Species distribution model of the Yosemite toad (*Anaxyrus [=Bufo] canorus*) in the Sierra National Forest, California

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male Yosemite toad

female Yosemite toad

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Abstract

Species distribution models are commonly used to identify the environmental characteristics that allow for the occurrence of a species in the landscape. The information gained from these models is particularly valuable for sensitive species and can be used to inform management decisions in protection and conservation efforts. Species distribution models for the Yosemite toad (*Anaxyrus [=Bufo] canorus*) were constructed 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. 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. The full model performed the best and had the highest discrimination for the data set. The two subset models also had good discrimination but the biophysical model performed better than the management model. 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.

Introduction

Modeling of species distributions is a common method to evaluate the species-environment relationship and to determine suitable habitat (Scott et al. 2002). 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 energy 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). The use of species distribution models has become widespread in addressing questions in biogeography, ecology and evolution as well as in conservation and management. For example, species distribution models have been used to quantify the environmental niche of a species (Elith et al. 2006, Kumar et al. 2009), predict species invasions (Giovanelli et al. 2008), estimate species distributions in the past (Svenning et al. 2008, Waltari and Guralnick 2009) and future climates (Jarnevich and Stohlgren 2009) or under different land uses (Riley at al. 2005), and in conservation planning and reserve design (Pawar et al. 2007, Fuller et al. 2008).

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 in California. The Yosemite toad (*Anaxyrus [=Bufo] canorus*) is a Federal candidate species for listing as threatened or endangered and a Forest Service sensitive species. The U.S Fish and Wildlife Service found that listing was warranted as threatened or endangered for this species however the listing was precluded at the time based on other higher priority issues (USFWS 2002). The species is managed as sensitive by the Pacific Southwest Region of the US Forest Service (1998). It 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 (Karlstrom 1958, Jennings and Hayes 1994). The Yosemite toad is a long-lived 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. The Yosemite toad breeds in late spring, usually at snowmelt, in areas of shallow water such as wet meadows, margins of ponds and lakes, and slow-moving streams (Stebbins 2003, Martin 2008). Breeding often only lasts 1-2 weeks, with adults then often moving to upland areas. Eggs and larvae develop in shallow water areas and metamorphosis occurs by late summer of the same year (Kagarise Sherman and Morton 1984, USFWS 2002).

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 related to 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).

To better understand the environmental requirements of the Yosemite toad in the southern portion of its range, species distribution modeling was performed to investigate possible environmental predictors. Possible predictors included biophysical factors such as elevation, amount of precipitation and vegetation type as well as factors that are subject to management such as timber activity and land use change. Evaluation of the different types of factors is useful in informing management decisions with the goal 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 the 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.

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). The Yosemite toad is currently found above 6000 feet elevation on the Sierra National Forest and is also the focus of several ongoing monitoring and research projects.

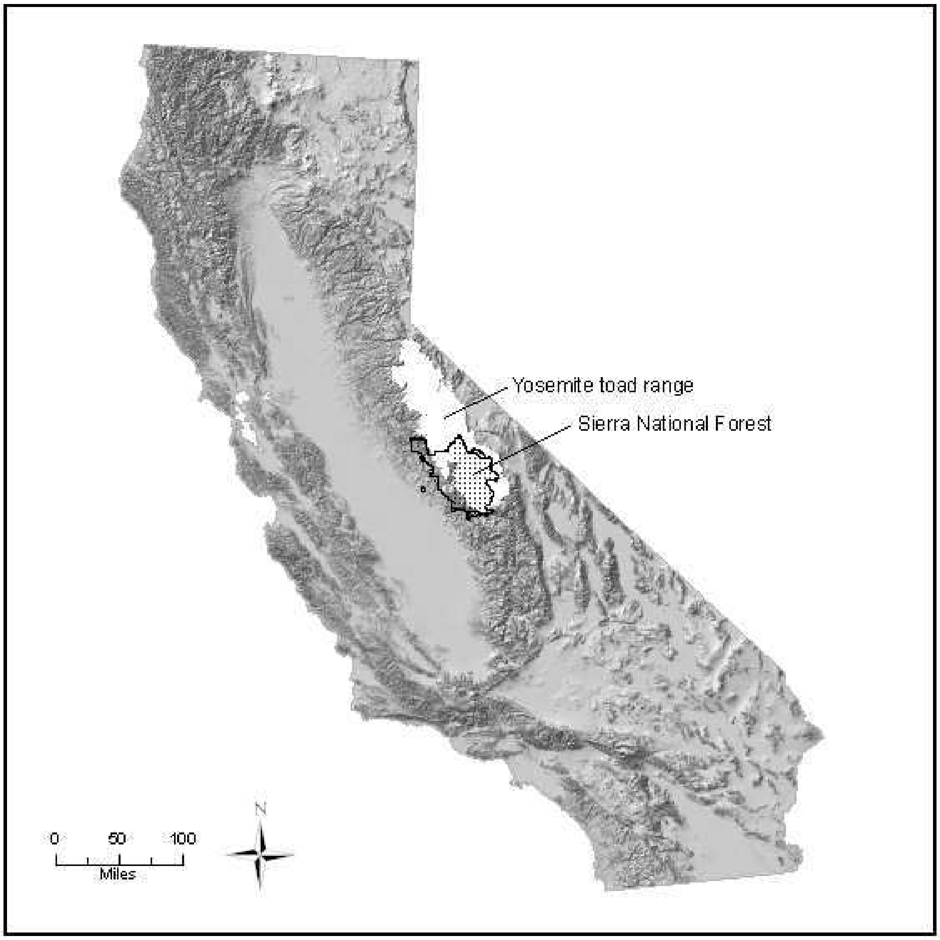

Figure 1. Yosemite toad range and the location of the Sierra National Forest in California.

From 2002 through 2004, protocol level surveys were conducted by trained Forest Service staff in potential breeding sites above 6000 feet in elevation. According to the protocol, the surveys were timed to coincide with tadpole presence which occurs in the late spring and summer. The surveys focused specifically on the Yosemite toad, though any 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, metamorphic toads, 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 difficulties in detectability for most life stages. Yosemite toads may not breed at sites every year and all life-stages are not equally detectable. Additional surveys may be necessary 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 2 shows the 2002-2004 Yosemite toad survey sites in the Sierra National Forest where toads were present or not observed.

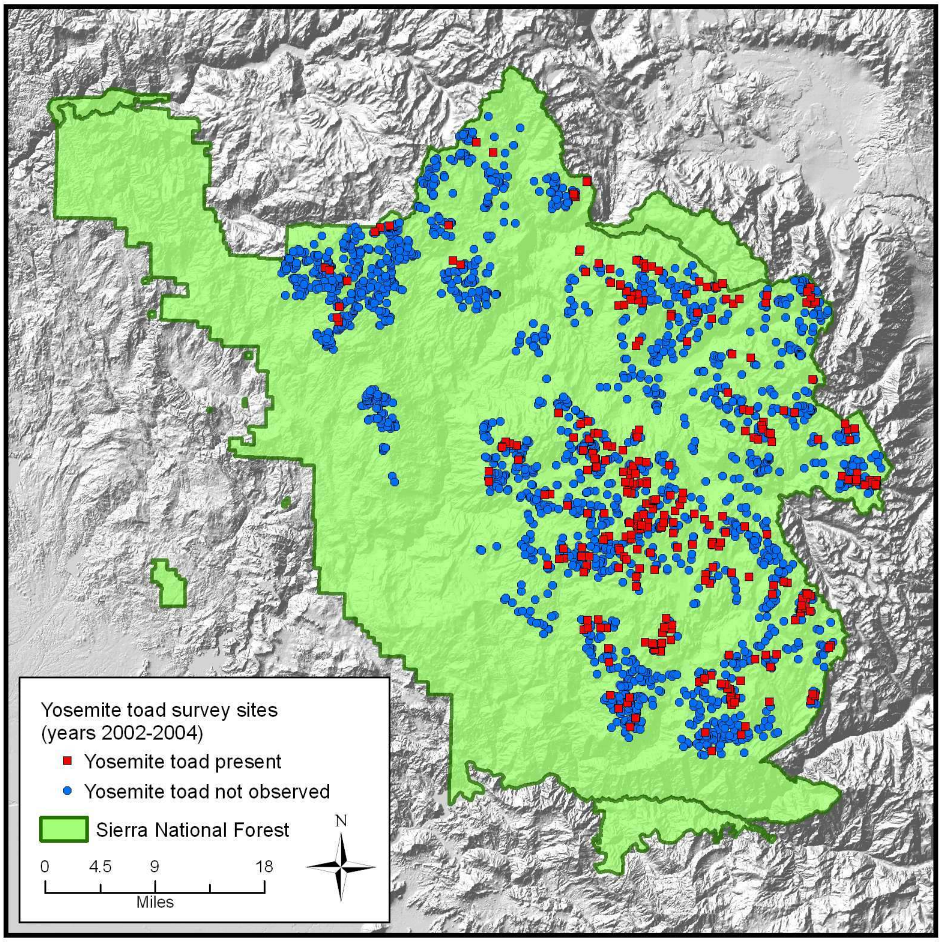

Figure 2. Yosemite toad 2002-2004 survey sites in the Sierra National Forest in California.

Environmental Predictor Variables

Fifty-four predictor variables were initially considered for the full model (Appendix 1). Variables were gathered from the field surveys and from environmental datasets 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. 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 (climatology normals 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 1500 meters of each surveyed site was added to the model (Dormann et al. 2007). The 1500 meter distance represents the maximum distance a Yosemite toad might travel (Kagarise Sherman 1980, Martin 2008, CT Liang *unpublished data*). In addition, the number of all sites (occupied or not) within 1500 meters of a surveyed site was calculated in GIS 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 uncorrelated 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). 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.

Table 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 1500 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
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.

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 the resampling analyses were averaged for a single estimation. The Somers' Dxy rank correlation statistic was used to compare the initial model to the resampled models. 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.

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.

Results

Full Model

The best full GLM model contained 16 environmental predictor variables (Table 2) and performed well for the data set with very good discrimination (AUC=0.90). Cross-validation showed that the model has 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 2).

In the model, the odds of Yosemite toad presence increased with higher values of elevation, aspect, water temperature, precipitation of the warmest quarter, annual SCA, survey time and the autocovariate. The odds also increased with seasonal water type compared to perennial water type, and with higher vegetative land cover compared to areas of little or no change. The odds of Yosemite toad presence decreased with higher values of acreage of the survey site, slope, air temperature, temperature seasonality, precipitation of the driest quarter, and the y-coordinate (i.e., the more northerly sites had a lower likelihood of Yosemite toad occupancy) (Table 2).

Table 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**	**Increase / Decrease**
Intercept	-7.86	21.55	-0.36	0.72			
AC	0.69	0.07	10.34	0.00	1.85	1.65 – 2.08	Increase
ACRES	-0.26	0.09	-2.99	0.00	0.91	0.86 – 0.97	Decrease
ASPECT	0.17	0.08	2.16	0.03	1.30	1.03 – 1.66	Increase
BBIN5	0.34	0.12	2.87	0.00	11.14	2.15 – 57.80	Increase
BIO4	-0.39	0.12	-3.19	0.00	0.63	0.47 – 0.84	Decrease
BIO17	-0.37	0.15	-2.47	0.01	0.67	0.49 – 0.92	Decrease
BIO18	0.37	0.12	3.05	0.00	1.72	1.21 – 2.44	Increase
CHG8591 (factor=2)	-0.13	0.86	-0.15	0.88	1.13	0.21 – 6.16	no effect
CHG8591 (factor=3)	1.93	1.26	1.53	0.13	7.80	1.23 – 49.40	Increase
CHG9095 (factor=4)	5.38	21.53	0.25	0.80	0.00	0.00 – 9.84 x 10^{15}	none
CHG9095 (factor=5)	6.49	21.54	0.30	0.76	3.03	1.87 – 4.91	Increase
CHG9095 (factor=6)	5.70	21.54	0.26	0.79	1.37	0.73 – 2.57	no effect
CHG9095 (factor=7)	6.43	21.57	0.30	0.77	2.84	0.26 – 30.87	no effect
CHG9095 (factor=8)	3.78	21.55	0.18	0.86	0.20	0.05 – 0.83	Decrease
CHG9095 (factor=9)	6.06	21.54	0.28	0.78	1.96	0.99 – 3.90	Increase
DEM	0.98	0.13	7.37	0.00	5.09	3.30 – 7.84	Increase
GPS_N	-0.27	0.11	-2.36	0.02	0.64	0.44 – 0.93	Decrease
SLOPE	-0.17	0.10	-1.80	0.07	0.81	0.65 – 1.02	Decrease
SURVEY_TOT	0.93	0.10	8.93	0.00	1.76	1.55 – 1.99	Increase
TEMPAIR_ST	-0.24	0.10	-2.45	0.01	0.71	0.54 – 0.93	Decrease
TEMPW	0.71	0.09	7.73	0.00	2.75	2.13 – 3.55	Increase
WTYPE	-0.44	0.18	-2.52	0.01	1.56	1.10 – 2.20	Increase

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)
* = reference category for odds ratio is factor 2
^ = reference category for odds ratio is factor 4
+ = 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

Biophysical Model

The best biophysical GLM model contained 11 predictor variables (Table 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 3).

In the model, the odds of Yosemite toad presence increased with higher values of acreage of the survey site, elevation, aspect, water temperature, precipitation of the warmest quarter, and the autocovariate. The odds of Yosemite toad presence decreased with higher values of the slope, air temperature, temperature seasonality, precipitation of the driest quarter, and the y-coordinate (Table 3).

Table 3. Biophysical model. Results of the best GLM model using biological and physical predictor variables to describe the occurrence of Yosemite toad.

Table 3					**Effects on Toad Presence**		
Predictor Variable	**Logistic Coefficient**	**Standard Error**	**Wald Z**	**P-value**	**Odds Ratio**	**95% CI**	**Increase / Decrease**
Intercept	-2.38	0.10	-23.77	0.00			
AC	0.75	0.06	12.03	0.00	1.95	1.75 – 2.18	Increase
ACRES	0.23	0.07	3.33	0.00	1.08	1.03 – 1.14	Increase
ASPECT	0.17	0.07	2.24	0.03	1.29	1.03 – 1.61	Increase
BIO4	-0.26	0.11	-2.50	0.01	0.73	0.57 – 0.93	Decrease
BIO17	-0.33	0.13	-2.43	0.01	0.70	0.53 – 0.93	Decrease

Table 3					**Effects on Toad Presence**		
Predictor Variable	**Logistic Coefficient**	**Standard Error**	**Wald Z**	**P-value**	**Odds Ratio**	**95% CI**	**Increase / Decrease**
BIO18	0.37	0.11	3.33	0.00	1.72	1.25 – 2.36	Increase
DEM	0.30	0.10	3.07	0.00	1.64	1.20 – 2.25	Increase
GPS_N	-0.20	0.10	-1.91	0.06	0.72	0.52 – 1.01	Decrease
SLOPE	-0.28	0.09	-3.00	0.00	0.72	0.58 – 0.89	Decrease
TEMPAIR_ST	-0.32	0.09	-3.55	0.00	0.63	0.49 – 0.81	Decrease
TEMPW	0.74	0.09	8.69	0.00	2.88	2.27 – 3.65	Increase

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

Management Model

The best management-related GLM model contained 6 predictor variables (Table 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$_{\text{model}}$=0.65, Somers' Dxy$_{\text{cross-validation}}$=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 4).

In the model, the odds of Yosemite toad presence increased with higher values of the x-coordinate and the autocovariate. The odds also increased with higher vegetative land cover compared to areas of little or no change. The odds of Yosemite toad presence decreased with greater distance to timber activity. The odds also 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 (Table 4).

Table 4. Management model. Results of the best GLM model using predictor variables subject to management to describe the occurrence of Yosemite toad.

Table 4					**Effects on Toad Presence**		
Predictor Variable	**Logistic Coefficient**	**Standard Error**	**Wald Z**	**P-value**	**Odds Ratio**	**95% CI**	**Increase / Decrease**
Intercept	-7.35	24.54	-0.30	0.76			
AC	0.79	0.06	12.67	0.00	2.02	1.82 – 2.26	Increase
CHG8591 (factor=2)*	-0.13	0.73	-0.18	0.86	1.14	0.27 – 4.71	no effect
CHG8591 (factor=3)	1.79	1.02	1.76	0.08	6.83	1.61 – 28.96	Increase
CHG9095 (factor=4)^	5.26	24.53	0.21	0.83	0.01	0.00 – 3.91 x 10^{18}	no effect

Table 4					**Effects on Toad Presence**		
Predictor Variable	**Logistic Coefficient**	**Standard Error**	**Wald Z**	**P-value**	**Odds Ratio**	**95% CI**	**Increase / Decrease**
CHG9095 (factor=5)	6.34	24.53	0.26	0.80	2.93	1.95 – 4.41	Increase
CHG9095 (factor=6)	5.83	24.53	0.24	0.81	1.76	1.05 – 2.96	Increase
CHG9095 (factor=7)	5.78	24.55	0.24	0.81	1.67	0.18 – 15.41	no effect
CHG9095 (factor=8)	4.30	24.54	0.18	0.86	0.38	0.11 – 1.35	no effect
CHG9095 (factor=9)	6.18	24.53	0.25	0.80	2.50	1.36 – 4.58	Increase
FireCond (factor=2)	0.01	0.18	0.07	0.94	1.01	0.71 – 1.44	no effect
FireCond (factor=3)	-0.94	0.34	-2.74	0.01	0.39	0.20 – 0.77	Decrease
FireCond (factor=9)	-0.15	0.24	-0.63	0.53	0.86	0.54 – 1.38	no effect
GPS_E	0.70	0.15	4.74	0.00	2.99	1.90 – 4.71	Increase
TIMB_DIST	-0.26	0.13	-1.92	0.05	0.69	0.48 – 1.01	Decrease

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

* = reference category for odds ratio is factor 2
^ = reference category for odds ratio is factor 4
$^{+}$ = 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
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

Predictor variables

Statistics (mean, standard deviation, 95% confidence interval) for predictor variables in any of the three models are shown in Table 5 along with their univariate relationship to Yosemite toad presence. A positive relationship indicates that the Yosemite toad is more likely at sites with higher values of the variable unit while a negative relationship indicates that the toad is more likely at sites with lower values. The direction of the relationship is reversed in the models for three variables: 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.

Table 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.

Table 5	**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*

Table 5	**Mean ± SD (95% CI)**		
Predictor variable (Units)	**Presence Sites**	**Absence Sites**	**Relationship to toad presence**
WTYPE (categorical variable)	0.56 ± 0.50 (0.51 – 0.62)	0.51 ± 0.50 (0.49 – 0.53)	not applicable for categorical variable

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)

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 combination 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 the data set used for modeling. The two subset models both performed well, with the biophysical model having better discrimination than the management model.

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). The model showed that Yosemite toads were more likely to be found at survey sites where warmer water temperature readings are documented. The variable had a large positive effect on Yosemite toad presence and it represents generalized information about the conditions of the survey site. 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* though 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 prefers 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. 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 selected. 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 will not affect the adult population dynamics until after the existing generation of adult Yosemite toads dies off in 12-15 years.

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 the degree of departure of the current vegetation and fuel conditions from the historic (pre-settlement) natural fire regime. This variable represents comparisons between current expected fires and historic fire regimes with regard to fire frequency, size and patchiness, and effects on key ecosystem elements and processes. 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. This suggests that the Yosemite toad is affected by some unknown and unmeasured ecosystem factors that are represented by this 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 future study

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 and management related variables. Future steps would be to test this model by predicting the distribution of the Yosemite toad in other parts of its range.

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Appendix 1. 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 1500 meters of survey site	calculated in R statistical program using X- and Y-coordinates with a distance of 1500 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
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

Variable (Units)	**Description**	**Derivation**	**Source**
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
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 imager	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

Variable (Units)	**Description**	**Derivation**	**Source**
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
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 1500 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 (°C)	air temperature at end of survey	survey data	2002-2004 surveys
TEMPAIR_ST (°C)*	air temperature at start of survey	survey data	2002-2004 surveys
TEMPW (°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 (°C x10^{-2})	annual minimum temperature, 1971-2000	GIS grid layer	PRISM, 1971-2000 climatology normals layer (800 meter resolution)
TMXANN (°C x10^{-2})	annual maximum temperature, 1971-2000	GIS grid layer	PRISM, 1971-2000 climatology normals layer (800 meter resolution)
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.