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# Validation Tests of Predictive Models of Butterfly Occurrence Based on Environmental Variables

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**Abstract:** *Ecologists often seek to predict species distributions as functions of abiotic environmental variables. Statistical models are useful for making predictions about the occurrence of species based on variables derived from remote sensing or geographic information systems. We previously used 14 topographically based environmental variables from 49 locations in the Toquima Range (Nevada, U.S.A.) and species inventories conducted over 4 years (1996-1999) to model logistically the occurrence of resident butterfly species. To test the models, we collected new validation data in 39 locations in the nearby Shoshone Mountains in 2000-2001. We used a series of "classification rules" based on conventional logistic and Bayesian criteria to assess the success rates of predictions. The classification rules represented a gradient of stringency in the "certainty" with which predictions were made. More stringent rules reduced the number of predictions made but greatly increased the success rate of predictions. For comparisons of classification rules making similar numbers of predictions, conventional logistic and Bayesian criteria produced similar outcomes. Success rates for predicted absences were uniformly higher than for predicted presences. Increasing the temporal extent of data from 1 to 2 years elevated success rates for predicted presences but decreased success rates for predicted absences, leaving the overall success rates essentially the same. Although species occurrence rates (the proportion of locations in which each species was found) were correlated between the modeling and validation data sets, occurrence rates for many species increased or decreased substantially; erroneous predictions were more likely for those taxa. Model fit (measured by the explained deviance) was an indicator of the probable success rate of predicted presences but not of predicted absences or overall success rates. We suggest that classification rules for predicting likely presences and absences may be decoupled to improve overall predictive success. Our general framework for modeling species occurrence is applicable to virtually any taxonomic group or ecosystem.*

## Pruebas de Validación de Modelos Predictivos de Ocurrencia de Mariposas Basados en Variables Ambientales

**Resumen:** *A menudo los ecólogos tratan de predecir la distribución de especies en función de variables ambientales abióticas. Los modelos estadísticos son útiles para hacer predicciones sobre la presencia de especies en base a variables derivadas de sistemas de percepción remota o de información geográfica. Previamente utilizamos 14 variables ambientales topográficas de 49 localidades en las Montañas Toquima (Nevada, EE.UU.) e inventarios de especies realizados a lo largo de cuatro años (1996-1999) para modelar lógicamente la presencia de especies de mariposas residentes. Para poner a prueba los modelos, recolectamos nuevos datos de validación en 39 localidades en las Montañas Shoshone cercanas en 2000 y 2001. Utilizamos una serie de "reglas de clasificación" basadas en criterios logísticos convencionales y Bayesianos para evaluar las tasas de éxito de las predicciones. Las reglas de clasificación representaron un gradiente de estrechez en cuanto a la "certidumbre" con la que se hicieron las predicciones. Las reglas más estrechas redujeron el número de predicciones pero incrementaron significativamente las tasas de éxito predictivo. Para comparaciones de reglas de clasificación con números de predicciones similares, los criterios logísticos convencionales*

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Paper submitted March 18, 2002; revised manuscript accepted July 15, 2002.

*y Bayesianos produjeron resultados similares. Las tasas de éxito para ausencias predichas fueron uniformemente superiores que las de presencias predichas. El incremento en la extensión temporal de los datos de un año a dos aumentó las tasas de éxito para presencias predichas pero disminuyó las tasas de éxito para ausencias predichas, con lo que las tasas de éxito en general permanecieron iguales. Aunque las tasas de presencia de especies (proporción de localidades en la que se encontró a cada especie) se correlacionaron entre los conjuntos de datos de modelación y los de validación, las tasas de presencia de muchas especies aumentaron o disminuyeron sustancialmente; para esos taxones las predicciones erróneas fueron más probables. El ajuste del modelo (medido por la desviación explicada) fue un indicador de la probable tasa de éxito de presencias predichas pero no de ausencias predichas ni tasas de éxito totales. Sugerimos que las reglas de clasificación utilizadas para predecir probables presencias y para predecir probables ausencias pueden ser desacopladas para mejorar el éxito predictivo total. Nuestro marco general para modelar la ocurrencia de especies es aplicable a virtualmente cualquier grupo taxonómico o ecosistema.*

## Introduction

Explaining and predicting distributions of species rank among the primary goals in ecology and biogeography. Distribution patterns reflect complex relationships between biogeographic history, interspecific interactions, resource requirements and tolerances, and in situ evolution (Huston 1994; Rosenzweig 1995; Roughgarden 1995). Although interspecific interactions and evolutionary responses traditionally have dominated studies of species distributions, the increasing availability of extensive databases, land models, and computing power has stimulated a pragmatic shift toward statistically based approaches (e.g., Austin et al. 1990; Guisan & Zimmermann 2000; Jackson et al. 2000; Bell 2001). Although the distributions of species of interest may overlap, occurrence patterns are often examined on a single-species basis (Cody 1986; Tardif & DesGranges 1998; Rubinoff 2001).

Modeling species occurrence as a function of environmental variables that can be quantified easily, at relatively small spatial grains, and over extensive areas is particularly appealing (Angermeier & Winston 1999; Cowley et al. 2000; Kerr et al. 2001). Although efforts to predict occurrence as a function of resource requirements, such as prey availability or nesting sites, are often successful (Hanski & Gilpin 1997; Hanski 1999; Miller & Cale 2000; Germaine & Wakeling 2001), obtaining these data can be expensive and labor-intensive. Indeed, conducting fine-grained measurement of habitat might require as much effort as surveying the focal biota itself. In contrast, data sets and methods for deriving topographic and climatic variables are becoming widely accessible, and obtaining values for these variables does not require field visits. In some cases, modeling species occurrence as a function of environmental variables also allows us to predict whether climate change or landscape reconstruction may alter occurrence probabilities (Loreau et al. 2001; Fleishman et al. 2001a).

To be useful, the predictions of species-occurrence models must be tested explicitly according to clearly defined criteria (Guisan & Zimmermann 2000; Jackson et al. 2000). The process of generating and testing model

predictions increases our understanding of relationships between organisms and environmental variables and contributes to the scientific foundation for regional conservation planning (Mac Nally & Bennett 1997; Hawkins et al. 2000; Mac Nally et al. 2000).

Our objective is to develop a general framework for building, testing, and refining models of species occurrence that can be applied to any taxonomic group or ecosystem. We previously built statistically significant models for 36 of the 56 resident species of butterflies recorded from the 1750-km<sup>2</sup> Toquima Range (Lander and Nye counties, Nevada, U.S.A.), a mountain range in the central Great Basin of western North America (Fleishman et al. 2001b). To test the models, we conducted 2 years of species inventories in the Shoshone Mountains, a 1600-km<sup>2</sup> mountain range 40 km west of the Toquima Range. The Toquima Range and Shoshone Mountains are within the same biogeographic subregion (Austin & Murphy 1987). The two ranges have similar climates, a common biogeographic past and ancestral biota, and comparable land-use histories.

In temperate regions, butterflies are excellent study organisms. They are well known ecologically, relatively amenable to field study, appealing to the general public, and sometimes able to respond rapidly to environmental change (Scott 1986; New 1991; Kremen 1992; Prendergast et al. 1993; Harding et al. 1995; Blair & Launer 1997). From a conservation perspective, the Great Basin is an appropriate focal system because the majority of the area is public land that is managed for multiple and often conflicting uses. Also, many native species in the Great Basin are threatened by climate change, modified disturbance regimes, and invasions of non-native species (McDonald & Brown 1992; Murphy & Weiss 1992; Fleishman et al. 1998, 2001a; Warren et al. 2001).

We based models of butterfly occurrence on 14 predictor variables derivable from digital elevation models. Each predictor variable was significant in a model for at least one species (Fleishman et al. 2001b). Quadratic (squared) versions of the predictor variables were also used to capture possible nonlinear responses (e.g., a species' preference for intermediate values of a variable).

We chose to test our models with data from a new mountain range because we were interested in evaluating the spatial extent of model applicability (i.e., whether models are “transferable” to new locations). Biogeographers sometimes have treated mountain ranges in the Great Basin as replicates (e.g., Brown 1978; McDonald & Brown 1992; Boggs & Murphy 1997; Murphy & Weiss 1992; but see Lawlor 1998). Thus, they assumed, at least implicitly, that species’ responses to environmental gradients would be comparable among mountain ranges. We have empirical evidence that relationships between measures of species diversity (such as species richness) and major environmental gradients (such as elevation and area) are not uniform among mountain ranges (Fleishman et al. 2000). Even when a measure of diversity is significantly associated with a particular environmental gradient in several mountain ranges, the functional relationship between diversity and the gradient may differ (Fleishman et al. 2001a; Mac Nally et al. 2002). Therefore, we specifically wanted to determine whether predictors of occurrence were similar among mountain ranges.

### Classification Rules

Statisticians have expended much effort in developing “classification rules” for characterizing predictive success. Because we relate success rates to the classification rule used, our assessments provide more information than if we merely tested whether our predictions were correct. We used two broad sets of rules. The first was a conventional set of rules based on ordinary logistic classification; the second set was based on posterior probability distributions of occurrence (presence or absence) derived from Bayesian calculations (Fleishman et al. 2001b; for a general overview of Bayesian statistical methods, see Bergerud & Reed 1998 and references therein). We examined the two sets of rules for similar results because some workers are strong advocates of Bayes approaches (e.g., Crome et al. 1996), but Bayes calculations are generally more difficult to do.

#### CONVENTIONAL LOGISTIC CLASSIFICATION

When data for predictor variables are substituted into a logistic-regression model for a species, the result is an estimated probability of occurrence,  $\hat{p}$ . Typically, if  $\hat{p} < 0.5$ , then the species is predicted to be absent. If  $\hat{p} \geq 0.5$ , the species is predicted to be present. However, more-stringent classification rules can be used; predictions can be made only for locations at which a species is predicted to be absent or present with a given degree of confidence. For example, one might predict that a species will be absent if  $\hat{p} \leq 0.2$  and present if  $\hat{p} \geq 0.8$ . Predictions would not be made for cases with intermediate values (e.g.,  $\hat{p} \sim 0.4$ ). Because the predictions for some

locations are highly uncertain, a consequence of using more-stringent rules is that fewer predictions are made.

#### BAYESIAN CLASSIFICATION

When using Bayes-based rules, we consider the posterior probability distribution of  $\hat{p}$ . Bayesian calculations involve the computation of a “joint posterior probability distribution” for all model parameters (and the data), including, in this case, the regression coefficients and location-specific probabilities of occurrence (i.e.,  $\hat{p}$ ). We think that the confidence of predictions of presence or absence relates to where the bulk of the probability for  $\hat{p}$  lies, so that if most of the probability mass is, say, in the region where  $\hat{p} \leq 0.2$ , then the species is expected to be absent (i.e., “very unlikely” present). Alternatively, if most of the mass is where  $\hat{p} \geq 0.8$ , then the species is expected to be present (i.e., “very likely” present). In these Bayesian rules, different levels of stringency are reached by using different proportions (e.g.,  $\geq 25\%$  or  $\geq 80\%$ ) of probability mass in either the very unlikely or very likely compartments of the posterior probability distribution.

### Objectives

We assessed overall success rates, the success rates of absence predictions, and the success rates of presence predictions with conventional and Bayesian suites of classification rules. In addition, because the point at which a “snapshot” of occupancy is taken can affect parameter estimation and model accuracy, we compared success rates relative to the number of years of inventory data (1 year vs. 2 years). A single snapshot of occupancy may be adequate if it represents longer-term occupancy patterns well, but parameters and validation tests based on temporally extensive data are generally expected to yield more-accurate predictions (Hanski 1994, 1999; Hanski et al. 1996; Moilanen 1999, 2000). We further explored whether success rates depend on the fit of the model, measured by the proportion of explained deviance during the model-building phase. We also considered success rates in light of the biology of individual species and the environmental characteristics of particular locations.

## Methods

### Study System and Field Methods

The Great Basin is an extensive region of internal drainage bounded by the Sierra Nevada in the west and the Wasatch Range in the east (Grayson 1993). The topography of the Great Basin is dominated by more than 200 mountain ranges that are climatically isolated from the surrounding valleys (Brown 1978; Grayson 1993). Re-

source agencies generally develop separate management plans for individual mountain ranges.

From 1996 to 1999, we used standard methods to conduct comprehensive inventories of butterflies in 10 canyons in the Toquima Range. We divided canyons into multiple segments from base to crest (49 total). Each segment was 100 m wide and extended for approximately 100 m change in elevation. Mean segment length was >1 km, which is greater than the dispersal distances of virtually all resident butterflies (Fleishman et al. 1997). The Toquima Range data were used to build our occurrence models.

From 2000 to 2001, we used the same field methods to conduct inventories of butterflies in a total of 39 segments in eight canyons in the nearby Shoshone Mountains. The Shoshone Mountain data were used to test the predictions of our occurrence models. During 2000, we conducted inventories of butterflies in 22 canyon segments in four canyons. During 2001, we continued to collect data from those 22 canyon segments and inventoried 17 additional segments in four new canyons. Thus, our validation data set included information on species occurrence from 39 new segments.

Butterfly inventory methods are described in extensive detail by Fleishman et al. (1998, 2000). Using these well-established methods, it is unlikely that we failed to detect species that actually were present in a given segment in a field season (Shapiro 1975; Thomas & Mallorie 1985; Swengel 1990; Kremen 1992; Pollard & Yates 1993; Harding et al. 1995). Moreover, field personnel were familiar with the regional butterfly fauna, and we restricted our inventories to weather most favorable for flight. It is reasonable to infer that a given butterfly species is absent if the area has been searched with these methods during the appropriate season and weather conditions (Pullin 1995; Reed 1996).

We delineated canyon segments by overlaying differentially corrected global positioning system locations on a 30-m (1:24,000) digital elevation model maintained on a geographic information system. For each canyon segment, we derived 14 predictor environmental variables that reasonably might be expected to affect and thus to predict butterfly distributions. These variables, including geographic coordinates, elevation, slope and aspect, length, precipitation, solar insolation, topographic exposure and heterogeneity, and distance to the nearest source of running or standing water (for a complete description see Fleishman et al. 2001b; Mac Nally et al. 2002) were derived from electronic sources of data in combination with ArcView 3.2 and Arc Macro Language scripts (Arc/Info 7 or 8.2).

Our approach to developing predictive models of species occurrence has four phases (for full details see Fleishman et al. 2001b). The first three phases—primary variable screening, secondary variable screening using logistic regression, and logistic model fitting—comprise

the model-building process. The fourth phase is model validation.

## Model Building

### PRIMARY VARIABLE SCREENING

Each species of butterfly was modeled separately. Prior to model calculations, all predictor variables were standardized by

$$X'_{ik} = (X_{ik} - \bar{X}_k) / s_k, \quad (1)$$

where the mean ( $\bar{X}$ ) and standard deviation ( $s$ ) of variable  $k$  were used for each canyon segment  $i$ . Because models were to be derived from 14 predictor variables and their squares, we had to evaluate millions of possible models for each species. We used an exhaustive-search screening of all models, selecting those that produced a minimum value of Schwarz's (1978) information criterion. This criterion is an optimization between model fit (measured by the proportion of explained deviance) and model complexity (measured by the number of predictor variables). The screening approach was based on ordinary multiple linear regression because this can be automated for many millions of models. Logistic-regression modeling relies on iterative procedures and therefore is much slower and difficult to automate. Thus, we assumed that the multiple linear regression approach would yield a suitable set of candidate predictor variables, although this initial modeling was not strictly appropriate.

### SECONDARY VARIABLE SCREENING USING CONVENTIONAL LOGISTIC MODELING

We used conventional logistic-based maximum-likelihood models to select the single most appropriate model for each species from the limited set of predictor variables derived from the first stage. In the second stage, we retained the most complex model statistically justifiable given model fit (Crawley 1993).

### LOGISTIC MODEL FITTING

Next, we fitted models using Bayesian logistic regression and computed them using the BUGS (Bayesian Updating using Gibbs Sampling) programming framework (Spielgelhalter et al. 1996). In the original Bayesian modeling, parameters were given "vague" priors because we had little information upon which to construct prior distributions for regression coefficients (Fleishman et al. 2001b).

The Bayesian framework provided not only estimated distributions for model parameters but also simulated "posterior" distributions of probabilities of occurrence (termed  $\pi_i$  values) for each canyon segment  $i$  given the values of the predictor variables. We divided the distribution into five probability compartments:  $0 \leq \pi_i < 0.2$  = very unlikely to be present,  $0.2 \leq \pi_i < 0.4$  = unlikely,  $0.4 \leq \pi_i <$

$0.6 =$  indeterminate,  $0.6 \leq \pi_i < 0.8 =$  likely, and  $0.8 \leq \pi_i \leq 1.0 =$  very likely. The proportion of the posterior probability mass in each compartment was an indicator of the species' probability of occurrence in segment  $i$ .

### Model Validation

We tested occurrence models for each species by using independent sets of data from the Shoshone Mountains that were not used to build the models. If values for a predictor variable at a validation site in a given model were outside the range of the data used in the model-building phase (for that variable), then the site was not included for the butterfly species involved. Otherwise, we standardized the values for the set of predictor variables for the validation segments by using the means and standard deviations from the model-building phase. The BUGS models with the computed regression-coefficient distributions from the model-building phase were used in conjunction with the standardized data from the new segments to generate posterior  $\pi$ -value distributions for those new segments. Our objective during this testing phase was to evaluate the success rates of the existing models. Therefore, we did not update parameter estimates for regression coefficients in the usual Bayesian way (e.g., Lee 1989). Bayesian updating would modify the models, which we did not yet wish to do.

We computed segment-specific predictions for each butterfly species with both conventional logistic and Bayesian classifications. Conventional logistic-regression calculations used the mean (approximate medians, given the observed high symmetry of distributions) regression-coefficient values derived from the Bayesian model-building process. These means were substituted into the appropriate equation along with standardized values for the predictor variables so that the values for  $\hat{p}$  could be derived by "back-calculation." For Bayesian calculations (BUGS framework), the distributions of regression coefficients (i.e., means and standard errors) were used in conjunction with the standardized values for the predictor variables to compute posterior probability distributions for  $\hat{p}$ . In effect, the uncertainties in values for the regression coefficients were built into the Bayesian calculations but not into the conventional logistic calculations, although it would be possible to do so in conventional calculations by using Monte Carlo sampling.

### VALIDATION CRITERIA

We tested the success rate of three types of occurrence predictions: (1) correct predictions of species absence (i.e., {predicted absent and observed absent = [0,0]} as a proportion of {predicted absent [0, 0 or 1]}); (2) correct predictions of species presence (i.e., {predicted present and observed present [1,1]} as a proportion of {predicted present [1, 0 or 1]}); and (3) correct predic-

tions compared with total predictions made (i.e.,  $([0,0] + [1,1]) / (\text{all predictions})$ ).

In a conventional test of a logistic-regression model for a species, data for predictor variables from new locations are used to produce an estimated probability of occurrence,  $\hat{p}$ , based on the model. If  $\hat{p} < 0.5$ , then the species is predicted to be absent; if  $\hat{p} \geq 0.5$ , the species is predicted to be present. We abbreviate this conventional classification rule as C(0.5, 0.5). To determine the sensitivity of success rates to rule stringency, we evaluated model predictions with six conventional classifications ranging from the standard C(0.5, 0.5) rule to a very stringent C(0.1, 0.9) rule (i.e.,  $\{\hat{p} \leq 0.1 \rightarrow \text{absence}; \hat{p} \geq 0.9 \rightarrow \text{presence}\}$ ).

For our Bayes-based approach, we used the posterior distributions of the  $\pi$  values to make classification rules. That is, we only tested predictions for new locations for which the model predicted a strong positive or negative probability of occurrence (for example,  $\geq 70\%$  of the  $\pi$ -probability mass distribution in either the very likely or very unlikely compartments, abbreviated as B[0.7]). As with the conventional classifications, we evaluated the success rate of model predictions with six Bayes-based classification rules ranging from a relatively lenient B(0.25) to a stringent B(0.8).

### LEVELS OF ANALYSIS

We conducted analyses at two levels, those of assemblage and the single species. For the assemblage-level analyses, we assessed success rates integrated over all butterfly species that were modeled. We compared the success rates of various conventional and Bayes-based classification rules relative to number of years of inventory data (2 years for some segments versus 1 year for others). Single-species success rates were considered in relation to differences in observed occurrence between data sets used for model building and for validation and in relation to model fit in the building phase. We were able to test the predictions of models for 35 species. Because values for predictor variables vary in space, and because models for different species included different predictor variables, the set of new segments for which predictions could be made was not identical for all species.

## Results

### Assemblage-Level Analyses

#### CONVENTIONAL VERSUS BAYES-BASED CRITERIA

There were 1026 possible predictions of species occurrence in canyon segments based on the single-species models and the environmental attributes of our inventory locations in the Shoshone Mountains. Predictions for some segments were tested with 2 years of inventory data,

whereas other segments could be tested with only 1 year of data. The difference in temporal extent is not crucial in these comparisons because we used the same set of data to compare the conventional and Bayes-based success rates.

Increasing the stringency of classification criteria greatly reduced the number of predictions made (Fig. 1). For example, the most stringent conventional rule, C(0.1, 0.9), produced only 480 predictions, or 47% of the possible total of 1026. The most stringent Bayes-based rule, B(0.8), produced only 459 predictions, 45% of the possible total.

Success rates for overall predictions, predicted absences, and predicted presences increased with greater stringency for both conventional and Bayes-based classification rules (Fig. 2). In all cases, success rates for predicted absences were substantially higher than for predicted presences. Although the success rates continued to increase as a function of stringency based on the conventional rules, there appeared to be a plateau in the Bayes-based rules beyond which increasing stringency yielded little further prediction success (e.g., B[0.6] was similar to B[0.8]).

When a pair of conventional and Bayes-based rules made a similar number of predictions, we compared the

overall success rates of the two rules. For example, C(0.15, 0.85) made 551 predictions and B(0.6) made 561. In five comparisons, there were no significant differences in overall success rates (all  $|t_{0.05,\infty}| < 0.76$ ,  $p > 0.4$ ; arcsin-square-root method; Sokal & Rohlf 1969).

After examining all these results, we chose to restrict the remainder of analyses to the Bayes-based classification rule B(0.7), as we advocated previously (Fleishman et al. 2001b).

#### TEMPORAL EXTENT OF DATA

Twenty-two of the 39 Shoshone Mountain segments were inventoried in both 2000 and 2001. For these segments, the success rates (B[0.7] rule) based on 2 years of data were not significantly higher than those based on the first year of data: for all predictions,  $t_{0.05,\infty} = 0.19$ ,  $p > 0.8$ ; for absence predictions,  $t_{0.05,\infty} = 1.69$ ,  $p > 0.09$ ; for presence predictions,  $t_{0.05,\infty} = 1.28$ ,  $p > 0.2$  (arcsin-square-root method; Sokal & Rohlf 1969).

We performed a similar comparison of the results for the segments that were inventoried in 2 years ( $n = 22$ ) versus the segments that were inventoried in only 1 year ( $n = 17$ ). Again, total success rates did not differ significantly ( $t_{0.05,\infty} = 0.25$ ,  $p > 0.8$ ). However, success rates for presence predictions were significantly greater for the 2-year segments than for the 1-year segments (74%

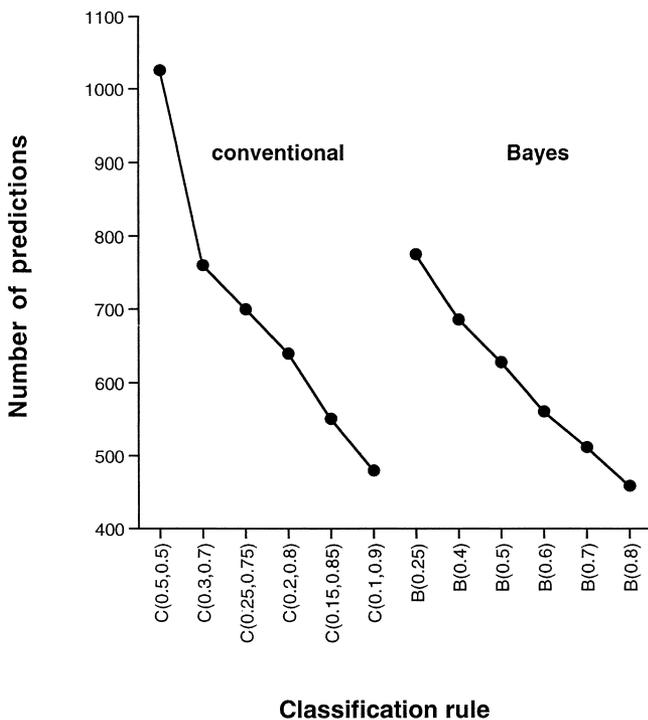


Figure 1. Numbers of predictions of species occurrence made as a function of logistic classification rules employed. "Conventional" and "Bayes-based" rules are defined in the text. The usual conventional rule, C(0.5, 0.5), made predictions for every species-canyon segment combination ( $n = 1026$ ). See methods for definitions of abbreviations for classification rules.

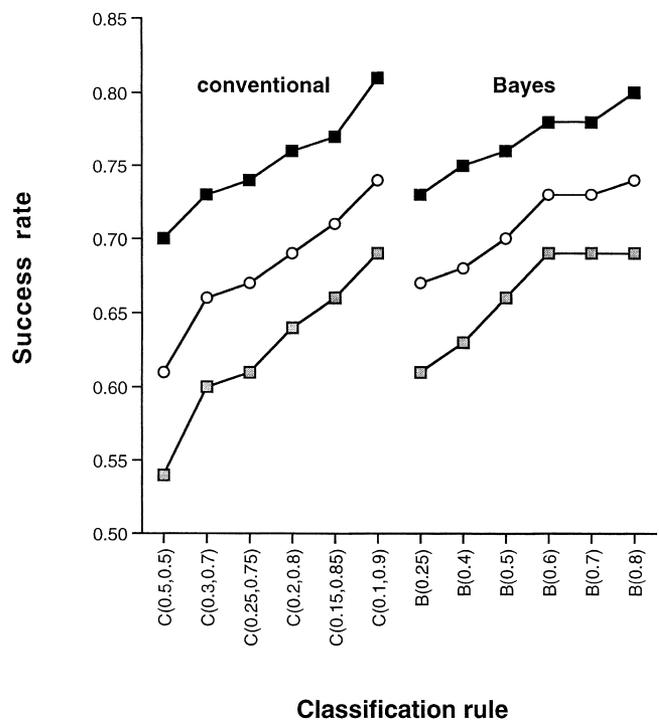


Figure 2. Prediction success rates as a function of classification rules employed. "Conventional" and "Bayes-based" rules are defined in the text. Key: black squares, predicted absences; open circles, overall predictions; grey squares, predicted presences.

vs. 62%,  $t_{0.05,\infty} = 2.17$ ,  $p \approx 0.03$ ), whereas the success rates for absence predictions were significantly lower for the 2-year segments than for the 1-year segments (71% vs. 89%,  $t_{0.05,\infty} = -3.42$ ,  $p < 0.001$ ).

### Single-Species Analyses

#### OVERALL OCCURRENCE RATES

There was a significant correlation between occurrence rates (the proportion of locations in which a species

was found) during the model-building phase (Toquima Range) and the model-validation phase (Shoshone Mountains) (Spearman's  $r_s$  [tie-corrected] = 0.56,  $p < 0.001$ ; Fig. 3a). The average occurrence rates in the model-building phase and validation phase were 0.48 and 0.41, respectively. However, the occurrence of some species during the two phases differed greatly (Appendix 1). The difference in occurrence may be a temporal effect (different sets of years, in which variation in weather conditions and resource availability may have been sufficient to affect butterfly distributions), a geo-

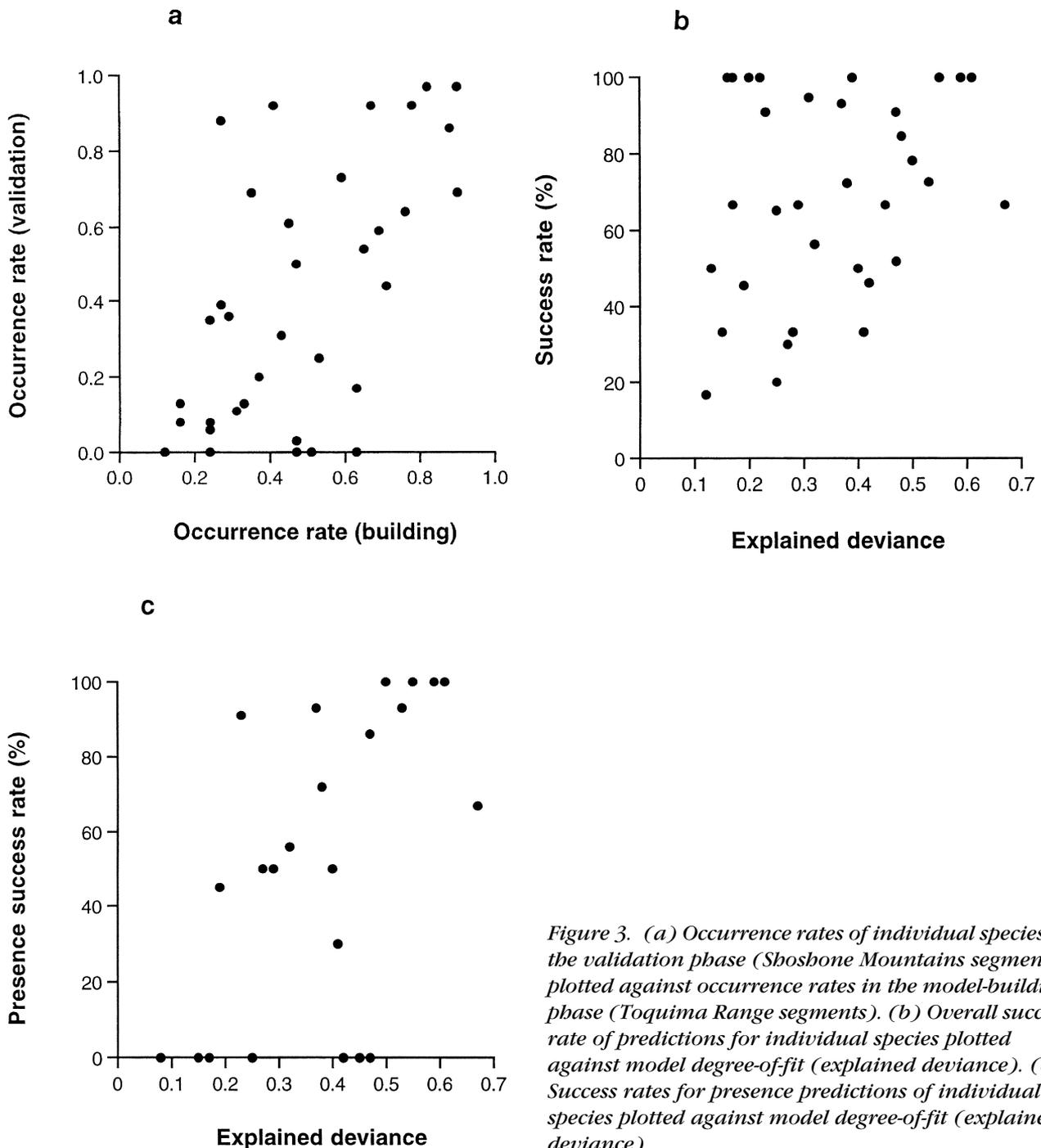


Figure 3. (a) Occurrence rates of individual species in the validation phase (Shoshone Mountains segments) plotted against occurrence rates in the model-building phase (Toquima Range segments). (b) Overall success rate of predictions for individual species plotted against model degree-of-fit (explained deviance). (c) Success rates for presence predictions of individual species plotted against model degree-of-fit (explained deviance).

graphic effect (Toquima Range vs. Shoshone Mountains), or both. Three species, *Euchloe hyantis*, *Callophrys affinis*, and *Neominois ridingsii*, with occurrences in the building phase of 0.12, 0.47, and 0.51, respectively, were not recorded during the validation phase in the Shoshone Mountains. All presences predicted for the latter three taxa in the Shoshone Mountains necessarily would be incorrect. Occurrence rates of another four species increased by more than 0.25 (*Speyeria callippe*, *S. zerene*, *Glaucopsyche piasus*, *Coenonympha tullia*). These increases probably elevated the error rates of absence predictions.

Mean species-specific success rate (B[0.7] rule) was  $67\% \pm 29\%$  (SD). Success rates of  $>90\%$  were recorded for 13 species, 8 of which were based on predictions for more than half of the canyon segments inventoried. For several of the latter 13 species, all predictions were either absences (e.g., *Euchloe hyantis*, *Hesperia uncas*, *Polygonia zephyrus*) or presences (e.g., *Lycaeides melissa*, *Cercyonis oetus*, *Icaricia icarioides*). The results that may prove most useful for management were for several species with high success rates for predictions of both absence and presence. *Mitoura siva*, for example, had a success rate of 100% (six correct absence predictions and three correct presence predictions), and *Icaricia sbasta* had a success rate of 91% (14 of 15 absence predictions correct and 6 of 7 presence predictions correct). Species with poor success rates for predictions based on more than one-third of the segments inventoried included *Satyrrium bebrii* (14 of 21 presence predictions incorrect, 33% success rate), *Glaucopsyche piasus* (8 of 12 absence predictions incorrect, 33% success rate) and *Speyeria callippe* (10 of 12 absence predictions incorrect, 17% success rate). At least for *G. piasus* and *S. callippe*, a high proportion of incorrect absence predictions was expected because the species had substantially higher occurrence rates in the validation phase than in the model-building phase (0.69 vs. 0.35 for *G. piasus*, 0.88 vs. 0.27 for *S. callippe*).

#### SUCCESS RATES AS A FUNCTION OF MODEL FIT

Overall success rates (B[0.7] rule) were not significantly correlated with the original model fit (measured by the proportion of explained deviance in the logistic model) (Spearman's  $r_s = 0.32$ ,  $p > 0.05$ ; Fig. 3b). For example, eight species had an overall prediction success rate of 100%, but the proportion of explained deviance in the model-building phase ranged from 0.16 (*Phyciodes pulchella*) to 0.61 (*Lycaeides melissa*). The success rate of absence predictions was also not correlated with model fit (Spearman's  $r_s = -0.05$ ,  $p \approx 0.8$ ).

However, model fit was correlated with the success rate of presence predictions (Spearman's  $r_s = 0.59$ ,  $p \approx 0.005$ ; Fig. 3c). Three species with predicted presence success rates of zero had much lower occurrence

rates in the Shoshone Mountains than in the Toquima Range (*Euphydryas editba*, 0.03 vs. 0.47; *Plebejus saepiolus*, 0 vs. 0.24; *Chlosyne acastus*, 0.17 vs. 0.68). When these three species were excluded, the rank correlation between the model fit and success rate of presence predictions increased to 0.77 ( $p < 0.001$ ).

## Discussion

### Importance of Model Validation

We believe that rigorous validation of statistical modeling of species distributions has not received sufficient attention. This has led to at least two adverse outcomes. First, workers may assume that models are correct and thus are reliable either for use in further research inference or for management planning. Lack of widespread validation also has a second, more important consequence: impeded learning. The model-building and validation process itself generates pertinent research questions by identifying where our ecological understanding could be improved.

To illustrate the latter point, consider differences in the occurrence rates of many species between our model-building data set (1996–1999, Toquima Range) and model-validation data set (2000–2001, Shoshone Mountains). These disparities suggested that as we continue to collect validation data with which to refine our models, we should simultaneously conduct inventories in some new canyon segments in the range used for model-building (i.e., “validation” *sensu stricto* within the same population of sites). This would allow us to determine whether changes in occurrence rates are strictly temporal, whether there are fundamental geographic differences between the two mountain ranges (i.e., whether models are “transferable”; Leftwich et al. 1997), or both. If the different occurrence rates largely reflect deterministic temporal trends, the models may not be successful even when applied to locations in the range from which they are based. The extent of geographic differences provides an indication of the possible spatial extent of the utility of models. One would expect a decay in model applicability with increasing distance from the locations used to build the models, but knowledge of that decay rate is crucial.

Ideally, models would be tested with a validation data set comparable in temporal and spatial extent to the model-building data set. In practice, data used to build a model may sometimes be collected over many years, but financial or other constraints often limit the collection of validation data to fewer years or even to just 1 year. The success of our models did not depend on the number of years of validation data, and we did not find a difference in total success rates between years (2000 vs. 2001). Thus, the main issue in improving data quality appears

to be discriminating between temporal and spatial sources of variability in occupancy rates and not necessarily simply collecting more years of validation data from the same set of locations.

Nonetheless, as the temporal extent of our data increased, we did obtain more successful presence predictions but fewer successful absence predictions. Species composition in almost every ecological system is temporally variable to some extent. On the one hand, it is possible that a species will be present at a study location in some years but absent in other years (perhaps because weather conditions are unfavorable). The apparent absence of a species from a location where it is sometimes present—because of temporal variability and the implemented survey program—is a “false negative.” Over time, the probability of false negatives decreases, so the success of presence predictions should increase. On the other hand, given a long enough period of time, many species will appear as “accidentals” in locations that are outside their typical distributional range. Thus, the success of absence predictions is likely to decrease somewhat over time.

#### Classification Rules: Tradeoffs between Quantity and Quality

Much practical information can be obtained by calculating prediction success rates with a range of classification rules, based on both conventional methods and Bayesian posterior probability distributions. There are many ways to make a prediction about a species' occurrence, and no single classification rule is best under all circumstances.

We believe that making inherently poor predictions for the sake of prediction is not profitable. More-stringent classification rules yield fewer predictions, but the quality of those predictions is greater. For instance, compare the results for the conventional C(0.5, 0.5) rule with a more stringent rule, such as B(0.7). The Bayes-based rule made 512 predictions, almost 50% fewer than the conventional rule. What was the success rate of the additional 514 predictions made under the C(0.5, 0.5) rule? The C(0.5, 0.5) rule predicted an additional 210 absences (i.e., that a given species would be absent in a given segment), 130 (62%) of which matched the observed field data. The C(0.5, 0.5) rule also made an additional 304 presence predictions, only 122 (40%) of which were correct. Thus, the overall success rate for the 514 extra predictions was just 49%, not much different from the rate expected by chance.

The difference in the success rates of the additional absence or presence predictions made using the C(0.5, 0.5) rule suggests that classification rules for predicting presences and for predicting absences may be decoupled to improve overall predictive success. In some decision-making scenarios, the 62% success rate of the additional absence predictions might fall within an acceptable

level of certainty, although the additional presence predictions would be eschewed. In principle, one might employ a mixed approach in which one used all C(0.5, 0.5) absence predictions (overall success rate of 70%), all the B(0.7) presence predictions (success rate of 69%), and, for species with a sufficiently high model fit (recall that success rates for presence predictions were positively correlated with model fit), the additional C(0.5, 0.5) presence predictions. This mixed approach would yield predictions for at least  $512 + 210 = 722$  species-segment combinations, possibly close to 800 overall, at a success rate of approximately 65%.

#### Interspecific and Spatial Variation

Among species and locations, there was considerable variation in the success of predictions. Moreover, regardless of whether the overall success rate was high or low, predictions for some species and locations were much better for presence than for absence, and vice versa. For example, although the overall success rate of predictions for *Coenonympha tullia* was high (73% using the B[0.7] rule), predictions for presence (93%) were much better than for absence (29%). In contrast, predictions for *Chlosyne acastus* were weak overall (33%). The success rate of absence predictions for *C. acastus* was high (86%), however, and much greater than for presence predictions (0%).

For some species, we can draw biological inferences about why models were successful or unsuccessful. A few of the species with extremely high success rates were either nearly ubiquitous or very rare in the Shoshone Mountains. *Cercyonis oetus*, *Lycaeides melissa*, and *Polygonia zephyrus*, with overall model success rates of >85%, and Shoshone Mountains occupancy rates of 97%, 97%, and 6%, respectively, are good examples. The high (approximately 90%) success rate of at least one species with intermediate occupancy rates in both mountain ranges, *Icaricia shasta*, may result from its known association with high elevations. Biological explanations for other successful models are not as apparent, suggesting that the models are a real improvement over the intuition of an experienced observer. For example, 100% of the B(0.7) predictions for *Mitoura siva* were correct. *Mitoura siva* had an intermediate degree of occupancy in both mountain ranges. In the field, the species does not appear to be restricted to locations with a characteristic topography, and its larval host-plant, the juniper tree (*Juniperus osteosperma*), is far more widespread than the butterfly. Thus, the occupancy model for *Mitoura siva* may be a valuable planning tool despite our current inability to provide an ecological rationale for its success. We can offer at least two explanations for some of the less successful models. First, as we noted, occupancy rates for several species were very different in the model-building and model-val-

validation data sets. Second, a few other species with <50% success rates, such as *Glaucopsyche piasus* and *Satyrium bebrii*, have highly stochastic temporal occurrence patterns (Fleishman et al. 1997).

We can also interpret some of the relatively high and low success rates for individual study locations using biological explanations. Several canyon segments had few resources for butterflies (e.g., larval host plants, adult nectar sources, and sources of water) or were climatically severe (e.g., the highest sampled elevations). In these cases, it is not surprising that success rates, especially for absence predictions, were high. In contrast, several of the canyon segments with the highest rates of successful presence predictions seemed to have relatively abundant resources and diverse topography, locations where one might expect a priori to encounter many species of butterflies.

### Model Refinement

Notwithstanding some major differences in occurrence rates of individual species and potential sources of temporal and geographic variability, our models of species occurrence were relatively successful (73% overall using the B[0.7] rule), especially for absence predictions (78%). Our modeling process continues, and we are pursuing several avenues for model refinement. First, new remote-sensing instruments and terrain-based geographic information system models can provide improved estimates of environmental variables such as precipitation, temperature, land-cover type and extent, and leaf-area index at a moderate spatial resolution (250 m to 1 km) and at a range of temporal resolutions. These data might offer greater modeling scope for some species.

Second, the existing set of validation data might be used to “update” model parameter estimates in the usual Bayesian way to refine models. The number of locations for which we currently have inventory data is almost double the number we used to build the initial models. These additional data potentially allow models with improved fit and/or predictive success to be constructed for species that were not modeled well in the first iteration. Third, it may prove worthwhile to use generalized link functions in the logistic modeling process. The logit transform is symmetrical about  $p = 0.5$  (Prentice 1976). It is possible to reframe the logistic link with an additional exponential parameter to better model species having occurrence rates substantially different from  $p = 0.5$  (Manel et al. 2001), which may improve overall modeling success.

Although we used butterflies as a study system, our methods for building, testing, and refining models of species occurrence constitute a general framework that can be applied to any taxonomic group or ecosystem. We do not advocate any single classification rule. In-

stead, we have provided information on tradeoffs between the number of predictions and the quality or certainty of those predictions which can be used to determine the best rule under a particular set of real-world circumstances. We hope our work will save managers and decisionmakers time and money by allowing them to predict species occurrence in existing landscapes or in landscapes that may be altered by climate change or reconstruction efforts.

### Acknowledgments

We thank A. Bennett, E. Main, and two anonymous reviewers for valuable comments on the manuscript and the Humboldt-Toiyabe National Forest for logistic support in the field. Financial support for this research was provided by the Nevada Biodiversity Research and Conservation Initiative; the Joint Fire Sciences Program via the Rocky Mountain Research Station, U.S. Forest Service; and the Australian Research Council.

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## Appendix 1. Occurrence rates of individual species in the model-building and model-validation phases.

Species	Occurrence rate	
	building	validation
<i>Cercyonis stbenele</i>	0.90	0.69
<i>Lycaeides melissa</i>	0.90	0.97
<i>Hesperia juba</i>	0.88	0.86
<i>Cercyonis oetus</i>	0.82	0.97
<i>Icaricia icarioides</i>	0.78	0.92
<i>Incisalia eryphon</i>	0.76	0.64
<i>Icaricia lupini</i>	0.71	0.44
<i>Euphydryas anicia</i>	0.69	0.59
<i>Coenonympha tullia</i>	0.67	0.92
<i>Limenitis weidemeyerii</i>	0.65	0.54
<i>Apodemia mormo</i>	0.63	0
<i>Chlosyne acastus</i>	0.63	0.17
<i>Ochlodes sylvanoides</i>	0.59	0.73
<i>Satyrrium bebrii</i>	0.53	0.25
<i>Neominois ridingsii</i>	0.51	0
<i>Callophrys affinis</i>	0.47	0
<i>Euphydryas editha</i>	0.47	0.03
<i>Neobasia menapia</i>	0.47	0.50
<i>Lycaena heteronea</i>	0.45	0.61
<i>Icaricia sbasta</i>	0.43	0.31
<i>Speyeria zerene</i>	0.41	0.92
<i>Papilio rutulus</i>	0.37	0.20
<i>Glaucopsyche piasus</i>	0.35	0.69
<i>Nymphalis antiopa</i>	0.33	0.13
<i>Phyciodes pulchella</i>	0.31	0.11
<i>Eucbloë ausonides</i>	0.29	0.36
<i>Euphilotes ancilla</i>	0.27	0.39
<i>Speyeria callippe</i>	0.27	0.88
<i>Mitoura siva</i>	0.24	0.35
<i>Plebejus saepiolus</i>	0.24	0
<i>Polygonia zephyrus</i>	0.24	0.06
<i>Satyrrium sylvinum</i>	0.24	0.08
<i>Hesperia uncas</i>	0.16	0.08
<i>Lycaena rubidus</i>	0.16	0.13
<i>Eucbloë hyantis</i>	0.12	0

