Habitat modeling and movements of the Yosemite toad (*Anaxyrus* (=*Bufo*) *canorus*)
in the Sierra Nevada, California

By

CHRISTINA TEH-PING LIANG
B.A. (University of California, Berkeley) 1994
B.S. (University of California, Berkeley) 1994
M.S. (University of Michigan, Ann Arbor) 1998

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Dr. James F. Quinn, Chair

Dr. Sharon P. Lawler

Dr. Amy J. Lind

Committee in Charge

2010

ABSTRACT

The Yosemite toad (*Anaxyrus* (=*Bufo*) *canorus)* is a high-elevation species endemic to the Sierra Nevada mountain range in California and is part of the world-wide amphibian declines phenomenon. The toad is thought to have disappeared from over 50% of its historic range even in seemingly undisturbed areas, and remaining populations appear to be in decline. The causes of the disappearance and decline are unknown, and this poses a particular challenge for management and conservation since there is little understanding on how to ensure the survival of remaining populations. In order to provide information that can be used to inform management and to aid in the conservation of the species, my research on the Yosemite toad consisted of three parts: (1) constructing species distribution models to identify environmental correlates; (2) identifying environmental correlates associated with different habitat patch types; and (3) determining movement patterns and habitat use in the terrestrial environment. In the first study, I used Yosemite toad survey data from over 2,200 sites in the Sierra National Forest in the southern part of the toad's range and related them to 54 environmental variables. I found that the Yosemite toad has a complex relationship with the environment and is correlated with both biophysical and management related variables. In the second study, I looked at 49 consistently occupied sites versus 27 intermittently occupied sites throughout the range of the Yosemite toad and related the two site types separately to 26 environmental variables. I found that the different site types were correlated with different environmental variables. In the third study, I radio-tracked 42 adult Yosemite toads and collected data on their movements and habitat use. I found that toads traveled up to 1.26 kilometers away from breeding sites, and the average distance moved was 275 meters. The toads were often found in burrows and extensively used the terrestrial environment. The results from my research help elucidate the environmental requirements of the Yosemite toad both in and away from breeding sites, and can be used to inform management decisions for protection of the species and its habitat.

ACKNOWLEDGEMENTS

My time at Davis has been exciting, challenging and overall very rewarding. I am grateful to all who have helped me through these past 6 years. First of all, thanks to my advisor Dr. Jim Quinn for providing a supportive research environment and for having an open-door policy. He has always been available when needed, and has given useful advice and guidance. Thanks also to Dr. Sharon Lawler for being on my committee and for helping me in my academic development. She has provided great feedback and has been very supportive and encouraging throughout my graduate school career.

Special thanks to the third member of my committee, Dr. Amy Lind, who was also my supervisor at the U.S. Forest Service Pacific Southwest Research Station (PSW). Amy was one of the first persons to introduce me to the Yosemite toad and she provided me with my research direction. She has always been supportive, enthusiastic and encouraging about my research. I am very grateful for the opportunities and guidance she has provided me. Thanks very much!

I thank all those who helped me with my research in the field. I was fortunate to have great field assistants on my project: Matthew Thornton in 2008 and Caitlin White in 2009. Thanks to Cathy Brown, Katie Kiehl, and Lucas Wilkinson of the U.S. Forest Service Sierra Nevada Amphibian Monitoring Program for their assistance as well as camaraderie during the start of the field seasons. Dr. Carolyn Hunsaker and Jason Adair from PSW provided logistical and field support. Stephanie Barnes and Holly Eddinger from the Sierra National Forest shared their knowledge about toads and provided field support. Phil Strand from the Sierra National Forest also provided field support as well as funding support.

I also thank those who have helped me with my modeling research. Thanks again to Stephanie, Holly and Amy for providing me with data and feedback. Tom Stohlgren of the USGS is an inspiration and I am grateful for the opportunity to have worked with him. His enthusiasm--for science and for life in general--is infectious.

Funding for my research came from several sources and I am grateful for all of them. The USDA Basu Scholarship paid for my tuition and fees, and gave me the outstanding opportunity to work at PSW as a student employee. Additional research support was provided by the sensitive species fund from the U.S. Fish & Wildlife Service; USFS special projects fund; UC Davis Jastro-Shields Graduate Research Scholarship Award; and UC Davis Graduate Group in Ecology block grant award.

I feel fortunate to have been a part of the Graduate Group in Ecology at UC Davis. All the students and faculty I have interacted with have been supportive and open. They have provided a stimulating academic environment that has encouraged my scientific growth and development, and are a major factor in my positive graduate school experience. Special thanks to Silvia Hillyer for all her support and for everything that she does to keep the GGE running.

I am most thankful for the family and friends that have made the past 6 years so meaningful and enjoyable. Thanks to Becky, Clare and Sara for their support, fun times and friendship. Thanks to Debbie and Greg for always being there and for their support and love. Finally, thanks to my parents for their unceasing support, encouragement and love. I am so grateful that you all are in my life!

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Amphibians are currently experiencing rapid worldwide population declines and extinctions, with more than 43% of species in some form of population decrease (Stuart et al. 2004). Habitat destruction and over-exploitation are leading causes of decline but many species in seemingly pristine areas are also disappearing for unknown reasons. These "enigmatic-decline" species pose a particular challenge for management and conservation since little is known about how to ensure the survival of these populations (Stuart et al. 2004). Many of the species are in high-elevation habitats even within protected areas. The Yosemite toad (*Anaxyrus* (= *Bufo*) *canorus*) is one of the "enigmatic-decline" species endemic to the Sierra Nevada mountain range in California. The toad appears to have disappeared from over 50% of its historic range although the causes of the disappearances are not known (USFWS 2002). In addition, remaining populations appear to be in decline (Sherman and Morton 1993, Drost and Fellers 1996). Potential factors in the disappearance and decline include airborne contaminants, infectious disease, drought, and habitat degradation due to anthropogenic causes such as development of roads, timber harvesting, grazing, and suppression of natural wildfire.

There is great interest in protecting the Yosemite toad; it is currently a candidate for federal listing as threatened or endangered, although higher priority actions and budget constraints preclude the listing of the toad at this time (USFWS 2002). The Yosemite toad is a California species of special concern and is managed as a sensitive species by the U.S. Forest Service Pacific Southwest Region. My research on the toad was aimed at providing information that can be used to inform management and to aid in the conservation of the species. Towards that goal, my research consisted of three parts: (1) constructing species distribution models for the toad in the Sierra National Forest; (2) investigating patch types occupied by the toad throughout its range; and (3) tracking habitat use by adult toads in the Bull Creek watershed within the Sierra National Forest.

In Chapter 1, I used comprehensive survey data collected in the Sierra National Forest (SNF) to construct species distribution models for the Yosemite toad. Species distribution models are empirical models that predict distributions by relating known occurrences to environmental predictor variables (Guisan and Thuiller 2005). The models quantify the species-environment relationship and provide information on species distributions in ecological and geographical space. Over 2,200 sites in the SNF were surveyed specifically for the Yosemite toad in 2002-2004 and occupancy at each site was recorded. The occupancy data were related to 54 environmental predictor variables that were collected in the field or through available data sources. Three separate distribution models were constructed using: (1) all available predictors, (2) biophysical variables only, and (3) only variables subject to management. The purpose of the models is to better understand the relationship between the Yosemite toad and its environment, and to identify potential stressors on the populations.

Chapter 2 looks at the habitat patch types occupied by the Yosemite toad during the breeding season. Patch type can be sites that are more consistently occupied (e.g., mainland or source sites) versus sites that are more intermittently occupied (e.g., island or sink sites) (Pulliam 1988, Harrison and Taylor 1997), and is likely determined by environmental heterogeneity and local environmental factors. For species like the Yosemite toad that occur in spatially structured populations, the patch type has important implications for population processes and persistence. I identified consistently and intermittently occupied sites throughout the range of the Yosemite toad from existing survey data collected over the past 5-15 years. I then modeled the sites separately to look at the environmental factors that relate to the different patch types. This is a novel approach to studies of species distributions and can be applied to other taxa in spatially structured populations.

Chapter 3 investigates the movement patterns and habitat use of adult Yosemite toads away from breeding sites. Movement is fundamental to population processes as well as to management and conservation issues (Clobert et al 2001). Understanding spatial and temporal aspects of animal movement is critical to fundamental ecological questions such as population regulation, community structure, metapopulation dynamics, and interspecific interactions. Movement is also central to conservation and management questions such as the design of reserves, impact of land use changes, spread of disease, and response to global climate change. For amphibians with a biphasic life cycle, population persistence is dependent on the movements of individuals to and from aquatic breeding sites and terrestrial habitats. In 2007-2009, I radio-tracked 42 adult Yosemite toads as they left the breeding sites. Data were collected on the location, habitat type and environmental conditions for each individual tracked throughout the summer. In conjunction with tracking adult movements, I surveyed plant communities in toad occupied and (presumed) unoccupied areas in order to identify the terrestrial communities associated with the Yosemite toad. The results of this study have implications for identifying population processes such as metapopulation dynamics, as well as for management purposes such as establishing the size of buffer zones and identifying sensitive habitat in the terrestrial environment.

In my research, I looked at the environmental correlates, habitat patch types, movement patterns, and habitat use of the Yosemite toad. The results help elucidate the environmental requirements of the toad both in and away from breeding sites. Land managers and conservationists can use information from this research to make more informed decisions for species-specific as well as ecosystem-level management plans, in order to protect the Yosemite toad and its habitat.

LITERATURE CITED

Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols. 2001. Dispersal. Oxford University Press, Oxford, U.K.

Drost, C.A. and G.M. Fellers. 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. Conservation Biology 10:414-425.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993-1009.

Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. pp. 27–42 In: I. Hanski and M. E. Gilpin, editors. Metapopulation dynamics: ecology, genetics and evolution. Academic Press, New York, New York, USA.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652-661.

Stuart, S., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L. Rodrigues, D.L. Fishman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783-1786.

Sherman, C.K. and M.L. Morton. 1993. Population declines of yosemite toads in the eastern Sierra Nevada of California. Journal of Herpetology 27:186-198.

U.S. Fish and Wildlife Service (USFWS). 2002. 12-month finding for a petition to list the Yosemite toad. Federal Register 67(237):75834-75843.

CHAPTER 1. SPECIES DISTRIBUTION MODEL OF THE YOSEMITE TOAD (*ANAXYRUS* (=*BUFO*) *CANORUS*) IN THE SIERRA NATIONAL FOREST, CALIFORNIA

Christina T. Liang[1,2], Stephanie L. Barnes[3], Holly Eddinger[4] , and Amy J. Lind[2]

[1]Department of Environmental Science and Policy, University of California at Davis, Davis, CA 95616

[2] USDA Forest Service, Pacific Southwest Research Station, Sierra Nevada Research Center, 1731 Research Park Drive, Davis, CA 95618

[3]USDA Forest Service, High Sierra Ranger Station, Sierra National Forest, 29688 Auberry Rd (PO BOX 559), Prather, CA 93651

[4]USDA Forest Service, Ecosystem Conservation Department, Lake Tahoe Basin Management Unit, 35 College Drive, South Lake Tahoe, CA 96150

ABSTRACT

We constructed species distribution models for the Yosemite toad (*Anaxyrus* (=*Bufo*) *canorus*) from comprehensive survey data gathered in the Sierra National Forest, California in 2002-2004. Three separate species distribution models were created to identify environmental variables related to the occurrence of the Yosemite toad based on 54 environmental variables collected in the field and through existing environmental datasets. The three models were: (a) a full model containing all available environmental variables; (b) a subset model containing only biological and physical variables; and (c) a subset model containing only variables subject to land management. The full model performed the best and had the highest discrimination for the data set. It contained 16 predictor variables including both biophysical and management-related variables. The two subset models also had good discrimination but the biophysical model performed better than the management model. The biophysical model contained 11 predictor variables and the management model contained 6 predictor variables. Overall, the Yosemite toad appears to have a complex relationship with the environment and is not dependent on a single set of environmental factors. Both biophysical and management-related variables influence Yosemite toad occurrence and need to be considered in order to understand the species distribution.

Keywords: Species distribution model, habitat distribution model, biophysical variables, management variables, Yosemite toad, *Anaxyrus canorus, Bufo canorus*

INTRODUCTION

Species distribution models are commonly used to identify the environmental characteristics that allow for the occurrence of a species in the landscape. This information is particularly valuable for species at risk, such as the Yosemite toad (*Anaxyrus* (=*Bufo*) *canorus*) in California. The Yosemite toad appears to have disappeared from over 50% of its historic range even in seemingly undisturbed areas (USFWS 2002). In addition, remaining populations appear to be in decline (Sherman and Morton 1993, Drost and Fellers 1996, Davidson et al. 2002). The cause or causes of the disappearance and decline are not known, although potential factors include airborne pesticides and other toxins, infectious disease, climate change, and habitat modification due to anthropogenic changes (USFWS 2002). Habitat modification resulting from livestock grazing, roads and timber harvest, vegetation and fire management activities, recreation, and dams and water diversion are all considered threats to the species (USFWS 2002). The Yosemite toad is a Federal candidate species for listing as threatened or endangered due to declines in distribution and abundance. The U.S. Fish and Wildlife Service found that listing the Yosemite toad as threatened or endangered was warranted, but listing was precluded by higher priority actions (USFWS 2002). The toad is managed as a sensitive species by the Pacific Southwest Region of the U.S. Forest Service (1998).

To better understand the environmental requirements and some of the potential stressors of the Yosemite toad, we used species distribution models to investigate the relationship between the toad and its environment. Species distribution models are statistical models that use various modeling algorithms to relate known occurrences of a species (response variable) to environmental predictor variables. Known occurrences provide information on the environmental requirements of the species and may be presence, presence-absence, or abundance data from field observations collected either systematically or opportunistically. Environmental predictors can be limiting factors such as temperature and moisture, resources that are used by the organism such as food and water, and anthropogenic or natural disturbances that affect the environment (Guisan and Thuiller 2005). Species distribution modeling uses algorithms to select significant predictor variables and determine how well they explain the response, examine the strength of association to evaluate if there is a good statistical fit between the predictors and the response, and predict habitat suitability where the distribution is unknown (Guisan et al 2002).

For the Yosemite toad species distribution models, potential predictor variables were gathered from field data and from available environmental datasets. Predictors included biophysical variables such as elevation, amount of precipitation and vegetation type; and variables related to management such as timber harvest activity and land cover changes. Evaluation of the two sets of variables is useful for informing management decisions in the context of protecting and conserving the species. Our objective in this paper was to create and compare three separate species distribution models to identify environmental variables related to Yosemite toad occurrence using a comprehensive survey conducted in the Sierra National Forest, California. The three models were: (a) a full model containing all available environmental variables; (b) a subset model containing only biological and physical variables; and (c) a subset model containing only variables subject to management.

Natural history of the Yosemite toad

The Yosemite toad is endemic to the Sierra Nevada mountains in California, historically ranging from Alpine County in the north to Fresno County in the south at elevations above 6,400 feet (1,950 meters) (Karlstrom 1958, Jennings and Hayes 1994). The toad is a long-lived anuran species with females documented to reach 15 years and males to reach 12 years of age (Kagarise Sherman and Morton 1984). It is associated with wet mountain meadows and adjacent upland forests, and is active primarily from late spring to early fall. Individuals emerge at snowmelt in the spring and enter hibernation in late September or early October (Karlstrom 1962, Kagarise Sherman 1980).

The Yosemite toad breeds in late spring typically in wet meadows but also in other shallow water areas such as slow-moving streams and margins of ponds and lakes (Karlstrom 1962, Kagarise Sherman 1980, Martin 2008). Females first breed at 4-6 years and males at 3-5 years of age (Kagarise Sherman and Morton 1984). Males emerge from hibernation for breeding as soon as snow melts from meadows and stay at breeding pools for a week or two; females enter the pools after the males begin calling and remain for only a few days (Kagarise Sherman and Morton 1984, Martin 2008). Breeding often only lasts 1-2 weeks, with adults often then moving to upland areas. Adults have been documented to move up to 1,260 meters from breeding to upland foraging sites although not all individuals leave the breeding meadows (CT Liang *unpublished data*). Eggs and larvae develop in the shallow water areas and metamorphosis occurs by late summer of the same year (Kagarise Sherman and Morton 1984, USFWS 2002). Metamorphs appear to overwinter their first year in the meadow habitat adjacent to their rearing site and move to more distant terrestrial habitat during mid-summer of their second year (Kagarise Sherman and Morton 1993).

METHODS

Study area and Yosemite toad surveys

The Sierra National Forest in California is located on the western slope of the central Sierra Nevada and encompasses 33% of the Yosemite toad's historic range, in the southern portion of the range (Figure 1.1). The Yosemite toad is currently found on the Sierra National Forest and is the focus of several ongoing monitoring and research projects. From 2002 through 2004, visual encounter surveys were conducted by trained Forest Service staff in potential breeding sites above 6,000 feet in elevation. According to the established protocol, the surveys were timed to coincide with tadpole presence, which occurs in the late spring and summer. The surveys were focused specifically on the Yosemite toad, though any other amphibian or reptile species observed at a site was also recorded. Survey sites were visited only once during the survey period. Data on species occurrence and indices of abundance were collected along with information on environmental variables such as air and water temperatures. Over 2,200 sites were surveyed representing a range of potential breeding habitats for Yosemite toads including meadows, streams within the meadows, and lakes.

Yosemite toad occurrence at the survey sites was recorded by life stage (egg, tadpole, metamorph, juvenile, adult) and abundance. Presence of any of the life stages was evidence of Yosemite toad presence at the site, and the site was considered occupied. If tadpoles were not observed during a survey, the site was considered a non-breeding site for that season. If none of the life stages were observed, the site was considered unoccupied for that season. It is important to recognize that not observing any life stages during a survey is not necessarily indicative of true absence, due to low detectability for some life stages. Yosemite toads may not breed at sites every year and not all life-stages are equally detectable. Additional surveys may be needed to determine true occupancy if potential habitat was present at unoccupied surveyed sites. However, for use in the species distribution model, sites where the Yosemite toad was not observed during the survey period were considered absent for the modeling and statistical analysis. Yosemite toad presence or absence was the dependent variable in the species distribution models. Figure 1.2 shows the 2002-2004 Yosemite toad survey sites in the Sierra National Forest where toads were either present or not observed.

Environmental predictor variables

Fifty-four predictor variables were initially considered for the full model (Appendix 1). Variables were gathered from the field survey data and from environmental datasets available in a geographic information system (GIS). The 2002-2004 survey data included geographic coordinates, date, total survey time, air temperature, water temperature, and water type (i.e., seasonal or perennial water source). Environmental variables such as vegetation, elevation, slope, and aspect were obtained in GIS. Anthropogenic impacts such as changes in surrounding land cover and distances to roads, agriculture and timber activity were also obtained in GIS. Bioclimatic variables relating to eco-physiological tolerances of species and based on annual mean temperature and precipitation were calculated from PRISM climate data (most recent climatology normals available for year 1971-2000, 800 meter resolution; http://www.prism.oregonstate.edu) using an ARC AML script (mkBCvars.aml; http://www.worldclim.org/mkBCvars.aml). Snow covered area (SCA) variables, such as annual SCA and melt dates, were obtained for watershed basins within the Sierra Nevada from Dozier et al. 2008 (500 meter resolution; ftp://ftp.snow.ucsb.edu/pub/org/snow/users/dozier/MODIS-TimeSeries/) (Appendix 1).

To account for spatial autocorrelation, an autocovariate term representing the distance-weighted number of occupied (present) sites within 1,500 meters of each surveyed site was added to the model (Dormann et al 2007). The 1,500 meter distance represents the maximum distance a Yosemite toad might travel based on observed data (Kagarise Sherman 1980, Martin 2008, CT Liang *unpublished data*). In addition, the number of all sites (occupied or not) within 1,500 meters of a surveyed site was calculated to account for the degree of site isolation and the amount of potential suitable habitat.

Multicollinearity was tested by examining cross-correlations for all variables. Only one variable from a highly correlated set of variables (Pearson's correlation coefficient ≥ ± 0.80) was included in the analyses. For example, many of the bioclimatic variables such as mean diurnal range, isothermality, and temperature annual range were correlated; only mean diurnal range was included in the analyses and the other variables were excluded. The included variable was determined by contribution to potential distribution and ecological relevance to the Yosemite toad, based on best judgment and available knowledge on how the variable might relate to the species. After the multicollinearity analysis, the remaining more independent predictor variables were used in developing the model.

Modeling method

There are numerous species distribution modeling methods (reviewed in Elith et al 2006, Guisan et al 2007) but the purpose of this paper was not to compare them. Instead, we used one well-established and common method, the generalized linear model (GLM), to create the model. GLMs relate a linear combination of the predictor variables to the mean of the response variable via a link function (Guisan et al 2002). The link function may be non-linear which allows for non-linear relationships between the dependent and independent variables and for non-normal error structures in the data. In this analysis, Yosemite toad occurrence data was analyzed using a binomial probability distribution and a logit link with species presence or absence as the response variable.

All statistical analyses were conducted using R statistical software (version 2.10.0; http://www.r-project.org).

Model selection and validation

Three separate modeling analyses were run for: (1) all environmental variables (full model); (2) biological and physical variables only (biophysical model); and (3) only variables subject to direct human activity and management (management model). There were 31 variables in the analysis for the full model, 23 variables for the biophysical model and 9 variables for the management model (Table 1.1). Continuous variables were centered and scaled prior to analysis in the GLM in order to reduce multicollinearity. All models used the same model selection and validation methods.

The dataset was cleaned up to remove records with errors or missing values. The resulting dataset contained 1,978 sites which were used in all the regression analyses (298 presence and 1680 absence records). The best GLM models were selected with step-wise selection (using both forward and backward selection) based on the lowest Akaike's Information Criterion (AIC) values. This criterion provides a balance between model fit and precision with the best models having the lowest AIC value (Burnham and Anderson 2002).

After model selection, a ten-fold cross-validation was performed on the models. Validation allows for an evaluation of how well the model fits data not used in model selection and development. The dataset was partitioned into ten subsamples, reserving one subsample for validation and using the remaining nine subsamples to estimate the model parameters. The model developed with the nine subsamples was used to estimate the probability of occurrence in the validation subsample. This process was repeated ten times with each subsample used once as the validation data. Results from this resampling analysis were averaged for a single estimation. The Somers' Dxy rank correlation statistic was used to compare the initial model to the resampled models. For the binary variable Y, Somers' Dxy looks at the predicted probability that Y=1 compared to Y=0 and is equal to 2(*c*-0.5) where *c* is the 'Area Under the Receiver Operating Characteristic Curve' or concordance probability (Newson 2006).

Models were evaluated using the threshold-independent measure, 'Area Under the Receiver Operating Characteristic Curve' (AUC), which quantifies model performance at all possible thresholds. AUC is obtained by plotting sensitivity (true positive rate) against 1-specificity (false positive rate) and calculating the area under the curve. It is a measure of the model's discrimination, which is the ability of the model to distinguish Yosemite toad presence from toad absence. AUC values vary from 0.5 for models performing no better than random to 1 for models with perfect discrimination (Fielding and Bell 1997). An AUC value above 0.90 can be considered 'very good' (Swets 1988).

Effect size was measured by the odds ratio, which can be used to determine the relative importance of the independent variables relative to the effect on the dependent variable's odds. In this study, the odds were the odds of Yosemite toad presence. When looking at the results, the odds increase if the odds ratio is greater than 1, decrease if the odds ratio is less than 1 and have no effect if the odds ratio is equal to 1. For continuous variables, the odds ratio represents the percent increase by which the odds change for a one-unit change in the variable. For categorical variables, the odds ratio represents the factor by which the odds change when comparing a categorical level to the reference category of the variable. Categorical variables in the dataset were land cover changes, fire condition class, vegetation type, and water type at survey site. Land cover changes are increases or decreases in vegetative cover over the five year period and can be caused by fire, timber harvest, or development along with mortality and regrowth. Fire condition class represents the degree of departure of the current vegetation and fuel conditions from the historic (pre-settlement) natural fire regime. Vegetation type used the California Wildlife Habitat Relationships classification system. Water type is either seasonal or perennial water source.

RESULTS

Full model

The best full GLM model contained 16 environmental predictor variables (Table 1.2) and performed well for the data set with very good discrimination (AUC=0.90). Cross-validation showed that the model has strong predictive ability (Somers' Dxy_{model}=0.80, Somers' $Dxy_{cross\text{-}validation}$=0.77). Predictor variables in the model were the biophysical variables: acreage of survey site, elevation, aspect, slope, air temperature, water temperature, temperature seasonality (seasonal variation calculated as the standard deviation of monthly mean temperatures), precipitation of driest quarter, precipitation of warmest quarter, annual SCA that is 75-100% covered in snow, and water type. Predictors also included variables subject to management: land cover classification changes from 1990-1995 and from 1985-1991. The y-coordinate of the site, total survey time and distance-weighted autocovariate were also included in the model. Most predictor variables in the model were significant ($p<0.05$) with the exceptions of slope and the land cover change categories (Table 1.2).

The odds of Yosemite toad presence increased with higher values of the following variables, listed in order of greatest to least effect size: annual SCA, land cover changes from 1985-1991 (increase with vegetation increase compared to areas of no change), elevation, land cover changes from 1990-1995 (increase with small increase in vegetation compared to areas of little of no change), water temperature, autocovariate, survey time, precipitation of warmest quarter, water type (increase with seasonal type compared to perennial type), and aspect (Table 1.2). The odds of Yosemite toad presence decreased with higher values of the following variables, listed in order of greatest to least effect size: temperature seasonality, y-coordinate (i.e., the more northerly sites had a lower likelihood of Yosemite toad occupancy), precipitation of driest quarter, air temperature, slope, and acreage of survey site (Table 1.2).

Biophysical model

The best biophysical GLM model contained 11 predictor variables (Table 1.3) and performed well for the data set with good discrimination (AUC=0.86). Cross-validation showed that the model has predictive ability (Somers' $Dxy_{model}=0.71$, Somers' $Dxy_{cross\text{-}validation}=0.70$). Predictor variables in the model were acreage, elevation, aspect, slope, air temperature, water temperature, temperature seasonality, precipitation of driest quarter, and precipitation of warmest quarter. The y-coordinate of survey site and distance-weighted autocovariate were also included in the model. Most individual predictor variables in the model were significant ($p<0.05$) with the exception of the y-coordinate (Table 1.3).

The odds of Yosemite toad presence increased with higher values of the following variables, listed in order of greatest to least effect size: water temperature, autocovariate, precipitation of warmest quarter, elevation, aspect, and acreage of the survey site (Table 1.3). The odds of Yosemite toad presence decreased with higher values of the following variables, listed in order of greatest to least effect size: air temperature, precipitation of driest quarter, slope, y-coordinate of survey site, and temperature seasonality (Table 1.3).

Management model

The best management-related GLM model contained 6 predictor variables (Table 1.4) and performed well for the data set with good discrimination (AUC=0.83). Cross-validation showed that the model has predictive ability (Somers' Dxy_{model}=0.65, Somers' $Dxy_{cross\text{-}validation}$=0.62). Predictor variables in the model were land cover classification changes from 1990-1995 and from 1985-1991, distance to timber harvest activity, fire condition class, and x-coordinate of the site. The distance-weighted autocovariate was also included in the model (Table 1.4).

The odds of Yosemite toad presence increased with higher values of the following variables, listed in order of greatest to least effect size: land cover changes from 1985-1991 (increase with small increase in vegetation compared to areas of little of no change), x-coordinate, land cover changes from 1990-1995 1995 (increase with small increase in vegetation compared to areas of little of no change), and the autocovariate (Table 1.4). The odds of Yosemite toad presence decreased in areas where the fire regime was significantly altered from the historical range compared to areas where the fire regime was within or near historical range. The odds also decreased to a lesser effect with greater distance to timber activity (Table 1.4).

Predictor variables

Statistics (mean, standard deviation, 95% confidence interval) for predictor variables in any of the three models are shown in Table 1.5 along with their univariate relationship to Yosemite toad presence. A positive relationship indicates that the Yosemite toad is more likely to occur at sites with higher values of the variable unit while a negative relationship indicates that the toad is more likely to occur at sites with lower values. The direction of the relationship is reversed in the models for four variables: acreage of survey site (ACRES; reversal in full model only), annual SCA that is 75-100% covered in snow (Bbin5), precipitation of the driest quarter (BIO17), and distance to timber activity (TIMB_DIST). The reversal is due to partial correlation, which is the contribution of a predictor in the regression model after the contributions of all other predictors have been removed from both that predictor and the dependent variable. The relationship between individual variables and the dependent variable in a multivariate analysis can differ from the relationship in a univariate analysis since the effects of other variables are taken into account.

DISCUSSION

All models showed that the distribution of the Yosemite toad on the Sierra National Forest is related to a number of factors and no one variable or small set of variables is the main predictor of Yosemite toad presence-absence. Although the biophysical or management-related subset models alone can predict Yosemite toad occurrences, the full model had the best discrimination for our data set. The two subset models both performed well, with the biophysical model having better discrimination than the management model based on AUC (0.86 vs 0.83).

Looking at all models, it appears that both biophysical and management-related variables influence Yosemite toad occurrence and both are needed to adequately describe the distribution of the species. The Yosemite toad appears to have a complex relationship with the environment and occurs across a range of conditions. The complexity of the species-environment relationship makes it difficult to evaluate the relationship as a whole but individual variables within the models can be assessed as to how they might influence Yosemite toad occurrence.

Biophysical variables

All variables in the biophysical model were in the full model and included geographic location and acreage of the breeding site; topographic variables such as elevation, aspect, slope; air and water temperature; and climatic variables such as temperature seasonality and precipitation. Although acreage of the survey site was statistically significant, the effect on Yosemite toad occurrence was small and the direction of its influence was switched in the two models. Thus it appears that Yosemite toads are just as likely to be found in small as in large sites and the size of the survey area is not biologically significant.

Topography had a large effect on Yosemite toad occurrence in the models. The Yosemite toad is considered a high-elevation endemic species (Stebbins 2003) and the models confirmed that it is more likely to occur at higher elevations. The models also indicated that the Yosemite toad was observed in relatively flat sites that are facing more southwesterly directions. (Note: since aspect is measured on a 1-360 degree scale, the univariate statistics along with plots of the data were used to interpret this variable.) These slope and aspect occurrences may be related to the drainage patterns in breeding sites and the amount of solar radiation that the sites receive. These factors can affect the timing of breeding by influencing when the breeding pools are free from snow and available for use. South facing sites receive more solar radiation and have faster snow melt. Drainage patterns and solar radiation can also affect the development of tadpoles by influencing how quickly the pools shrink after breeding has occurred. An association between breeding pool duration, breeding synchrony, development rate, and larval development has been shown for other amphibian species such as spadefoot toads (Morey and Reznick. 2004)

Air and water temperatures were taken during the surveys and were significant variables in the models. Yosemite toad presence was related to cooler air temperatures. Air temperature is affected by elevation, and higher elevations where Yosemite toads are more likely to be found have cooler temperatures. Water temperature within a site is not uniform and varies due to water source, depth and flow at the measurement location. During the surveys, water temperature was taken at a random point within the survey site and not necessarily at actual or potential breeding pools or where individuals were observed. The water temperature readings then were not directly connected to Yosemite toad occurrence, and more sampling in the breeding pools and other habitats within the surveys sites are needed to determine the exact relationship between water temperature and occupancy. Laboratory studies show that tadpoles of other species prefer warmer temperatures (Bancroft 2008) and it is appears that Yosemite toad tadpoles also prefer warmer temperatures in the field (Mullally 1953). While the water temperature reading is not directly related to occupied pools, it does represent generalized information about the conditions of the survey site. The model showed that Yosemite toads were more likely to be found at survey sites where warmer water temperature readings are documented, and the variable had a large positive effect on toad presence. The water temperature reading is likely related to unmeasured site characteristics such as water flow or other hydrologic variables that have an effect on the breeding pools within the site.

Climatic variables influenced Yosemite toad occurrence and the models showed that the Yosemite toad is more likely to be found in areas with less variation in mean annual air temperature. Air temperature has been identified as an important habitat component for the closely related boreal toad *Anaxyrus* (=*Bufo*) *boreas*, although it is minimum daily winter air temperature that is positively correlated with survival (Scherer et al 2008). Precipitation was also related to toad occurrence though the timing of the precipitation affected the direction of the effect. Yosemite toads were more likely to be found in areas with more precipitation in the warmest quarter but less precipitation in the driest quarter. Although the warmest and driest quarters might potentially cover some of the same time period, precipitation in the two quarters was not highly correlated and so the time periods appear to be distinguishably different. Overall, it appears that the

Yosemite toad are more likely to occur at more temperate sites that have relatively less climatic variation.

Annual snow covered area and water type were significant variables in the full model but not in the environmental model. SCA had a very large effect on Yosemite toad occurrence, and sites that are 75-100% covered in snow for longer periods during the water year were more likely to have Yosemite toads. SCA is affected by topography and other climatic variables, and the effect that it had on Yosemite toad occurrence likely may have been related to these factors as well. With regard to water type, Yosemite toad presence was more likely in surveyed areas with seasonal water bodies relative to surveyed areas with perennial water bodies. Seasonal water bodies include ephemeral or intermittent streams and pools which may be the preferred breeding habitat for the Yosemite toad because they are likely to be shallower and warmer, resulting in shorter time to metamorphosis (CT Liang, AJ Lind *personal observations*).

Management related variables

Management variables related to Yosemite toad presence included land cover changes and fire condition class. Land cover changes are changes to vegetation amount and type that may be caused by fire, timber harvest or development as well as mortality and regrowth. The likelihood of Yosemite toad presence increased in areas with small to moderate increases in vegetation relative to areas with no change. It is notable that land cover changes from 1990-1995 and 1985-1991 but not land cover changes from 1997-2001 were retained in the models. This indicates that there may be a delay in the Yosemite toad's response to changes in the environment, possibly due to the long-lived nature of this species. Changes that affect early life-stages and prevent recruitment into the adult stage may not affect the adult population for one or more generations (5 to 10 years or more).

The management model contained two environmental factors not contained in the full model: distance to timber activity and fire condition class. Distance to timber activity was not included in the full model analysis due to its high correlation with elevation. In the management model, Yosemite toads were more likely to occur in areas closer to timber activity. Due to the correlation, it could also be a proxy for elevation which was a strong predictor in the full model. Timber harvest activities also involve removal of canopy trees and may maintain the open breeding sites by clearing the canopy and perhaps by preventing tree encroachment into the sites. Semlitsch et al (2009) found that two frog species benefitted from clearcut tree removal though only in the reproduction and larval development stages. They predict that species requiring early successional or open habitat for breeding would benefit from timber activity.

Fire condition class represents comparisons between current expected fires and historic (pre-settlement) fire regimes with regard to fire frequency, size and patchiness, and effects on key ecosystem elements and processes. The historic fire regime throughout most of the Sierra Nevada had fire return intervals that were generally less than 20 years (McKelvey et al. 1996). This regime was disrupted when a policy of fire suppression was enacted in the early 20th century leading to changes in forest structure and composition. In the management model, Yosemite toads were less likely to occur in areas where the fire regime was significantly altered from the historical range compared to areas where the fire regime was within or near the historic regime. The classification of significantly altered is defined by the data source originators as “where fire frequencies have changed from natural frequencies by multiple return intervals.” This suggests that the Yosemite toad is affected by some unknown and unmeasured ecosystem factors that are represented by this fire condition variable. Takaoka and Swanson (2008) suggest that changes from the historic fire regime in the central Cascades in Oregon may limit both expansion of meadows and maintenance of recent meadows, as well as support encroachment of trees into meadows.

Survey variables

There were two variables related to field surveys themelves that were included in the set of potential variables for the full model but not in potential variable sets for either the biophysical or management models: date of survey and total time of survey. Although date of survey was included in the analysis it was not selected in the model. In contrast, total time of survey was a highly significant predictor in the full model and had a large positive effect on Yosemite toad presence. Survey time was influenced by habitat complexity as well as number of individuals observed during the survey since the presence of more potentially suitable habitat and more species would require more time to survey. Drier areas without any potential breeding pools did not take as long to assess although each survey site was given an equal effort. Also, since most life stages of Yosemite toads can be very cryptic in their environment, longer surveys could potentially decrease the detection error. This would be true regardless of the size of the survey area; survey time was not correlated with survey site acreage.

Spatial autocorrelation

The distance-weighted autocovariate was highly significant with large effects in all models, indicating that Yosemite toad occupancy exhibits strong spatial autocorrelation. This spatial autocorrelation may be due to several factors including adult movement and synchronous population dynamics (Knapp et al 2003). Adults have been observed to move between breeding sites in search of mates (CT Liang *personal observation*) and perhaps better quality sites. It is also possible that adults in crowded sites may move to less crowded lower-quality sites for breeding, as in a source-sink population dynamic (Pulliam 1988) such has been suggested for the common toad *Bufo bufo* (Martinez-Solano and Gonzalez 2008). Adult movement would thus cause spatial autocorrelation in the distribution of larvae.

Synchronous population dynamics may also lead to spatial autocorrelation of Yosemite toad occupancy. Sites that are closer together may experience similar climatic or other environmental conditions compared to sites that are further apart, resulting in similar population dynamics and cycles of low and high abundance (Moran effect; Ranta et al. 1997, Koenig 2002). Sites that are closer together may also experience the same diseases or disturbances that can concurrently affect species populations, as has been reported for the mountain yellow legged frog *Rana muscosa* (Knapp et al 2003).

Caveats and conclusions

While species distribution models can identify variables that are predictors of Yosemite toad occurrence, there are some caveats that come with the analysis. The survey data are based on a single visit to each site and Yosemite toad presence may not have been observed during the visit due to year-to-year variation in toad breeding. Since breeding sites may not be utilized every year and post-metamorphic life stages can be difficult to detect, the recorded non-detections may not be true absences.

Variables in the model may be statistically significant predictors but not biologically significant for the Yosemite toad. Thus, variables in the model may be statistical artifacts that do not actually relate to Yosemite toad occurrence. Also, the true predictors of toad occurrence may be difficult to identify when variables are correlated or interact with one another. Highly cross-correlated variables were excluded from the analysis based on probable relevance to Yosemite toads, but they may in fact be better predictors than the variables that were included. Finally, the model may be missing unknown or unmeasured variables that influence Yosemite toad occurrence.

However, given these caveats, the species distribution models developed in this analysis all performed well and had good discrimination of the data based on the AUC values. The models are a means of investigating the species-environment relationship and add to the overall understanding of the distribution of the Yosemite toad. The results can be used to inform management decisions with regard to protecting, conserving or restoring habitat for the Yosemite toad in both current and future conditions. Modeling efforts can also complement other studies such as field experiments or data collection, and as data from other studies become available they can be used to further refine the model.

In this analysis, we identified several predictors of Yosemite toad occurrence in the Sierra National Forest. The Yosemite toad has a complex species-environment relationship and is affected by both biophysical variables such as water temperature and topography as well as management related variables such as land cover changes. Future steps would be to test this model by predicting the distribution of the Yosemite toad in other parts of its range.

ACKNOWLEDGEMENTS

We thank the field crews from the Sierra National Forest for conducting the surveys. R. Grasso, S. Lawler, and J. Quinn provided helpful reviews on earlier versions of the manuscript. J. Baldwin and N. Willits provided statistical assistance. Funding was provided by the Sacramento USDI Fish and Wildlife Service office and the USDA Forest Service.

Literature Cited

Bancroft, B. A., N. J. Baker, C. L. Searle, T. S. Garcia, and A. R. Blaustein. 2008. Larval amphibians seek warm temperatures and do not avoid harmful UVB radiation. Behavioral Ecology 19:879-886.

Burnham, K.P. and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York.

Dormann, F.C., J.M. McPherson, M.B. Araújo, R. Bivand, J. Bolliger, G. Carl, R.G. Davies, A. Hirzel, W. Jetz, W.D. Kissling, I. Kühn, R. Ohlemüller, P.R. Peres-Neto, B. Reineking, B. Schröder, F.M. Schurr, and R.Wilson. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609–628

Dozier, J., T.H. Painter, K. Rittger, and J.E. Frew. 2008. Time-space continuity of daily maps of fractional snow cover and albedo from MODIS. Advances in Water Resources 31:1515-1526.

Drost, C.A. and G.M. Fellers. 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. Conservation Biology 10:414-425.

Evangelista, P. H., S. Kumar, T. J. Stohlgren, C. S. Jarnevich, A. W. Crall, J. B. Norman III, and D. T. Barnett. 2008. Modelling invasion for a habitat generalist and a specialist plant species. Diversity and Distributions 14:808-817.

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.

Guisan, A., T.C. Edwards, Jr., and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157:89-100.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993-1009.

Guisan, A., N.E. Zimmermann, J. Elith, C.H. Graham, S. Phillips, and A.T. Peterson. 2007. What matters for predicting the occurrences of trees: techniques, data or species' characteristics? Ecological Monographs 77:615-630.

Jennings, M. R. and M. P. Hayes. 1994. Amphibian and reptile species of special concern in California. California Department of Fish and Game, Rancho Cordova.

Kagarise Sherman, C. 1980. A comparison of the natural history and mating system of two Anurans: Yosemite Toads (*Bufo canorus*) and Black Toads (*Bufo exsul*). PhD dissertation. University of Michigan, Ann Arbor.

Kagarise Sherman, C. and M.L. Morton. 1984. The toad that stays on its toes. Natural History 93:72–78.

Karlstrom, E. L. 1958. Sympatry of the Yosemite and western toads in California. Copeia 1958:152-153.

Karlstrom, E. L. 1962. The toad genus *Bufo* in the Sierra Nevada of California. University of California Publications in Zoology 62:1-104.

Knapp, R. A., K. R. Matthews, H. K. Preisler, and R. Jellison. 2003. Developing probabilistic models to predict amphibian site occupancy in a patchy landscape. Ecological Applications 13:1069-1082.

Koenig, W. D. 2002. Global patterns of environmental synchrony and the Moran effect. Ecography 25:283–288.

Martin, D. 2008. Decline, movement and habitat utilization of the Yosemite toad (*Bufo canorus*): an endangered anuran endemic to the Sierra Nevada of California. PhD dissertation. University of California, Santa Barbara.

Martinez-Solano, I., and E. G. Gonzalez. 2008. Patterns of gene flow and source-sink dynamics in high altitude populations of the common toad Bufo bufo (Anura: Bufonidae). Biological Journal Of The Linnean Society 95:824-839.

McKelvey, K. S., C. N. Skinner, C. Chang, D. C. Erman, S. J. Husari, D. J. Parsons, J. W. van Wagtendonk, and C. P. Weatherspoon. 1996. An overview of fire in the Sierra Nevada. In: Sierra Nevada Ecosystem Project: Final report to Congress, vol. II: Assessments and scientific basis for management options. Water Resources Center Report No. 37. Centers for Water and Wildland Resources, University of California, Davis.

Morey, S. R., and D. N. Reznick. 2004. The relationship between habitat permanence and larval development in California spadefoot toads: field and laboratory comparisons of developmental plasticity. Oikos 104:172-190.

Mullally, D. P. 1953. Observations on the ecology of the toad *Bufo canorus*. Copeia 1953:182-183.

Newson, R. 2006. Confidence intervals for rank statistics: Somers' D and extensions. Stata Journal 6:309-334.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Ranta, E., V. Kaitala, J. Lindstrom, and E. Helle. 1997. The Moran effect and synchrony in population dynamics. Oikos 78:136–142.

Scherer, R. D., E. Muths, and B. A. Lambert. 2008. Effects of weather on survival in populations of boreal toads in Colorado. Journal of Herpetology 42:508-517.

Semlitsch, R. D., B. D. Todd, S. M. Blomquist, A. J. K. Calhoun, J. W. Gibbons, J. P. Gibbs, G. J. Graeter, E. B. Harper, D. J. Hocking, M. L. Hunter Jr., D. A. Patrick, T. A. G. Rittenhouse, and B. B. Rothermel. 2009. Effects of timber harvest on amphibian population: understanding mechanisms from forest experiments. BioScience 59:853-862.

Sherman, C.K. and M.L. Morton. 1993. Population declines of yosemite toads in the eastern Sierra Nevada of California. Journal of Herpetology 27:186-198.

Stebbins, R.C. 2003. A field guide to western reptiles and amphibians, third edition. Houghton Mifflin Company, New York.

Swets, J.A. 1988. Measuring the accuracy of diagnostic systems. Science 240:1285-1293.

Takaoka, S. and F. J. Swanson. 2008. Change in extent of meadows and shrub fields in thecentral western Cascade Range, Oregon. The Professional Geographer 60:527-540.

U.S. Fish and Wildlife Service (USFWS). 2002. 12-month finding for a petition to list the Yosemite toad. Federal Register 67(237):75834-75843.

U.S. Forest Service. 1998. Sensitive species list for the Pacific Southwest Region of the U.S. Forest Service.

Table 1.1. Environmental variables analyzed in the full (F), biophysical (B), and management (M) models.

Variable Code	Description	Models
AC	distance-weighted autocovariate	F, B, M
ACRES	acreage of survey site	F, B
ASPECT	aspect	F, B
BBIN2	annual snow covered area; percentage of water year that the basin is 10-25% covered in snow	F, B
BBIN3	annual snow covered area; percentage of water year that the basin is 25-50% covered in snow	F, B
BBIN5	annual snow covered area; percentage of water year that the basin is 75-100% covered in snow	F, B
BIO2	mean diurnal range	F, B
BIO4	temperature seasonality (standard deviation of monthly mean temperatures)	F, B
BIO14	precipitation of driest month	F, B
BIO15	precipitation seasonality (coefficient of variation for monthly precipitation estimates)	F, B
BIO17	precipitation of driest quarter (note: quarter is a period of three months)	F, B
BIO18	precipitation of warmest quarter (note: quarter is a period of three months)	F, B
BPLUS75	last date in 2004 water year that the basin was >75% snow covered	F, B
CHG8591	classification of land cover change between 1985 and 1991 based on satellite imager	F, M
CHG9095	classification of land cover change between 1990 and 1995 based on satellite imagery	F, M
CHG9701	classification of land cover change between 1997 and 2001 based on satellite imagery	F, M
DATE	date of survey	F
DEM	elevation	F, B
FIRECOND	fire condition class (general deviation of ecosystems from their presettlement natural fire regime)	F, M
FIREP_DIST	straight-line distance to nearest fire perimeter	F, M
GPS_E	x-coordinate of the survey site	F, B, M
GPS_N	y-coordinate of the survey site	F, B, M
MDW_COUNT	number of meadows within 1,500 meters of survey site	F, B
PPTANN	annual precipitation, 1971-2000	F, B
ROAD_DIST	straight-line distance to nearest road	F, M
SLOPE	slope	F, B
SURVEY_TOT	total survey time	F
TEMPAIR_ST	air temperature at start of survey	F, B

Table 1.1, continued

Variable Code	Description	Models
TEMPW	water temperature at survey site	F, B
TIMB_DIST*	straight-line distance to nearest harvest activity area	M
WHR	vegetation type (California Wildlife-Habitat Relationships classification)	F, B
WTYPE	water type at survey site (seasonal/perennial)	F, B

*Variable not included in analysis of full model due to cross-correlation.

Table 1.2. Full model. Results of the best GLM model using all predictor variables to describe the occurrence of Yosemite toad.

					Effects on Toad Presence		
Predictor Variable	**Logistic Coefficient**	**Standard Error**	**Wald Z**	**P-value**	**Odds Ratio**	**95% CI**	**Effect**
Intercept	-7.86	21.55	-0.36	0.72			
AC	0.69	0.07	10.34	0.00	1.85	1.65 – 2.08	+
ACRES	-0.26	0.09	-2.99	0.00	0.91	0.86 – 0.97	–
ASPECT	0.17	0.08	2.16	0.03	1.30	1.03 – 1.66	+
BBIN5	0.34	0.12	2.87	0.00	11.14	2.15 – 57.80	+
BIO4	-0.39	0.12	-3.19	0.00	0.63	0.47 – 0.84	–
BIO17	-0.37	0.15	-2.47	0.01	0.67	0.49 – 0.92	–
BIO18	0.37	0.12	3.05	0.00	1.72	1.21 – 2.44	+
CHG8591 (factor=2)*	-0.13	0.86	-0.15	0.88	1.13	0.21 – 6.16	0
CHG8591 (factor=3)	1.93	1.26	1.53	0.13	7.80	1.23 – 49.40	+
CHG9095 (factor=4)^	5.38	21.53	0.25	0.80	0.00	0.00 – 9.84×10^{15}	0
CHG9095 (factor=5)	6.49	21.54	0.30	0.76	3.03	1.87 – 4.91	+
CHG9095 (factor=6)	5.70	21.54	0.26	0.79	1.37	0.73 – 2.57	0

Table 1.2, continued

					Effects on Toad Presence		
Predictor Variable	**Logistic Coefficient**	**Standard Error**	**Wald Z**	**P-value**	**Odds Ratio**	**95% CI**	**Effect**
CHG9095 (factor=7)	6.43	21.57	0.30	0.77	2.84	0.26 – 30.87	0
CHG9095 (factor=8)	3.78	21.55	0.18	0.86	0.20	0.05 – 0.83	–
CHG9095 (factor=9)	6.06	21.54	0.28	0.78	1.96	0.99 – 3.90	+
DEM	0.98	0.13	7.37	0.00	5.09	3.30 – 7.84	+
GPS_N	-0.27	0.11	-2.36	0.02	0.64	0.44 – 0.93	–
SLOPE	-0.17	0.10	-1.80	0.07	0.81	0.65 – 1.02	–
SURVEY_TOT	0.93	0.10	8.93	0.00	1.76	1.55 – 1.99	+
TEMPAIR_ST	-0.24	0.10	-2.45	0.01	0.71	0.54 – 0.93	–
TEMPW	0.71	0.09	7.73	0.00	2.75	2.13 – 3.55	+
WTYPE+	-0.44	0.18	-2.52	0.01	1.56	1.10 – 2.20	+

AC=distance-weighted auto-covariate; ACRES=acreage of meadow survey site; ASPECT=aspect; BBIN5=annual snow covered area, percentage of water year that the basin is 75-100% covered in snow; BIO4=temperature seasonality; BIO17=precipitation of driest quarter (note: quarter is a period of three months); BIO18=precipitation of warmest quarter; *CHG8591(categorical variable)=classification of land cover change between 1985 and 1991 based on satellite imagery; ^CHG9095(categorical variable)=classification of land cover change between 1990 and 1995 based on satellite imagery; DEM=elevation; GPS_N=y-coordinate of the survey site; SLOPE=slope; SURVEY_TOT=total survey time; TEMPAIR_ST=air temperature; TEMPW=water temperature; +WTYPE(categorical variable)=water type at survey site (seasonal/perennial)

Table 1.2, continued

* = for CHG8591, reference category for odds ratio is factor 2
^ = for CHG0905, reference category for odds ratio is factor 4
+ = for WTYPE, reference category for odds ratio is factor 1

Factors in categorical variables:
CHG8591 (factor=1) vegetation decrease
CHG8591 (factor=2) no change
CHG8591 (factor=3) vegetation increase
CHG9095 (factor=3) small decrease in vegetation
CHG9095 (factor=4) little or no change
CHG9095 (factor=5) small increase in vegetation
CHG9095 (factor=6) mod increase in vegetation
CHG9095 (factor=7) large increase in vegetation
CHG9095 (factor=8) non-vegetation change
CHG9095 (factor=9) terrain shadow or wet
WTYPE (factor=0) seasonal
WTYPE (factor=1) perennial

Table 1.3. Biophysical model. Results of the best GLM model using biological and physical predictor variables to describe the occurrence of Yosemite toad.

					Effects on Toad Presence		
Predictor Variable	**Logistic Coefficient**	**Standard Error**	**Wald Z**	**P-value**	**Odds Ratio**	**95% CI**	**Effect**
Intercept	-2.38	0.10	-23.77	0.00			
AC	0.75	0.06	12.03	0.00	1.95	1.75 – 2.18	+
ACRES	0.23	0.07	3.33	0.00	1.08	1.03 – 1.14	+
ASPECT	0.17	0.07	2.24	0.03	1.29	1.03 – 1.61	+
BIO4	-0.26	0.11	-2.50	0.01	0.73	0.57 – 0.93	–
BIO17	-0.33	0.13	-2.43	0.01	0.70	0.53 – 0.93	–
BIO18	0.37	0.11	3.33	0.00	1.72	1.25 – 2.36	+
DEM	0.30	0.10	3.07	0.00	1.64	1.20 – 2.25	+
GPS_N	-0.20	0.10	-1.91	0.06	0.72	0.52 – 1.01	–
SLOPE	-0.28	0.09	-3.00	0.00	0.72	0.58 – 0.89	–
TEMPAIR_ST	-0.32	0.09	-3.55	0.00	0.63	0.49 – 0.81	–
TEMPW	0.74	0.09	8.69	0.00	2.88	2.27 – 3.65	+

AC=distance-weighted auto-covariate; ACRES=acreage of meadow survey site; ASPECT=aspect; BIO4=temperature seasonality; BIO17=precipitation of driest quarter (note: quarter is a period of three months); BIO18=precipitation of warmest quarter; DEM=elevation; GPS_N=y-coordinate of the survey site; SLOPE=slope; TEMPAIR_ST=air temperature; TEMPW=water temperature

Table 1.4. Management model. Results of the best GLM model using predictor variables subject to management to describe the occurrence of Yosemite toad.

					Effects on Toad Presence		
Predictor Variable	**Logistic Coefficient**	**Standard Error**	**Wald Z**	**P-value**	**Odds Ratio**	**95% CI**	**Effect**
Intercept	-7.35	24.54	-0.30	0.76			
AC	0.79	0.06	12.67	0.00	2.02	1.82 – 2.26	+
CHG8591 (factor=2)*	-0.13	0.73	-0.18	0.86	1.14	0.27 – 4.71	0
CHG8591 (factor=3)	1.79	1.02	1.76	0.08	6.83	1.61 – 28.96	+
CHG9095 (factor=4)^	5.26	24.53	0.21	0.83	0.01	0.00 – 3.91 x 10^{18}	0
CHG9095 (factor=5)	6.34	24.53	0.26	0.80	2.93	1.95 – 4.41	+
CHG9095 (factor=6)	5.83	24.53	0.24	0.81	1.76	1.05 – 2.96	+
CHG9095 (factor=7)	5.78	24.55	0.24	0.81	1.67	0.18 – 15.41	0
CHG9095 (factor=8)	4.30	24.54	0.18	0.86	0.38	0.11 – 1.35	0
CHG9095 (factor=9)	6.18	24.53	0.25	0.80	2.50	1.36 – 4.58	+

Table 1.4, continued

					Effects on Toad Presence		
Predictor Variable	**Logistic Coefficient**	**Standard Error**	**Wald Z**	**P-value**	**Odds Ratio**	**95% CI**	**Effect**
FireCond (factor=2)	0.01	0.18	0.07	0.94	1.01	0.71 – 1.44	0
FireCond (factor=3)	-0.94	0.34	-2.74	0.01	0.39	0.20 – 0.77	–
FireCond (factor=9)	-0.15	0.24	-0.63	0.53	0.86	0.54 – 1.38	0
GPS_E	0.70	0.15	4.74	0.00	2.99	1.90 – 4.71	+
TIMB_DIST	-0.26	0.13	-1.92	0.05	0.69	0.48 – 1.01	–

AC=distance-weighted auto-covariate; *CHG8591(categorical variable)=classification of land cover change between 1985 and 1991 based on satellite imagery; ^CHG9095(categorical variable)=classification of land cover change between 1990 and 1995 based on satellite imagery; [+]FireCond(categorical variable)=fire condition class; GPS_E=x-coordinate of the survey site; TIMB_DIST=distance to timber harvest area

* = for CHG8591, reference category for odds ratio is factor 2
^ = for CHG9095, reference category for odds ratio is factor 4
[+] = for FireCond, reference category for odds ratio is factor 1

Factors in categorical variables:
CHG8591 (factor=1) vegetation decrease
CHG8591 (factor=2) no change
CHG8591 (factor=3) vegetation increase
FireCond (factor=1) fire regime w/in or near historical range
FireCond (factor=2) fire regime moderately altered from historical range
FireCond (factor=3) fire regime significantly altered from historical range
FireCond (factor=9) none assigned
CHG9095 (factor=3) small decrease in vegetation
CHG9095 (factor=4) little or no change
CHG9095 (factor=5) small increase in vegetation
CHG9095 (factor=6) mod increase in vegetation
CHG9095 (factor=7) large increase in vegetation
CHG9095 (factor=8) non-vegetation change
CHG9095 (factor=9) terrain shadow or wet

Table 1.5. Means, standard deviations and 95% confidence intervals for predictor variables in all models (full, biophysical, management). Positive relationship indicates that toad presence is more likely at sites with higher values of the variable. Relationships with an asterisk (*) are reversed in the models due to partial correlations.

	Mean ± SD (95% CI)		
Predictor variable (Units)	**Presence Sites**	**Absence Sites**	**Relationship to toad presence**
AC	0.37 ± 0.30 (0.34 – 0.41)	0.10 ± 0.19 (0.10 – 0.11)	positive
ACRES	12.73 ± 24.21 (9.98 - 15.48)	6.02 ± 13.16 (5.39 – 6.65)	positive
ASPECT (degrees)	200.67 ± 94.67 (189.92 - 211.42)	190.21 ± 97.80 (185.53 – 194.88)	positive
BBIN5 (percentage)	1.58 ± 5.83 (0.92 - 2.25)	2.41 ± 7.63 (2.05 – 2.78)	negative*
BIO4 (SD x 100)	5,817.80 ± 165.81 (5,798.98 – 5,836.63)	5,870.62 ± 175.26 (5,862.24 – 5,879.00)	negative
BIO17 (mm)	26.75 ± 4.99 (26.18 – 27.32)	25.39 ± 5.60 (25.13 – 25.66)	positive*
BIO18 (mm)	35.50 ± 11.28 (34.22 – 36.78)	32.20 ± 11.49 (31.65 – 32.75)	positive
CHG8591 (categorical variable)	2.00 ± 0.15 (1.99 – 2.02)	1.99 ± 0.12 (1.99 – 2.00)	not applicable for categorical variable
CHG9095 (categorical variable)	4.77 ± 1.38 (4.61 – 4.92)	4.58 ± 1.25 (4.52 – 4.64)	not applicable for categorical variable
DEM (m)	2,819.06 ± 297.57 (2,785.28 – 2,852.85)	2,592.91 ± 432.70 (2,572.22 – 2,613.60)	positive
FireCond (categorical variable)	2.43 ± 2.50 (2.14 – 2.71)	2.69 ± 2.43 (2.57 – 2.80)	not applicable for categorical variable
GPS_E (m)	322,452 ± 13,807 (320,884 – 324,019)	312,711 ± 20,833 (311,715 – 313,707)	positive
GPS_N (m)	4,122,762 ± 18,425 (4,120,670 – 4,124,854)	4,129,246 ± 21,383 (4,128,223 – 4,130,268)	negative
SLOPE (degrees)	4.27 ± 3.32 (3.89 – 4.64)	5.92 ± 4.47 (5.70 – 6.13)	negative
SURVEY_TOT (min)	53.27 ± 55.41 (46.97 – 59.56)	26.57 ± 25.12 (25.37 – 27.77)	positive
TEMPAIR_ST (^{o}C)	19.58 ± 3.72 (19.16 – 20.00)	20.72 ± 4.60 (20.50 – 20.94)	negative
TEMPW (^{o}C)	22.77 ± 5.80 (22.11 – 23.42)	18.72 ± 5.96 (18.43 – 19.00)	positive
TIMB_DIST (m)	12,163.33 ± 8,461.14 (11,202.66 – 13,124.01)	9,473.06 ± 9,417.84 (9,022.71 – 9,923.41)	positive*
WTYPE (categorical variable)	0.56 ± 0.50 (0.51 – 0.62)	0.51 ± 0.50 (0.49 – 0.53)	not applicable for categorical variable

Table 1.5, continued

AC=distance-weighted auto-covariate; ACRES=acreage of meadow survey site; ASPECT=aspect; BBIN5=annual snow covered area, percentage of water year that the basin is 75-100% covered in snow; BIO4=temperature seasonality; BIO17=precipitation of driest quarter (note: quarter is a period of three months); BIO18=precipitation of warmest quarter; CHG8591(categorical variable)=classification of land cover change between 1985 and 1991 based on satellite imagery; CHG9095(categorical variable)=classification of land cover change between 1990 and 1995 based on satellite imagery; DEM=elevation; FireCond(categorical variable)=fire condition class; GPS_E=x-coordinate of the survey site; GPS_N=y-coordinate of the survey site; SLOPE=slope; SURVEY_TOT=total survey time; TEMPAIR_ST=air temperature; TEMPW=water temperature; TIMB_DIST=distance to timber harvest area; WTYPE(categorical variable)=water type at survey site (seasonal/perennial)

Figure 1.1. Yosemite toad range and the location of the Sierra National Forest in California.

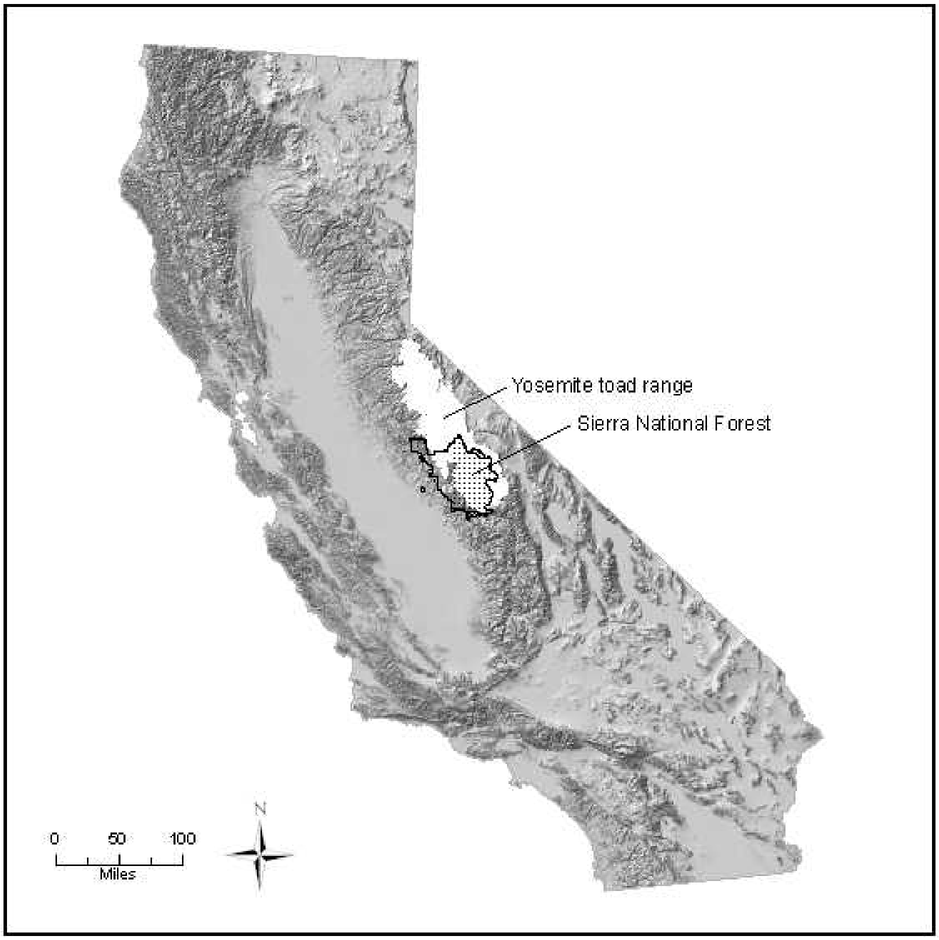
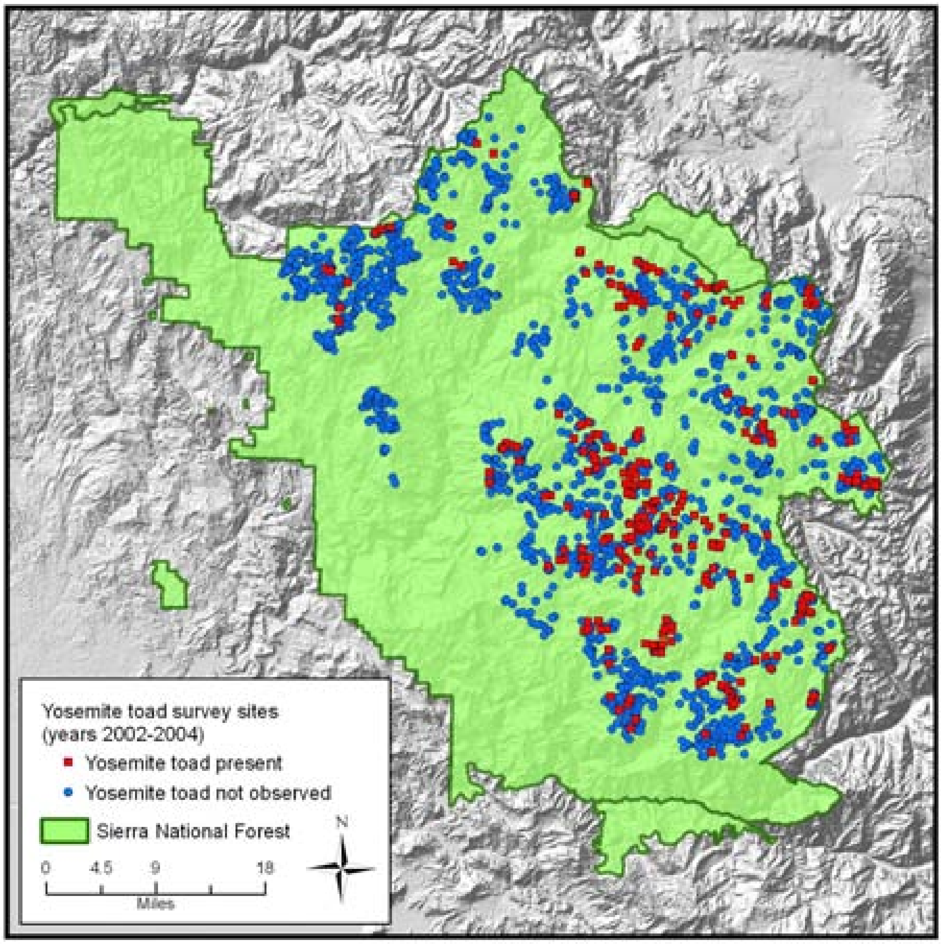


Figure 1.2. Yosemite toad 2002-2004 survey sites in the Sierra National Forest in California.



Appendix 1.A. Fifty-four predictor variables considered for the species distribution model. Variables with an asterisk (*) were included in the modeling analysis after the results of the cross-correlation analysis.

Variable (Units)	**Description**	**Derivation**	**Source**
AC*	distance-weighted autocovariate; weighted number of occupied sites within 1,500 meters of survey site	calculated in R statistical program using X- and Y-coordinates with a distance of 1,500 meters	survey data; statistical calculation
ACRES*	acreage of meadow site	meadow boundary delineated in GIS using aerial photograph	Sierra National Forest
AG_DIST (m)	straight-line distance to nearest agricultural land	calculated in GIS from landcover grid layer	California Fire Resources Assessment Program, land cover layer (100 meter resolution)
ASPECT (degrees)*	aspect	calculated in GIS from DEM grid layer	United States Geological Survey, Digital Elevation Model layer (10 meter resolution)
BBIN1 (percentage)	annual snow covered area binned as percentage of water year that the basin is 0-10% covered in snow	table data attached to GIS basin vector layer	Dozier et al. 2008 (500 meter resolution)
BBIN2 (percentage)*	annual snow covered area binned as percentage of water year that the basin is 10-25% covered in snow	table data attached to GIS basin vector layer	Dozier et al. 2008 (500 meter resolution)
BBIN3 (percentage)*	annual snow covered area binned as percentage of water year that the basin is 25-50% covered in snow	table data attached to GIS basin vector layer	Dozier et al. 2008 (500 meter resolution)
BBIN4 (percentage)	annual snow covered area binned as percentage of water year that the basin is 50-75% covered in snow	table data attached to GIS basin vector layer	Dozier et al. 2008 (500 meter resolution)
BBIN5 (percentage)*	annual snow covered area binned as percentage of water year that the basin is 75-100% covered in snow	table data attached to GIS basin vector layer	Dozier et al. 2008 (500 meter resolution)
BIO1 (^{o}C x 10)	annual mean temperature	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO2 (^{o}C x 10)*	mean diurnal range (mean of monthly (max temp - min temp))	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation

Appendix 1.A, continued

Variable (Units)	Description	Derivation	Source
BIO3 (unitless)	isothermality (mean diurnal range/temperature annual range)	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO4 (SD x 100)*	temperature seasonality (standard deviation)	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO5 (^{o}C x 10)	maximum temperature of warmest month	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO6 (^{o}C x 10)	minimum temperature of coldest month	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO7 (^{o}C x 10)	temperature annual range (max temp of wamest month - min temp of coldest month)	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO8 (^{o}C x 10)	mean temperature of wettest quarter (note: quarter is a period of three months)	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO9 (^{o}C x 10)	mean temperature of driest quarter (note: quarter is a period of three months)	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO10 (^{o}C x 10)	mean temperature of warmest quarter (note: quarter is a period of three months)	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO11 (^{o}C x 10)	mean tempearture of coldest quarter (note:quarter is a period of three months)	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO12 (mm)	annual precipitation	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO13 (mm)	precipitation of wettest month	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO14 (mm)*	precipitation of driest month	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO15 (CV)*	precipitation seasonality (coefficient of variation)	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO16 (mm)	precipitation of wettest quarter (note: quarter is a period of three months)	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO17 (mm)*	precipitation of driest quarter (note: quarter is a period of three months)	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation

Appendix 1.A, continued

Variable (Units)	Description	Derivation	Source
BIO18 (mm)*	precipitation of warmest quarter (note: quarter is a period of three months)	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BIO19 (mm)	precipitation of coldest quarter (note: quarter is a period of three months)	calculated in GIS from PRISM climate data	PRISM, 1971-2000 climatology normals layer (800 meter resolution); WorldClim calculation
BPLUS10 (date)	last date in 2004 water year that the basin was >10% snow covered (note: "water year" is October thru September with the ending year designated as the water year)	table data attached to GIS basin vector layer	Dozier et al. 2008 (500 meter resolution)
BPLUS25 (date)	last date in 2004 water year that the basin was >25% snow covered (note: "water year" is October thru September with the ending year designated as the water year)	table data attached to GIS basin vector layer	Dozier et al. 2008 (500 meter resolution)
BPLUS50 (date)	last date in 2004 water year that the basin was >50% snow covered (note: "water year" is October thru September with the ending year designated as the water year)	table data attached to GIS basin vector layer	Dozier et al. 2008 (500 meter resolution)
BPLUS75 (date)*	last date in 2004 water year that the basin was >75% snow covered (note: "water year" is October thru September with the ending year designated as the water year)	table data attached to GIS basin vector layer	Dozier et al. 2008 (500 meter resolution)
CHG8591*	classification of land cover change between 1985 and 1991 based on satellite imagery	GIS grid layer	California Fire Resources Assessment Program, Land Cover Mapping & Monitoring Program layer (30 meter resolution)
CHG9095*	classification of land cover change between 1990 and 1995 based on satellite imagery	GIS vector layer	California Fire Resources Assessment Program, Land Cover Mapping & Monitoring Program layer
CHG9701*	classification of land cover change between 1997 and 2001 based on satellite imagery	GIS vector layer	California Fire Resources Assessment Program, Land Cover Mapping & Monitoring Program layer
DATE (Julian)*	date of survey	survey data	2002-2004 surveys

Appendix 1.A, continued

Variable (Units)	**Description**	**Derivation**	**Source**
DEM (m)*	elevation	GIS grid layer	United States Geological Survey, Digital Elevation Model layer (10 meter resolution)
FIRECOND*	fire condition class (general deviation of ecosystems from their presettlement natural fire regime)	GIS grid layer	California Fire Resources Assessment Program, Fire Regime and Condition Class layer (100 meter resolution)
FIREP_DIST (m)*	straight-line distance to nearest fire perimeter	calculated in GIS from fire perimeter vector layer	California Fire Resources Assessment Program, Fire Perimeters layer
GPS_E (m)*	x-coordinate of the survey site	survey data, verified in GIS	2002-2004 surveys
GPS_N (m)*	y-coordinate of the survey site	survey data, verified in GIS	2002-2004 surveys
MDW_COUNT*	number of meadows within 1,500 meters of survey site	calculated in GIS from survey data	2002-2004 surveys
PPTANN (mm x10^{-2})*	annual precipitation, 1971-2000	GIS grid layer	PRISM, 1971-2000 climatology normals layer (800 meter resolution)
ROAD_DIST (m)*	straight-line distance to nearest road	calculated in GIS from road vector layer	United States Forest Service, Pacific Southwest Region GIS Clearinghouse, road layer
SLOPE (degrees)*	slope	calculated in GIS from DEM grid layer	United States Geological Survey, Digital Elevation Model layer (10 meter resolution)
SURVEY_TOT (min)*	total survey time	survey data	2002-2004 surveys
TEMPAIR_EN (^{o}C)	air temperature at end of survey	survey data	2002-2004 surveys
TEMPAIR_ST (^{o}C)*	air temperature at start of survey	survey data	2002-2004 surveys
TEMPW (^{o}C)*	water temperature in survey site	survey data	2002-2004 surveys
TIMB_DIST (m)*[1]	straight-line distance to nearest harvest activity area	calculated in GIS from accomplished harvest activity vector layer	United States Forest Service, Pacific Southwest Region GIS Clearinghouse, FACTS Accomplished Harvest Activities layer
TMNANN (^{o}C x10^{-2})	annual minimum temperature, 1971-2000	GIS grid layer	PRISM, 1971-2000 climatology normals layer (800 meter resolution)
TMXANN (^{o}C x10^{-2})	annual maximum temperature, 1971-2000	GIS grid layer	PRISM, 1971-2000 climatology normals layer (800 meter resolution)

Appendix 1.A, continued

Variable (Units)	**Description**	**Derivation**	**Source**
WHR*	vegetation type (California Wildlife-Habitat Relationships classification)	GIS vector layer	United States Forest Service, Pacific Southwest Region GIS Clearinghouse, CALVEG layer
WTYPE*	water type at survey site (seasonal/perennial)	survey data	2002-2004 surveys

*[1] = only included in management model analysis
SD = standard deviation, CV = coefficient of variation.

CHAPTER 2. HABITAT SUITABILITY OF PATCH TYPES: A CASE STUDY OF THE YOSEMITE TOAD

Christina T. Liang[1,2] and Thomas J. Stohlgren[3]

[1]Department of Environmental Science and Policy, University of California at Davis, Davis, CA 95616

[2] USDA Forest Service, Pacific Southwest Research Station, Sierra Nevada Research Center, 1731 Research Park Drive, Davis, CA 95618

[3] U.S. Geological Survey Science, Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, CO 80526

ABSTRACT

Understanding patch variability is crucial in understanding the spatial population structure of wildlife species, especially for rare or threatened species. We used a well-tested maximum entropy species distribution model (Maxent) to map the Yosemite toad (*Anaxyrus (=Bufo) canorus*) in the Sierra Nevada mountains of California. Twenty-six environmental variables were included in the model representing climate, topography, land cover type, and disturbance factors (e.g., distances to agricultural lands, fire perimeters, and timber harvest areas) throughout the historic range of the toad. We then took a novel approach to the study of spatially structured populations by applying the species-environmental matching model separately for 49 consistently occupied sites of the Yosemite toad compared to 27 intermittently occupied sites. We found that the distribution of the entire population was highly predictable, and associated with low slopes, specific vegetation types (wet meadow, alpine-dwarf shrub, montane chaparral, red fir, and subalpine conifer), and warm temperatures. The consistently occupied sites were also associated with these same factors, and they were also highly predictable. However, the intermittently occupied sites were associated with distance to fire perimeter, a slightly different response to vegetation types, distance to timber harvests, and a much broader set of aspect classes. We conclude that many studies of species distributions may benefit by modeling spatially structured populations separately. Modeling and monitoring consistently-occupied sites may provide a realistic snapshot of current species-environment relationships, important climatic and topographic patterns associated with species persistence patterns, and an understanding of the plasticity of the species to respond to varying climate regimes across its range. Meanwhile, modeling and monitoring of widely dispersing individuals and intermittently occupied sites may uncover environmental thresholds and human-related threats to population persistence.

Keywords: Species-environmental matching model, species distribution model, Maxent, metapopulation, Yosemite toad, *Anaxyrus canorus*, *Bufo canorus*

INTRODUCTION

Knowledge of species distributions is fundamental to ecology and the distribution of species is largely determined by the environment. Species-environmental matching models are an increasingly common tool to investigate suitable habitat and species distributions (Phillips et al. 2004, Elith et al. 2006). Species distribution models are statistical models that quantify species-environment relationships by relating species occurrences to environmental predictor variables. The models use various algorithms to model the distribution of the known locations (response variable), select significant predictor variables and determine their fit, evaluate the strength of association between predictors and response, and predict habitat suitability in areas where the distribution is unknown (output is known as a habitat suitability map). The advancement of modeling methods has led to the wide-spread use of species distribution models in addressing issues in biogeography, ecology and evolution, and for species conservation and management. For example, species distribution models have been used to quantify the environmental niche of a species (Phillips et al. 2004, Elith et al. 2006, Kumar et al. 2009), predict species invasions (Evangelista et al. 2008, Giovanelli et al. 2008), estimate species distributions in the past (Svenning et al. 2008, Waltari and Guralnick 2009) and in future climates (Jarnevich and Stohlgren 2008) or under different land uses (Riley at al. 2005), and in conservation planning and reserve selection (Pawar et al. 2007, Fuller et al. 2008).

However, species distribution models commonly assume that all recorded locations of a species are qualitatively the same, and do not take into account habitat heterogeneity such as in spatially subdivided local populations. We found no publications where species distribution models have been used specifically to assess spatially structured populations in discrete habitat patches. Spatially structured populations can be organized in a variety of ways along a continuum of connectivity and patch structure (Harrison and Taylor 1997). Three main population structures, listed in order of decreasing connectivity, are: patchy population, metapopulation, and isolated populations. In a patchy population, multiple patches are well connected by dispersal and there is little potential for local extinction within individual patches. In a metapopulation, multiple local populations are reciprocally linked by less frequent dispersal (Levins 1969). Local populations are prone to extinction from both stochastic and deterministic causes and persist only at the regional level through recolonization (Hanski 1999). In isolated populations, there is no movement between patches and patches that go extinct will not be recolonized (Frankham et al 2002). These structures are based on connectivity but do not take into account variation in local patch size, location or quality.

Patch variability leads to variants of the patchy population or metapopulation structure, which differ in their mechanisms of persistence and coexistence. In a mainland-island population system, there is substantial variation in the size of patches or populations (Harrison and Taylor 1997). Larger “mainland” populations are less prone to extinction whereas smaller “island” populations are more susceptible to stochastic extinction. In a source-sink population system, there is variation in the quality of patches with higher quality “source” patches and lower quality “sink” patches (Pulliam 1988). The quality of the patch is identified by the before-dispersal population growth rate, which is positive in source patches and negative in sink patches. Dispersal from mainland or source patches supports the island or sink patches, and recruitment in the islands or sinks is from immigration rather than from within the local patch. Mainland-island and source-sink systems can apply to both patchy population and metapopulation structures.

Spatially structured population models have been applied to the study of a number of taxa including wetland-breeding amphibians. Breeding areas are discrete habitat patches that can be connected by migrating individuals and the rate of migration is often low due to high site fidelity, low vagility and physiological constraints that restrict movement to moist areas. This has led to the generalization that many amphibians have a metapopulation structure (Alford and Richards 1999) although this generalization may be overstated (Marsh and Trenham 2001, Smith and Green 2005) and some species are in patchy populations rather than metapopulations (Petranka and Holbrook 2006). However, regardless of the exact population structure, the patch is an important feature that needs to be considered in any research, management, restoration, or conservation effort (Marsh and Trenham 2001, Petranka and Holbrook 2006). Patch variability results in sites that are more consistently occupied (mainland or source sites) versus sites that are more intermittently occupied (island or sink sites). Patch type is likely determined by environmental heterogeneity and local environmental factors.

The Yosemite toad (*Anaxyrus (=Bufo) canorus*) provides an ideal case study of a species that is spatially structured in discrete patches. It is endemic to the Sierra Nevada mountains in California at elevations above 6,400 ft (1,950 m) and is associated with wet mountain meadows and adjacent forests (Karlstrom 1962). The Yosemite toad breeds in late spring in areas of shallow water such as wet meadows, margins of ponds and lakes, and slow-moving streams. Breeding usually only lasts 1-2 weeks after which adults typically move to upland areas. Eggs and larvae develop in the shallow water areas and metamorphosis occurs by late summer of the same year. Adults tend to breed in a single site and appear to be highly philopatric, although individuals can move between breeding areas (CT Liang *dissertation chapter 3*). Breeding sites exhibit variation in year-to-year occupancy and some sites are consistently occupied while others are intermittently occupied. There also is variation in population sizes at the breeding sites. It appears highly likely that mainland-island or source-sink dynamics are occurring in this species though the exact population structure is not known. Regardless, it is evident that patch types vary for the Yosemite toad throughout its range.

The Yosemite toad is a candidate for federal listing as endangered or threatened and a California state species of special concern due to its apparent disappearance from over 50% of its historic range even in seemingly undisturbed areas. In addition, remaining populations appear to be in decline (Sherman and Morton 1993, Drost and Fellers 1996, Davidson et al. 2002). The cause(s) of the disappearance and decline are not known, although potential factors include airborne pesticides and other toxins, infectious disease, climate change, and habitat modification due to anthropogenic changes. Habitat modification related to livestock grazing, roads, timber harvest, vegetation and fire management activities, recreation, and dams and water diversion are all considered threats to the species (USFWS 2002).

Our objectives were to: (1) determine the Yosemite toad's response to environmental variables throughout its range to develop better conservation strategies for this rare species; and (2) demonstrate the general utility of modeling species-environmental relationships separately for consistently occupied sites compared to intermittently occupied sites to understand patch variability and potential threats to the species' persistence.

METHODS

Yosemite toad locations

Numerous surveys related to the Yosemite toad have been conducted in the national forests and parks within its range. Visual encounter survey for any life stage is the typical method. Some sites have been repeatedly visited over the past 10-15 years to survey for breeding adults, eggs and/or tadpoles. Based on available survey information, 49 consistently occupied sites and 27 intermittently occupied sites were identified in the Inyo National Forest, Sequoia and Kings Canyon National Park, Sierra National Forest, Stanislaus National Forest, and Yosemite National Park (Figure 2.1). Consistent sites were defined as being occupied on a yearly basis in ≥50% of total surveys for the site and with a relatively constant population in all occupied years; intermittent sites were not occupied on a yearly basis in <50% of site surveys and had relatively few individuals when occupied. A site was considered occupied if any Yosemite toad life stage was found during the survey. The classification of "consistent" and "intermittent" was based on the best available knowledge of the sites although sites were not necessarily surveyed consecutively over multiple years or with standardized levels of effort. The classification was used only to identify two different patch types which the Yosemite toad occupies and does not make any assumptions about the population structure (e.g., patchy population, metapopulation), which cannot be determined from the available data and is not the focus of this paper.

Environmental variables

Twenty-six environmental variables were originally considered for the models representing climate, topography (elevation, aspect and slope), land cover type, and disturbance factors (distances to agricultural lands, fire perimeters, and timber harvest areas) throughout the historic range of the Yosemite toad (Appendix A). Nineteen bioclimatic variables defining ecophysiological tolerances of species based on annual mean temperature and precipitation were calculated from PRISM climate data (http://www.prism.oregonstate.edu) using an ARC AML script (mkBCvars.aml; http://www.worldclim.org/mkBCvars.aml). Vegetation type was based on the California Wildlife-Habitat Relationships (WHR) classification. All environmental variables were gathered in a geographic information system (GIS) and resampled to 30 meter resolution to match the digital elevation model layer. GIS analyses were conducted using Environmental Systems Research Institute's (ESRI, Redlands, California, USA) ArcGIS 9.2.

Multicollinearity was tested by examining cross-correlations for all variables. Only one variable from a highly correlated set of variables (Pearson's correlation coefficient ≥ ± 0.80) was included in the analyses, based on contribution to potential distribution and ecological relevance to the Yosemite toad. For example, many of the bioclimatic variables were correlated such as mean diurnal range, isothermality, and temperature annual range; only mean diurnal range was included in the analyses and the other variables were excluded. Subsequently, only six of the nineteen bioclimatic variables (mean diurnal range, temperature seasonality, maximum temperature of warmest month, annual precipitation, precipitation of driest quarter, and precipitation of coldest quarter) were included in the analyses. Overall, a total of twelve environmental variables that were not correlated were used in the models (Appendix A).

Maxent model

There are numerous species distribution modeling methods, but the purpose of this paper was not to compare them. Instead, we used one relatively newer method which has consistently fared well in model comparison studies (Elith et al 2006; Kumar et al. 2009; Li et al. 2009). The maximum entropy model, Maxent, is a general purpose predictive model that uses presence-only data (Phillips et al. 2004, 2006b). It is based on the principle of maximum entropy, using available information as constraints and obtaining the least-biased inferences when insufficient information is available. This method estimates the probability distribution of a species by finding the probability distribution of maximum entropy, which is a probability that is closest to uniform (Phillips et al. 2006b). Maxent 3.3.0 was used for the modeling and is freely available from the authors (www.cs.princeton.edu/~schapire/maxent/).

Model development and validation

Three separate Maxent models were run for (1) all occurrence locations (with all 76 sites); (2) the 49 consistent sites, and (3) the 27 intermittent sites, using the 12 environmental predictors. We ran each model 25 times with a 25-fold cross-validation, and model results were averaged for all runs. The validation of predictive model outputs from Maxent is accomplished in several ways. First, the user has the option of defining a percentage of the data which: (1) allows for testing and training omissions against threshold; (2) provides predicted area against threshold; and (3) calculates the receiver operating characteristic curve (ROC). The area under the ROC curve (AUC) is calculated for each. Second, a jackknife option allows the estimation of the bias and standard error in the statistics, and tests of variable importance (Phillips et al. 2004, 2006b). Finally, Maxent generates response curves for each predictor variable. Maxent has had favorable reviews with predicting species distributions from small sample sizes (e.g., geckos in

Madagascar; *Uroplatus sp*.; Pearson et al. 2007; American bullfrogs across the globe; *Rana catesbeiana*; Ficetola et al. 2007).

Patch connectivity and patch size

Patch connectivity and size are important components in defining a spatially structured population and may play a role in identifying patch type. However, patch connectivity (measured by distance to nearest occupied site) and patch size (measured by site acreage) were not included in the Maxent model because they do not have meaningful measurable values in the landscape outside the sites, and thus cannot be modeled by the maximum entropy probability distribution. To evaluate the importance of these variables in determining patch type, classification and regression trees (CART) method was utilized with a 10-fold cross-validation. The two patch types were classified by CART using the 12 uncorrelated environmental variables plus distance to nearest occupied site and site acreage. Distance to nearest occupied site was calculated in a geographic information system (ArcGIS 9.3) based on known occupied sites. Site acreage was gathered from the survey dataset of Yosemite toad locations. Statistical analysis was performed with R software (version 2.11.0; http://www.r-project.org) using the rpart package.

RESULTS

All-sites species-environmental matching

The Maxent model results for all sites showed suitable habitat for the Yosemite toad in areas from El Dorado National Forest in the north, through Yosemite National

Park and down to Sierra National Forest and Sequoia-Kings Canyon National Park in the south (Figure 2.2a). Highly suitable habitats primarily have low slopes, are in specific vegetation types (wet meadow, alpine-dwarf shrub, montane chaparral, red fir, and subalpine conifer), and have warm temperatures; greater distance to fire perimeter, low aspect classes and mean diurnal temperature range between approximately 10-14° C are also associated with suitable habitat to a lesser degree (Table 2.1). The Maxent model performed well for all the Yosemite toad sites (AUC=0.95 ± 0.03 SD). Variable response curves for the top six predictors showed mostly non-linear responses for the factors, excepting vegetation type and aspect which were categorical factors (Figure 2.3). Slope displayed a reverse sigmoid response with a fairly steep decline. The bioclimatic variables showed unimodal responses, with a fairly broad range of suitability for these variables. Distance to fire perimeter showed a linear response until it reached a threshold value.

Consistent sites species-environmental matching

The Maxent model results for consistent sites showed more limited suitable habitat for the Yosemite toad for the same study area (Figure 2.2b). Similar to the model for all Yosemite toad occurrence sites, highly suitable consistent-site habitats have low slopes, specific vegetation types (primarily wet meadow, alpine-dwarf shrub, montane chaparral, red fir, and subalpine conifer), and warm temperatures; low aspect-classes, precipitation range between approximately 500-800 mm during the coldest quarter, and mean diurnal temperature range between approximately 9-15° C further define consistent-site habitat (Table 2.1). The Maxent models performed well for the Yosemite toad consistent sites (AUC=0.95 ± 0.05 SD). Variable response curves for the top six predictors show similar non-linear responses as the all-occurrence model for most of the factors as well as similar results for the categorical variables (Figure 2.4).

Intermittent sites species-environmental matching

The Maxent model results for intermittent sites differed markedly from the models for all-occurrence sites and consistent sites (Figure 2.2c). Intermittent-site habitat is more extensive throughout the range of the Yosemite toad than for consistent sites. The primary factors associated with intermittent-site habitat included distance to fire perimeter, a slightly different response to vegetation types, distance to timber harvest activity, and aspect class (Table 2.1). More than half of variable contributions to the model were a combination of distance to fire perimeter (41.8%) and distance to timber harvest activity (10.1%). Certain vegetation types such as lodgepole pine were used more by intermittent-site populations than by consistent-site populations, while montane chaparral was used less.

Fewer variables contributed more than 5% to the intermittent-site habitat compared to the all-occurrence habitat and consistent-site habitat (Table 2.1). Slope was not a significant predictor in the intermittent-site model (4% contribution to the predicted potential geographic distribution)**,** unlike the all-occurrence and consistent-site models where slope had the highest contribution. Intermittent sites were associated with a wider spectrum of slopes, as the slope response curve was more gradual for intermittent sites (Figure 2.5) compared to all-occurrence sites (Figure 2.3) and consistent sites (Figure

2.4). The Maxent models performed well for the Yosemite toad intermittent sites (AUC=0.90 ± 0.11 SD).

Area of consistent- and intermittent-site habitats

Results show that habitat suitability for consistent sites is more restricted than either the all-occurrence sites or the intermittent sites (Table 2.2). For probability of occurrence greater than 0.5, consistent sites have 87% of the all-occurrence area and 61% of the intermittent sites area. Intermittent sites have the most extensive habitat suitability, with 141% of the all-occurrence area.

Patch connectivity and patch size

The classification tree results for predicting patch type (i.e., consistent sites versus intermittent sites) did not include distance to nearest occupied site or site acreage in any of the tree nodes. The root node was split based on distance to fire perimeter (≥ 92.9), the second node was separated on the easting coordinates (≤ 119.8), the third node was separated on aspect (= southeast, south, southwest, west categories), and the final node was split based on the maximum temperature of the warmest month (≥ 201.5). Root node error was 0.355.

DISCUSSION

Consistent- and intermittent- site differences for the Yosemite Toad

The two major conclusions from our study were: (1) modeling all occurrences of a species may mask important differences in consistent and intermittent sites; and (2) modeling intermittent-site populations may expose threats to population persistence better than models of all-occurrences or consistent sites. Cleary, disturbance factors contributed more to the distribution model for intermittent sites (Table 2.1). This suggests that highly suitable habitat for breeding populations may be affected by fire and timber harvest. Consistent with what is already known about the Yosemite toad, the models show that the species is generally associated with the wet meadow vegetation type and flat areas. However, modeling consistently occupied sites and intermittently occupied sites separately allowed our first look into the broadening of habitat features associated with marginal habitat. For example, intermittent sites included a broader suite of slopes than consistent sites. In addition, there are fewer significant environmental factors and thus fewer constraints associated with intermittent-site habitat (Table 2.1). Highly suitable habitat associated with intermittent sites is thus increased relative to that of all-occurrence or consistent sites (Table 2.2).

For the Yosemite toad, there are several variables that correlate with the presence of the species at both consistent and intermittent sites. This indicates that the species does not have a simple relationship with the environment, and is found within a range of environmental conditions. The distribution of consistently occupied sites is influenced by topographic and bioclimatic factors and shows tolerance for a fairly broad range of temperature and precipitation gradients (Figure 2.4). This indicates that the Yosemite toad may be relatively insensitive to changes in bioclimatic conditions within its current elevational range. However, the Yosemite toad may be less able to respond to widespread changes in land management related to fire management and timber harvest (Figure 2.5). Fire can have negative effects directly though mortality or indirectly through destruction of habitat. In a review of amphibian responses to fire and fire management practices, Pilliod et al. (2003) found that responses can be spatially and temporally variable. However, the negative effects of fire may be greatest for species in regions with long fire-return intervals (such as in the Sierra Nevada which has been subject to fire suppression activities over the past century) and for habitat specialists like the Yosemite toad. Conversely, timber removal may have a beneficial effect on the species by preventing encroachment of conifers into breeding meadows (Semlitsch et al 2009) or by changing local mico-climate conditions (e.g., temperature, solar radiation) in cleared areas.

Our study suggests that persistence of the Yosemite toad may depend, in part, on: (1) maintaining highly suitable breeding habitat (and many consistent-site populations) across broad environmental gradients; and (2) reducing threats to consistent-site populations over a smaller area than would be identified if the entire population were modeled (Table 2.2). Additional monitoring is needed to assess changes in consistent and intermittent sites over time.

Caveats

There are many caveats associated with species-environmental matching models. All such models are affected by sample size, the clustering of presence points, and the resolution and accuracy of predictive layers (Phillips et al. 2004, 2006b). There are also caveats associated with the data for the Yosemite toad. The classification of “consistent” and “intermittent” sites is somewhat subjective and can be confounded by detectability issues. Sites may only be surveyed once during the year or may not be surveyed in consecutive years, and life-stages other than calling males can be difficult to detect and are easily missed. The classification of a site as consistently occupied versus only intermittently occupied then may not be true in all cases.

In our case study, we had almost twice as many consistent sites (49 vs. 27), but both types of sites were broadly distributed over the same area of interest. A wide range of environmental variables was associated with population distributions, yet the accuracy of models (in terms of AUC) was very high. Thus, we feel that the models performed well enough to provide a preliminary understanding of the primary differences between consistent- and intermittent-type population sites.

General utility of modeling patch types

There is considerable theoretical interest in patch quality and metrics and increasing empirical evidence that patch quality is influential in species' distributions and spatial population structure (see review by Mortelliti et al. 2010). Though there is recognition that the habitat and quality within patches can vary (Lloyd 2008, Heisswolf et al. 2009), most studies focus on how patch characteristics relate to overall occupancy (Bradford et al. 2003, Schooley and Branch 2009). Patch occupancy is treated as a bivariate state (occupied versus not occupied) and once a patch is found to be occupied it remains classified as such. Data gathered from all occupied patches are then typically used in models and analyses. However, occupancy can be intermittent and changeable resulting in different types of occupied patches (e.g., mainlands and islands, sources and sinks). The different patch types vary in their size, location and environmental characteristics and it is not surprising that these variations influence the species-environment relationship and lead to different predictions of suitable habitat. Modeling of patch types separately identifies their associated environmental variables and provides a more complete picture of overall environmental requirements of a species and potential constraints.

Patch type is often thought to be highly related to patch metrics such as connectivity and size since these variables are the principal determinants of the existence and nature of a spatial population structure (Pulliam 1988, Harrison and Taylor 1997). Our results, however, indicate that patch type for the Yosemite toad is determined more by environmental variables than by distance to nearest occupied site or site acreage. The results of the CART analysis, similar to the Maxent models, showed that disturbance, topographic and bioclimatic variables are primary factors in differentiating patch type. Although this result may not be true for all species, it illustrates the importance of looking beyond patch metrics when investigating patch types.

Species with spatially structured populations are not uncommon (Pulliam 1988, Mortelliti et al. 2010), so the lessons learned here may have broad applications. Furthermore, dispersal is a necessary risk for a species to extend its range, with individuals likely moving into intermittently occupied patches first. While dispersal may be risky to the individual, “the long-term survival of populations depends on having a sufficient number of individuals that move, find each other, and locate suitable breeding habitats” (Kokko and Lo´pez-Sepulcre 2006). For example, Columbia spotted frogs (*Rana luteiventris*) in the northern Rocky Mountains “had exceptionally high juvenile dispersal rates (up to 62% annually) over long distances (>5km), large elevation gains (>750m) and steep inclines (36° incline over 2km)” (Funk et al. 2005). Dispersal increases gene flow, assuming the dispersers survive and reproduce. In addition to extending a species range, and thus extending the environmental gradients associated with range expansion, dispersion may accelerate evolution. For example, the leading edge of invasive Cane toads (*Bufo marinus*) in Australia resulted in longer legs for dispersing individuals (Phillips et al. 2006a). For all these reasons, it may be particularly important to map, model, and monitor dispersing individuals in intermittent-site populations separately from the more stable consistent-site populations of the same species.

We conclude that many studies of species distributions may benefit by modeling patch types separately. Modeling and monitoring consistently occupied sites may provide a realistic snapshot of current species-environment relationships, important climatic and topographic patterns associated with species distribution patterns, and an understanding of the plasticity of the species in response to varying climate regimes across its range. Meanwhile, modeling and monitoring widely dispersing individuals and intermittently occupied sites may uncover environmental thresholds and human-related threats to population persistence. This may be particularly important for rare and threatened species. Model outputs may help guide future data collection, identify suitable habitat, and guide restoration efforts. Iterative mapping, monitoring, and modeling over time may be needed to assure the persistence of sensitive species.

ACKNOWLEDGMENTS

R. Grasso of the USDA Forest Service, Sierra Nevada Research Center, assisted in classifying Yosemite toad locations. Data were provided by the Inyo National Forest, Sierra National Forest, Stanislaus National Forest, Sequoia-Kings Canyon National Park, and Yosemite National Park. S. Kumar provided Maxent training. The Natural Resource

Ecology Laboratory at Colorado State University provided logistical support. Funding for C.T.L. was provided by the University of California at Davis. Funding for T.J.S. was provided by the U.S. Geological Survey. S. Kumar, T. Holcombe, A. Lind, S. Lawler, and J. Quinn provided helpful reviews on earlier versions of the manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Two anonymous peer reviewers provided additional comments. To all we are grateful.

LITERATURE CITED

Alford, R. A., and S. J. Richards. 1999. Global amphibian declines: A problem in applied ecology. Annual Review of Ecology and Systematics 30:133-165.

Bradford, D. F., A. C. Neale, M. S. Nash, D. W. Sada, and J. R. Jaeger. 2003. Habitat patch occupancy by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. Ecology 84:1012-1023.

Davidson, C., H. B. Shaffer, and M. R. Jennings. 2002. Spatial tests of the pesticide drift, habitat destruction, UV-B, and climate-change hypotheses for California amphibian declines. Conservation Biology 16:1588-1601.

Drost, C. A., and G. M. Fellers. 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. Conservation Biology 10:414-425.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Lohmann, G. Manion, C. Moritz, J. M. Overton, A. T. Peterson, S. J. Phillips, M. Nakamura, Y. Nakazawa, R. E. Schapire, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129-151.

Evangelista, P. H., S. Kumar, T. J. Stohlgren, C. S. Jarnevich, A. W. Crall, J. B. Norman III, and D. T. Barnett. 2008. Modelling invasion for a habitat generalist and a specialist plant species. Diversity and Distributions 14:808-817.

Ficetola, G. F., W. Thuiller, and C. Miaud. 2007. Prediction and validation of the potential global distribution of a problematic alien invasive species—the American bullfrog. Diversity and Distributions 13:476–485.

Frankham, R., J. D. Ballou, and D. A. Briscoe. 2002. Introduction to conservation genetics. Cambridge University Press, Cambridge, UK.

Fuller, T., D. P. Morton, and S. Sarkar. 2008. Incorporating uncertainty about species' potential distributions under climate change into the selection of conservation areas with a case study from the Arctic Coastal Plain of Alaska. Biological Conservation 141:1547-1559.

Funk, W. C., A. E. Greene, P. S. Corn, and F. W. Allendorf. 2005. High dispersal in a frog species suggests that it is vulnerable to habitat fragmentation. Biological Letters 1:13-16.

Giovanelli, J. G. R., C. F. B. Haddad, and J. Alexandrino. 2008. Predicting the potential distribution of the alien invasive American bullfrog (Lithobates catesbeianus) in Brazil. Biological Invasions 10:585–590.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, New York, New York, USA.

Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. pp. 27–42 In: I. Hanski and M. E. Gilpin, editors. Metapopulation dynamics: ecology, genetics and evolution. Academic Press, New York, New York, USA.

Heisswolf A, S. Reichmann, H. J. Poethke, B. Schrader, and E. Obermaier. 2009. Habitat quality matters for the distribution of an endangered leaf beetle and its egg parasitoid in a fragmented landscape. Journal of Insect Conservation 13:165–175.

Jarnevich, C. S., and T. J. Stohlgren. 2009. Near term climate projections for invasive species distributions. Biological Invasions 11(6):1373-1379.

Karlstrom, E. L. 1962. The toad genus Bufo in the Sierra Nevada of California. University of California Publications in Zoology 62:1-104.

Kokko, H., and A. Lo´pez-Sepulcre. 2006. From individual dispersal to species ranges: perspectives for a changing world. Science 313: 789–791.

Kumar, S., S. A. Spaulding, T. J. Stohlgren, K. A. Hermann, T. S. Schmidt, and L. L. Bahls. 2009. Predicting habitat distribution for freshwater diatom Didymosphenia geminata in the continental United States. Frontiers in Ecology and the Environment 7:415-420.

Levins, R. A. 1969. Some demographic and evolutionary consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237-240.

Li, M. Y., Y. W. Ju, S. Kumar, and T. J. Stohlgren. 2008. Modeling potential habitats for alien species Dreissena polymorpha (Zebra mussel) in the Continental USA. Acta Ecologica Sinica 28: 4253-4258.

Lloyd, H. 2008. Influence of within-patch habitat quality on high- Andean Polylepis bird abundance. Ibis 150:735–745.

Marsh, D. M., and P. C. Trenham. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology 15:40-49.

Mortelliti, A., A. G. Amori, and L. Boitani. 2010. The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. Oecologia 163:535–547.

Pawar, S., M. S. Koo, C. Kelley, M. F. Ahmed, S. Chaudhuri, and S. Sarkar. 2007. Conservation assessment and prioritization of areas in Northeast India: Priorities for amphibians and reptiles. Biological Conservation 136:346-361.

Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. T. Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34:102-117.

Petranka, J. W., and C.T. Holbrook. 2006. Wetland restoration for amphibians: should local sites be designed to support metapopulations or patchy populations? Restoration Ecology 14**:**404-411.

Phillips, B. L., G. P. Brown, J. K. Webb, and R.Shine. 2006a. Invasion and the evolution of speed in toads. Nature 439:803.

Phillips, S. J., M. Dudik, and R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. pp. 655–662 In: Proceedings of the 21st International Conference on Machine Learning, ACM Press, New York, USA.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006b. Maximum entropy modeling of species geographic distributions. Ecological Modeling 190:231-259.

Pilliod, D.S., R. B. Bury, E. J. Hyde, C. A. Pearl, and P. S. Corn. 2003. Fire and amphibians in North America. Forest Ecology and Management 178:163–181.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652-661.

Riley, S. P. D., G. T. Busteed, L. B. Kats, T. L. Vandergon, L. F. S. Lee, R. G. Dagit, J. L. Kerby, R. N. Fisher, and R. M Sauvajot. 2005. Effects of urbanization on the distribution and abundance of amphibians and invasive species in Southern California streams. Conservation Biology 19:1894-1907.

Schooley, R. L, and L. C. Branch. 2009. Enhancing the area–isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal. Ecological Applications 19:1708-1722.

Semlitsch, R. D., B. D. Todd, S. M. Blomquist, A. J. K. Calhoun, J. W. Gibbons, J. P. Gibbs, G. J. Graeter, E. B. Harper, D. J. Hocking, M. L. Hunter Jr., D. A. Patrick, T. A. G. Rittenhouse, and B. B. Rothermel. 2009. Effects of timber harvest on amphibian population: understanding mechanisms from forest experiments. BioScience 59:853-862.

Sherman, C. K., and M. L. Morton. 1993. Population declines of Yosemite toads in the eastern Sierra Nevada of California. Journal of Herpetology 27:186-198.

Smith, M. A., and D. M. Green. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28:110-128.

Svenning, J.-C., S. Normand, and M. Kageyama. 2008. Glacial refugia of temperate trees in Europe: insights from species distribution modelling. Journal of Ecology 96:1117-1127.

U.S. Fish and Wildlife Service (USFWS). 2002. 12-month finding for a petition to list the Yosemite toad. Federal Register 67(237):75834-75843.

Waltari, E., and R. P. Guralnick. 2009. Ecological niche modelling of montane mammals in the Great Basin, North America: examining past and present connectivity of species across basins and ranges. Journal of Biogeography 36:148-161.

Table 2.1. Relative contributions of predictor variables to the three predicted potential geographic distribution models (models using all sites, consistent sites only, and intermittent sites only) for Yosemite toad. Only variables that have greater than or equal to 5% contribution are included in the table.

	% Contribution		
Variable	**All sites**	**Consistent sites**	**Intermittent sites**
Slope	35.8	35.5	---
Vegetation Type	13.4	15.0	20.9
Max Temp. Warmest Month	10.5	13.7	---
Distance to Fire Perimeter	9.9	---	41.8
Aspect	8.6	9.2	7.8
Mean Diurnal Range	8.4	5.0	---
Precip. Coldest Quarter	---	8.5	---
Distance to Timber Harvest	---	---	10.1

Table 2.2. Areas of predicted occurrence for Yosemite toad in the three geographic distribution models (all sites, consistent sites only, and intermittent sites only).

	Area (hectares)		
Probability of occurrence	**All Sites**	**Consistent sites**	**Intermittent sites**
0.9 – 1.0	1,355	1,439	1,395
0.8 – 0.9	6,580	6,010	9,762
0.7 – 0.8	12,564	10,312	17,522
0.6 – 0.7	17,308	14,666	24,738
0.5 – 0.6	23,064	20,315	32,499
Sum	60,871	52,742	85,916

Figure 2.1. Yosemite toad locations, classified into consistent and intermittent sites.

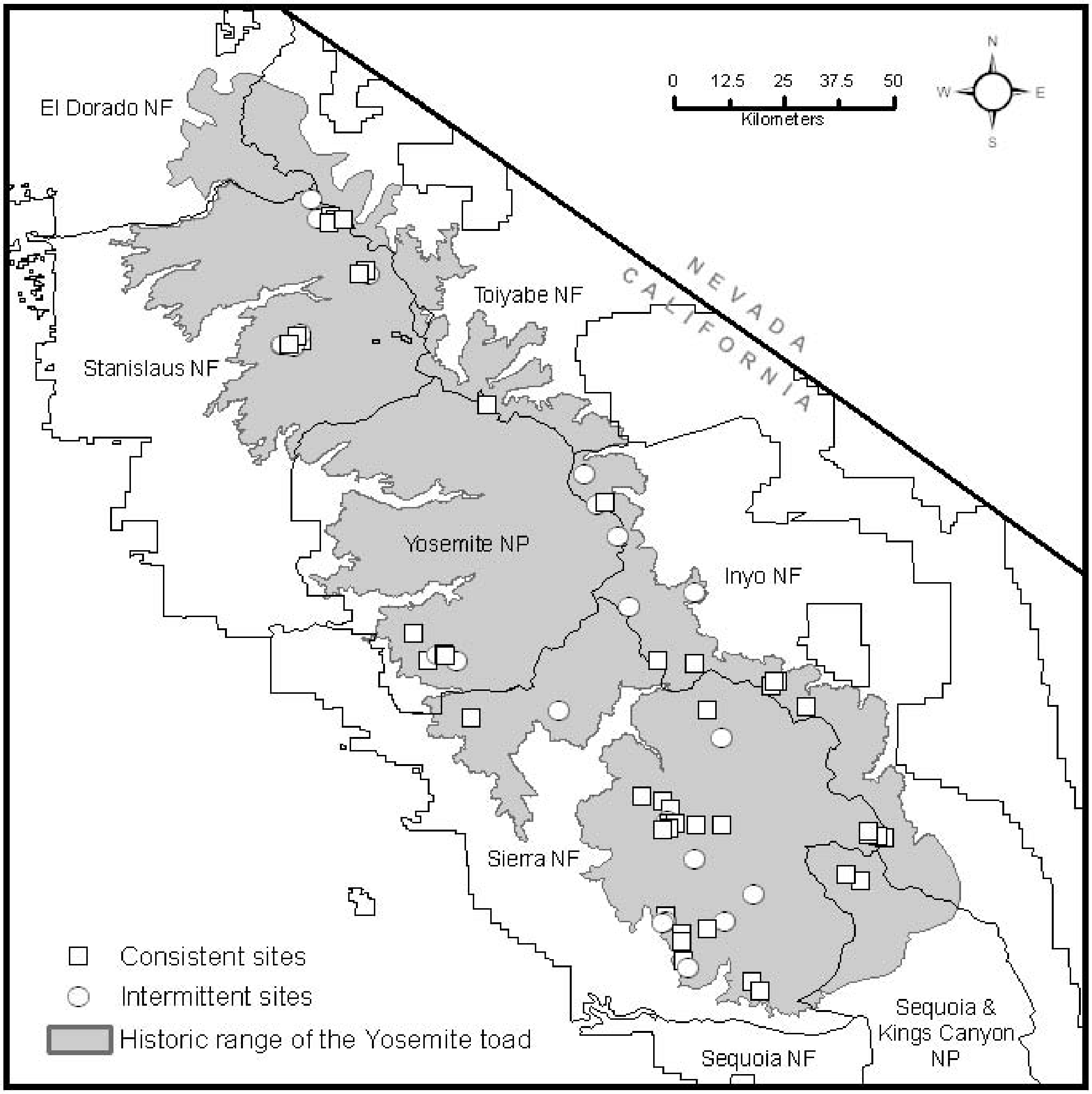


Figure 2.2. Predicted potential geographic distribution for Yosemite toad: (a) all sites; (b) sites that are consistently occupied with relatively robust populations (consistent sites); and (c) sites that are intermittently occupied with few individuals when occupied (intermittent sites).

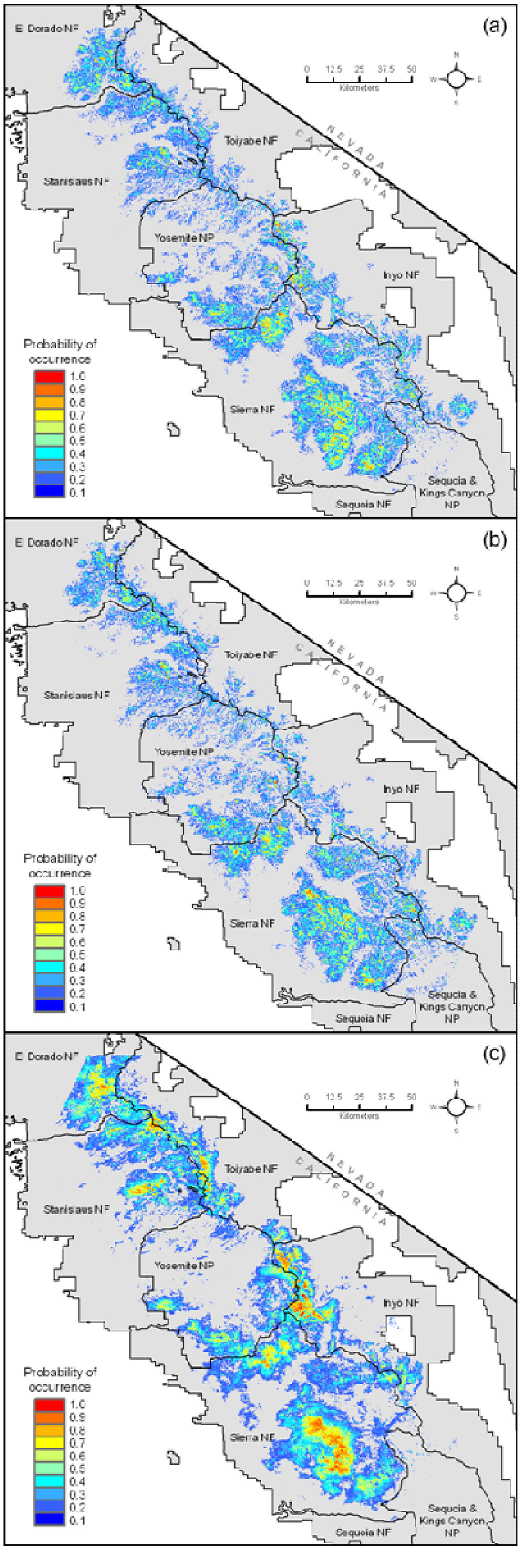
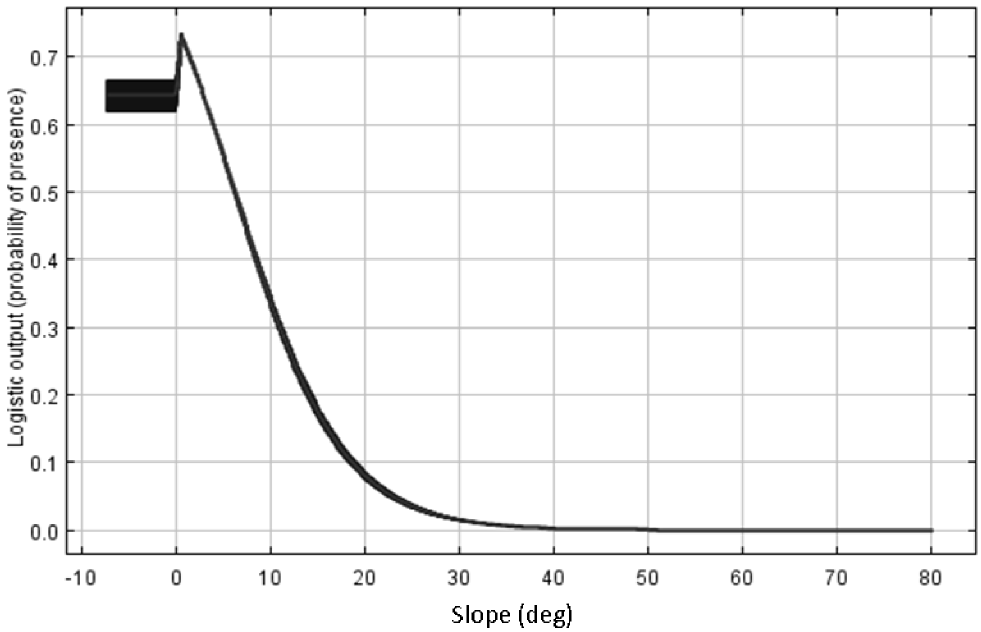
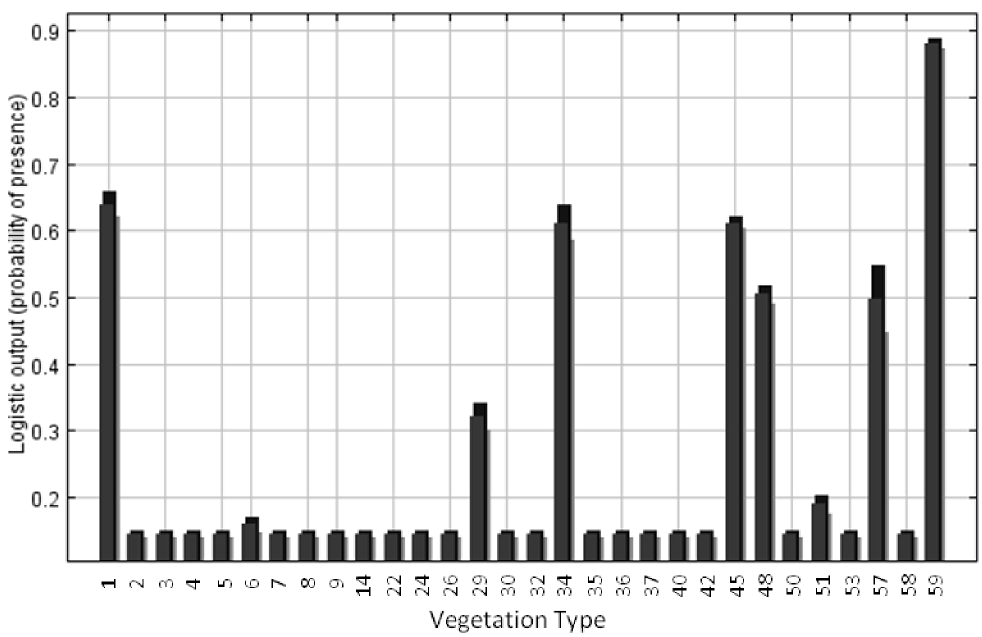


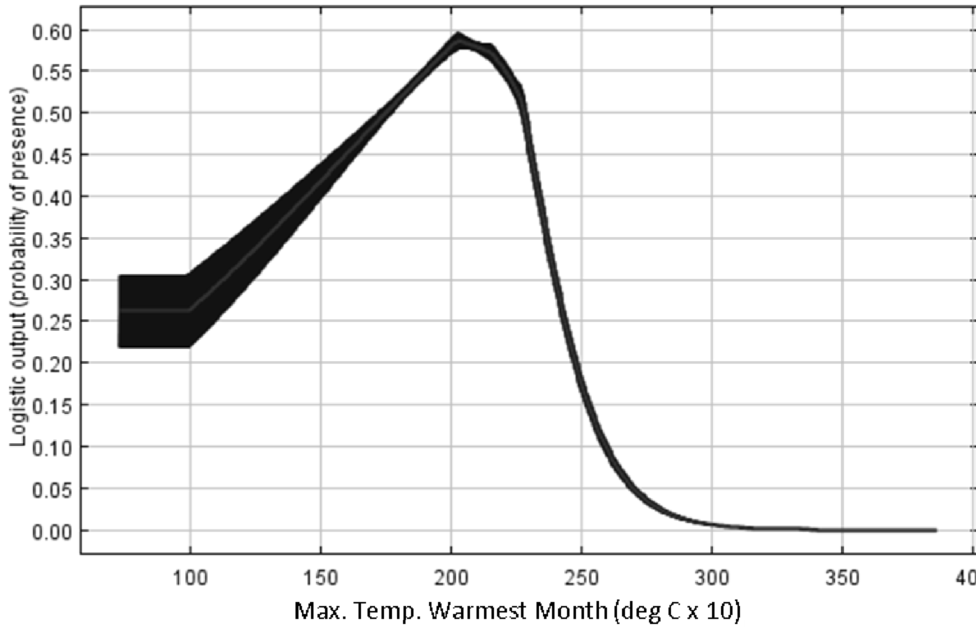
Figure 2.3a. Variable response curves for the top six predictors in the Maxent model prediction for all Yosemite toad sites (consistent plus intermittent sites).





1	Alpine-Dwarf Shrub	22	Freshwater Emergent Wetland	40	Pinyon-Juniper
2	Agriculture	24	Jeffrey Pine	42	Ponderosa Pine
3	Annual Grassland	26	Juniper	45	Red Fir
4	Alkali Desert Scrub	29	Lodgepole Pine	48	Subalpine Conifer
5	Aspen	30	Low Sage	50	Sagebrush
6	Barren	32	Mixed Chaparral	51	Sierran Mixed Conifer
7	Bitterbrush	34	Montane Chaparral	53	Urban
8	Blue Oak-Foothill Pine	35	Montane Hardwood-Conifer	57	Water
9	Blue Oak Woodland	36	Montane Hardwood	58	White Fir
14	Douglas-Fir	37	Montane Riparian	59	Wet Meadow

Figure 2.3b. Variable response curves for the top six predictors in the Maxent model prediction for all Yosemite toad sites (consistent plus intermittent sites).



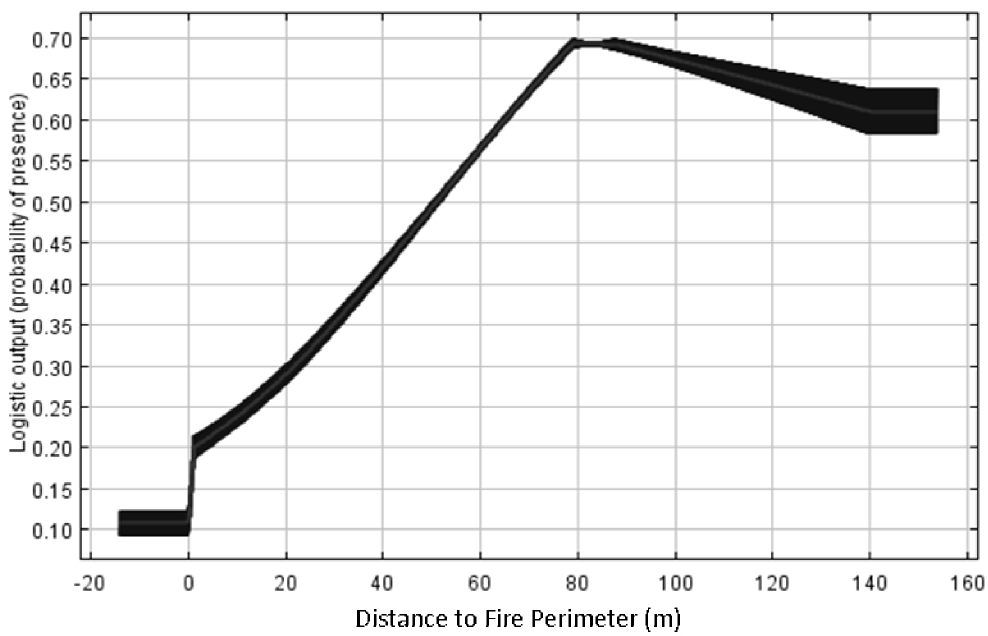
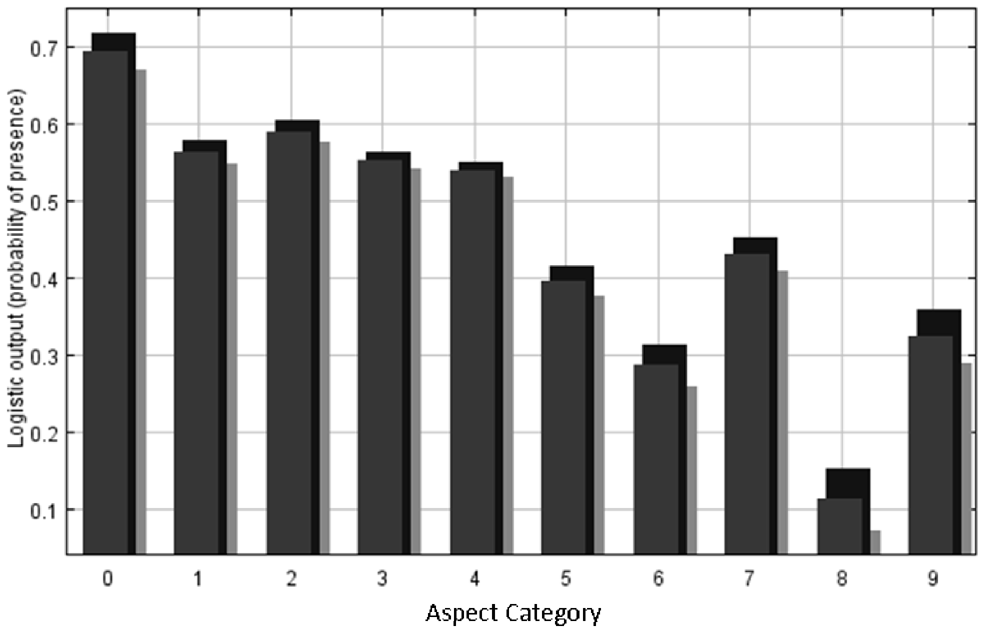


Figure 2.3c. Variable response curves for the top six predictors in the Maxent model prediction for all Yosemite toad sites (consistent plus intermittent sites).



0	Flat (-1)	3	East (67.5-112.5)	6	Southwest (202.5-247.5)
1,9	North (0-22.5, 337.5-360)	4	Southeast (112.5-157.5)	7	West (247.5-292.5)
2	Northeast (22.5-67.5)	5	South (157.5-202.5)	8	Northwest (292.5-337.5)

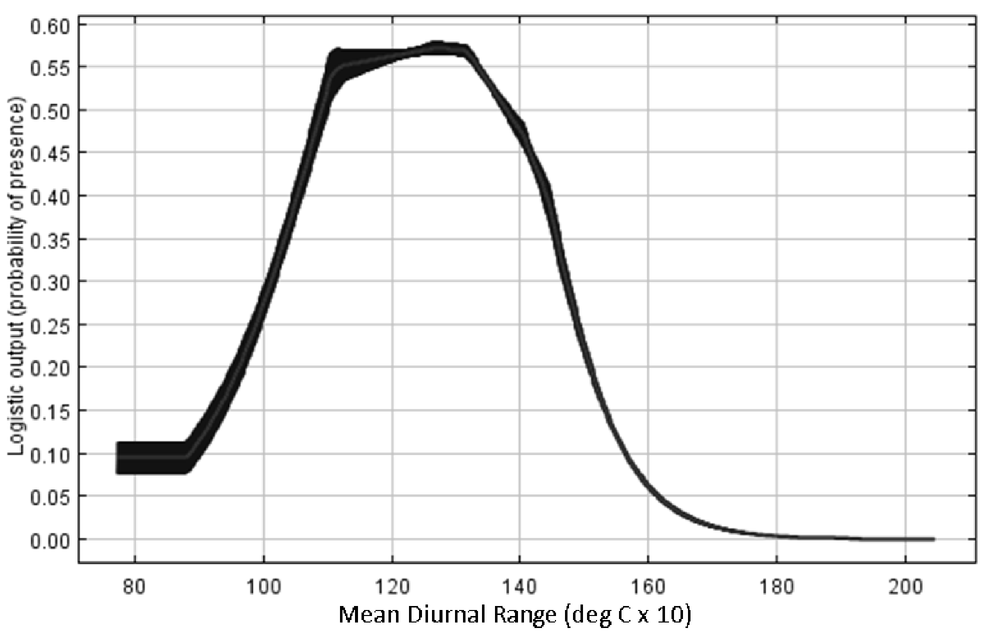
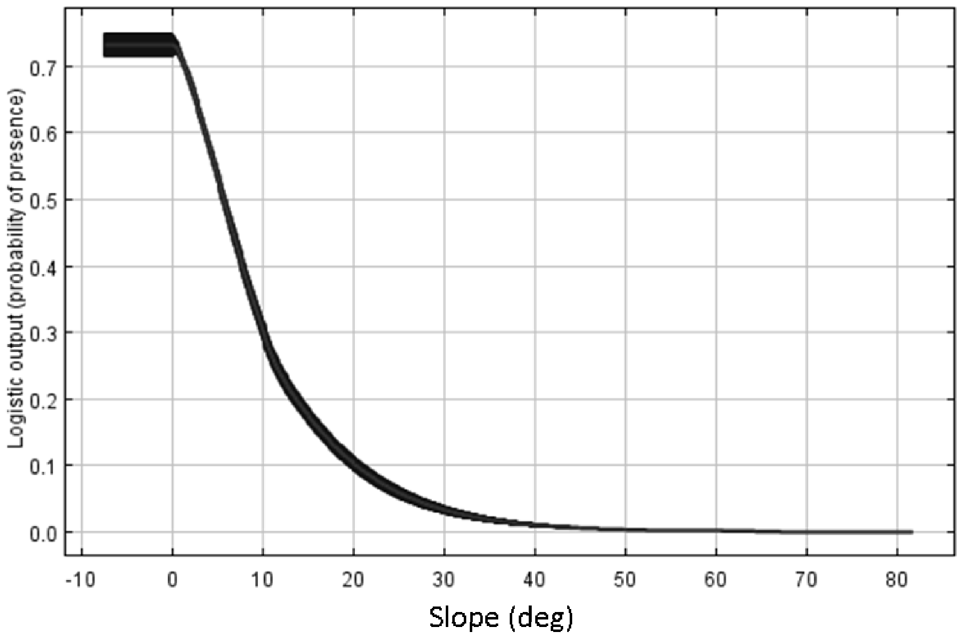
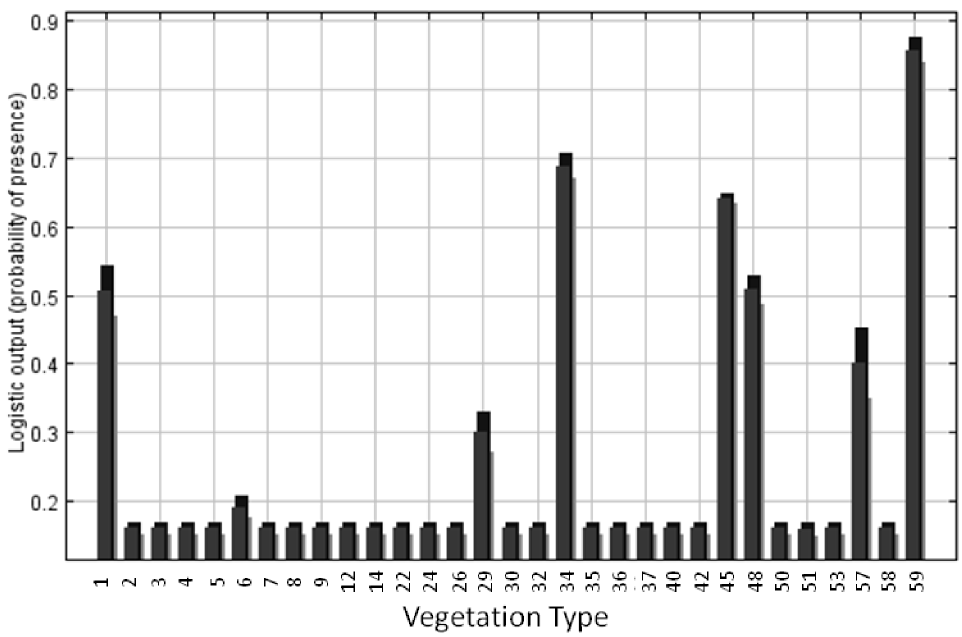


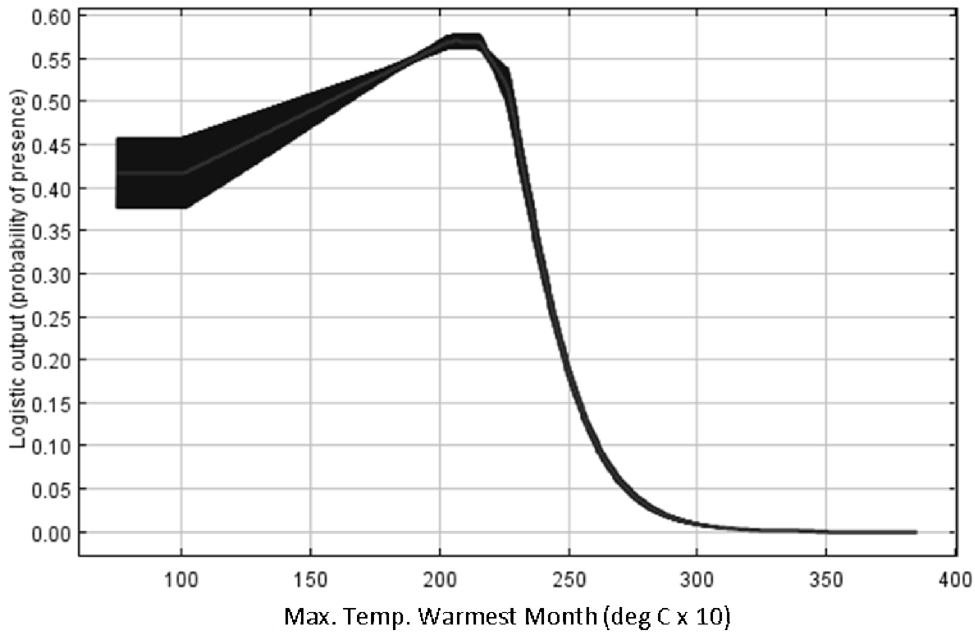
Figure 2.4a. Variable response curves for the top six predictors in the Maxent model prediction for Yosemite toad sites that are consistently occupied.

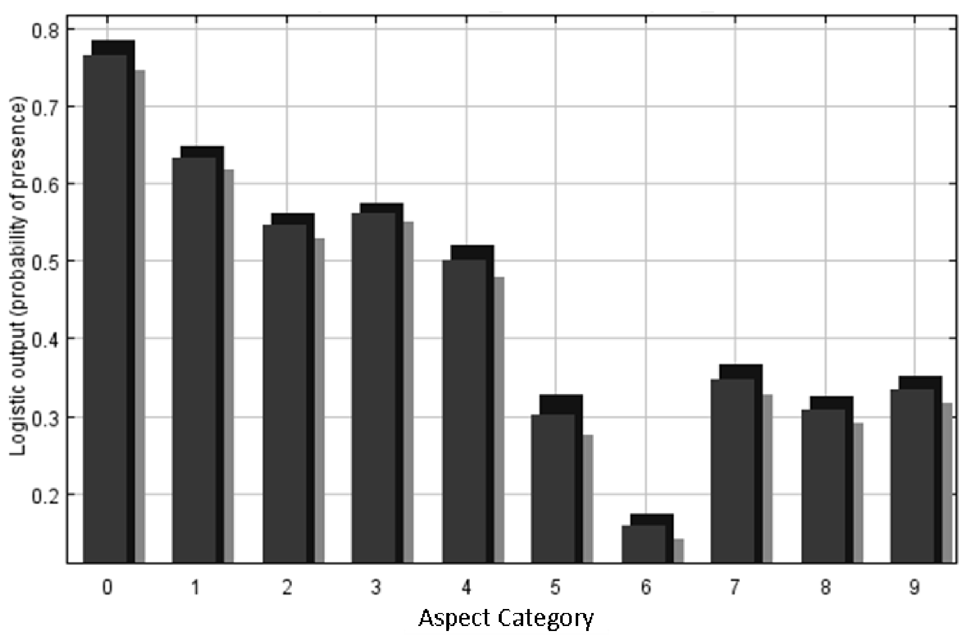




1	Alpine-Dwarf Shrub	14	Douglas-Fir	37	Montane Riparian
2	Agriculture	22	Freshwater Emergent Wetland	40	Pinyon-Juniper
3	Annual Grassland	24	Jeffrey Pine	42	Ponderosa Pine
4	Alkali Desert Scrub	26	Juniper	45	Red Fir
5	Aspen	29	Lodgepole Pine	48	Subalpine Conifer
6	Barren	30	Low Sage	50	Sagebrush
7	Bitterbrush	32	Mixed Chaparral	51	Sierran Mixed Conifer
8	Blue Oak-Foothill Pine	34	Montane Chaparral	53	Urban
9	Blue Oak Woodland	35	Montane Hardwood-Conifer	57	Water
12	Chamise-Redshank Chaparral	36	Montane Hardwood	58	White Fir
				59	Wet Meadow

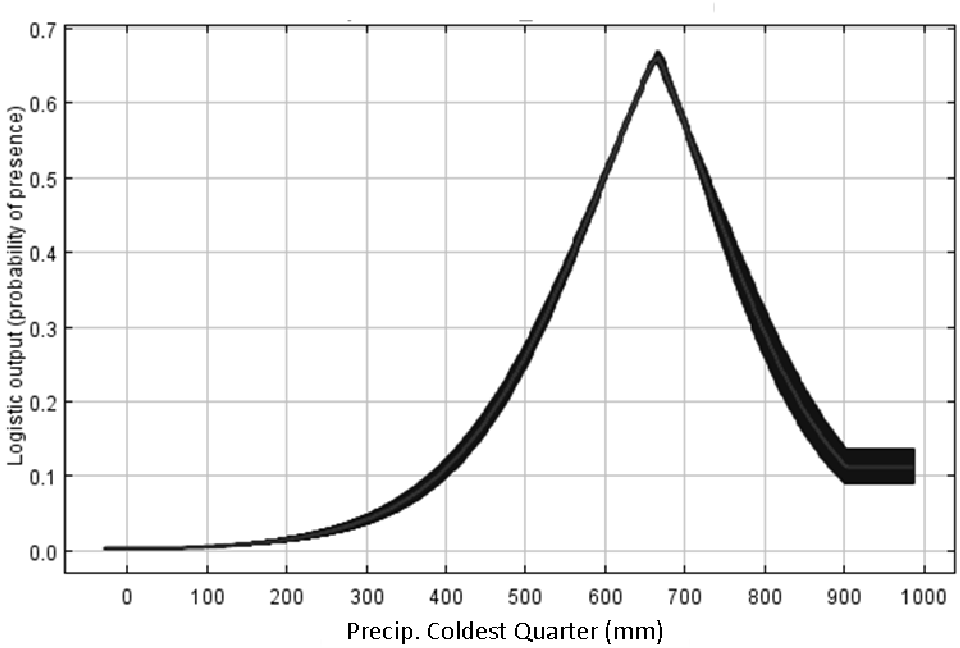
Figure 2.4b. Variable response curves for the top six predictors in the Maxent model prediction for Yosemite toad sites that are consistently occupied.





0	Flat (-1)	3	East (67.5-112.5)	6	Southwest (202.5-247.5)
1,9	North (0-22.5, 337.5-360)	4	Southeast (112.5-157.5)	7	West (247.5-292.5)
2	Northeast (22.5-67.5)	5	South (157.5-202.5)	8	Northwest (292.5-337.5)

Figure 2.4c. Variable response curves for the top six predictors in the Maxent model prediction for Yosemite toad sites that are consistently occupied.



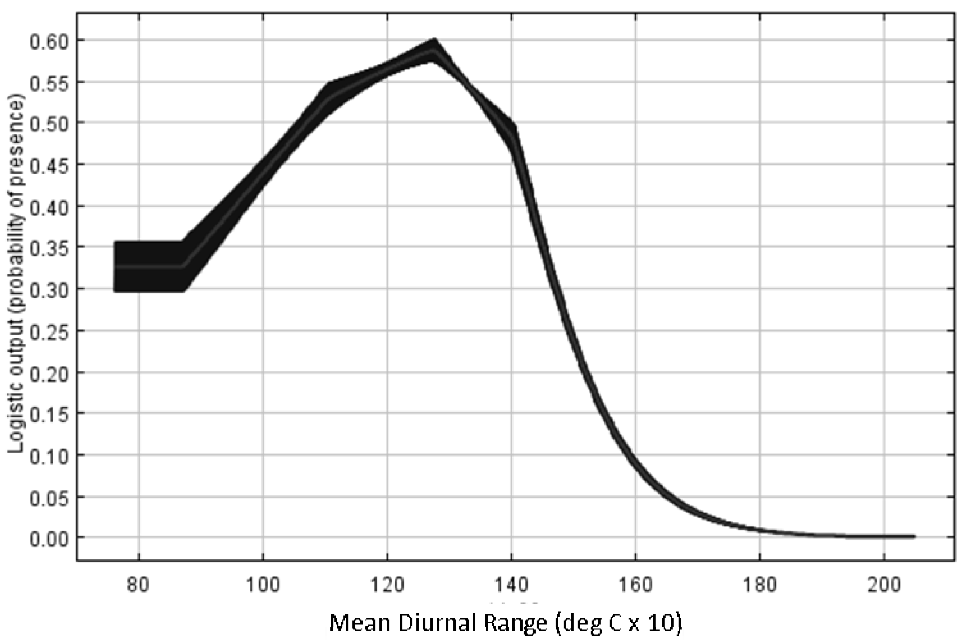
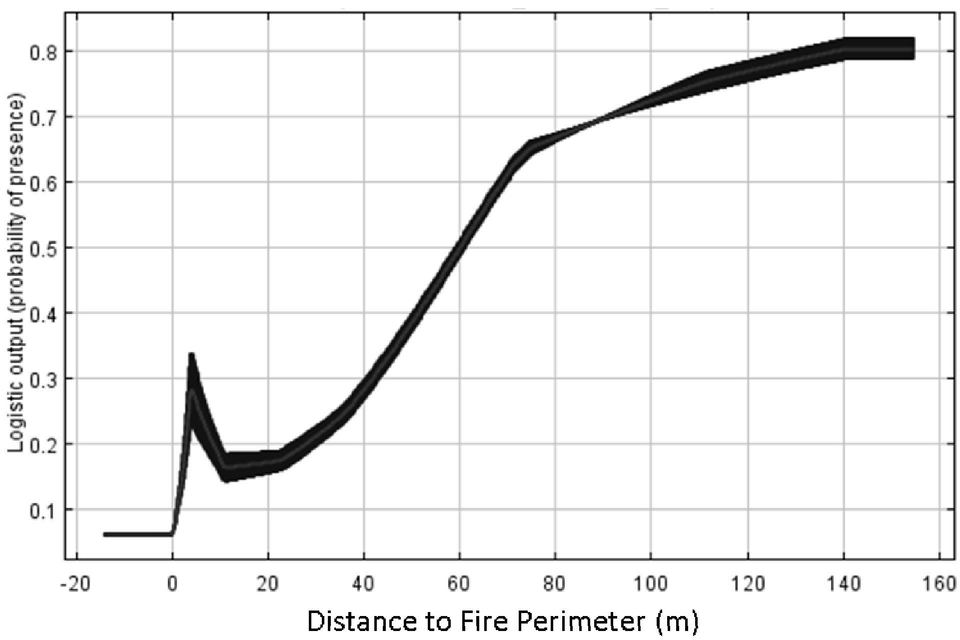
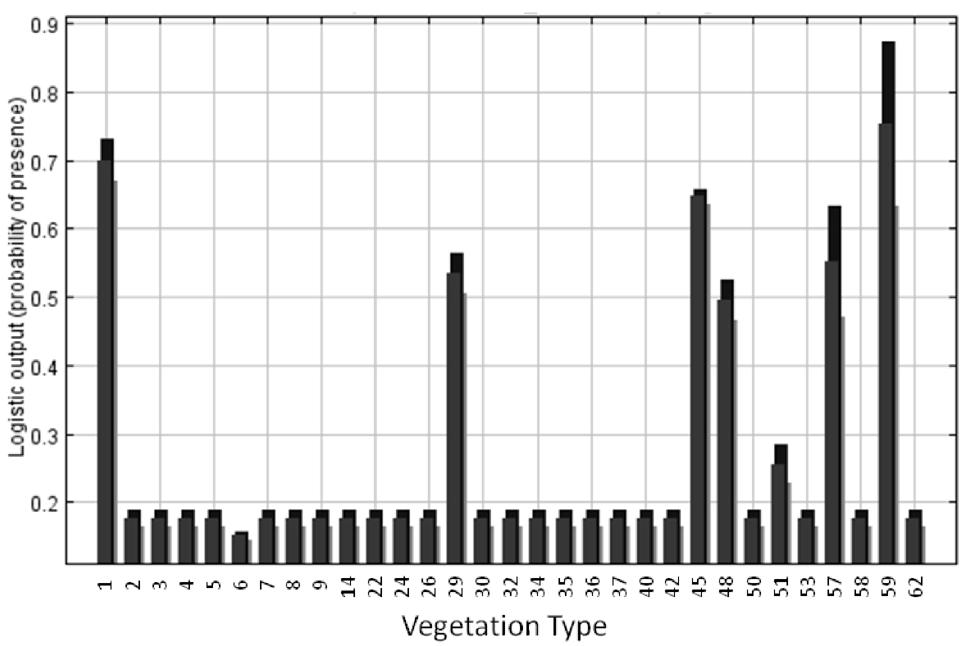


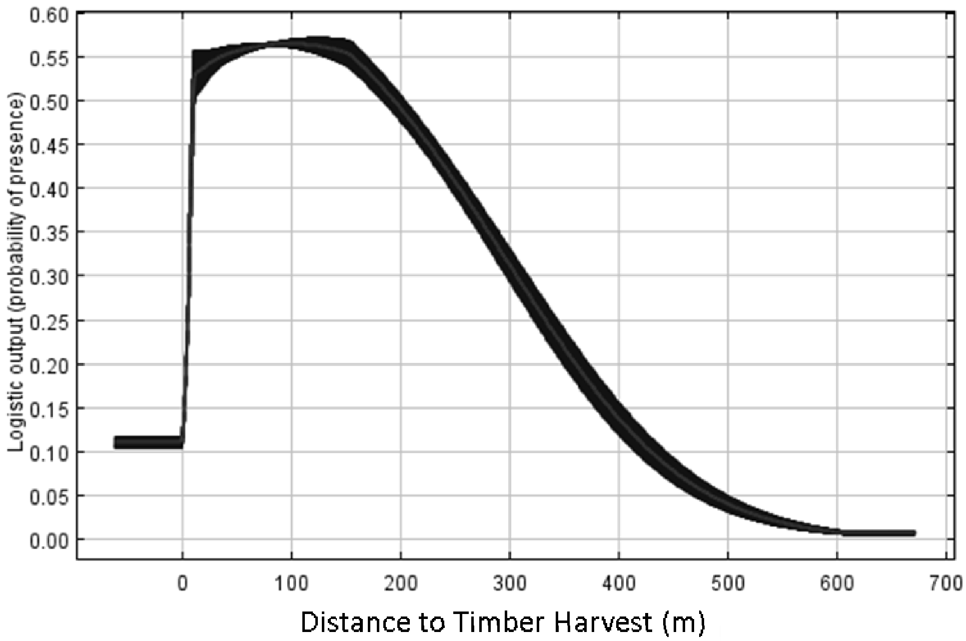
Figure 2.5a. Variable response curves for the top four predictors in the Maxent model prediction for Yosemite toad sites that are intermittently occupied.

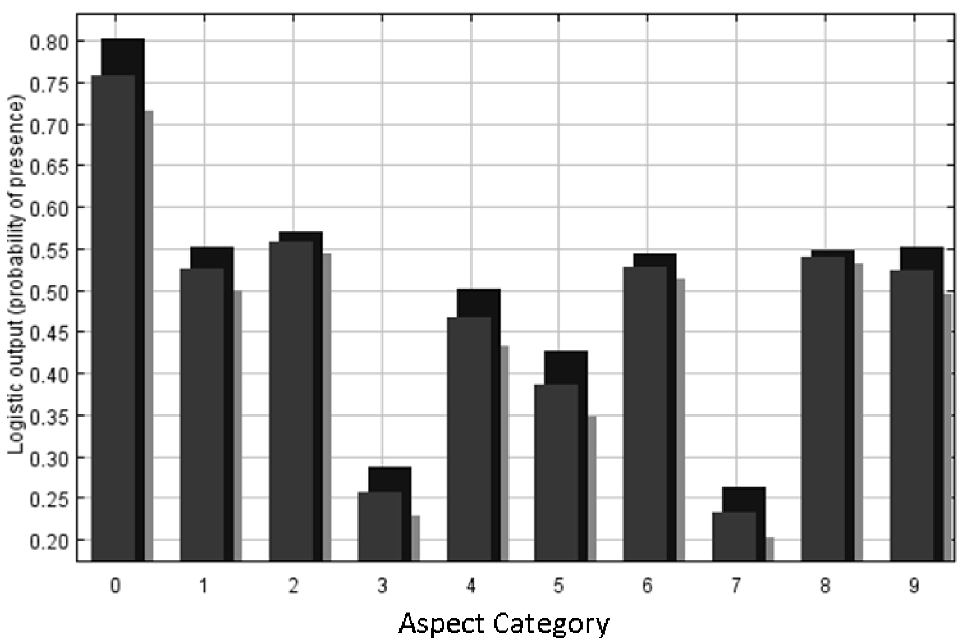




1	Alpine-Dwarf Shrub	22	Freshwater Emergent Wetland	40	Pinyon-Juniper
2	Agriculture	24	Jeffrey Pine	42	Ponderosa Pine
3	Annual Grassland	26	Juniper	45	Red Fir
4	Alkali Desert Scrub	29	Lodgepole Pine	48	Subalpine Conifer
5	Aspen	30	Low Sage	50	Sagebrush
6	Barren	32	Mixed Chaparral	51	Sierran Mixed Conifer
7	Bitterbrush	34	Montane Chaparral	53	Urban
8	Blue Oak-Foothill Pine	35	Montane Hardwood-Conifer	57	Water
9	Blue Oak Woodland	36	Montane Hardwood	58	White Fir
14	Douglas-Fir	37	Montane Riparian	59	Wet Meadow
				62	Unknown shrub type

Figure 2.5b. Variable response curves for the top four predictors in the Maxent model prediction for Yosemite toad sites that are intermittently occupied.





0	Flat (-1)	3	East (67.5-112.5)	6	Southwest (202.5-247.5)
1,9	North (0-22.5, 337.5-360)	4	Southeast (112.5-157.5)	7	West (247.5-292.5)
2	Northeast (22.5-67.5)	5	South (157.5-202.5)	8	Northwest (292.5-337.5)

Appendix 2.A. Environmental predictor variables considered for the Maxent models. Variables with an asterisk (*) were included in the models after analysis of cross-correlations.

Variable	**Source**
Elevation (m)	USGS National Elevation Dataset
*Aspect (category based on degrees)	USGS National Elevation Dataset
*Slope (degrees)	USGS National Elevation Dataset
*Vegetation (WHR type)	United States Forest Service, Pacific Southwest Region GIS Clearinghouse; CALVEG layer
*Distance to agricultural land (m)	California Fire Resources Assessment Program; land cover layer
*Distance to fire perimeter (m)	United States Forest Service, Pacific Southwest Region GIS Clearinghouse; FACTS Accomplished Harvest Activities layer
*Distance to timber harvest activity (m)	California Fire Resources Assessment Program; Fire Perimeters layer
Annual mean temperature (BIO1; ^{o}Cx10)	PRISM climate data, WorldClim calculation
*Mean diurnal range (BIO2; ^{o}C x10)	PRISM climate data, WorldClim calculation
Isothermality (BIO3)	PRISM climate data, WorldClim calculation
*Temperature seasonality (BIO4; SDx100)	PRISM climate data, WorldClim calculation
*Max. temp of warmest month (BIO5; ^{o}Cx10)	PRISM climate data, WorldClim calculation
Min. temp of coldest month (BIO6; ^{o}Cx10)	PRISM climate data, WorldClim calculation
Temperature annual range (BIO7; ^{o}Cx10)	PRISM climate data, WorldClim calculation
Mean temp of wettest quarter (BIO8; ^{o}Cx10)	PRISM climate data, WorldClim calculation
Mean temp of driest quarter (BIO9; ^{o}Cx10)	PRISM climate data, WorldClim calculation
Mean temp of warmest quarter (BIO10; ^{o}Cx10)	PRISM climate data, WorldClim calculation
Mean temp of coldest quarter (BIO11; ^{o}Cx10)	PRISM climate data, WorldClim calculation
*Annual precipitation (BIO12; mm)	PRISM climate data, WorldClim calculation

Appendix 2.A, continued

Variable	Source
Precipitation of wettest month (BIO13; mm)	PRISM climate data, WorldClim calculation
Precipitation of driest month (BIO14; mm)	PRISM climate data, WorldClim calculation
Precipitation seasonality (BIO15; CV)	PRISM climate data, WorldClim calculation
Precipitation of wettest quarter (BIO16; mm)	PRISM climate data, WorldClim calculation
*Precipitation of driest quarter (BIO17; mm)	PRISM climate data, WorldClim calculation
Precipitation of warmest quarter (BIO18; mm)	PRISM climate data, WorldClim calculation
*Precipitation of coldest quarter (BIO19; mm)	PRISM climate data, WorldClim calculation

Note: WHR is the California Wildlife-Habitat Relationships vegetation classification. BIO represents the ‘bioclim’ variable calculated from PRISM climate data (http://www.prism.oregonstate.edu) using an ARC AML script (mkBCvars.aml; http://www.worldclim.org/mkBCvars.aml). SD is standard deviation, CV is coefficient of variation.

CHAPTER 3. MOVEMENTS AND HABITAT USE OF YOSEMITE TOADS (*ANAXYRUS* (=*BUFO*) *CANORUS*) IN THE SIERRA NATIONAL FOREST, CALIFORNIA

Christina T. Liang[1,2]

[1]Department of Environmental Science and Policy, University of California at Davis, Davis, CA 95616

[2] USDA Forest Service, Pacific Southwest Research Station, Sierra Nevada Research Center, 1731 Research Park Drive, Davis, CA 95618 email: ctliang@ucdavis.edu

ABSTRACT

I conducted a study on the movements and habitat utilization of adult Yosemite toads (*Anaxyrus* (=*Bufo*) *canorus*) in the Sierra National Forest in late spring and summer of 2007-2009. Forty-two adult toads were captured from breeding meadows, outfitted with radio transmitters and radio-tracked as they left the breeding sites. I collected data on the location, habitat and microsite type, and environmental conditions for each individual tracked. Yosemite toads moved up to 1.26 kilometers away from breeding meadows and the average distance was 275 meters. Females moved significantly longer distances than males and had a larger home range. Distance traveled was related to Julian day as well as the interaction between day and sex. Yosemite toads used terrestrial environments extensively and were found throughout the mixed-conifer forest. Burrows were the most commonly used microsite but other protective cover such as logs, rocks and tree stumps were also used. The locations occupied by Yosemite toads in the terrestrial environment were more open with less canopy and fewer woody species than surrounding areas. The results of this study have implications for identifying population processes such as

metapopulation dynamics, as well as for management purposes such as establishing the size of buffer zones and identifying sensitive habitat in the terrestrial environment.

Keywords: Species movement, habitat utilization, Yosemite toad, *Anaxyrus canorus*, *Bufo canorus*

INTRODUCTION

The Yosemite toad (*Anaxyrus* (=*Bufo*) *canorus*) is a high-elevation species endemic to the Sierra Nevada mountains in California. The toad is found in both wetland and terrestrial habitats, moving from breeding sites in wetland areas to upland foraging areas (Martin 2008). Movement data are important for determining spatial population structure in metapopulations or patchy populations (Harrison and Taylor 1997) and for management purposes such as establishing buffers around meadows (Lee et al. 2004) and identifying movement corridors (Chetkiewicz et al. 2006). Movement information is also necessary for identifying animals' habitat requirements and use patterns. Understanding movement is especially important for species of special concern such as the Yosemite toad, whose populations appear to be in decline for unknown reasons (USFWS 2002). There is minimal information regarding adult movements of the toad away from breeding sites and associated habitat use (Kagarise Sherman 1980, Martin 2008).

The Yosemite toad breeds in the late spring in areas of shallow water such as wet meadows, edges of ponds and lakes, and slow-moving streams. Breeding typically lasts for 1-2 weeks, after which adults move into other parts of the wetland area or into the terrestrial environment. The species is sexually dimorphic and adult females are generally larger than adult males in both mass and length (Karlstrom 1962, Kagarise Sherman 1980). The aims of this study were to: (1) determine mean and maximum distances traveled by Yosemite toads away from breeding sites; (2) analyze differences in distance traveled by sex and by meadow location; (3) examine microsite usage by Yosemite toads; and (4) examine terrestrial vegetation communities in sites with and without Yosemite toads.

METHODS

Study area

I conducted this study in the Bull Creek watershed within the Dinkey Creek drainage in the Sierra National Forest (SNF). The SNF is on the western slope of the central Sierra Nevada mountains and is within the southern part of the Yosemite toad's historic range. The Bull Creek watershed is in the southern portion of the SNF at elevations of approximately 7,000 – 8,000 ft (2,130 – 2,440 m) in mixed-conifer forest. In 2007, I captured adult toads at two breeding meadows (520M15, 520M20) in the Bull Creek watershed. In 2008 and 2009, I captured adult toads in two additional breeding meadows (520M14, 520M25) for a total of four meadows in the Bull Creek watershed (Figure 3.1).

Yosemite toad radio-tracking

I radio-tracked 35 adult Yosemite toads (16 females, 19 males) in 2007-2009. Six of the toads were captured and tracked in multiple years: two females in two years, three males in two years, and one male in all three years of the study. A total of 42 sets of tracking locations (18 females, 24 males) were collected and used in the data analysis. I captured toads by hand at breeding meadows in April-June, weighed them using a field scale, measured them with a ruler for snout-vent length (SVL), and implanted them with a PIT (passive integrated transponder) tag for identification purposes. The PIT tag was inserted under the skin along the dorsum and maneuvered into position near the base of the spine. I only captured individual females after they had finished mating and were no longer gravid; I captured males opportunistically.

I outfitted individual toads with radio transmitters and tracked them as they left the breeding meadows. G3-1V transmitters from AVM Instrument Company with expected battery life of 5-12 weeks were used in 2007; SOPR-2070 transmitters from Wildlife Materials with expected battery life of 18-21 weeks were used in 2008 and 2009. I attached the transmitters to the adults using a belt system modified after Muths (2003). Flexible, surgical grade polyethylene tubing (inside diameter=0.58 mm, outside diameter=0.99 mm) was placed through an opening in the transmitter casing. A nylon coated stainless steel wire was threaded inside the rubber tubing and crimped shut with a sterling silver bead. Wire ends were cut flush to the crimp. I sized the tubing and wire belt to fit over the widest part of the toad’s thighs when the legs were fully extended and held together. The transmitter and belt apparatus was then maneuvered over the legs and placed it around the waist of the toad with the transmitter situated on the dorsal side of the animal. The total mass of the transmitter and belt was approximately 2 grams. I only attached transmitters to toads that weighed 20 grams or more, so that the transmitter and belt apparatus was equal to or less than 10% of the individual’s mass.

I used a Telonics TR-2 receiver and H-type directional antenna to track Yosemite toads every 1-19 days, which allowed enough time for independence of observations (Swihart and Slade 1985). Toad locations were recorded with a GPS (Garmin eTrex Legend). Along with location, I collected data on environmental conditions (air and ground temperature, relative humidity, cloud cover and wind) and general habitat type and cover. I removed transmitters in August-September before the battery life was expected to expire, or earlier if the transmitter began to send erratic signals.

Straight-line distance from the capture site in the meadow to every recorded location was calculated for each adult Yosemite toad using GIS (ESRI ArcGIS 9.3). Home range for each individual was calculated by the minimum convex polygon method for comparison purposes using Hawth's Analysis Tools v3.27 for GIS. I used t-test and one-factor ANOVA to compare differences in straight-line distance and home range by sex or meadow, using log-transformed values to meet the assumption of normality.

I analyzed distance using a mixed model with sex, meadow and Julian day as fixed factors and toad as the random subject on which repeated measurements were taken. Year was not included in the model because it was highly correlated with toad. To analyze the within-subject variance-covariance structure, I ran separate models for compound symmetry, unstructured, autoregressive, and autoregressive with heterogeneous variances. I chose the model with the lowest Akaike's information criterion value for the covariance structure. Irregularly spaced time points were accounted for by using a multilevel model with time as a linear effect, shown in the following equations.

Level 1 (day): distance = $\beta_{0j} + \beta_{1j}$ (day) + e_{ij}

Level 2 (toad): $\beta_{0j} = \gamma_{00} + \gamma_{01}$(sex) + γ_{02}(meadow) + γ_{03}(sex * meadow) + u_{0j}

Level 2 (toad): $\beta_{1j} = \gamma_{10} + \gamma_{11}$(sex) + γ_{12}(meadow) + γ_{13}(sex * meadow) + u_{1j}

(1)

where *i* refers to the level 1 unit (i.e., day) and *j* refers to the level 2 unit (i.e., toad). In the level 1 model, the intercept (β_{0j}) and slope (β_{1j}) are random variables defined by the level 2 equations and the residual (e_{ij}) is the standard linear model residual term. In the level 2 model, the intercepts (γ_{00}, γ_{10}) and regression coefficients (γ_{0n}, γ_{1n} for n=1, 2, 3) are the standard linear regression model variables. The residuals (u_{0j} , u_{1j}) are random variables with parameters $E(u_{0j}) = E(u_{1j}) = 0$, $var(u_{0j}) = \sigma^2$, $var(u_{1j}) = \sigma^2$, $cov(u_{1j}, u_{1j}) = \sigma_{u01}$.

Substituting the level 2 model into the level 1 model results in the following single equation, with the random variables in square brackets.

distance = $\gamma_{00} + \gamma_{01}$(sex) + γ_{02}(meadow) + γ_{03}(sex * meadow) + γ_{10}(day) + γ_{11}(sex * day) + γ_{12}(meadow * day) + γ_{13}(sex * meadow * day) + [$u_{0j} + u_{1j}$(day) + e_{ij}]

(2)

To model the possible quadratic effect of time, I added a day*day term to (2).

$$\text{distance} = \gamma_{00} + \gamma_{01}(\text{sex}) + \gamma_{02}(\text{meadow}) + \gamma_{03}(\text{sex} * \text{meadow}) + \gamma_{10}(\text{day}) + \gamma_{11}(\text{sex} * \text{day}) + \gamma_{12}(\text{meadow} * \text{day}) + \gamma_{13}(\text{sex} * \text{meadow} * \text{day}) + \gamma_{20}(\text{day*day}) + \gamma_{21}(\text{sex} * \text{day*day}) + \gamma_{22}(\text{meadow} * \text{day*day}) + \gamma_{23}(\text{sex} * \text{meadow} * \text{day*day}) [u_{0j} + u_{1j}(\text{day}) + u_{2j}(\text{day*day}) + e_{ij}] \quad (3)$$

I used the model in (3) to look at distance traveled by Yosemite toad as a function of sex, meadow and time as Julian day. Time was also included as a quadratic term to account for the possible non-linear rate of movement, whereby distance traveled varies during different time periods. I analyzed the data with R version 2.11.1 (http://www.r-project.org/) using the nlme package.

Yosemite toad microsites

Microsite type was recorded when I radio-tracked the location of Yosemite toads. Microsites were classified into nine categories: burrow, depression, downed wood, log, open/no cover, rock, stump, vegetation, water. The burrow category included both shallow burrows and more extensive underground burrows. The depression category was used for small concavities in the ground surface. Downed wood included smaller pieces of wood such as branches and bark which were not as large as downed logs. The open/no cover category was used when toads were exposed in the environment, in both terrestrial and wetland habitats. The rock category included rocks of all sizes, from small flat rocks to boulders. Stump was used for tree stumps in the terrestrial habitat. The vegetation category included herbaceous and woody cover. The water category included meadow pools and streams.

Microsite usage data from each Yosemite toad was compared using a Friedman one-way repeated measures analysis of variance by ranks. It is a non-parametric test similar to parametric repeated measures ANOVA. A parallel coordinates plot was constructed with cover type categories along the vertical axes; lines in the graph connect cover type usage for each individual toad. Post-hoc tests for multiple comparison analysis of ranked data were performed, analogous to Tukey's HSD for ANOVA. I analyzed the data with R version 2.11.1 using the coin and multcomp packages, and the Friedman post-hoc R code from Galili (2010) performing the Wilcoxon-Nemenyi-McDonald-Thompson test (Hollander and Wolfe 1999).

Vegetation sampling

I conducted vegetation sampling to compare habitat with and without Yosemite toads in upland terrestrial locations. Occupied locations were found by radio-tracking the toads. Unoccupied locations were randomly selected from a set of grid points spaced 150 meters apart that were established within the Bull Creek watershed for the US Forest Service King's River Experimental Watershed (KREW) project (Hunsaker and Eagan 2003). Yosemite toads were presumed to be absent from these locations although this could not be definitively verified. However, none of the tracked toads were found in or near the locations assumed to be unoccupied. I sampled a total of 38 occupied and unoccupied locations in 2008-2009; 26 were sampled in 2008 (13 occupied, 13 unoccupied) and 12 were sampled in 2009 (6 occupied, 6 unoccupied).

At each occupied and unoccupied location, I placed a 22 meter transect in a random direction. I conducted three types of sampling: quadrat sampling for herbaceous plants, line-intercept sampling for shrubs and canopy, and belt transect sampling for trees. Sampling methods followed the protocol established and used by KREW personnel (protocol updated 8/30/05, *personal communication*). In quadrat sampling, I placed a 1m x 1m quadrat on the left side of the transect axis (when facing from 0 to 22 m) at 2 m, 7 m and 12 m. One side of the quadrat was the transect axis so that the quadrats were at 2-3 m, 7-8 m and 12-13 m along the transect. I estimated percent cover for all species within the quadrat along with percent cover of rock, gravel, soil, moss, and downed dead wood all under 1 m. Cover was estimated to the nearest 1% up to 20% and to the nearest 5% above 20%, and total coverage could exceed 100% due to species overlap. In line-intercept sampling, I recorded all woody species that intersected the transect at two levels: 2 m or below and above 2 m. Intersection below 2 m was determined by holding a meter stick perpendicular to level. Intersection above 2 m was determined using a densitometer. I recorded data at every meter along the transect from 2 to 21 m, resulting in 20 sampled points. In the belt transect sampling, I counted all free-standing woody species taller than 2 m within 5 m on both sides of the transect from 2 to 22 m, resulting in a 10 m x 20 m survey area. I identified all vegetation to species if possible, otherwise to genus following Hickman (1993).

I calculated Sørensen dissimilarity for all possible pairs of locations to compare vegetation communities at locations with Yosemite toads to those without toads. Sørensen dissimilarity is a distance measure used to evaluate the disimilarities of two communities, with low dissimilarity values indicating more similar communities and high values indicating different communities. For each transect, I calculated the mean Sørensen values comparing the transect both to Yosemite toad occupied locations and to toad unoccupied locations for the three vegetation layers (herbaceous, shrub and canopy, and trees). T-tests were used to test for differences in the mean dissimilarity scores of the transects at locations with toads versus locations without toads. I analyzed the data with R version 2.11.1 using the ecodist package.

RESULTS

Radio-tracking

The mass of the Yosemite toads used for tracking averaged 46.4 g (SD 8.7) for females and 30.0 g (SD 5.0) for males; SVL averaged 76 mm (SD 5) for females and 67 mm (SD 4) for males. The length of time that each Yosemite toad was tracked ranged from 13 to 127 days and the number of locations ranged from 5 to 38 (Table 3.1). The length of time individual toads could be tracked was sometimes limited by transmitter failure or the shedding of the transmitter by the toad. Maximum distance traveled was 1,260.9 m for a female (F4-09) and 865.2 m for a male (M02-08). Distances traveled by each Yosemite toad are shown in Figure 3.2. The average distance traveled by females was twice as large as by males and the average home range for females was more than 1.5 times as large as for males (Table 3.2). Differences between females and males were significant for mean distance traveled (two-sided t-test $p=0.004$, $df=31$) and maximum distance traveled (two-sided t-test $p=0.048$, $df=30$) but not for home range (two-sided t-test $p=0.376$, $df=33$). There were no significant differences between toads from different meadows for mean distance traveled (ANOVA p=0.335, df=3,38), maximum distance traveled (ANOVA p=0.697, df=3,38), or home range (ANOVA p=0.641, df=3,38).

The mixed model was used to look at differences in distance traveled based on sex, meadow, Julian day, and interactions between all variables. The variance-covariance model with the lowest AIC value was the autoregressive with heterogeneous variances and this covariance structure was used in the mixed model. Day, day*day and sex*day were all highly significant ($p<0.001$); neither sex nor meadow were significant variables (Table 3.3). Most of the longer distances traveled occurred within 60 days of leaving the breeding site (Figure 3.3).

Microsite use

Yosemite toads were most often found in burrows (Figure 3.4) and results of the Friedman test showed that there was a significant difference in cover type use ($p<0.0000$). Post-hoc analysis showed that burrows were used significantly more than all other cover types except for vegetation and water ($p<0.01$ for all significant comparisons). Downed wood was used less than the open/no cover, vegetation, water as well as burrow cover types ($p<0.05$ for all comparisons). All other cover type comparisons were not significant (p=0.05 level).

Vegetation sampling

Mean Sørensen dissimilarity was significantly lower between Yosemite toad occupied locations than between toad occupied and unoccupied locations for all vegetation layers (Table 3.4). Vegetation communities in occupied locations were more similar to one another than to vegetation communities in unoccupied locations. Herbaceous, shrub and tree species from 20 different families were identified during the vegetation sampling (Table 3.5).

Locations with toads generally had higher percent coverage of herbaceous plants such as *Lupinus* and *Lotus* species, but contained fewer woody plants and had less canopy cover. Locations without toads generally had more trees and shrubs such as red fir (*Abies magnifica*), white fir (*Abies concolor*) and bush chinquapin (*Chrysolepis sempervirens*). Woody species were found in the ground layer as well as the understory and overstory in locations without toads but not in locations with toads.

DISCUSSION

Yosemite toad movements

Adult Yosemite toads moved up to 1,260.9 m away from breeding meadows during this study and the average distance was 275.1 m (SD 260.7). This maximum distance is greater than previously reported dispersal distances of 150-750 m for this species (Karlstrom 1962, Kagarise Sherman 1980, Morton 1981, Kagarise Sherman & Morton 1984). The only other radio-tracking study of adult Yosemite toads, conducted by Martin (2008) in 1995-1997 on 10 toads, reported a maximum distance traveled of 657.4 m away from breeding pools. Toads in that study were tracked in the northern part of their range, in the Highland Lakes area on the Stanislaus National Forest which is at higher elevation (2,620 m) than the Bull Creek watershed and in alpine forest in a glacial cut valley. The mean distance traveled was 278.6 m (which is very similar to the results from this study.

Collectively these studies suggest that the mean distance traveled is representative of the species but maximum distance might be affected by elevation, forest type or terrain.

The maximum distance traveled by the Yosemite toad is not atypical for an amphibian species. Smith and Green (2005) reviewed 166 studies of 90 amphibian species and found that the mean maximum distance moved was 2,023.5 m (SD 4,895.6). For anurans, the mean maximum distance was 2,922.5 km (SD 5,929.9) in 102 studies of 52 species. The majority of anuran species (56%) traveled a maximum distance of less than 1 km and 31% of species traveled less than 400 m, but 7% of anurans moved a maximum distance of more than 10 km. Overall, amphibians show a wide range of movement patterns (Smith and Green 2005).

Female Yosemite toads moved significantly greater distances and had larger home ranges than males. The closely related boreal toad (*Anaxyrus* (=*Bufo*) *boreas*) exhibits the same pattern, with females moving significantly farther from breeding sites than males (Bartelt 2000, Muths 2003). Females of both species are larger than their male counterparts and may have greater water storage capability, allowing for longer distance movement away from wetland areas or water sources. Females may also have higher energy requirements for egg production and so use a larger foraging area in order to meet their energetic needs (Muths 2003, Bartelt et al. 2004). Female Yosemite toads do not necessarily breed every year (Kagarise Sherman 1980, Morton 1982) and might not be as philopatric as males. Bartelt et al. (2004) postulated that males remain closer to breeding sites in order to have a competitive advantage when mating begins in the spring.

Julian day was a significant factor in Yosemite toad movement both as a linear and quadratic predictor. Toads left the breeding sites after mating finished in May-June and moved into the terrestrial habitat or other areas of the meadows. Most long-distance movement was accomplished within the first 60 days after leaving the breeding sites though some toads did move long distances after that period. Yosemite toads were observed to stay in the same location for several days or weeks before moving again. The length of time that a toad spent in a given area was variable. Some individuals stayed in the same area for weeks and did not move any further after the initial travel away from the meadow. There was a significant interaction between Julian day and sex in toad movement. Females leave breeding areas as soon as they finish laying eggs while males stay in breeding areas for longer periods of time to try to mate with as many females as possible. Kagarise Sherman (1980) found that males that mated successfully tended to have stayed at breeding sites longer.

Yosemite toads did not follow an obvious path through the environment as they moved from the breeding meadows into the upland terrestrial environment. Although some individuals did move along drainages, most did not use these drainages or other moist environments as they moved. All toads appeared to travel longer distances during the night, perhaps to minimize evaporative water loss (Tracy et al. 1993, Bartelt et al. 2004). Toads also did not appear to follow man-made roads or trails as they moved but they did cross the roads. Individuals were found to have crossed wide, graded roads with vehicular activity and were periodically located in burrows or under rocks within 1 m of these roads.

Microsite use

Previous studies reported that Yosemite toads were often found in subterranean rodent burrows made by species such as mountain meadow voles (*Microtus montanus*) and pocket gophers (*Thomomys monticola*) (Mullally 1953, Mullally and Cunningham 1956, Karlstrom 1962). Burrows provide protection from cold overnight temperatures and offer a moister microclimate than the surrounding open environment. This study confirmed that toads were found more often in burrows and they used shallow burrows where the toad could be seen by looking inside the burrow as well as subterranean burrows where the toad was not visible. However, Yosemite toads also used a variety of other microsites such as logs, rocks and tree stumps. They appeared to opportunistically select microsites and to remain in ones that perhaps provide adequate thermal insulation and favorable moisture conditions (Martins 2008). Individuals were often found in the same microsite for several days to weeks and possibly overwintered in these sites.

Yosemite toads were occasionally found basking out in the open, although they usually moved into cover when approached by an observer. Toads that were not in the open were difficult to locate and were well concealed in the environment. It would be challenging to find toads in their microsites without the use of an attached transmitter to identify their exact locations. Transmitters did not appear to interfere with toad activity, either during breeding (for males) or during movement and habitat use in aquatic or terrestrial environments.

Yosemite toads showed site fidelity to terrestrial microsites as well as to breeding sites. Site fidelity to breeding sites was strong, and the majority of individuals identified in multiple years (though not necessarily tracked) were found in the same meadow pools during the breeding period (CT Liang *personal observation*). Site fidelity to upland terrestrial microsites also was evident, as some of the individuals tracked in multiple years returned to the same upland areas. Two of the repeat males were located in the exact same microsites (rock and tree stump) in multiple years. The other four repeat individuals were found in the same general areas in multiple years but did not return to the exact same microsites. Site fidelity to both breeding sites and cover types have been documented for many amphibian species (examples in Smith and Green 2005).

Terrestrial habitat

Little attention has been paid to the terrestrial habitat used by the Yosemite toad. Most of the previous studies focused on wetland areas because toads were assumed to prefer this habitat (Mullally 1953, Karlstrom 1962, Kagarise Sherman 1980, Kagarise Sherman and Morton 1984). Toads are also difficult to locate in the terrestrial environment without the aid of tracking devices, which restricted previous investigations in these upland areas. The radio-tracking study by Martin (2008) was the first to examine terrestrial habitat use and over-wintering burrows. He found that toads extensively used the upland foraging habitat, described as "located in the lush vegetation near seeps and/or springs on the steeply sloping mountain sides above the breeding meadows that are dominated by willow thickets and/or lupine stands." This study confirms that Yosemite toads regularly use the upland terrestrial environment and are not only found in the wetland environment. However, unlike Martin (2008), toads were found in areas away from water sources and in vegetation communities other than willow thickets and lupine stands. Toads were found throughout the mixed-conifer forest and were associated with a variety of plant species (Table 3.5).

Within the mixed-conifer forest in this study, the Yosemite toad was found in locations that were more open than surrounding areas. There were fewer trees and shrubs and less canopy and woody litter in toad occupied sites compared to random sites in the watershed. Microsites were generally in clearings and not under woody plants. These clearings often had higher percent cover of herbaceous species in the ground layer. Some of the herbaceous plants such as lupines and *Lotus* species prefer full sun. These plants also attract insects such as ants and bees, which are preyed upon by toads (Mullally1953, Kagarise and Sherman 1984).

Summary and conclusions

This study found that Yosemite toads moved further than previously reported, up to 1.26 km away from breeding meadows. The average distance traveled was 275 m. This has implications for determining the type of spatial population structure formed by Yosemite toads. Amphibians are often thought to exhibit a metapopulation structure, which is a population of populations connected by dispersal (Levins 1969). One of the requirements of a metapopulation is limited dispersal between breeding sites (Hanski et al. 1995, Hanski 1999) although this condition has rarely been tested for in amphibians (Smith and Green 2005). This study shows that Yosemite toads do have the capability to travel distances between breeding meadows (average distance between known occupied meadows in the Bull Creek watershed is approximately 800 m) but most individuals do not move that far. Thus it is possible that toads are in a metapopulation structure since the requirement of limited dispersal is met, although other requirements such as asynchronous dynamics in breeding meadows need to be evaluated. If Yosemite toads are in a metapopulation structure, landscape connectivity will have an important role in population persistence.

These movement data also have important implications for management, where 30.5 m (100 ft) buffers are usually put in place to protect riparian and wetland species (Clinnick 1985, Lee et al. 2004). These buffers may not be adequate to encompass both the wetland and upland terrestrial habitats used by Yosemite toads and new buffer zones should be considered; factors to consider when establishing a buffer zone size for anurans are time of year and sex (Goates 2007). In a meta-analysis of the effectiveness of riparian buffers for species conservation, Marczak et al. (2010) analyzed 397 studies comparing species abundance in riparian buffer zones and unmanipulated reference riparian sites. They found that current buffer zones are not adequate for many riparian species. Response to buffer zones varied by taxonomic group, and amphibian abundance decreased overall in buffer zones compared to reference sites. For all taxa, wider buffer zones (greater than 50 m) did not have a greater effect on species abundance in comparison to narrower buffers; buffer zones less than 50 m had more variable responses with both large positive and negative effects on species abundance (Marczak et al. 2010). Wider buffer zones alone may not be sufficient to fully protect riparian species. Olsen et al. (2007) suggest that targeted protection of sensitive habitat may be a better management approach, instead of offering limited protection everywhere. For mobile species such as the Yosemite toad which can travel over 1 km, this necessitates the identification of sensitive habitat in the upland terrestrial environment.

This study confirmed that Yosemite toads made extensive use of the terrestrial habitat and were found throughout the upland environment. In the non-breeding season, toads were not tied to moist areas and were found in locations away from water sources. Burrows were the most used microsites but other protective microsites such as rocks and tree stumps were also used. The locations occupied by Yosemite toads in the terrestrial environment were more open with less canopy and fewer woody species than surrounding areas. These occupied locations may be more similar to historic vegetation communities under pre-fire suppression conditions. Fire suppression in the past century has benefited the growth of shade tolerant species such as white fir (*Abies concolor*) and red fir (Abies *magnifica*) and led to an increase in tree densities (Kilgore and Taylor 1979, Parsons and DeBendeetti 1979, Stephens et al. 2009). Forest management practices that reduce woody biomass may have beneficial effects for the Yosemite toad. However, more study on the potential effects of ground disturbance on Yosemite toad terrestrial microsites and consideration of the seasonality of forest management operations are needed.

ACKNOWLEDGEMENTS

I thank M. Thornton, C. White, A. Lind, R. Grasso, C. Brown, K. Kiehl, L. Wilkinson, J. Adair, C. Hunsaker, S. Barnes, and P. Strand for assistance and support for this project. A. Lind, S. Lawler, and J. Quinn provided helpful reviews on earlier versions of the manuscript. Funding was provided by the USDA Forest Service-Sierra Nevada Research Center, the Sierra National Forest, and UC Davis (Jastro-Shields Graduate Research Scholarship Award and Graduate Group in Ecology Block Grant Award).

LITERATURE CITED

Bartelt, P. E. 2000. A biophysical analysis of habitat selection in western toads (Bufo boreas) in southeastern Idaho. Ph.D. dissertation. Idaho State University.

Bartelt, P. E., C. R. Peterson, and R. W. Klaver. 2004. Sexual differences in the post-breeding movements and habitats selected by western toads (Bufo boreas) in southeastern Idaho. Herpetologica 60:455-467.

Chetkiewicz, C.-L. B., C. C. St. Clair, and M. S. Boyce. 2006. Corridors for conservation: integrating pattern and process. Annual Review of Ecology Evolution and Systematics 37:317–342.

Clinnick, P.F. 1985. Buffer strip management in forest operations: a review. Australian Forestry 48:34–45.

Galili, T. 2010. Post hoc analysis for Friedman's Test (R code). R-statistics blog. Retrieved June 7, 2010, from http://www.r-statistics.com/2010/02/post-hoc-analysis-for-friedmans-test-r-code.

Goates, M. C., K. A. Hatch, and D. L. Eggett. The need to ground truth 30.5 m buffers: a case study of the boreal toad (Bufo boreas). Biological Conservation 138:474-483.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, UK.

Hanski, I., T. Pakkala, M. Kuussaari, and G. Lei. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos 72: 21-28.

Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. pp. 27–42 In: I. Hanski and M. E. Gilpin, editors. Metapopulation dynamics: ecology, genetics and evolution. Academic Press, New York, New York, USA.

Hickman, J. (ed.). 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, CA.

Hollander, M., and D. E. Wolfe. 1999. Nonparametric Statistical Methods, 2nd edition. John Wiley, New York, New York, USA.

Hunsaker, C. T., and S. M. Eagan. 2003. Small stream ecosystem variability in the Sierra Nevada of California. pp. 716-721 In: K.G. Renard, S.A. McElroy, W.J. Gburek, H.E. Canfield, and R.L. Scott, editors. First Interagency Conference on Research in the Watersheds, October 27-30, 2003. U.S. Department of Agriculture, Agricultural Research Service.

Kagarise Sherman, C. 1980. A comparison of the natural history and mating system of two anurans: Yosemite toads (Bufo canorus) and Black toads (Bufo exsul). Ph.D. dissertation. University of Michigan, Ann Arbor.

Kagarise Sherman, C., and M. L. Morton. 1984. The toad that stays on its toes. Natural History 93:72-78.

Karlstrom, E. L. 1962. The toad genus Bufo in the Sierra Nevada of California. University of California Publications in Zoology 62:1-104.

Kilgore, B. M., and D. Taylor. 1979. Fire history of a sequoiamixed conifer forest. Ecology 60:129–142.

Lee, P., C. Smyth, and S. Boutin. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. Journal of Environmental Management 70:165–180.

Levins, R. A. 1969. Some demographic and evolutionary consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237-240.

Marczak, L. B., T. Sakamaki, S. L. Turvey, I. Deguise, S. L. R. Wood, and J. S. Richardson. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. Ecological Applications 20:126-134.

Martin, D. 2008. Decline, movement and habitat utilization of the Yosemite toad (Bufo canorus): an endangered anuran endemic to the Sierra Nevada of California. Ph.D. dissertation. University of California, Santa Barbara.

Morton, M. L. 1981. Seasonal changes in total body lipid and liver weight in the Yosemite toad. Copeia 1981:234-238.

Morton, M. L. 1982. Natural history of the Yosemite toad. National Geographic Society Research Reports 14:499-503.

Mullally, D. P. 1953. Observations on the ecology of the toad Bufo canorus. Copeia 1953:182-183.

Mullally, D. P., and J. D. Cunningham. 1956. Aspects of the thermal ecology of the Yosemite toad. Herpetologica 12:57-67.

Muths, E. 2003. Home range and movements of boreal toads in undisturbed habitats. Copeia 2003:160-165.

Olsen, D. H., P. Anderson, C. A. Frissell, H. H. Welsh, Jr., and D. F. Bradford. 2007. Biodiversity management approaches for stream-riparian areas: perspectives for Pacific Northwest headwater forests, microclimates and amphibians. Forest Ecology and Management 246:81–107.

Parsons, D. J., and S. H. DeBendeetti. 1979. Impact of fire suppression on a mixed-conifer forest. Forest Ecology and Management 2:21–33.

Smith, M. A., and D. M. Green. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28: 110-128.

Stephens, S. L., J. J. Moghaddas, C. Edminster, C. E. Fiedler, S. Haase, M. Harrington, J. E. Keeley, E. E. Knapp, J. D. McIver, K. Metlen, C. N. Skinner, and A. Youngblood. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. Ecological Applications 19:305-320.

Swihart, K., and N. A. Slade. 1985. Testing for independence of observation in animal movements. Ecology 66:1176-1184.

Tracy, C. R., K. A. Christian, M. P. O’Connor, and C. R. Tracy. 1993. Behavioral thermoregulation by Bufo americanus: the importance of the hydric environment. Herpetologica 49:375–382.

U.S. Fish and Wildlife Service (USFWS). 2002. 12-month finding for a petition to list the Yosemite toad. Federal Register 67(237):75834-75843.

Table 3.1. The sex, meadow of origin, dates tracked, number of days tracked , number of locations, maximum distance traveled, and home range for radio-tracked Yosemite toads.

Toad ID	Sex	Meadow	Dates Tracked	Number of Days Tracked	Number of Locations	Maximum Distance (m)	Home range (m2)
F2-07	F	520M20	Apr-May 2007	13	7	216.5	3,096
F4-07	F	520M15	May-Aug 2007	93	22	570.3	23,177
F5-07	F	520M15	May-Jun 2007	26	7	179.8	5,340
F6-07[1]	F	520M15	May-Jul 2007	64	14	1,089.3	71,273
F7-07[2]	F	520M20	Jun-Aug 2007	67	17	69.4	1,834
M1-07[3]	M	520M20	Apr-May 2007	22	10	103.8	1,514
M3-07	M	520M15	May-Jun 2007	39	11	188.4	4,062
M4-07	M	520M15	May-Jul 2007	66	17	149.0	4,032
M7-07	M	520M15	May-Aug 2007	94	23	127.4	5,686
F1-08	F	520M20	May-Aug 2008	101	35	962.2	107,896
F2-08	F	520M20	May-Sep 2008	122	35	864.4	110,200
F3-08	F	520M20	May-Sep 2008	122	34	908.6	55,568
F4-08	F	520M15	May-Jun 2008	37	17	199.9	7,706
F5-08	F	520M15	May-Aug 2008	86	28	277.8	27,026
F6-08	F	520M15	May-Aug 2008	91	31	115.7	4,729
F7-08	F	520M15	May-Aug 2008	91	28	335.9	22,281
F8-08	F	520M25	May-Sep 2008	117	32	742.9	58,010

Table 3.1, continued

Toad ID	Sex	Meadow	Dates Tracked	Number of Days Tracked	Number of Locations	Maximum Distance (m)	Home range (m2)
F9-08[1]	F	520M14	Jun-Jul 2008	23	7	83.5	548
M01-08[4]	M	520M20	May-Sep 2008	127	38	480.8	68,193
M02-08	M	520M20	May-Aug 2008	98	35	865.2	79,767
M03-08[3]	M	520M20	May-Aug 2008	99	33	230.0	20,082
M04-08	M	520M25	May-Aug 2008	95	29	191.6	16,410
M05-08[5]	M	520M25	May-Aug 2008	95	31	447.8	36,155
M06-08[6]	M	520M25	May-Aug 2008	95	31	295.6	22,303
M07-08	M	520M15	May-Aug 2008	94	32	244.2	24,569
M08-08	M	520M15	May-Aug 2008	91	30	303.8	19,369
M10-08	M	520M15	May-Jul 2008	57	22	101.5	3,700
M11-08	M	520M15	Jun-Aug 2008	76	23	309.0	25,811
M12-08	M	520M25	Jun-Aug 2008	74	22	400.7	17,707
M14-08	M	520M14	Jun-Aug 2008	73	22	742.6	36,528
M15-08	M	520M14	Jun-Aug 2008	73	23	200.3	16,338
F1-09	F	520M20	May-Aug 2009	99	15	474.0	12,387
F2-09[2]	F	520M20	May-Aug 2009	96	14	678.6	51,826
F3-09	F	520M15	May-Aug 2009	102	15	624.6	49,865
F4-09	F	520M15	May-Aug 2009	96	12	1,260.9	31,102

Table 3.1, continued

Toad ID	**Sex**	**Meadow**	**Dates Tracked**	**Number of Days Tracked**	**Number of Locations**	**Maximum Distance (m)**	**Home range (m2)**
M1-09[3]	M	520M20	May-Aug 2009	101	16	92.1	3,799
M2-09[4]	M	520M20	May-Aug 2009	98	15	319.2	22,892
M3-09	M	520M15	May-Aug 2009	96	13	325.5	22,321
M5-09[5]	M	520M25	May-Jun 2009	35	5	107.3	824
M6-09[6]	M	520M25	May-Aug 2009	96	13	124.7	5,316
M7-09	M	520M14	May-Aug 2009	95	13	427.1	49,584
M8-09	M	520M14	May-Jul 2009	67	9	76.7	1,249
Total locations: F = 370, M = 516							

Table 3.2. Mean distance traveled, mean maximum distance traveled and mean home range for radio-tracked Yosemite toads by year and by sex.

Year	Sex	N	Mean distance (SD) (m)	Mean maximum distance (SD) (m)	Mean home range (SD) (m2)
2007	F	5	292.0 (299.3)	425.1 (416.1)	20,944 (29,433)
	M	4	109.1 (42.8)	142.1 (36.0)	3,824 (1,723)
2008	F	9	389.0 (287.0)	499.0 (364.0)	43,773 (42,282)
	M	13	194.9 (181.4)	370.2 (220.8)	29,764 (21,500)
2009	F	4	649.2 (317.2)	759.5 (345.3)	36,295 (18,474)
	M	7	146.5 (115.6)	210.4 (142.5)	15,141 (17,894)
2007 through 2009	F	18	419.9 (308.7)	536.4 (374.5)	35,770 (34,699)
	M	24	166.4 (148.5)	285.6 (200.6)	21,175 (20,742)
	both	42	275.1 (260.7)	393.1 (310.6)	27,430 (28,178)

Table 3.3. Results of the mixed model for analyzing distance traveled by radio-tracked Yosemite toads.

	numerator df	**denominator df**	**F value**	***P* value**
(Intercept)	1	828	19.9195	<0.0001
factor(Sex)	1	34	2.9578	0.0946
factor(Meadow)	3	34	1.4406	0.2481
Day	1	828	40.6399	<0.0001*
Day*Day	1	828	30.5140	<0.0001*
factor(Sex):factor(Meadow)	3	34	0.9373	0.4334
factor(Sex):Day	1	828	11.1904	0.0009*
factor(Meadow):Day	3	828	0.6968	0.5541
factor(Sex):Day*Day	1	828	0.4288	0.5128
factor(Meadow):Day*Day	3	828	0.2237	0.8799
factor(Sex):factor(Meadow):Day	3	828	0.3955	0.7563
factor(Sex):factor(Meadow):Day*Day	3	828	0.6057	0.6114

*significant at the p<0.001 level

Table 3.4. Mean Sørensen dissimilarity values comparing locations with Yosemite toads to one another and to locations without Yosemite toads.

	mean Sørensen dissimilarity between locations with toads (SD)	**mean Sørensen dissimilarity between locations with and without toads (SD)**	**t value**	**df**	***P* value**
quadrat	0.46 (0.05)	0.52 (0.03)	-4.4854	31.58	0.0001
line-intercept (under 2m)	0.65 (0.13)	0.75 (0.11)	-2.3733	34.93	0.0233
line-intercept (over 2m)	0.38 (0.10)	0.56 (0.05)	-6.9979	27.50	0.0000
belt transect	0.25 (0.07)	0.43 (0.07)	-7.7857	35.75	0.0000

Table 3.5. Plant list for vegetation sampling in locations with and without Yosemite toads.

Genus	Species	Family	Locations with toads	Locations without toads
Abies	*concolor*	Pinaceae	x	x
Abies	*magnifica*	Pinaceae	x	x
Allium	*campanulatum*	Liliaceae	x	
Arabis	*platysperma*	Brassicaceae	x	
Arctostaphylos	*nevadensis*	Ericaceae	x	x
Arctostaphylos	*patula*	Ericaceae	x	x
Calyptridium	*umbellatum*	Portulaceae	x	x
Ceanothus	*cordulatus*	Rhamnaceae	x	x
Chrysolepis	*sempervirens*	Fagaceae	x	x
Collinsia	*torreyi*	Scrophulariaceae	x	x
Erigeron	*breweri*	Asteraceae	x	x
Eriogonum	*nudum*	Polygonaceae	x	
Eriogonum	*spergulinum*	Polygonaceae	x	
Gayophytum	*diffusum*	Onagraceae	x	x
Gayophytum	*eriospermum*	Onagraceae		x
Hackelia	*mundula*	Boraginaceae	x	x
Hieraceum	*albiflorum*	Asteraceae		x
Kelloggia	*galioides*	Rubiaceae	x	
Lomatium	*sp.*	Apiaceae	x	
Lotus	*sp.*	Fabaceae	x	x
Lupinus	*sp.*	Fabaceae	x	x
Monardella	*odoratissima*	Lamiaceae	x	x
Pedicularis	*semibarbata*	Scrophulariaceae	x	x
Pellaea	*bridgesii*	Polypodiaceae	x	
Phacelia	*hydrophylloides*	Hydrophyllaceae	x	x
Phacelia	*racemosa*	Hydrophyllaceae	x	
Pinus	*contorta*	Pinaceae	x	
Pinus	*lambertiana*	Pinaceae	x	x
Ribes	*sp.*	Grossulariaceae		x
Senecio	*aronicoides*	Asteraceae		x
Solidago	*canadensis*	Asteraceae		x
Streptanthus	*tortuosus*	Brassicaceae	x	
Symphoricarpos	*mollis*	Caprifoliaceae	x	x

Figure 3.1. Meadow locations within the Bull Creek watershed in the Sierra National Forest, California. Meadows 520M14, 520M15, 520M20, and 520M25 were used in the study.

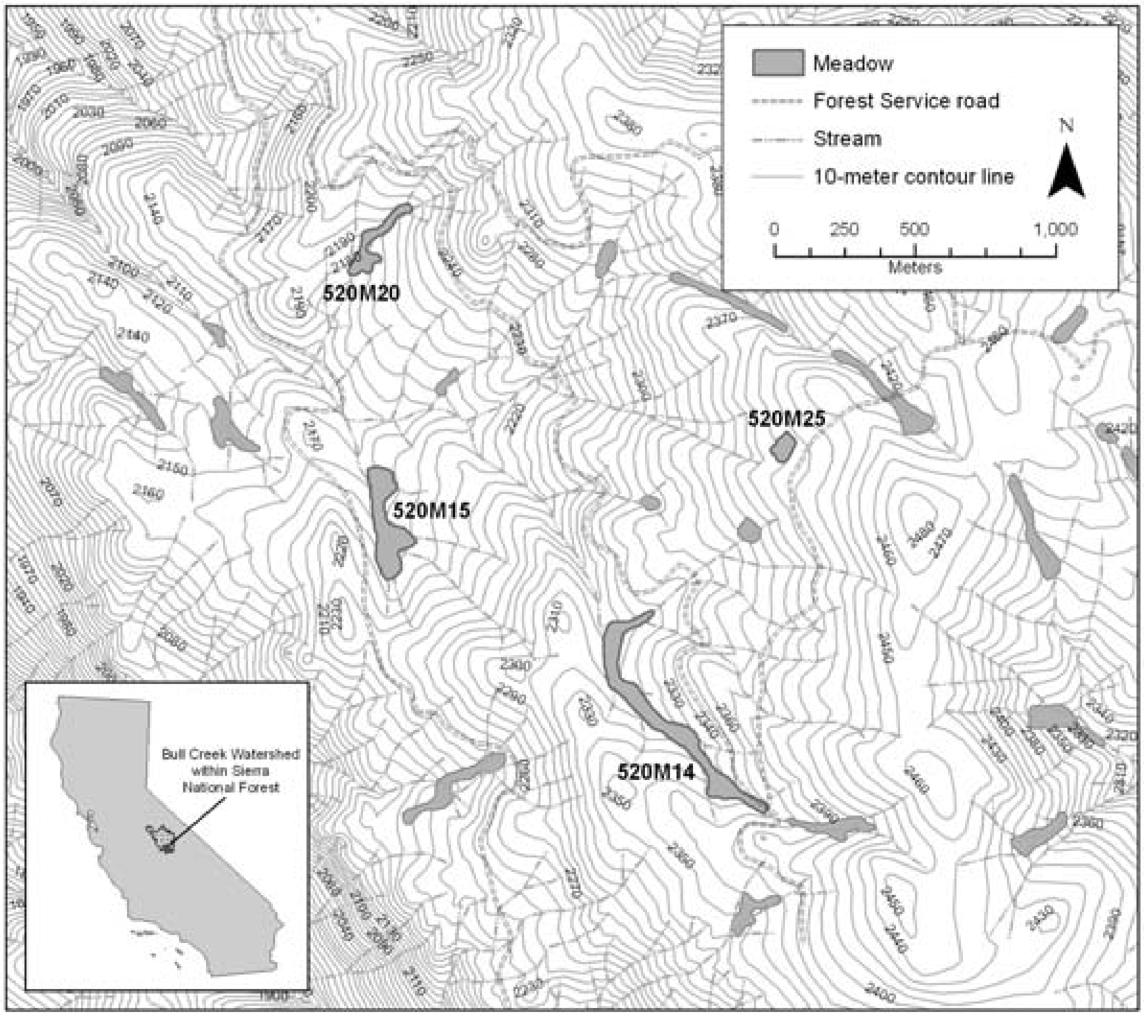


Figure 3.2. Distances traveled by radio-tracked Yosemite toads by sex and Julian day.

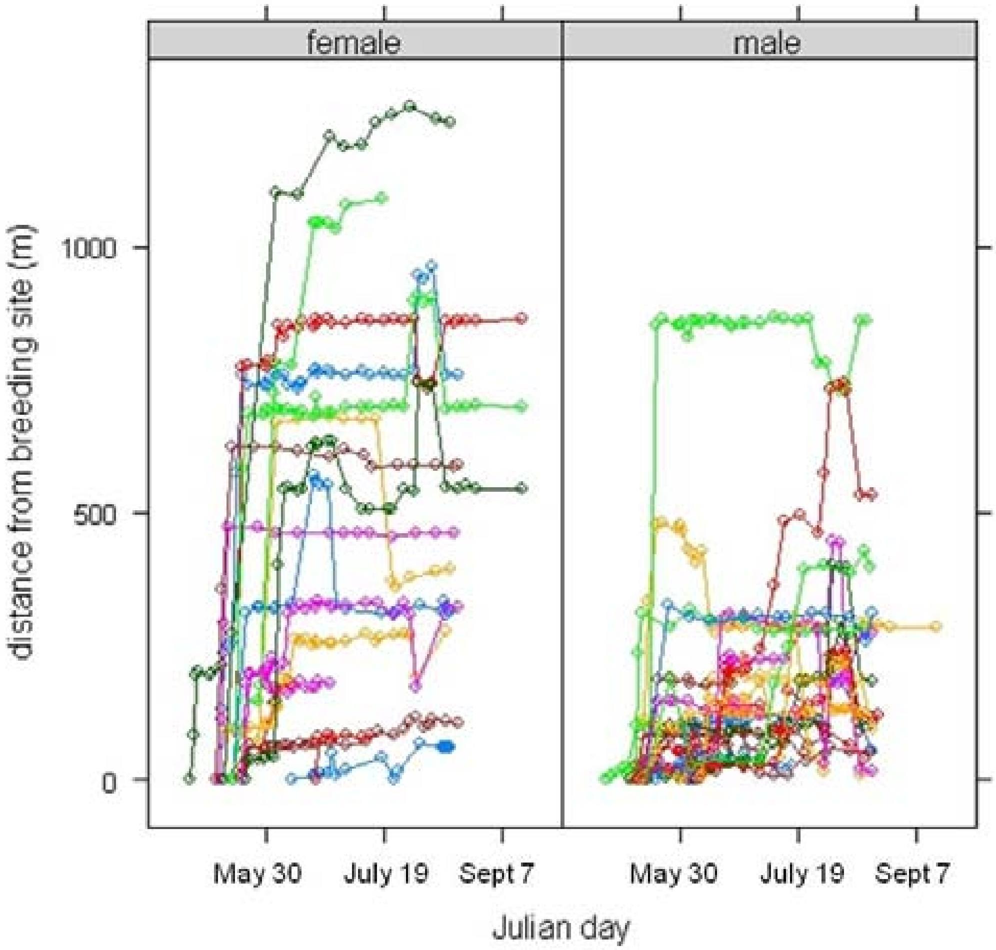


Figure 3.3. Scatter plot of days since first tracked versus distance traveled between tracking locations with loess-fitted smooth curve.

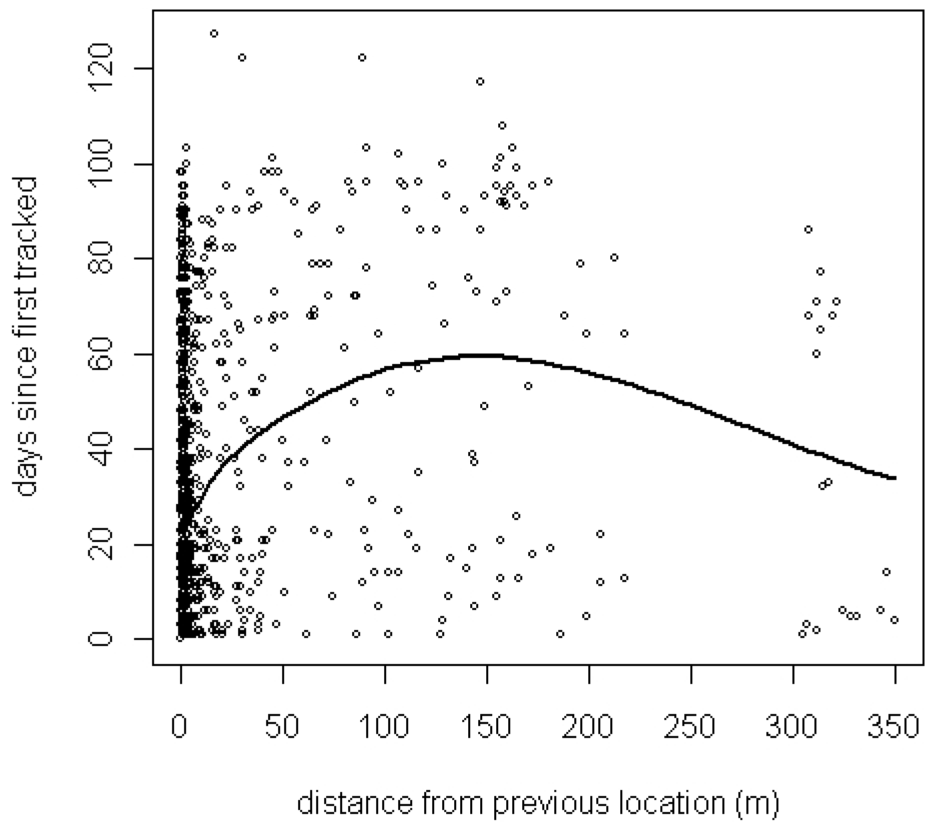


Figure 3.4. Parallel coodinates plot for microsite use by Yosemite toads. Lines in the graph connect cover type use for each individual toad. The Xs show the mean use by all individuals for the cover type.