



Use of guilds for modelling avian responses to vegetation in the Intermountain West (USA)

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ABSTRACT

Aim Individually focused conservation management of many species is expensive and logistically impractical. Mesofilter conservation methods may facilitate the simultaneous management of multiple species. We used data on distributions of two sets of avian guilds, based on dependence on riparian vegetation and on nest location, to relate occurrence rates to environmental variables. Variables were selected by expert opinion and are likely to be affected by changes in climate and land use.

Location Data were collected from 2001–06 in four adjacent mountain ranges in the central Great Basin (Lander, Nye and Eureka counties, Nevada, USA): the Shoshone Mountains and the Toiyabe, Toiyabe and Monitor ranges.

Methods Data on occurrence of birds, vegetation composition and vegetation structure were obtained in the field. Geographical coordinates and the normalized difference vegetation index were derived from a digital elevation model and a satellite image. To construct a general model for guilds as a whole, while allowing flexibility for variation in the functional responses of individual species, we applied multivariate adaptive regression splines.

Results The predictive capacity of expert knowledge of relationships between birds and vegetation was inconsistent. Latitude, longitude and elevation may constrain the response of some guilds to changes in vegetation structure and composition. Guild-based models were useful for modelling species with sparse distributions, which are difficult to model individually. In essence, this method supplements models for the individual species with patterns for the guild to which they belong.

Main conclusions Guilds of birds appeared to have predictable associations with selected attributes of vegetation structure and composition. The criteria by which species are grouped into guilds may affect the success of predictions and management interventions. Our derived models offer the potential to predict effects on the avifauna of management or climate-driven change in vegetation.

Keywords

Avian guilds, climate change, expert opinion, MARS, multispecies modelling, prescribed fire, riparian, sagebrush steppe.

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INTRODUCTION

The strategy of mesofilter conservation explicitly seeks to manage ecosystems to benefit many species simultaneously (Hunter, 2005). By emphasizing elements of the landscape (e.g. riparian cover) or ecological processes (e.g. fire) that provide resources for multiple species, the number of species that require individually tailored interventions may be reduced. The effectiveness of

mesofilter conservation relies on our ability to identify environmental components that are critical to many species, and to predict the response of a high proportion of those species to perturbations in those key components.

Potential responses of species to environmental variables and environmental change can be modelled at several levels, from species to assemblages (Lemoine *et al.*, 2007). Models for individual species identify ecological variables with the greatest

influence on occurrence of that species. Models at the assemblage or community level examine environmental correlates of patterns of species richness or turnover (e.g. Downes *et al.*, 1998), but often do not account explicitly for species identity. Multiresponse models are a balance between modelling individual species, which may be problematic for some species (e.g. rare species), and modelling assemblage-level attributes (e.g. Olden, 2003; Leathwick *et al.*, 2005). Multiresponse methods examine collectively many species using a common set of key variables, but retain information about the responses of individual species. Most previous examples of multispecies models (Olden, 2003; Leathwick *et al.*, 2005) have simultaneously modelled all species in an assemblage or taxonomic group. Several workers have reported that multispecies models can improve prediction of occurrence for species that are rare or for which few data exist (Leathwick *et al.*, 2006; Elith & Leathwick, 2007). Here, we build guild-based models, in which ecologically similar species of birds are grouped together for modelling. Species in a guild are more likely than an entire assemblage or taxonomic group to respond to a common subset of environmental variables.

The structure and composition of vegetation often strongly influences the distribution of birds (Rotenberry, 1985). Birds are commonly monitored to assess the biological consequences of management of specific land-cover types and disturbances (George & Dobkin, 2002; Knick *et al.*, 2003). In the Intermountain West, USA, major drivers of land-cover change currently include climate change, human appropriation of water, fire regime, livestock grazing, oil and gas development, woodland expansion and invasion of non-native plants (Knick *et al.*, 2003).

Mean annual temperatures in the Great Basin increased by 0.3 to 0.6 °C during the 20th century and are projected to increase by another 2 to 5 °C before 2100 (Cubash *et al.*, 2001; Smith *et al.*, 2001). Projected changes in regional precipitation are inconsistent with respect to sign, but the average changes are near zero (Cubash *et al.*, 2001). As temperatures increase, the availability of water to native flora and fauna is likely to decrease. The ratio of rain to snow is increasing, snowpack is melting earlier and peaks in stream flow are occurring earlier (Mote *et al.*, 2005). Also, any increases in precipitation are likely to be offset by higher evapotranspiration and longer growing seasons. Scarcity and variability of precipitation is exacerbated by increasing use of water by humans. As rates of instream flow and incidence of natural flooding decrease, non-native invasive species such as saltcedar (*Tamarix ramosissima*) can more easily establish and dominate riparian zones (Sher *et al.*, 2000). Much land management in the Intermountain West focuses on the maintenance and restoration of riparian areas (Chambers & Miller, 2004).

Since the mid-1800s, the cover, density and mean age of two of the most characteristic trees in the Great Basin, pinyon (*Pinus monophylla*) and juniper (*Juniperus* spp., primarily *Juniperus osteosperma*), have increased across the region. As fuel loads have increased, so has the frequency and intensity of fires in pinyon–juniper woodlands and adjacent riparian woodlands (Swetnam *et al.*, 1999). Fuel loads have also increased because of invasion of fire-adapted, non-native annual grasses, especially cheatgrass (*Bromus tectorum*). Replacement of native by non-native vegetation

is expected to reduce habitat quality for species that occupy sagebrush steppe and woodland (Knick *et al.*, 2005; Rowland *et al.*, 2006). Climate change will probably further increase invasion rates and fire frequency (Westerling *et al.*, 2006). Prescribed fire and other fuel-reduction treatments may be mechanisms to manage these risks. Relationships between vegetation, climate and fire are reasonably well understood. However, relatively little empirical information exists to predict how potential changes in vegetation structure and composition resulting from alternative fire regimes may affect assemblages of native animals (Knick *et al.*, 2005).

Here, we combine guild-based species classification with multiresponse statistical models to derive distribution models for many species based on a relatively small set of environmental attributes. We classified birds according to their degree of reliance on riparian vegetation and location of nest sites. Our selection of guilds was guided in part by ongoing and projected environmental changes in the Great Basin. As noted above, both the availability of water and the status of native riparian vegetation are likely to decline in response to climate change and human demands. Structural complexity of vegetation and the relative proportion of cover in the understorey, shrub layer and canopy encompass a suite of characteristics (e.g. risk of nest predation, abundance and diversity of food resources, microclimate) that strongly affect the quality of habitat for nesting and the relative nest success of birds (Martin, 1998; Jones, 2001), and these vegetation attributes are likely to shift in response to changes in climate, fire regime and land use.

Our approach was to identify a priori a few (no more than three) vegetation variables that might reasonably be expected to strongly influence the distribution of species in each guild based on their natural history. The variables we selected are also likely to be affected by natural or anthropogenic environmental changes as described above. The use of a small number of potential predictor variables makes interpretation easier and is more useful for management. Our goal was to evaluate the predictive ability of a small set of variables that are relevant to management rather than to identify the most ecologically important variables (the 'best models') for individual species based on a comprehensive pool of variables. We did not question the general validity of expert opinion about relationships between guilds and vegetation variables. Instead, our intent was to examine whether these relationships have predictive capacity. For example, despite extensive knowledge of correlative and causal associations between plants and their environment in the central Great Basin (e.g. the sedge *Carex nebrascensis* occurs at high water tables), the predictability of relationships among vegetation, geomorphology and hydrology differs spatially (e.g. across abiotic gradients) and temporally (e.g. variability in water table depth increases as depth to water table increases) (Chambers *et al.*, 2004). Likewise, riparian obligate birds may often nest in dense riparian vegetation, but the probability of presence of those birds may not have a functional relationship to the proportion of riparian vegetation in the canopy. We also included latitude, longitude and elevation because these variables influence the distribution of birds in this and many other systems (Terborgh, 1977; Fleishman & Dobkin, 2008).

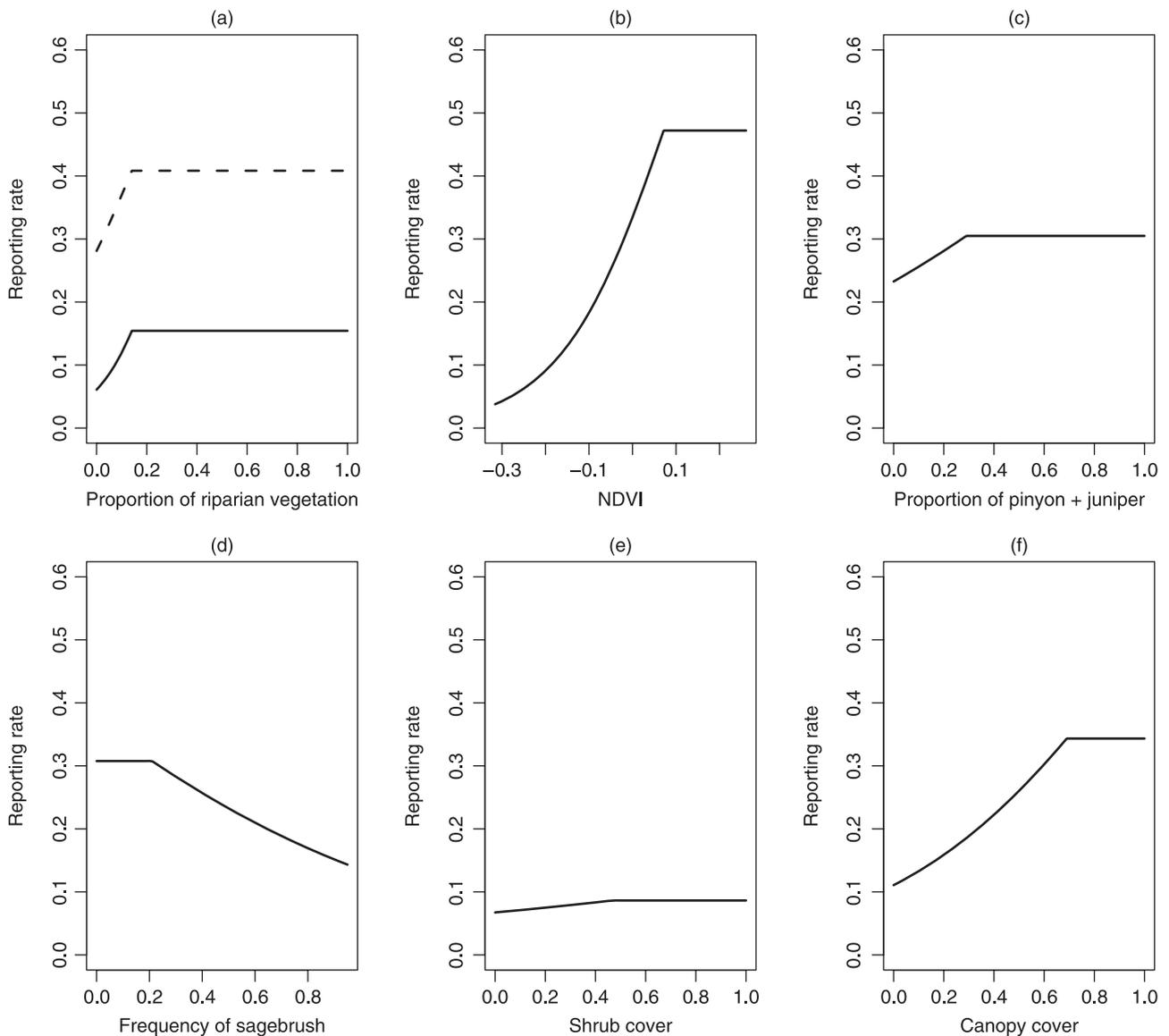


Figure 1 Typical responses of species within riparian dependence (a–d) and nesting (e, f) guilds to vegetation variables. Variables shown were initially selected on the basis of expert opinion and were subsequently retained in multivariate adaptive regression spline (MARS) basis functions for additive, guild-based models. We applied the median coefficient for all species in a guild to the corresponding basis functions and took the inverse link function (logit) to show how reporting rates of a typical species in that guild respond to each variable: (a) riparian obligate (solid line) and intermediate riparian (dashed line) guild, (b) riparian obligate guild, (c) non-riparian guild, (d) non-riparian guild, (e) ground or low-shrub cup nesters, (f) high shrub or canopy cup nesters.

Understanding current relationships between guilds and vegetation may allow us to anticipate how changes in vegetation, arising from management or climate change, are likely to affect these guilds. Few hypotheses or expert opinions regarding such relationships have been evaluated rigorously with empirical data, so our work should inform these issues.

METHODS

Data were collected in four adjacent mountain ranges with similar biogeographical and human land-use histories: the Shoshone Mountains, Toiyabe Range, Toquima Range and Monitor Range

(Lander, Eureka and Nye counties, Nevada, USA; see Mac Nally *et al.*, 2004, Fig. 1). The area bounding the ranges is about 125×125 km, centred near 39° N latitude and 117° W longitude. Canyons, many of which have perennial or ephemeral streams, drain the east and west slopes of the ranges.

We surveyed birds during the breeding seasons (late May and June) of 2001–06 using 75-m variable-radius point counts. Transient species that do not breed in these mountains were omitted from analyses. Most point centres were > 350 m apart. Points were located along the full elevational gradient of every canyon we sampled, typically with two or three points per 100-m vertical elevation change. Points were positioned to sample, in

proportion to areal extent, the dominant vegetation types throughout the canyons [e.g. aspen (*Populus tremuloides*), willow (*Salix* spp.), pinyon–juniper woodland, wet meadow, sagebrush (*Artemisia tridentata* ssp.)]. Dominant vegetation was consistent within the point. We did not attempt to classify land use because livestock grazing and human recreation, the ubiquitous dominant uses in this region, vary considerably through time.

During each visit, we recorded by sound or sight all birds using terrestrial habitat within the point. Point counts were conducted only in calm weather, and none were conducted > 3.5 h after dawn. Each point was surveyed three times a year for 5 min per visit. Three surveys usually are sufficient to determine the species of birds that are present at point count locations in a given year (Siegel *et al.*, 2001). Species accumulation curves generally approached an asymptote before the third round of surveys. Although we did not calculate detection probability for all species, related work suggested that single-visit detection probabilities generally exceeded > 66%, sufficient to be 95% confident that apparent point-level absences for a given year were true absences (Pellet *et al.*, 2007). Most points (82% of 314) were surveyed in two or more years. There were 53 points in the Shoshone Mountains, 75 in the Toquima Range, 151 in the Toiyabe Range and 35 in the Monitor Range.

To characterize the composition and structure of vegetation we established plots centred on the bird-survey points. We measured three radial 30-m lines from the centre of the point. Lines were separated from each other by 120°. The distal end of each line was the centre of a circular vegetation sampling unit with radius 11.3 m (0.04 ha). Within each circle, we recorded the identities and sizes of all live trees [either diameter at breast height (d.b.h.) or basal diameter, depending on plant morphology]. We recorded the identities and sizes of standing and fallen dead trees. Vegetation at each plot was measured once. Most vegetation measures changed little during the study (J. Chambers, personal communication).

We used a concave spherical densiometer to estimate the proportion of canopy cover. To estimate the frequency of shrubs and ground vegetation, we used an ocular tube with measurements taken at a 45° angle downward from the line of sight (Noon, 1981). We recorded occurrence of *c.* 30 dominant trees, shrubs and herbaceous taxa. We collected 21 densiometer and ocular tube readings at each plot: one each at 8 m, 16 m and 24 m along the 30-m line from the centre of the plot to the perimeter of each circle, and one while facing in each of the four cardinal directions from the centre of each circle. Cover values for the canopy were averaged for each bird-survey point. Frequency values for shrubs and ground vegetation, and occurrence data for dominant plant species, were aggregated into a relative measure of frequency at each point.

We measured the geographical coordinates of each point with a global positioning system; points were differentially corrected. Elevation was estimated by overlaying the corrected locations on a 30-m (1:24,000) digital elevation model. We derived measures of the normalized difference vegetation index (NDVI), which is associated with primary productivity, from a single cloud-free, geo-corrected Landsat Thematic Mapper image (WRS 41/33). This image was acquired in June 2000, coincident with the peak

of the regional growing season and the breeding season for birds. NDVI in a given location and spatial patterns of NDVI are generally not highly variable among years in the region (K. Seto & B. Bradley, personal communication).

We investigated relationships of bird species grouped by dependence on riparian habitat and by nest site. The assignment of species to categories within these guilds was relatively unambiguous based on extensive research experience with these species in the western United States (e.g. Dobkin & Wilcox, 1986; Thomson *et al.*, 2005; Fleishman & Dobkin, 2008) and the substantive natural history literature for North American birds (e.g. Ehrlich *et al.*, 1988). Assignment of species to these guilds is more reliable and equally or more effective analytically (Tewksbury *et al.*, 2002; Earnst *et al.*, 2005) than assignment based on other characteristics (e.g. foraging strategy, migratory status) that exhibit greater intraspecific geographical variation, and for which we lack adequate information for populations in the Great Basin. Riparian-dependence guild categories were: (1) obligate, (2) intermediate and (3) non-riparian. Nest-site guild categories were: (1) ground or low shrub cup, (2) high shrub or canopy cup and (3) tree cavity. Sample sizes of other nest types were too small to include in our analyses.

Vegetation variables for riparian obligates were the proportion of riparian vegetation in the canopy [aspen, cottonwood (*Populus fremontii*), water birch (*Betula occidentalis*), willow and chokecherry (*Prunus virginiana*)] and NDVI. For intermediate riparian species, candidate predictors were proportion of riparian vegetation in the canopy, NDVI and shrub cover. Vegetation variables for non-riparian species were proportion of pinyon and juniper in the canopy, frequency of sagebrush and frequency of bare ground.

For the guild of ground or low shrub cup nesters, vegetation variables were shrub cover and ground cover. Candidate predictors for high shrub or canopy cup nesters were canopy cover and proportion of trees with d.b.h. ≥ 18 cm (Saab *et al.*, 1995 and references therein). For the guild of tree cavity nesters, vegetation variables were mean diameter of all trees and the proportion of trees with d.b.h. ≥ 18 cm (Dobkin *et al.*, 1995).

Correlations among all 12 candidate predictor variables (vegetation variables, latitude, longitude and elevation) were weak (maximum $|r| = 0.51$, median $|r| = 0.11$).

Model building

The response variable was reporting rate, the proportion of years that a species was present at a sampling point during one or more visits (Thomson *et al.*, 2005). We modelled reporting rate as the probability that a species will be present at a given sampling point in a single year. We expect a positive correlation between the proportion of years that a sampling point is occupied by a given species and habitat quality of the sampling point for that species.

We modelled species reporting rates as functions of environmental variables using multivariate adaptive regression splines (MARS; Friedman, 1991). This adaptive method uses piecewise linear basis functions to define nonlinear relationships between a response variable and a set of predictor variables. We had no a

priori assumptions or hypotheses about the functional form of these relationships. We used a multiple response option in the MARS algorithm ('mda' package for R, Hastie & Tibshirani, 1996) to generate, from the pertinent set of vegetation and topographic variables, a common set of basis functions for each guild (Leathwick *et al.*, 2005). We then fitted a binomial generalized linear mixed model (GLMM) for each species relating reporting rate to these basis functions via the logit link. This step ensured that the probabilities of occurrence were between 0 and 1 (Leathwick *et al.*, 2005).

We built two sets of models for each guild. One set of models allowed only additive effects of predictor variables. The other set allowed two-way interactions between predictors. MARS can accommodate more complex interaction effects, but our goal was to keep the models simple.

Modelling details

See Appendix S1 in Supplementary Material for a more complete description of modelling details.

MARS models relationships between a response variable and a predictor variable as a series of linear segments of different slopes (Friedman, 1991; Leathwick *et al.*, 2005). These segments are specified by transforming a predictor x into a set of basis functions B , which are defined in pairs and have the form

$$B_n = \max(0, t - x); B_{n+1} = \max(0, x - t),$$

where x is the value of the predictor variable and t is a 'knot,' or break point, specifying a value within the range of x at which the slope of the fitted function changes. The slopes are determined by coefficients applied to each basis function. Multiple knots (i.e. multiple changes in slope) can be defined for each predictor variable and localized interactions (confined to subranges of variables) between predictor variables can be defined by including multiple predictors in the basis functions.

We fitted the final models as Bayesian GLMMs with binomial errors (Leathwick *et al.*, 2005) and point-level (i.e. survey point) random error terms. Point-level random errors allow for 'extra-binomial' variance that is constant among years at a point. Bayesian fitting accommodates missing covariate values (of which we had several), which are treated as unknown random variables whose values were estimated as part of the joint posterior distribution. Survey points with missing covariate values were omitted from the generation of MARS basis functions (the current MARS implementation in R does not support missing covariate values), but included in the final Bayesian models by assigning normal prior distributions to the missing values for basis functions (i.e. transformed covariates). The prior means and variances for the missing values were estimated from the existing values of the corresponding basis function.

The model for the reporting rate of species j at point i was

$$y_{ij} \sim \text{binomial}(p_{ij}, n_{ij}); \log\left(\frac{p_{ij}}{1 - p_{ij}}\right) = f_j(x_i) + \varepsilon_{ij};$$

$$f_j(x_i) = \sum_{k=1}^K \beta_{jk} B_k(x_i).$$

y_{ij} is the number of years that species j was observed at point i over n_{ij} survey years and p_{ij} is reporting rate, the probability of observing species j at point i in any one year. B is a set of K basis functions common to all species in the guild, β_j is a vector of species-specific regression coefficients, and ε_{ij} is the site level random error term for species j . Model coefficients were made exchangeable (Gelman *et al.*, 2003) by assigning a joint normal prior distribution with mean zero and unknown variance v_j^2 , $\beta_{jk} \sim N(0, v_j^2)$. We gave the corresponding standard deviation, v_j , a uniform prior over the interval (0, 10) (Gelman, 2005). This shrinks coefficients towards zero, with shrinkage proportional to the variance (Gelman *et al.*, 2003), and overcame the problem of separation (Heinze & Schemper, 2002) for species with few presence records.

We fitted Bayesian models for all species in a guild simultaneously and included an error component that was common to all species in that guild by specifying a hierarchical prior distribution for the site-level random errors: $\varepsilon_{ij} \sim N(\bar{\varepsilon}_i, \sigma_j^2)$; $\bar{\varepsilon}_i \sim N(0, \bar{\sigma}^2)$. Inclusion of an error component common to all species in the guild, $\bar{\varepsilon}_i$, allows for site-level factors not otherwise accounted for in the model that have a similar effect on the local reporting rates of all members of the guild, while allowing for species-specific errors, ε_{ij} . We specified uniform priors on the interval (0, 10) for the standard deviations of the random error terms ($\bar{\sigma}, \sigma_j$). Posterior distributions using these priors were essentially identical to those obtained with two alternative prior distributions for standard deviations: uniform on the interval (0, 5) and inverse gamma.

We standardized all covariates prior to generating the MARS basis functions. We fitted the final GLMMs with WinBUGS software (Spiegelhalter *et al.*, 2003). We allowed 10,000 Markov chain Monte Carlo (MCMC) iterations for burn-in and monitored posterior distributions for a further 10,000 iterations. We ran three MCMC chains and checked MCMC mixing and convergence using Gelman–Rubin statistics (Brooks & Gelman, 1998).

Model evaluation

We used a bootstrap procedure to evaluate the expected predictive capacity of models. Estimates of prediction error calculated by applying the fitted model to the model building data (in-sample estimates) are overly optimistic. Bootstrapping adjusts the in-sample validation statistic by an estimate of its optimism derived from simulations of model building and model testing performed on bootstrap samples. We used the 0.632+ bootstrap method (Efron & Tibshirani, 1997) with 50 bootstrap samples to estimate the expected predictive capacity for each model. We repeated the full model-building procedure, including selection of basis functions and subsequent fitting of GLMMs, for each bootstrap sample. The 0.632+ estimate is a weighted average of the in-sample statistic and the mean out-of-sample statistic of models fitted to the bootstrap samples. We report on the area under the relative operating characteristics (ROC) curves (Pearce & Ferrier, 2000); root mean square errors also were computed (using observed and predicted reporting rates) and were completely consistent with the ROC outcomes.

We calculated ROC values by expanding the data for each point into n_i point-by-year Bernoulli (presence-absence) cases, where n_i is the number of survey years for point i , with probability of occurrence equal to the point-level reporting rate rr_i . In this context, the ROC is the probability that an occupied point-by-year combination has a higher predicted probability of occurrence (i.e. point-level reporting rate) than an unoccupied point-by-year combination. Models were not intended to discriminate among years within a sampling point (all n_i cases from point i have equal probability but may be presences or absences if $0 < rr_i < 1$), making ROC = 1 impossible for most species. The potential maximum ROC value for a model that predicted the observed reporting rates perfectly ranged from 0.91–1. We adopted the criterion that for binary responses, models with bootstrap ROC values > 0.7 offer useful predictions (Pearce & Ferrier, 2000). The tendency for ROC values to underestimate predictive performance because ROC = 1 was impossible for all but one species is compensated because bootstrap estimates still may be optimistic (unbiased model evaluation requires completely independent data).

Out-of-sample predictions for bootstrap models were estimated simultaneously with MCMC model fitting in WinBUGS by treating y values (and therefore reporting rates, p) for the out-of-sample points as unknown parameters. To make computing time manageable, final GLMMs for bootstrap models were fitted in WinBUGS with 2000 burn-in iterations and 3000 sampled iterations.

Comparison of model-building approaches

We compared guild-based models with three other strategies for building MARS models: (1) models with a single set of basis functions for all species, regardless of guild (assemblage approach), (2) models built independently for each species and (3) models derived from random classification of species into three pseudo-guilds. The pseudo-guild approach was designed to test whether differences in performance between assemblage-based and guild-based approaches were attributable to the use of ecological information rather than to the use of fewer species in deriving basis functions. For (1) and (3), we included all 12 vegetation and geographical location variables as candidate predictors. For (2), we initially used the environmental variables identified as important for the species' riparian-dependence guild. Species in the same guild still shared a common set of candidate predictor variables, but the basis functions (i.e. retained variables and knots) were selected for each species separately. To test whether a priori selection of predictor variables improved model performance over automated variable selection, we also evaluated guild and individual-species models built with all 12 variables as candidate predictors. The 12 candidate variables were identified from expert opinion about environmental influences on the distribution of breeding birds and, collectively, are a small fraction of the available environmental data. Thus, even the 12 variables were effectively conditioned on expert opinion.

We fitted models for these comparisons as binomial GLMs by penalized maximum likelihood because fitting so many models (50 bootstrap models per combination of grouping strategy and

candidate predictor set) by MCMC would have been prohibitively slow. Shrinkage to deal with separation was achieved using Firth's penalty function (Firth, 1993; 'brlr' package for R, Heinze & Schemper, 2002). This always yielded finite estimates and standard errors for model parameters. Maximum likelihood models did not include point-level random error terms.

RESULTS

Guild-based relationships to environmental variables

We included the proportion of riparian vegetation in the canopy and NDVI as candidate predictors for the obligate riparian guild. Both variables were retained in the final set of basis functions for this guild. However, at least one vegetation variable was pruned from the final set of basis functions for all other guilds based on riparian dependence or nest site (Table 1), suggesting that the

Table 1 Number of knots (changes in slope of the fitted species-environment relationship) for variables in guild-based multivariate adaptive regression spline (MARS) models. Zero (0) indicates that a variable was included in the initial set of predictor variables for a guild but then was pruned from the final set of basis functions for each guild.

Predictor variables	Riparian guilds		
	Obligate	Intermediate	Non-riparian
Riparian vegetation*	1	1	
NDVI	1	0	
Shrub cover		0	
Pinyon-juniper†			1
Sagebrush‡			1
Bare ground§			0
Latitude	1	1	1
Longitude	1	1	1
Elevation	1	1	1
Predictor variables	Nest-site guilds		
	Ground/ low shrub cup	High shrub/ canopy cup	Cavity
Shrub cover	1		
Ground cover	0		
Canopy cover		1	
Mean tree diameter			0
Trees ≥ 18 cm d.b.h.¶		0	0
Latitude	3	3	1
Longitude	3	2	3
Elevation	2	1	1

*Proportion of riparian vegetation in the canopy.

†Proportion of pinyon and juniper in the canopy.

‡Frequency of sagebrush.

§Frequency of bare ground.

¶Diameter at breast height, proportion of all trees.

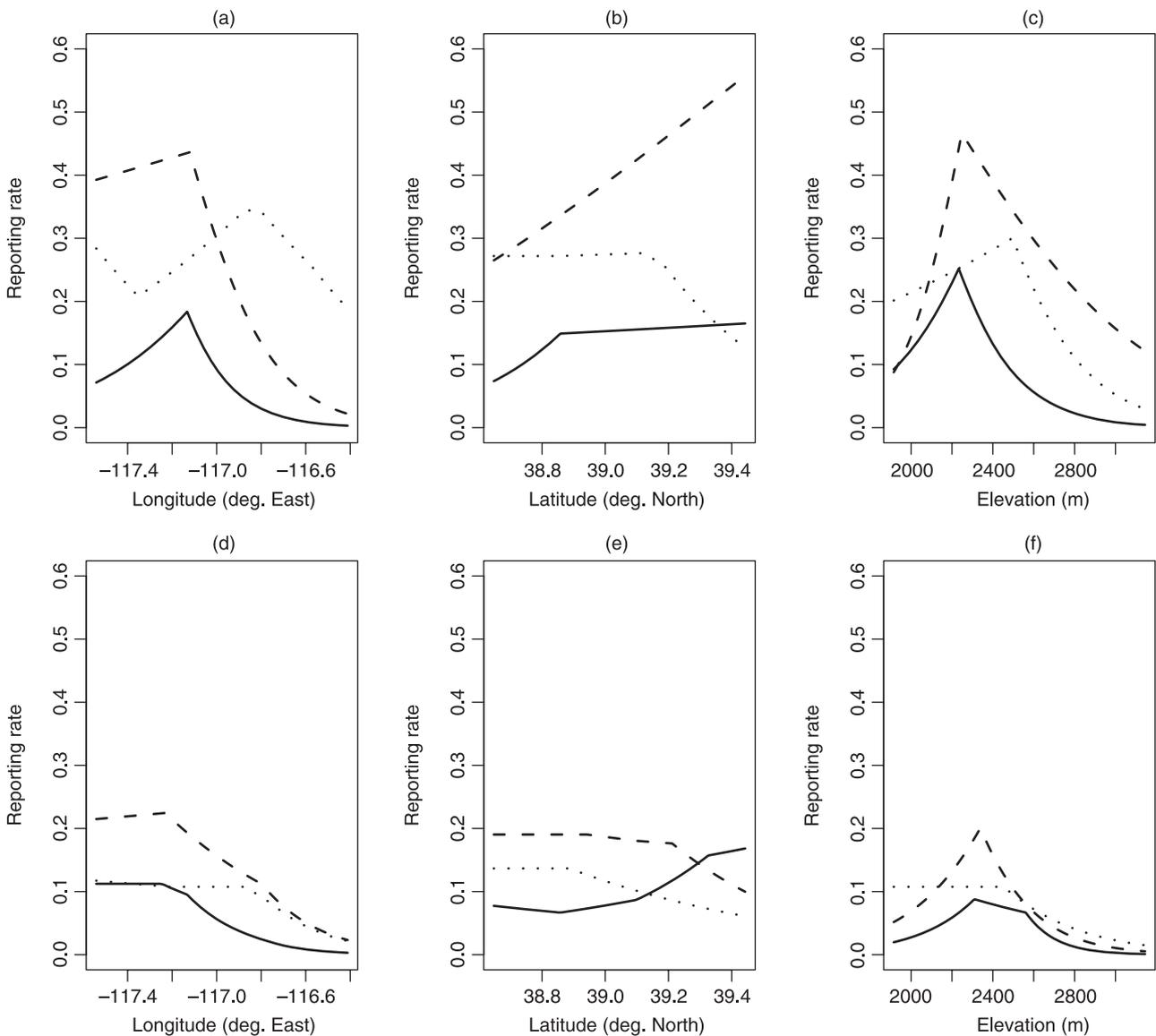


Figure 2 Typical responses of species within riparian dependence (a–c) and nesting (d–f) guilds to longitude (a, d), latitude (b, e) and elevation (c, f). Results obtained from additive, guild-based models that also included vegetation variables selected on the basis of expert opinion. For panels (a)–(c), solid lines = riparian obligate guild, dashed lines = intermediate riparian guild and dotted lines = non-riparian guild. For panels (d)–(f), solid lines = ground or low-shrub cup nester guild, dashed lines = high shrub or canopy cup nester guild and dotted lines = cavity nester guild.

predictive capacity of expert knowledge of relationships between birds and vegetation is inconsistent. Latitude, longitude and elevation were retained in the final set for all guilds. Retained basis functions for vegetation variables had only one knot (i.e. one change in slope) in all guild-based additive models, which implies relatively simple, asymptotic relationships between response and predictor variables (Fig. 1, Fig. 2). Geographical coordinates often had multiple knots, implying complex spatial patterns.

From posterior means of model coefficients, 20 of 22 riparian obligate species had positive relationships with the proportion of riparian vegetation in the canopy, and all had positive associations with NDVI (see Appendix S2). Posterior means of the model coefficients indicated the direction and magnitude of a given species' relationship to different variables. The environmental

variables retained in the final set of basis functions are constrained to be applicable to all species in the guild, rather than particular to each species. Nineteen of 25 intermediate riparian species had positive relationships to the proportion of riparian vegetation (Appendix S2, Fig. 1). Thirteen non-riparian species had positive relationships to the proportion of cover of the dominant conifers, pinyon and juniper, and negative relationships to frequency of sagebrush. Six non-riparian species had negative relationships to the dominant conifers and positive relationships to sagebrush (Appendix S2, Fig. 1). Six non-riparian species had negative relationships to both sagebrush and conifers, and four species had positive relationships to both variables (Appendix S2, Fig. 1).

Relationships to vegetation variables differed among nest-site guilds, although the majority of species had relationships that

Table 2 Median naïve (fit) evaluation statistics and bootstrap evaluation statistics for guild-based multivariate adaptive regression spline (MARS) models fitted as Bayesian generalized linear mixed models. Species were assigned to one of three riparian guilds (obligate, intermediate, or non-riparian) and one of three nest-site guilds (ground or low shrub cup, high shrub or canopy cup, or cavity). The MARS algorithm was used to create a set of common basis functions for species within each guild. Results of additive models are shown for each guild and combined across guild types (riparian or nest-site). Combined results only are shown for interactive (degree-2 MARS) models.

Guild	<i>n</i> *	ROC† fit	ROC† bootstrap	No. (%) of good models‡
Riparian guilds	76	0.95	0.76	55 (72%)
Obligate	22	0.96	0.81	16 (73%)
Intermediate	25	0.94	0.73	19 (76%)
Non-riparian	29	0.95	0.77	20 (69%)
Nest-site guilds	70§	0.95	0.74	47 (62%)
Ground or low shrub cup	28	0.96	0.77	19 (68%)
High shrub or canopy cup	28	0.92	0.73	18 (64%)
Cavity	14	0.97	0.74	8 (57%)
Riparian (interactive)	76	0.95	0.76	52 (68%)
Nest-site (interactive)	76	0.96	0.77	49 (64%)

*Number of species (hence number of models) in each guild or group of species.

†Area under receiver operator characteristics curve.

‡Bootstrap ROC values > 0.7.

§Six species with cliff-ledge or rock-crevice nest sites excluded (see Appendix S2).

were consistent with prior expectations. Eighteen of 28 ground or low shrub cup nesters were associated positively with increasing shrub cover, and 18 of 28 high shrub or canopy cup nesters had positive relationships to increasing canopy cover.

Most species in all guilds had unimodal relationships with elevation, with maxima between 2200 m and 2500 m. Reporting rates were very low for all species in the eastern-most mountain range, the Monitor Range, and were generally highest in one of the two western-most mountain ranges (Shoshone or Toiyabe). Reporting rates of riparian obligate and non-riparian species mostly decreased as latitude increased, whereas reporting rates of intermediate riparian species mostly increased as latitude increased (Fig. 2). There were no consistent latitudinal patterns among nest-site guilds other than a decreasing trend as latitude increased for cavity nesters, which comprised only 14 species.

The bootstrap results of models with basis functions derived from species grouped according to riparian status were better than the bootstrap results of models based on nest-site guilds (Table 2). The inclusion of interaction terms did not improve bootstrap results of models based on riparian dependence, but slightly improved results of models based on nest site (Table 2). Additive models derived from riparian guilds produced the greatest number (55, or 72% of modelled species) of models with bootstrap ROC > 0.7.

Comparison of model-building approaches

Models fitted by maximum likelihood lacking point-level errors did not fit or predict (bootstrap trials) the data as well as corresponding Bayesian models including point-level errors (Table 3). Nevertheless, comparisons among maximum likelihood models remain useful for comparing methods (guild, assemblage, single-species and pseudo-guild) for selecting basis functions. The addition of point-level error terms, to which we attribute most of the improved performance of the Bayesian models, is unlikely to alter substantially the relative rankings of the different approaches.

All multiple-species approaches produced better results than single-species models (Table 3). Differences in performance among multiple-species approaches were smaller than differences between each multiple-species approach and the single-species approach, but guild-based models with expert-selected variables produced the most consistent results (Table 3). The better performance of multiple-species approaches primarily reflected the superior prediction of reporting rates for less common species.

DISCUSSION

Guilds of birds in the Intermountain West appear to have predictable associations with selected attributes of vegetation structure and composition that are likely to change over coming decades in response to anthropogenic and natural drivers. Spatially explicit scenarios of vegetation change can be developed as a function of current trends, climate and land-use projections and management priorities. Projections of avifaunal occupancy then can be developed as statistical functions of alternative future scenarios of vegetation change. However, we found that the criteria by which species are grouped into guilds may affect the success of predictions and, by extension, the success of management interventions based on an understanding of guild-level responses to environmental change. Moreover, our work demonstrated that well-established natural history or expert knowledge about relationships between birds and vegetation is sometimes insufficient to develop reliable predictive models. Environmental gradients (often represented directly or indirectly by latitude, longitude and elevation) may constrain the response of at least some guilds to changes in vegetation structure and composition.

It was not our objective to identify threshold values of predictor variables, so assumptions that MARS knots reflect such thresholds should be made cautiously. However, instances in which a single knot was evident, and the majority of species within the guild had similar responses, may suggest a guild-level threshold that might benefit from evaluation with new empirical data. We identified several potential thresholds of guild-level responses to environmental variables – especially vegetation variables – that we intend to evaluate with further, targeted collection of data. For example, the reporting rate for the non-riparian guild appeared to decline when the frequency of sagebrush exceeded 0.2 (Fig. 1d).

In the central Great Basin, where water is typically the most limiting resource for the majority of animals and plants, classification

Table 3 Summary of results for all model-fitting approaches, sorted in descending order of number of good models. Good models are defined as those with bootstrap values of the area under relative operative characteristics (ROC) curve > 0.7.

(a) Bayesian fitting

Variable selection*	Approach†	Interactive model‡	ROC§ fit	ROC§ bootstrap	No. of good models
Expert	Riparian guild		0.95	0.76	55
All	Riparian guild		0.97	0.77	52
All	Riparian guild	x	0.96	0.77	52
Expert	Riparian guild	x	0.95	0.76	52
All	Nest-site guild		0.94	0.76	51
Expert	Nest-site guild	x	0.96	0.77	49
All	Nest-site guild	x	0.95	0.75	49
Expert	Nest-site guild		0.95	0.74	47

(b) Maximum likelihood fitting

Candidate variables*	Approach†	Interactive model‡	ROC§ fit	ROC§ bootstrap	No. of good models
Expert	Riparian guild		0.83	0.73	41
Expert	Nest-site guild	x	0.83	0.72	41
Expert	Riparian guild	x	0.84	0.71	40
All	Assemblage	x	0.82	0.72	39
All	Pseudo-guild		0.84	0.72	37
All	Assemblage		0.83	0.71	37
All	Nest-site guild		0.83	0.70	34
Expert	Nest-site guild		0.81	0.70	34
All	Nest-site guild	x	0.82	0.69	33
All	Riparian guild		0.83	0.69	33
All	Pseudo-guild	x	0.83	0.69	30
All	Riparian guild	x	0.83	0.69	30
Expert (riparian)	Individual species	x	0.83	0.66	27
Expert (riparian)	Individual species		0.83	0.66	26
All	Individual species	x	0.83	0.66	24
All	Individual species		0.85	0.64	21

*Expert selection: models included ≤ 6 candidate predictors for each guild identified on the basis of expert opinion. All: models included all 12 variables identified as candidate predictors for any guild.

†Approaches to selecting basis functions were guild, assemblage, individual species and pseudo-guild. See text for details.

‡Interactive models were degree-2 multivariate adaptive regression splines (MARS).

§Area under receiver operator characteristics curve.

of birds by riparian dependence appeared to provide a more useful basis for guild-based models of birds than nest-site classification. Our best models were additive models with expert-selected variables based on classification of riparian dependence. Most obligate and intermediate riparian species were associated positively with the proportion of riparian vegetation in the canopy, which underscores the importance of maintaining riparian vegetation in the face of declines in water availability and increases in human appropriation of water. When variables for both additive models and interactive models were selected by an automated process, riparian vegetation also emerged as a useful predictor of presence-absence patterns for all nest-site guilds. In addition to providing shelter and food – densities of insects and plants are greater in riparian areas than in uplands – riparian vegetation may be a surrogate for availability of water or for structural complexity of vegetation.

Elevation appeared to strongly affect the occurrence of birds across the central Great Basin. Species richness of birds appeared to have a unimodal response to elevation in individual and multiple mountain ranges, and elevation is a principal driver of the richness and occurrence of butterflies in the Great Basin (Fleishman & Dobkin, 2008). For breeding birds, structure and composition of riparian areas at intermediate elevations seemed more critical than at relatively low elevations.

Invasive herbaceous and woody species, including saltcedar, are currently a major concern for land managers in the region. Invasive plants are currently most prevalent at lower elevations. Selective cutting in patches dominated by saltcedar, although preferable ecologically, is not always feasible. If a reasonable amount of riparian vegetation is retained at intermediate elevations, aggressive management to control saltcedar and other non-native invasive species at lower elevations may be less likely

to conflict with regional conservation of native birds. Loss of habitat for Neotropical migrants and other species of birds generally is undesirable. However, there may be a trade-off between conserving existing habitat in the short term and preventing the dominance of that habitat by non-native invasive vegetation over the long term. A reduction in reporting rates of birds from west to east may reflect regional gradients in precipitation or tree cover among mountain ranges. Although there is local variation in precipitation and water availability, precipitation tends to decrease from west to east across the central Great Basin as the influence of prevailing winter storms from the Pacific Coast weakens. Analyses of satellite images suggest that over the past 20 years increases in tree cover have been greatest in the western portion of our study area.

Neither mean diameter of trees nor proportion of larger trees (≥ 18 cm d.b.h.), two attributes that might be affected positively or negatively by harvest or thinning in relatively old stands and in relatively dense stands of trees, were selected in models for nest-site guilds. However, most non-riparian species responded positively to cover of pinyon–juniper woodland and frequency of shrubs. Species that nest close to the ground had a positive response to shrub frequency. There was no reason to expect a priori, on the basis of expert opinion, that species would have a more consistent relationship to cover of woodland than to mean size of trees. However, natural loss or human removal of tree canopy and shrubs, especially in riparian areas, may have negative effects on breeding birds. Minimizing frequency and intensity of fire in riparian areas, while encouraging the growth of riparian understorey and canopy may encourage colonization or consistent occupancy of breeding birds. Although these results and inferences would have been reasonable a priori, we emphasize the importance of empirically supporting expert judgement about relationships among species, key environmental gradients and land cover. Expert opinion may be generally correct, yet may not yield reliable predictions.

For most species of birds, multiple-species approaches produced more reliable predictions than single-species modelling, at least with these variables and this modelling method (MARS). Other modelling methods (e.g. Elith *et al.*, 2006; Thomson *et al.*, 2007) might outperform MARS in building single-species models, and some species may be better modelled with variables not used here. However, modelling species individually would probably reduce efficiency for informing tractable management actions and may reduce the reliability of models. One of the reasons for the superior performance of the multiple-species approach is that constraining models to a common set of variables and basis functions for all guild members reduces the risk of overfitting models, or of finding spurious species–environment relationships. The greatest improvements in bootstrap results for guild-based models relative to single-species models were for species with low prevalence. Leathwick *et al.* (2006) and Elith & Leathwick (2007) also have reported that multispecies MARS models can improve prediction of occurrence of rare species or species for which few data exist.

We obtained the best model predictions by grouping species into ecological guilds and selecting a limited set of candidate

predictor variables relevant to each guild before modelling. Expert selection of predictor variables can increase the probability that models include important drivers of species occurrence rather than poor surrogates of those drivers or spurious predictors. Grouping species into ecological guilds facilitates the use of natural history and other knowledge to identify a set of variables to which all species in the guild are likely to respond.

Objective, statistical methods for explaining and predicting ecological relationships are generally preferable to reliance on expert opinion alone (Sutherland, 2006). By incorporating expert knowledge directly into statistical models, the limits and uncertainty associated with experience or intuition can be assessed (Johnson & Gillingham, 2004). Our work supports the inclusion of expert information into statistical models for situations where there is much expert knowledge, but few empirical data (Martin *et al.*, 2005).

Our models can be linked to spatially explicit scenarios of environmental change, such as quantitative projections of changes in key variables in response to climate or land-use trends, to predict assemblage-level responses. A species-based approach is more useful for anticipating such faunal change than modelling collective properties like species richness or turnover. Given that our guild-based modelling retains information on species identity and allows species-specific responses, we can identify species likely to have negative responses to a given type of land cover or land-use change. Such knowledge may facilitate regional planning that will maintain a high proportion of species. Identification of these species using statistical models may yield greater predictive accuracy than expert knowledge that is not vetted quantitatively.

ACKNOWLEDGEMENTS

Thanks to M. Ban, C. Betrus, L. P. Bulluck, G. Horrocks, G. Johnson, N. Losin, G. Markoff, N. McDonal and J. Smith for collection of field data integral to this work. Thanks to J. Fay and K. Seto for technical support. José Alexandre Diniz-Filho and two anonymous referees provided many helpful comments on the manuscript. Financial support was provided by the Australian Research Council, Nevada Biodiversity Research and Conservation Initiative, National Fish and Wildlife Foundation, and the Joint Fire Science Program via the Rocky Mountain Research Station, US Department of Agriculture Forest Service. This is contribution 115 from the Australian Centre for Biodiversity: Analysis, Policy and Management.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Complete description of modelling methods.

Appendix S2 Guild associations of bird species, relationship to predictor variables and predictive ability of guild-based models.

This material is available as part of the online article from:

<http://www.blackwell-synergy.com/doi/abs/10.1111/j.1466-8238.2008.00409.x>

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Editor: José Alexandre Diniz-Filho