

Bayesian Small Area Models for Assessing Wildlife Conservation Risk in Patchy Populations

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Abstract: Species conservation risk assessments require accurate, probabilistic, and biologically meaningful maps of population distribution. In patchy populations, the reasons for discontinuities are not often well understood. We tested a novel approach to habitat modeling in which methods of small area estimation were used within a hierarchical Bayesian framework. Amphibian occurrence was modeled with logistic regression that included third-order drainages as hierarchical effects to account for patchy populations. Models including the random drainage effects adequately represented species occurrences in patchy populations of 4 amphibian species in the Oregon Coast Range (U.S.A.). Amphibian surveys from other locations within the same drainage were used to calibrate local drainage-scale effects. Cross-validation showed that prediction errors for calibrated models were 77% to 86% lower than comparable regionally constructed models, depending on species. When calibration data were unavailable, small area and regional models performed similarly, although poorly. Small area estimation models complement wildlife ecology and habitat studies, and can help managers develop a regional picture of the conservation status for relatively rare species.

Keywords: amphibian conservation, *Ascaphus truei*, *Dicamptodon tenebrosus*, hierarchical Bayesian models, *Rhyacotriton kezeri*, *Rhyacotriton variegatus*, risk assessment

Modelos Bayesianos de Área Reducida para Evaluar el Riesgo de Conservación de Vida Silvestre en Poblaciones Fragmentadas

Resumen: Las evaluaciones de riesgo de conservación de especies requieren de mapas precisos, probabilísticos y biológicamente significativos de la distribución de la población. En poblaciones fragmentadas, las razones de las discontinuidades a menudo no son bien entendidas. Probamos un nuevo método para modelar hábitats en el que se usaron métodos de estimación de áreas pequeñas en un marco Bayesiano jerárquico. La ocurrencia de anfibios fue modelada con regresión logística que incluyó escurrimientos de tercer orden como efectos jerárquicos para explicar las poblaciones fragmentadas. Los modelos que incluyeron los efectos de los escurrimientos aleatorios representaron adecuadamente la ocurrencia de especies en poblaciones fragmentadas de cuatro especies de anfibios en la Cordillera Costera de Oregon (E.U.A.). Utilizamos muestreos de anfibios en otras localidades en el mismo escurrimiento para calibrar los efectos del escurrimiento a escala local. La validación cruzada mostró que los errores de predicción para los modelos calibrados fueron entre 77% y 86% menores que los modelos comparables construidos regionalmente, dependiendo de la especie. Cuando no se disponía de datos de calibración, los modelos de áreas pequeñas y regionales funcionaron similarmente, aunque pobremente. Los modelos de estimación de áreas pequeñas complementan los estudios de ecología y hábitat de vida silvestre, y pueden ayudar a que los manejadores desarrollen una visión regional del estatus de conservación de especies relativamente raras.

Palabras Clave: *Ascaphus truei*, conservación de anfibios, *Dicamptodon tenebrosus*, evaluación de riesgo, modelos Bayesianos jerárquicos, *Rhyacotriton kezeri*, *Rhyacotriton variegatus*

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Introduction

Most wildlife species have patchy, discontinuous populations (Wiens 1976) that are not often well represented by broad-scale, regionally constructed habitat models (Cushman et al. 2008). These regional models do not have the flexibility to incorporate factors influencing distributions that are often highly spatially variable across the region of interest; examples include inconsistent historical effects (e.g., disease or stream sedimentation), patchy predator distributions (Knapp et al. 2003), or localized geomorphology (Russell et al. 2004). There is little hope for developing regional models that account for all of the cumulative effects that commonly result in discontinuous, patchy distributions. Funding is limited and models cannot be developed for each species within each local area. Models that do not account for patchy populations, in effect, apply regional averages to predict highly variable local conditions.

One alternative is to combine regional and local scales through small area estimation (SAE) techniques (Rao 2003). Small area models have been used to help predict average income for small municipalities when sample coverage was sparse (Fay & Herriot 1979), to estimate crop coverage of counties, and are widely used in epidemiology (Ghosh & Rao 1994). The small areas are commonly defined as cities, counties, or even states, depending on the objectives. These SAE methods develop regional models as a collection of smaller areas to better reflect local conditions (Rao 2003). The small areas (third-order drainages in our context) are related through a common, higher-level process that allows consistent predictions and substantially better parameter estimates for local areas with scant data (Rao 2003). Furthermore, SAE models can incorporate local survey data to help make better predictions at local scales.

A more common approach to account for patchy wildlife populations is to directly model spatial autocorrelation (Augustin et al. 1996; Knapp et al. 2003). Small area models do not necessarily consider the spatial structure of the population (i.e., spatial correlation between neighboring small areas) and can therefore be developed with less data. Small area models may also be preferred where adjacent small areas are expected to be independent.

Our objective was to test the suitability of SAE models for characterizing patchy amphibian populations in the Oregon Coast Range to help assess possible risks to their conservation. Managers need reliable estimates of wildlife abundance because misidentifying areas as having locally high or low populations can lead to inefficient conservation efforts or missed opportunities. We also examined situations in which SAE models might suggest different conservation approaches compared with regional models.

We considered Pacific giant salamanders (*Dicamptodon tenebrosus*), larval and adult tailed frogs (*Ascaphus truei*), southern torrent salamanders (*Rhyacotriton variegatus*), and Columbia torrent salamanders (*Rhyacotriton kezeri*). Pacific giant salamanders are relatively common. Torrent salamanders and tailed frogs are federally listed species of concern (FEMAT 1993) and have patchy distributions across their range (Welsh & Lind 1996), which makes information on local populations especially important. The SAE models incorporated local survey information from a drainage to help make better predictions for unsurveyed areas. We used a hierarchical Bayesian approach to provide a probabilistic interpretation of the results (Gelman & Hill 2007). The combined Bayesian and SAE approaches provided the necessary information for risk assessment, a critical but underutilized technique for species conservation.

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Methods

Study Area and Amphibian Surveys

The study area encompassed Bureau of Land Management (BLM) lands along the eastern side of the Oregon Coast Range (U.S.A.). This region has a moist and cool maritime climate, with a prolonged summer drought. The area is within the *Tsuga heterophylla* zone (Franklin & Dyrness 1973), and the forests were predominately *Psuedotsuga menziesii*, with significant components of *Tsuga heterophylla*, *Thuja plicata*, *Alnus rubra*, *Acer macrophyllum*, and other minor species. We sampled headwater streams primarily in second-growth forests regenerated following logging and burning or in younger plantations. Headwater streams with intermittent or perennial stream flow were common. Riparian areas around these streams often had more deciduous trees than bordering stands and a diverse shrub and herbaceous component.

We surveyed 4 amphibian species within 16 third-order drainages randomly chosen from BLM lands of the Eugene and Salem districts. Drainages were 90 to 200 ha, with midpoint elevations between 200 and 660 m. Within each drainage, we surveyed amphibians at 35 to 50 randomly chosen 2-m-long stream sections (sample points) that had intermittent or perennial surface flow ≤ 0.5 m deep. Surveys followed standard protocols for area-constrained searches (Bury & Corn 1991). We grouped sample points into stands on the basis of age class of the adjacent forests (classes: 0–15, 16–55, 55–105, and >105 years). Stands contained between 1 and 34 sample points (mean 4.6). Drainages contained between 3 and 15 stands (mean 9.6). We surveyed 702 sample points across 153 stands in the summers of 1998 and 1999. Sample locations were randomly assigned to early, mid, and late summer to avoid possible seasonal bias (Stoddard & Hayes 2005).

Habitat was characterized at the stand and drainage scales from digital elevation maps (DEMs) and aerial photographs. Covariate selection was guided by the analyses

of Stoddard and Hayes (2005), who identified biologically relevant habitat variables for these species. At the stand scale these included heat index (heat) and the stream gradient (grad) averaged across all sample points. The heat index was calculated as $[1 - \cos(\text{aspect} - 45)]/2$, which scaled from 0–1 (near 0, low solar insolation [north, northeast aspect]; near 1, higher levels [south, southwest aspect]). We used a categorical variable to indicate the presence (1) or absence (0) of a buffer ≥ 46 m wide of older forest (>55 years) on both sides of the stream (stbuf). This buffer width corresponded to the riparian buffer for permanently flowing nonfish bearing streams under the Northwest Forest Plan for federal ownerships (FEMAT 1993). The relative elevation of each stand within a drainage (stelev) was computed as the elevation difference between the stand and the midpoint elevation of the drainage. At the drainage scale, variables included the percentage of the drainage with slope $\geq 60\%$ (slope), midpoint elevation (delev), and percentage of drainage area containing young (<15 years) stands (%young). Road density (roads) was kilometers of roads per hectare. Drainage aspect (aspect) was the DEM-calculated average aspect of sample points along the mainstem and was cosine transformed. Finally, we computed the percentage of the drainage with an older forest (>55 years) buffer at least 46 m wide on both sides of the stream (%dbuf). Several drainage-scale variables were included because they were expected to be indicative of disturbance history; for example, stream sedimentation is expected to be correlated with road density, average slope, and harvest intensity (Jones et al. 2000). Fine-scale habitat variables measured at the 2-m sample points were initially considered, but excluded from the analysis for reasons detailed later.

Presence or absence in each 2-m stream section was recorded for Pacific giant salamanders, larval, and adult tailed frogs, southern torrent salamanders, and Columbia torrent salamanders. The torrent salamander species were geographically separate but have similar habitat associations (Welsh & Lind 1996), so we combined them for analyses. At least one species was found at 59% of the stream sections. The mean probability of occurrence across all 702 sample points was 0.53, 0.095, 0.162, and 0.046 for giant salamanders, torrent salamanders, and larval and adult tailed frogs, respectively. A complete description of the study area and sampling methods is in Stoddard and Hayes (2005).

Bayesian Modeling

We used a hierarchical Bayesian model to analyze presence–absence data for amphibians (Wade 2000; Gelman et al. 2003; Gelman & Hill 2007). At the stand scale we used binomial regression to characterize a habitat model:

$$Y_{ijk} \sim \text{binomial}(p_{ijk}, n_{ijk}), \quad (1)$$

where Y_{ijk} is the number of sample points with species i present in stand j and drainage k . The number of sample points within a stand is n_{ijk} . The probability of occurrence (p) was modeled with a logit link function:

$$\begin{aligned} \text{logit}(p_{ijk}) = & \beta_{0i} + \alpha_{ik} + \beta_{1i}(\text{grad}_{jk}) + \beta_{2i}(\text{stelev}_{jk}) \\ & + \beta_{3i}(\text{stbuf}_{jk}) + \beta_{4i}(\text{heat}_{jk}). \end{aligned} \quad (2)$$

Drainage-scale effects were included as higher-level covariates and modified the intercept (β_0) in a hierarchical manner,

$$\alpha_{ik} \sim \text{MVN}(\mu, \Sigma), \quad (3)$$

where the drainage means (μ_{ik}) were assumed distributed multivariate normal (MVN). These means were modeled as a function of drainage-scale covariates:

$$\begin{aligned} \mu_{ik} = & \gamma_{1i}(\text{slope}_k) + \gamma_{2i}(\%dbuf_k) + \gamma_{3i}(\text{delev}_k) \\ & + \gamma_{4i}(\text{roads}_k) + \gamma_{5i}(\%young_k) + \gamma_{6i}(\text{aspect}_k). \end{aligned} \quad (4)$$

The variance–covariance matrix Σ was given a noninformative Wishart prior with 4 df, equal to the number of parameters (Gelman et al. 2003). The scale of the prior variances was set to 0.5 on the basis of a separate analysis with a generalized mixed linear model, whereas the scale of the prior covariances was set to zero. The model was relatively insensitive to the scale of the prior variances within a somewhat narrow range of 0.05 to 1. Noninformative priors were specified for all other parameters (β_{0-4} and γ_{1-6}) as $\sim N(0, 0.001)$, specified with precisions ($1/\sigma^2$). Model parameters (β , γ , and Σ) were given prior distributions, as required for all Bayesian analyses. These priors were updated with data and Bayes theorem and resulted in the posterior distributions for the parameters (i.e., parameter estimates). For comparison, a nonhierarchical regional model was fitted that did not include random drainage effects (α_{ik}), but that retained the same stand- and drainage-scale covariates.

All noncategorical habitat variables, with the exception of aspect, were standardized prior to analysis by subtracting the mean and dividing by the standard deviation. Bayesian analyses are scale independent, so the standardization only influenced the parameter interpretation. Standardized parameters are interpreted as the change in probability expected (on the logit scale) for a one standard deviation change in the value of the habitat covariate (Gelman et al. 2003).

All analyses were done with WinBUGS 1.4.1 (Lunn et al. 2000), which uses a Markov chain Monte Carlo (MCMC) approach to characterize the posterior distributions (Gelman et al. 2003). We based results on 100,000 MCMC simulations and retained every 10th sample to reduce autocorrelation following a 20,000 iteration tuning, or “burn-in” period, for the Markov chain to converge

to the target (i.e., posterior) distribution. Habitat covariate selection was guided by a lowest deviance information criterion (DIC) to select a parsimonious model with high predictive ability. Model selection was performed in a stepwise manner, with covariates dropped first that had estimates closest to zero. Covariates were retained if their 95% credibility interval (CI; Bayesian equivalent to the confidence interval) did not overlap with zero. The change in DIC was also assessed before dropping a covariate.

The final model with the MVN structure (Σ) as indicated had the lowest DIC of alternative options. Model convergence and fit were checked with multiple MCMC simulations and posterior predictive checks, respectively (Gelman et al. 2003).

Drainage-scale covariates were incorporated as a hierarchical effect; therefore, γ_{1-6} were constant across drainages, similar to fixed effects in a mixed linear model. In a hierarchical model, these effects are interpreted in a very specific way. Heuristically, the variances, $\sigma_{\alpha_i}^2$, estimate the additional "spread" or deviation of stands from the same drainage beyond that explained by the drainage-scale covariates. If the drainage-scale covariates explain all the drainage-scale mean differences (conditioned on the stand-scale covariates), then $\sigma_{\alpha_i}^2 = 0$ and the model collapses into a nonhierarchical model with stand- and drainage-scale covariates. These additional deviations from the drainage means (μ_{ik}) were computed during the MCMC simulations as $\text{dev}_{ik} = \alpha_{ik} - \mu_{ik}$, and represent local drainage effects. Species correlations were computed from Σ and estimate the correlation among deviations (dev_{ik}) between species within a drainage. A positive correlation indicated that drainages appearing to be of better quality than the drainage-scale covariates predicted for one species also tended to be better for the other species, and vice versa.

Fine-scale habitat variables measured at the 2-m sample points, such as stream width, percent undercut bank, and coarse woody debris were investigated as potentially useful predictors. First, we used a variance components model to partition the total variance of each fine-scale habitat variable into drainage, stand, and residual (i.e., within stand) sources. Second, we averaged fine-scale covariates at the stand scale, included them in the model (Eq. 1), and assessed their predictive ability with DIC.

We used a hierarchical Bayesian model to fit Eq. 1 for several reasons. First, such models are difficult to implement with frequentist methods, such as mixed linear models (Gelman & Hill 2007). Second, Bayesian model predictions for new stands are interpreted probabilistically, which is necessary for risk assessment. Finally, the model structure connects species at the drainage scale through Σ , which can result in better predictions for one species when data from a drainage are available for any of the 4 species (see Wilson et al. [2008] for an example).

Cross-Validation

We used cross-validation to compare the regional and SAE approaches. The models are intended for use by managers to make stand-scale predictions within new drainages; therefore, we used cross-validation to assess model accuracy and precision under this scenario. For the regional and SAE approaches, we sequentially excluded all data from a single drainage and fitted the models to this reduced data set, for a total of 16 simulations (reflecting the number of drainages). For the regional model, species occurrence predictions were made for stands in the excluded drainage directly from the estimated model parameters. For the SAE model, the available survey data within the excluded drainage were used for model calibration (i.e., estimating dev_{ik}). That is, for an excluded drainage with survey data available for 10 stands, 9 were used for calibration, and predictions were made for the remaining stand with the calibrated model. Predictions were made sequentially in this manner for all 153 stands. No other parameters (i.e., β , γ , or σ_{α}^2) were affected by this calibration. New predictions were made simultaneously with model fitting in WinBUGS and used the MCMC posterior distributions for the model parameters. For comparison, predictions were also made for an uncalibrated SAE model ($\text{dev}_{ik} = 0$, which is the average value across drainages).

The regional and SAE models were fitted to exactly the same data in the cross-validation, with the only difference being the SAE model used additional survey data for calibration. The regional models have no direct capacity for incorporating the additional survey data within a drainage. That is, regional models will make the same predictions for a stand, regardless of whether neighboring stands are known to have abnormally higher or lower amphibian abundances. The SAE models made use of this additional information in the calibration (Lappi 1991). The SAE model calibration incorporated the maximum amount of available data, so it represented a best-case scenario. We computed average prediction error $(Y_i - \hat{Y}_i)^2$, bias $(Y_i - \hat{Y}_i)$, and absolute prediction differences $|Y_i - \hat{Y}_i|$ from the observed (Y) and mean predicted (\hat{Y}) occurrences for each species. Further, variance predictions $\sigma_{\alpha_i}^2$ from the reduced data sets (15 drainages each) were compared with results from the full data set in a sensitivity analysis.

Simulations

One objective was to illustrate the use of local survey information within a regional habitat model. Local information (i.e., surveyed stands within a drainage) was simulated for new drainages with varying levels of additional local information. That is, a variable number (0–15) of new surveyed stands were included within a drainage with $n_{ijk} = 10$ and constant p_{ijk} for a species ($p_{ijk} = 0.5$,

0.1, 0.2, and 0.1 for giant salamanders, torrent salamanders, and larval and adult tailed frogs, respectively). The simulations were performed simultaneous to model fitting in WinBUGS with the MCMC posterior distributions for the model parameters. We used the “cut” function within WinBUGS to isolate parameter estimates fitted by the model from the simulated data.

As the amount of survey data within a drainage increased, the precision of the predicted local dev_{ik} effects increased. We assessed how practical the SAE models were by examining how steeply the precision increased with additional stands available for calibration. Precision was judged by the standard errors of the dev_{ik} prediction, which were computed directly from the posterior distribution on the logit scale. Because local dev_{ik} effects were conditional on the stand and drainage covariates, these were assigned known values as follows. Stand-scale covariates (on standardized scales) were *grad*, 0; *stlev*, 0; and *stbuf*, 1. Drainage-scale standardized covariates were *slope*, 0.25; *%dbuf*, -0.25 ; *delev*, 0; *%young*, 0.25; and *aspect*, 0.25. Predictions for species in the new stands were presented probabilistically as the predicted mean number of occurrences out of 10 randomly selected surveyed points. These predictions are given as a distribution of possible results in a Bayesian analysis. This aids with risk assessment because it shows the likelihood of a high or low population, rather than simply presenting a point (i.e., mean) prediction. We also examined how local survey information could alter management decisions by comparing regional and local model predictions for several of the 153 surveyed stands. To illustrate the typical differences, we made predictions for each species in drainages with average, high, and low predicted local effects. We used the actual stand- and drainage-scale co-

variates from a randomly selected stand in each drainage and estimated the probability of finding 0–10 individuals at 10 sample points within the stand.

Results

Local Habitat Models

The small area models adequately represented these highly patchy amphibian populations. The final model accounted for 25% of the residual deviance over a null (intercept only) model, with an adjusted R^2 of 0.34 (Nagelkerke 1991). Incorporating the MVN error structure showed a slight improvement in model fit indicated by a 4.2-point drop in DIC versus a non-MVN error. Posterior predictive checks showed good agreement with survey data, and residuals were adequately distributed. The sensitivity analysis showed the estimated drainage variances with a single-drainage excluded, which were all within the 95% CI of σ_{α_i} estimated with the full data set.

Predicted drainage effects varied between -2.0 and 2.6 on the logit scale for adult tailed frogs (Fig. 1b), indicating large differences in drainage-scale abundance. Other species showed a similar range. For reference, predicted effects of 3 and -3 on the logit scale result in changes on the probability scale from 0.5 to 0.95 and 0.05, respectively. A substantial portion of the drainage effects was due to extra deviation not accounted for by the drainage-scale covariates, which was indicated by the relatively large variances, $\sigma_{\alpha_i}^2$. These deviations from the mean drainage effects were interpreted as local drainage effects (dev_{ik}) with standard deviations on the logit scale (σ_{α_i})

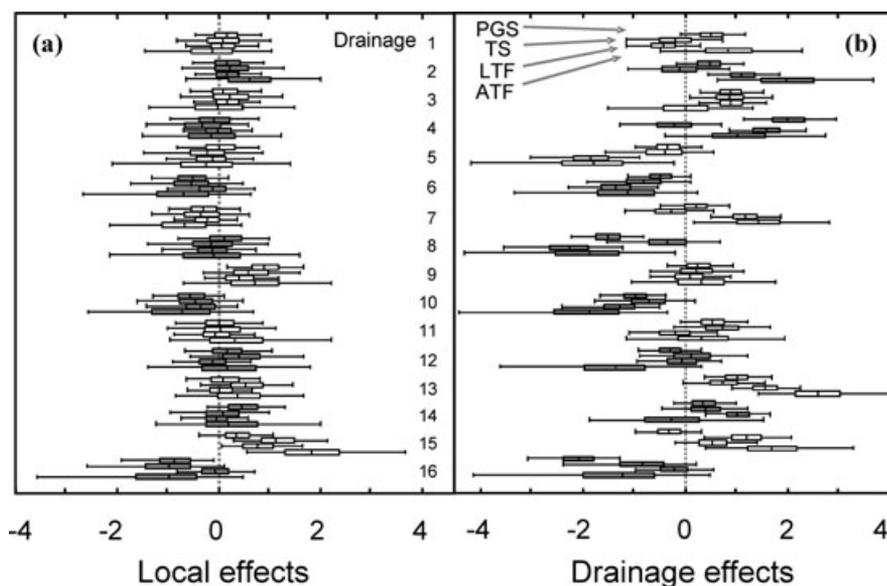


Figure 1. Posterior distributions for (a) estimated local effects (dev_{ik}) and (b) drainage effects (α_{ik}) for each species, shown as modified box plots on the logit scale. The center line indicates the median value. Bar ends are the 25th and 75th percentiles. The solid lines span the 95% credibility intervals for the predictions. The vertical dashed line at zero is the regional average for each species. Species are ordered as indicated by arrows for each drainage. Alternating gray shading was used to help distinguish drainages. Abbreviations: PGS, Pacific giant salamander; TS, torrent salamander; LTF larval tailed frog; ATF, adult tailed frog.

Table 1. Cross-validation results to compare model precision and accuracy between the small area estimation and regional modeling approaches for predicting amphibian occurrence.^a

Species ^b	Mean prediction error			Mean absolute difference		Mean bias	
	regional	SAE	SAE uncalibrated	regional	SAE	regional	SAE
PGS	1.725	0.241	1.858	0.967	0.389	-0.006	0.041
TS	0.778	0.140	0.813	0.514	0.251	0.070	-0.017
LTF	0.679	0.155	0.685	0.529	0.281	-0.008	-0.018
ATF	0.227	0.047	0.254	0.249	0.120	0.005	-0.017

^aPrediction error = $(Y_i - \hat{Y}_i)^2$, absolute difference = $|Y_i - \hat{Y}_i|$, and bias = $(Y_i - \hat{Y}_i)$ for the *i*th species. The regional model omitted local drainage effects. Calibrated small area estimation (SAE) model, with local drainage effects (dev_{ik}) estimated with available survey information within the same drainage. Uncalibrated SAE model, with dev_{ik} set to the regional average ($dev_{ik} = 0$).

^bAbbreviations: PGS, Pacific giant salamander; TS, torrent salamander; LTF, larval tailed frog; ATF, adult tailed frog.

between 0.49 and 1.05 for the different species (Table 2). If these local effects were insignificant or nonexistent, then $\sigma_{\alpha_i}^2$ would be close to zero. The direction of local drainage effects was consistent across all species, with correlation coefficients between 0.29 and 0.66.

The SAE model appeared superior to a regional model that omitted random drainage effects (i.e., local effects) but retained the stand- and drainage-scale covariates. The SAE model showed a 42-point drop in DIC over the non-SAE approach (with the full data set). Cross-validation also showed lower prediction errors for the calibrated SAE model over a comparable regional model (Table 1). Prediction error for giant salamanders was reduced by 86%, decreasing from 1.73 for the regional model to 0.24 for the calibrated SAE model (Table 1). Other species showed a 77% to 82% reduction. Similarly, the SAE model showed lower absolute prediction differences for each species (Table 1). Both models had low bias. Prediction errors for the regional and uncalibrated SAE models were similar (Table 1).

Species responded differently to the stand- and drainage-scale habitat variables (Table 2). Streamside

buffers of older forest (stbuf) had a strong positive effect on all species. Aspect was the most consistent covariate. All species except adult tailed frogs showed a positive response to cooler north aspects (Table 2). Drainage-scale covariates indicative of disturbance, such as slope and %young, were significant for each of the species (Table 2). The variables heat and roads did not improve model fit and were dropped. None of the stand- or drainage-scale covariates were highly correlated (extreme $r = 0.30$ and -0.46 , respectively).

The model predicted considerable variability in amphibian occurrence across surveyed stands, despite accounting for a moderate amount of the total deviance. For giant salamanders, the mean probability of occurrence was 0.496 and had a range of 0.07–0.94; other species had similarly wide ranges. For torrent salamanders, larval and adult tailed frogs, the highest probabilities were 0.48, 0.59, and 0.28, respectively, and the lowest were <0.01 .

Fine-scale habitat variables measured at 2-m sample points were ultimately excluded from the model. This could lead to biased predictions if these were aggregated at the stand-scale because variables such as fine sediment

Table 2. Parameter estimates (Eq. 1) for models predicting amphibian occurrence in the Oregon Coast Range with stand- and drainage-scale habitat variables.*

Parameter	Species			
	Pacific giant salamander	torrent salamander	larval tailed frog	adult tailed frog
Stand scale				
β_0	-0.182 (0.207)	-3.359 (0.365)	-2.504 (0.265)	-4.477 (0.618)
β_1	-0.164 (0.128)	0.589 (0.176)	-	0.505 (0.261)
β_2	-0.278 (0.112)	0.455 (0.182)	-0.716 (0.144)	-
β_3	0.611 (0.207)	1.18 (0.341)	0.455 (0.297)	0.496 (0.554)
Drainage scale				
γ_1	0.753 (0.224)	-	-	-
γ_2	-	-0.261 (0.284)	-	1.081 (0.429)
γ_3	-	-	-	0.661 (0.351)
γ_5	0.284 (0.227)	-	-0.733 (0.228)	-
γ_6	1.142 (0.267)	0.514 (0.341)	0.805 (0.254)	-
σ_{α_i}	0.59 (0.166)	0.74 (0.239)	0.49 (0.160)	1.05 (0.429)

*1 Parameter estimates are Bayesian posterior means, with posterior SDs in parentheses (-, variable did not contribute to the model fit and was dropped).

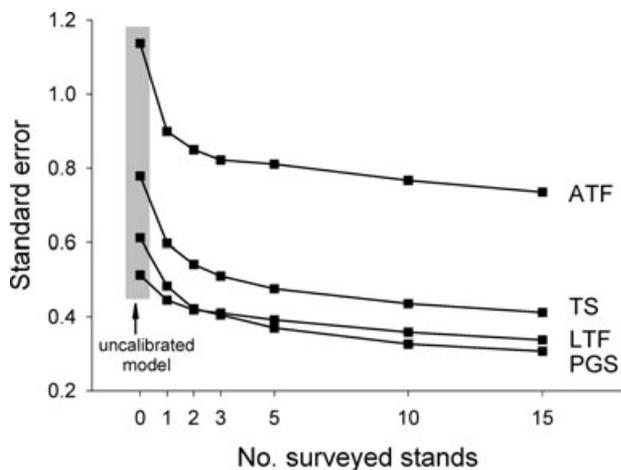


Figure 2. Predicted standard errors of local drainage effects (dev_{ik}) in a new stand within drainages that were unsurveyed (identified as uncalibrated model) or with varying numbers of additional surveyed stands within the drainage available for model calibration. See “Simulations” for assigned habitat covariate values and local survey information. Standard errors were the SD of the posterior distributions of dev_{ik} . Abbreviations: PGS, Pacific giant salamander; TS, torrent salamander; LTF larval tailed frog; ATF, adult tailed frog.

or water velocity influence how species segregate at very fine scales (<2 m) (Welsh & Lind 1996). The variance components model showed that stand effects accounted for between 3% and 31% of total variance, depending on the fine-scale habitat variable. Similarly, drainage effects accounted for between 4% and 25% of total variance. The low-variance components indicated that fine-scale habitat features were not aggregated at either scale. Furthermore, including the fine-scale covariates in Eq. 1 did not improve model fit, as judged by DIC.

Simulations

Even when only 1 or 2 additional surveyed stands were available for calibrating the model, precision of the estimated local effects, dev_{ik} , increased (Fig. 2). Because none of the $\sigma_{\alpha_i}^2$ were zero, it follows that precision of the dev_{ik} estimates will increase with higher numbers of surveyed stands available for calibration within a drainage. This pattern of increasing precision with more survey information is axiomatic within SAE models, so it was expected. Nevertheless, the utility of SAE models relies on reducing error with a reasonable number of additional surveyed stands. As the number of surveyed stands increases, the standard errors in Fig. 2 will reach an asymptote that represents uncertainty in the respective drainage-scale covariates and the drainage variance pa-

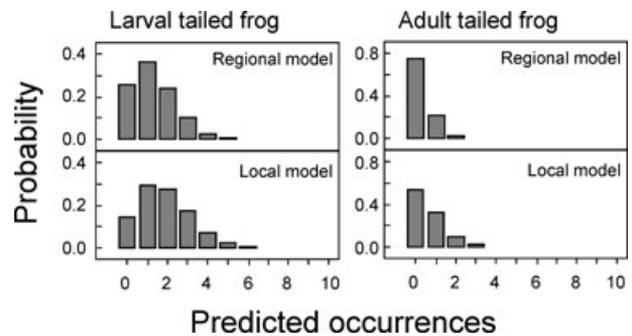


Figure 3. Posterior predictions from the model contrasting inferences from regional versus local (SAE) models. Shown are the predicted number of occurrences of larval and adult tailed frogs at 10 sample points within a new stand. See “Simulations” for assigned habitat covariate values and local survey information. Predictions for the local model were calibrated with 15 surveyed stands from within the same drainage.

rameters (Table 2; posterior SDs). The cross-validation also indicated that calibration resulted in a substantial reduction in prediction error relative to an uncalibrated SAE model (Table 1).

Inferential differences between the SAE and regional models were demonstrated through predictions for new stands with and without calibration data; the same stand- and drainage-scale covariates as those in the simulations were used. Species predictions were presented as the probability of finding 0–10 amphibians at 10 randomly located survey points within the stand. For example, when dev_{ik} was precisely estimated with the SAE model (i.e., with 15 stands), the probability of finding adult tailed frogs in the stand was considerably higher than predicted by the regional model (Fig. 3). For larval tailed frogs, inferences were only slightly altered; the stand appeared to be of high quality in both models. Obviously, field applications will vary depending on the actual survey data and species investigated. To further illustrate regional and SAE model differences, we used the models to predict torrent salamander occurrence for a randomly selected stand in drainages 1, 15, and 16, which represented average, high, and low predicted local effects, respectively (Fig. 1a). Predictions were made with the measured habitat covariates for the stand and drainage (Fig. 4). In general, calibrated SAE and regional models were quite different. For instance, the stand in drainage 15 appeared to be of much higher quality in the SAE model than the regional model for torrent salamanders (Fig. 4). Similar contrasting results were found for other species in drainages where the estimated local effects were higher or lower than average.

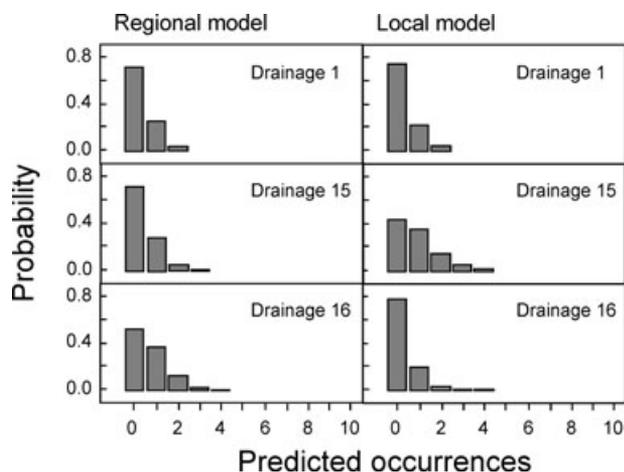


Figure 4. Posterior predictions for torrent salamanders from the regional and local (SAE) models. Shown are the predicted number of occurrences at 10 sample points for a randomly selected stand within drainages 1, 15, and 16, computed with the measured habitat covariates. The local-model predictions were based on the estimated local effects for the indicated drainages (dev_{ik}).

Discussion

Problems with Regional Habitat Models

Random local effects (dev_{ik}) explained a substantial portion of the data beyond the drainage-scale covariates and adequately represented these patchy populations. In contrast, regional models had no capacity to incorporate such location-specific information, which decreased their precision for predicting patchy local populations. Such regional models are still unbiased, but provide naive estimates when we recognize—but fail to incorporate—significant local effects that are not explained by the covariates. Patchy populations are common in wildlife (Wiens 1976), particularly for specialist animals with short dispersal distances. Small mammals (Bowman et al. 2000) and year-long resident birds develop patchy distributions that arise from influences at longer time scales or broader regional scales than captured by models. Site fidelity or social information may be other causes of patchiness for Neotropical songbirds (Betts et al. 2008). We suspect that most amphibians have patchy, discontinuous distributions such as those found here (Knapp et al. 2003).

The SAE models precisely predicted abundance in these patchy populations and provided the information necessary to make correct inferences. Nevertheless, SAE models require a larger investment in surveys than regional models, because local surveys are necessary to predict local effects. The hierarchical methods can reduce the data requirements, but this will vary among

species and regions. How far SAE models can reduce prediction error is not predictable a priori, but the reduction will be greatest for relatively rare species with patchy distributions. Without survey data available for calibration, the SAE and regional models performed similarly, but relatively poorly. This was expected in patchy populations such as these and highlights the critical need for good local information. Spatial modeling of populations (Augustin et al. 1996; Knapp et al. 2003) is another approach to account for patchiness, but was not suitable in this study due to the low number of sampled drainages and sparse geographic coverage.

The Bayesian approach provides the information necessary for risk assessment due to the probabilistic interpretation of the results (Clark 2003). For wildlife this information includes a prediction of the population size or habitat quality. For low-mobility species, such as amphibians, stand- and drainage-scale habitat assessments may be adequate, but if the populations are patchy, local abundance estimates become more critical. The other crucial piece of information for risk assessment is an assessment of uncertainty in the estimate. Point estimates (i.e., means) of population size are commonly derived from regional models, but without a way to assess their accuracy these have little utility for making location-specific decisions (Clark 2003). Consider the scenario outlined in Fig. 3 for adult tailed frog populations. The regional model indicated that the stand was almost certainly of low habitat quality, which suggests that concern for the species would be low if the stand was scheduled for harvest (but this stand may still be important within a regional context). On the other hand, good local information interjected substantial uncertainty into our population estimate. The local model allowed the possibility (albeit slight) of a substantial adult tailed frog population, and such uncertainty will alter the perceived risk and may alter management decisions. The scenario could also be reversed, where the local model shows low habitat quality with high certainty. Such scenarios were common in the data set, particularly for rare species such as torrent salamanders (Fig. 4; drainage 16).

Managers respond to perceived risk in a risk-adverse, risk-neutral, or risk-tolerant way (e.g., Burgman 2005), depending on many factors. In the previous scenario (Fig. 3), provided with good local information the risk-adverse manager would likely directly survey the stand in question. Avoiding harvest operations or stipulating extensive streamside buffers might also be decided without further surveys. Alternative choices based on the manager's risk attitude could be to assume low habitat quality or low population risk (possibly due to nearby set-aside areas of high quality). Nevertheless, deciding among these options cannot be considered with only point estimates of species prevalence. The perception of risk arose from the (slight) chance of high adult tailed frog populations, not from the mean (i.e., point estimate) probability. Point

estimates, often taken as fact, have little use in risk management.

Developing Local Habitat Models

Most wildlife management occurs at the stand or drainage scales and thus requires a fine-scale resolution that only model-based estimates can realistically provide (Thompson 2002). Design-based inferences at the same resolution are derived from extensive surveys and are usually cost-prohibitive. In contrast, the stand and drainage covariates we used could easily be estimated from aerial photos and information from geographic information systems over the entire Coast Range. Further incorporating local effects into the models would require more extensive surveys. Efforts such as the Survey and Manage Program in the U.S. Pacific Northwest (Olson 1999) have generated large numbers of surveys across the region for numerous plant and animal species. Although the coverage of third-order drainages will be sparse, even a small number of surveyed stands within a drainage can substantially reduce prediction error. Alternatively, changing the small-areas to higher-order drainages would increase sample size, with perhaps similar prediction ability.

Survey and Manage stands are not randomly chosen, and this could result in different inferences regarding amphibian populations than would a completely randomized sample design (Thompson 2002). A useful aspect of model-based inference is that the local surveys do not need to be randomly located, but relaxing the randomization requirement depends on the realism of the model to represent the population. More formally, it depends on the data being independent under the assumed model (Thompson 2002). In other words, stands within the same drainage are expected to be more similar than randomly chosen stands taken from the region (realized through the drainage effects). Nevertheless, the model assumes that stands within a drainage are independent, conditioned on the measured stand-scale covariates. This is unlikely to be strictly true, but we did not know how strongly correlated the errors actually were. Randomization of new surveys can guard against model failures and is strongly suggested until a better assessment of the independence assumption can be made.

If previous survey information is available, we suggest incorporating these data into the SAE models. Nevertheless, we suggest caution, particularly when using data with different survey designs, key habitat types of interest (e.g., riparian areas), season of sampling, or possible temporal trends following disturbance. For example, the 2-m stream-length surveys we used are not comparable to greater area- or time-intensive surveys, which would likely have different inferences on probability of occurrence (e.g., Kroll et al. 2008). Stream amphibians also have low detectability, which is strongly related to in-stream structure (coarse wood, percentage pools,

coarse sediment) (N. Chelgren, personal communication). We could not assess detectability because of the sampling design, and this likely biased our model predictions downward for stands and drainages with uniformly high in-stream structure (MacKenzie et al. 2002). Sampling within each drainage occurred on random dates throughout the summer, which should have minimized problems with seasonally changing detectability (Kroll et al. 2008).

The SAE methods and local habitat models we developed complement the numerous amphibian ecology and habitat studies in the region. We took a hierarchical Bayesian approach, so our results did not match those from the previous analysis (Stoddard & Hayes 2005). Nevertheless, many of the inferences regarding habitat covariates were similar to those from Stoddard and Hayes (2005) and related studies (e.g., Vesely & McComb 2002). Such ecological studies provide the basis for robust predictions with model choice partly based on the ecology and life history of the species (Burnham & Anderson 2002). Nevertheless, species-habitat studies are often restricted to answering fine-scale (e.g., stream- or stand-level) questions. Regional conservation of these species requires a regional picture of the current population status. For patchy populations, regional habitat models are inadequate to provide this. The SAE models we developed can help managers compile a regional view of the conservation status for many species drainage by drainage and thereby identify conservation gaps.

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