cave length, as well as between bat abundance and trench length (Figure 9), though outliers produced some complexity in this pattern.

Table 4. Performance metrics for the boosted regression tree model describing hibernating bat abundance in volcanic caves surveyed from 2010-2017 at Lava Beds National Monument, Siskiyou County, CA.

Number of Predictor Variables	CV deviance	CV deviance SE	CV correlation	CV correlation SE	Optimal number of trees	Number of sites (n)
7	30.387	13.12	0.387	0.092	3750	191

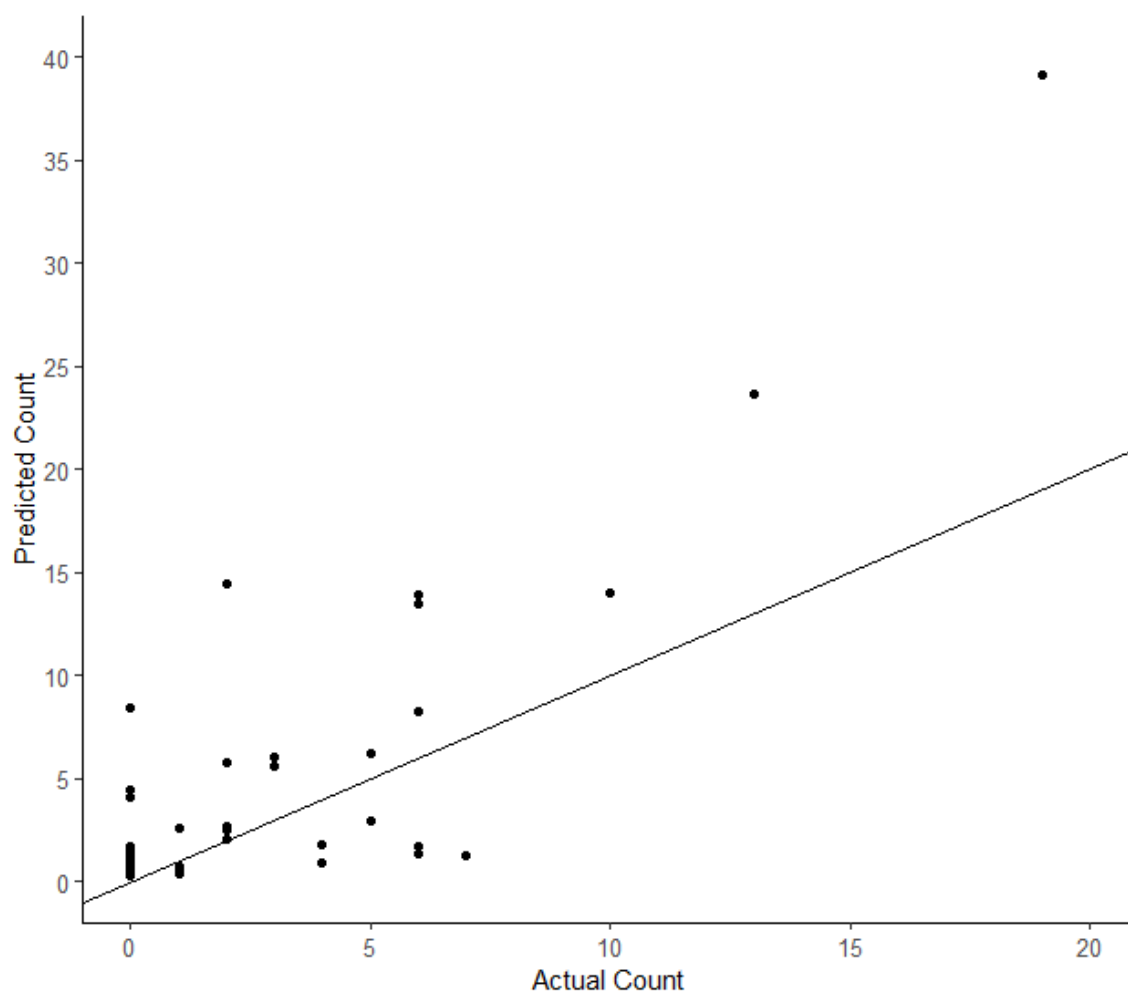


Figure 6. Comparison of predicted and observed bat abundance for a set of caves (n=50) used to validate the boosted regression tree model built from an extensive dataset (n=191) with seven predictor variables. Performance is moderate as shown by a distribution of points close to the 1:1 line, though several points show distinct over-predictions.

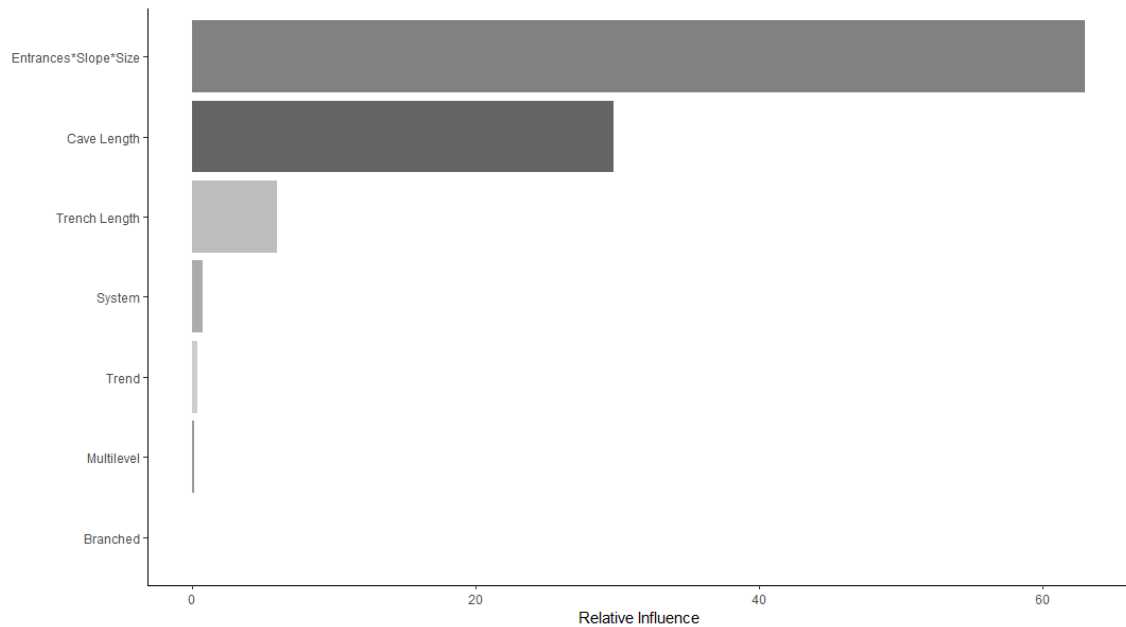


Figure 7. Relative influence plot showing the importance of predictor variables in creating the boosted regression tree model used to predict bat abundance. Morphology category (entrances*slope*size) provides the most influence (63%), followed by cave length (30%) and trench length (6%) while the other four variables (system, trend, multilevel, and branched) collectively provide just 1% of the relative influence.

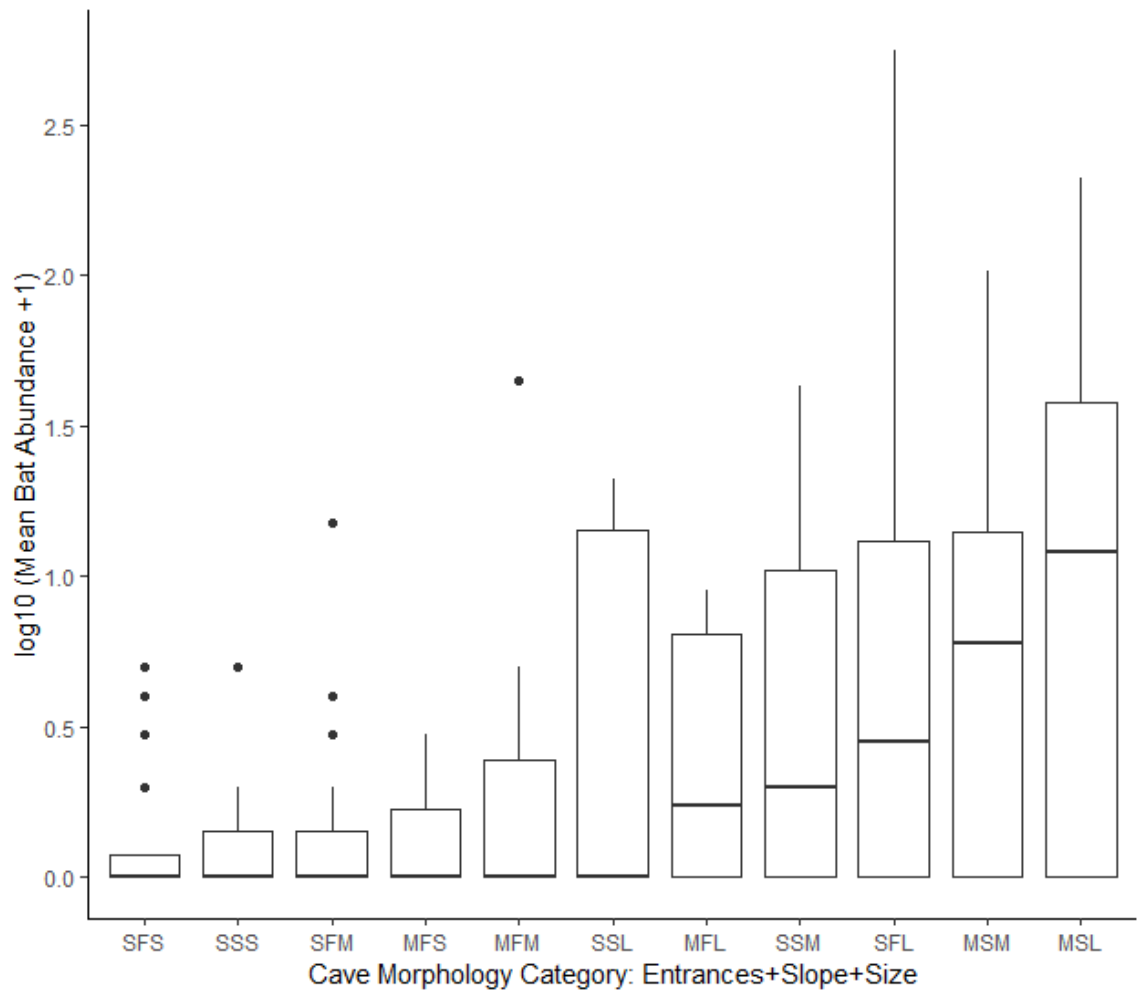


Figure 8. Boxplot describes log10-transformed mean bat abundance in relation to eleven possible combinations of cave morphology categories assigned based on information gathered from cave maps. Codes reflect single or multiple entrances (S/E), flat or sloped (F/S) passages, and small (<1.5 m), medium (1.5-6m), or large (>6m) ceiling heights (S/M/L). For example, SFS describes a cave with a single entrance, flat passages, and small ceiling heights.

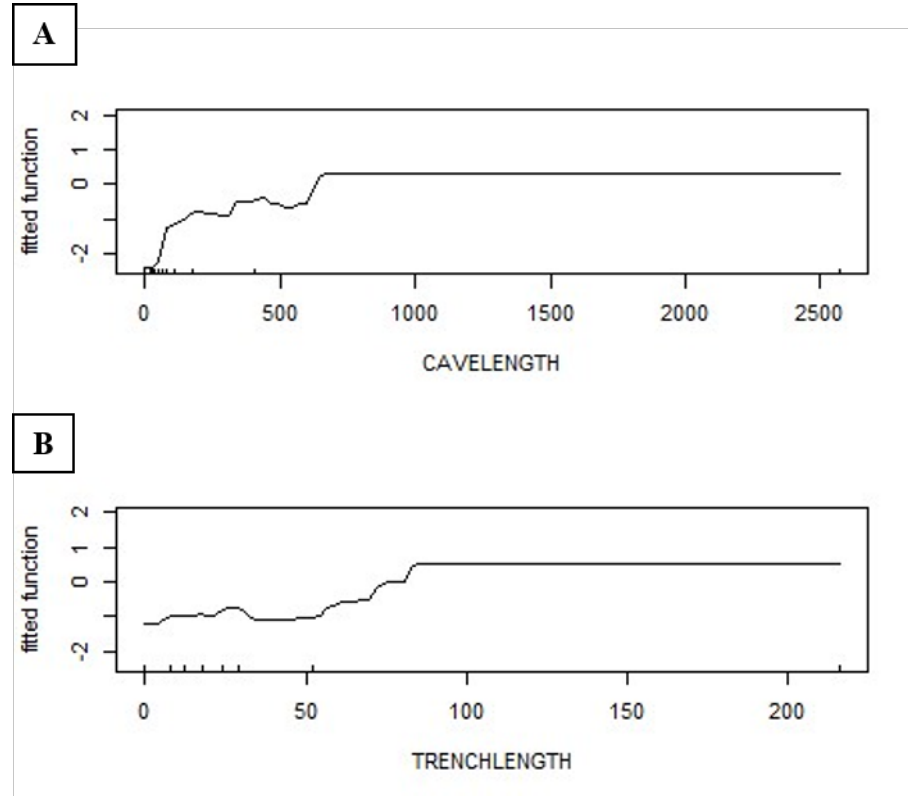


Figure 9. Partial dependence plots for predictor variables used in boosted regression tree models showing positive relationships between bat abundance and cave length in meters (9A) as well as between bat abundance and trench length in meters (9B). Outliers with the longest cave and trench lengths produce a plateau in fitted function values.

DISCUSSION

Cave Temperature

The relationship between cold cave microclimate and high bat abundance has been well documented across several species in volcanic caves, limestone caves, mines, and rock crevices (Tuttle & Stevenson 1978, Perry 2012). Data from the deep zones of volcanic caves at Lava Beds National Monument showed similar patterns of high bat abundance in caves with mean winter temperatures between 0° and 4° Celsius (Figures 2 and 3). The inverse relationship between cave temperature and bat abundance was stronger among occupied sites (Figure 3A), whereas increased variability in temperature among unoccupied sites generate a weaker relationship (Figure 3B). Year-round ice deposits may deter bats, as these caves otherwise provided similar temperatures to those caves with the highest bat abundance. As the ice volume in these caves changes over time (Zoltan & Thomas, 2014; Smith, 2014), changes in bat abundance at these sites will be important to document. Perhaps as the microclimate in these sites becomes too warm for ice in the future, it may instead provide ideal conditions for hibernating bats.

Further efforts could be made to clarify the relationship between cave microclimate and bat abundance in pursuit of a better understanding of *C. townsendii* ecology. For example, dataloggers measured temperature at easy-to-reach locations on the floors and walls below actual bat roost locations. Further analysis of microclimate variation within occupied caves could improve understanding of variation in abundance

among sites, where occupied caves may have more passage area with suitable temperature conditions than unoccupied caves. Stability of microclimate may also influence habitat selection for *C. townsendii* in volcanic caves, though that issue was not addressed in this analysis. Further, patterns between relative humidity and bat abundance could be clarified but were excluded here due to their multicollinearity with temperature. Instead, this analysis prioritized improvement of site selection based on cave morphology variables that were easier to measure than precise temperature for more efficient application to hundreds of caves.

Cave Morphology

Though cave microclimate may be directly influencing bat abundance in hibernacula, this metric is expensive and time-intensive to monitor. Instead, I used cave morphology as a proxy for cave microclimate to predict bat abundance in hibernacula because morphology metrics are more cost-effective and less time-intensive to measure. Cave microclimates are created by airflow exchange between the surface and cave passages (DeFreitas & Littlejohn 1987, Tuttle & Stevensen 1978). Passage configuration can have a large influence on this airflow exchange. For example, cold air can sink and be stored in caves with large passage volume located in deep chambers below entrances and chimney effects can occur between multiple entrances (Halliday 1954, Tuttle & Stevensen 1978).

In the intensive dataset (n=30), important cave morphology variables identified through PCA and used in linear regression to describe mean winter cave temperature included trench length, trench depth, and constriction area (Figures 4 and 5). Though the loadings plot showed visual patterns indicating trench length, trench depth, and constriction area might be indicative of cave temperature, the scores plot showed little to no clustering among caves in relation to the abundance categories used for site selection. This may suggest that the variables and sites in this dataset do not accurately reflect bat abundance patterns among all caves in the monument. Trench length and trench depth defined microtopographic variation on the surface near cave entrances, potentially providing an above-ground cold air sink similar to those developed in ice caves described by Halliday (1954). Constriction area represented an abrupt change in passage size known to increase or restrict airflow within a cave (Tuttle & Stevensen 1978).

In the extensive dataset (n=191), boosted regression tree models suggested that interactions between the number of entrances, passage slope, and passage size were the most influential predictor of bat abundance. Cave length and trench length followed in relative importance of creating bat abundance predictions, respectively. This combination of cave morphology metrics may best describe the complexity of airflow within a cave, where larger, longer caves could provide a more unique microclimate within the deep zone as compared to microclimates available on the surface (Tuttle and Stevensen 1978, DeFreitas & Littlejohn 1987, Ransome 1990). Trench length may be further differentiating available microclimate between surface and cave environments.

In other studies of cave and mine hibernacula, entrance size and aspect have been strong predictors of bat presence (Barnhart & Gillam 2017, Gilles 2014, Dixon 2011, Sherwin et al. 2000). Models using topographic variables found elevation, slope, and vegetation cover to be indicative of mean annual cave temperature (Hejna et al. 2015, Sherwin et al. 2000, Barnhart & Gillam 2017). Though many of these same studies reported non-significant results of cave length as a predictor, conclusions often alluded to the variability of length measurements based on braided passages and multiple levels, creating complexity in standardizing cave length measurements. In a study that included mines, Sherwin et al. (2000) found passage dimensions and complexity to be insignificant predictors of *C. townsendii* abundance. However, many of these studies reflected larger study areas with more landscape variation than is present within Lava Beds National Monument, which may have led to differences found between this analysis and those studies.

Of the studies that focused on cave morphology, hibernating *C. townsendii* selected sites far from cave or mine entrances (Humphrey & Kuntz 1976). In a study of 13 volcanic caves in Idaho, probability of occupancy by hibernating *C. townsendii* was correlated with presence of a collapse or constriction and lower mean ceiling height (Gillies et al. 2014). A similar study in Utah predicted a greater probability of occupancy at caves and mines with entrances less than 1.5 meters in height (Sherwin et al. 2000). further supports the use of cave morphology as moderately powerful predictors of bat abundance. These studies, along with the analysis presented here, provide further support

for the use of cave morphology variables as a proxy for temperature in predicting bat abundance.

Evaluation of Predictive Model

Though many studies have used landscape topography or cave morphology metrics to predict cave temperature or bat abundance, very few studies go on to validate these predictions. Though this model generally overpredicted bat abundance, the difference between predicted and observed values was only a few individuals for most sites. The patterns shown by evaluation of the interactive morphology term and partial dependence plots (Figures 8 & 9) suggested that short caves with low ceiling height have the lowest bat abundance. This analysis provides a unique opportunity to increase monitoring program efficiency by avoiding surveys at unoccupied sites that contribute little to the population census.

Overall, moderate predictive performance requires relatively little data collection effort, as the relative influence plots (Figure 7) suggested just three predictor variables were needed to explain most of the variation in bat abundance. Identification of these variables for the remaining 322 unsurveyed caves is possible, as data was collected from aerial imagery and cave maps. Though there may be a small portion of the unsurveyed caves for which accurate maps do not yet exist, most of these unsurveyed sites could be classified according to predictor variable categories used in this analysis.

If this model is used to prioritize sites for or eliminate sites from future surveys, there will likely be some errors associated with imperfect predictions. This could be

caused by missing or erroneous data from incomplete or inaccurate cave maps. Though reliable cave maps are available for approximately 70% of the caves in the monument, we may be unable to accurately classify morphology metrics at those sites without maps which could lead to complexity in future analysis. However, the monument partners with an extensive network of cave surveyors through the Cave Research Foundation; this partnership could be used to complete prioritized survey projects.

Though data related to spatial movement, social interaction, population demographics were not included in this analysis, these factors likely contribute to habitat selection and may improve future modeling efforts. Roost selection may vary by age, and sex, and latitude (Ransome 1990). Learned response and conspecific attraction may also be important, as bats communicate using a variety of techniques, including local enhancement, social facilitation, imitative learning, and intentional signaling (Wilkinson 1995). Further, habitat selection may vary among bats that roost individually and those that roost in direct contact with other bats, where thermoregulatory function or social interaction may influence bat abundance within or among potential hibernacula. Future efforts to describe *C. townsendii* ecology should consider these hypotheses.

Management Suggestions

Use of this model to prioritize unsurveyed sites could lead to faster discovery of important hibernacula, given the large number of caves to be surveyed and that most of them are unlikely to be occupied. Discovery of new hibernacula would increase the

monitored proportion of the *C. townsendii* population that resides within Lava Beds NM, potentially providing a more accurate population monitoring program. As this *C. townsendii* population monitoring program provides the most consistent data at some of the largest known hibernacula in the western U.S., continued development and implementation of this program is critical to informing decisions related to this species of special concern.

Application of the predictive model would require additional time spent assigning and compiling the identified predictor variables for the remaining 322 unsurveyed caves of interest. The most influential predictor (a categorical term describing the number of entrances, passage slope, and passage size) would require the most time to compile (approximately 80 hours) as this requires locating and interpreting individual cave maps. Some cave maps may be underdeveloped with insufficient detail to accurately assign morphology categories. The proportion of caves for which this applies is currently unknown and could create complexity in future analysis.

Alternatively, future site selection could simply eliminate caves below a length and maximum ceiling height threshold, an expansion of methods used to eliminate surface tubes and bridges from the sample frame before this analysis. This approach still requires interpretation of cave maps but requires only a single metric to be recorded from maps. Further analysis would be required to evaluate the exact cutoff values and potential errors associated with eliminating these sites from future surveys.

Application of these models will not be an effective approach to population monitoring for other hibernating bat species present in volcanic caves (*Myotis* spp. and

Eptesicus fuscus) at Lava Beds NM. Records are sparse with no clear relation to cave morphology or temperature (NPS unpublished data). In addition, *Myotis* spp. and *E. fuscus* are often found roosting inside crevices with only part of the body visible, making species identification difficult (Szewczak et al. 1998, NPS unpublished data). These species may be roosting in talus slopes, rock crevices, basal tree hollows, or human-developed structures, making site identification difficult without intensive telemetry research (Evelyn et al. 2004). Effective monitoring for these species will require acoustic techniques. Pilot acoustic monitoring efforts during summer months of 2016-2017 shows ubiquitous occurrence of several species across the monument (NPS unpublished data). The North American Bat Monitoring program may be a suitable framework to consider in development of new population trend, activity level, or occupancy monitoring programs for species other than *C. townsendii*.

Though alternative approaches to population monitoring will be required for bat species other than *C. townsendii*, the predictive modeling methods developed and presented here could be applied to other aggregating wildlife species with identifiable habitat associations. Maximizing efficiency of surveys by selecting sites more likely to be occupied by the species of interest will reduce monitoring costs when the objective is to maximize the proportion of the population monitored. Alternatively, surveying sites that are potential habitat but are unoccupied is important when the objective is to study change over time in the area occupied. This is an important consideration for the long-term implementation of this monitoring program in relation to the potential effects of white-nose syndrome on roosting behavior and habitat selection, as bats may roost in

smaller numbers at more dispersed locations to reduce disease-related mortality. The approaches described here, combining efficient site-level habitat metrics with machine learning analyses, could be used to improve the efficiency of monitoring site selection in either of these situations. Overall, the efficient use of survey effort via targeted monitoring to inform active decision-making is critical to the effectiveness of ecological conservation (Nichols & Williams 2006).

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APPENDIX A. CLASSIFICATION OF SURFACE TUBES AND BRIDGES

For the purpose of preliminary prioritization of unsurveyed caves, experienced NPS staff identified surface tubes and bridges according to the following designations. These site types have internal microclimates very similar to the surface microclimate and are assumed to be unoccupied or have extremely low bat abundance. These assumptions are supported by data from 137 surveys at these site types showing mean bat abundance of 0.22 (SE=0.07) bats per surface tube or bridge (NPS unpublished data).

Surface Tube: Shallow cave, small overburden, often at the end of a flow with dendritic/braided channels. Downward slope of floor usually not greater than -10° . No deep zone is present. From Lava Beds NM's cave database, the following records were identified as surface tubes: 1) Any cave record with notes from previous surveyors indicating 'surface tube' or 'no dark zone'. 2) Any cave record with length less than 50 feet AND no indication of unexplored leads. 3) Any cave record with maximum ceiling height less than or equal to five feet, regardless of length.

Bridge: Usually shorter than it is wide. If not, no deep zone is present due to multiple large entrances that allow substantial airflow and light infiltration. Depth usually less than 50 feet. From Lava Beds NM's cave database, the following records were identified as bridges: 1) Any cave record with notes from previous surveyors indicating 'bridge' AND 'no dark zone'. 2) Any cave named 'Bridge' with length less than 100 feet and two entrances OR length less than 200 feet long and three or more entrances.

APPENDIX B. CAVE MORPHOLOGY CATEGORY HISTOGRAM

