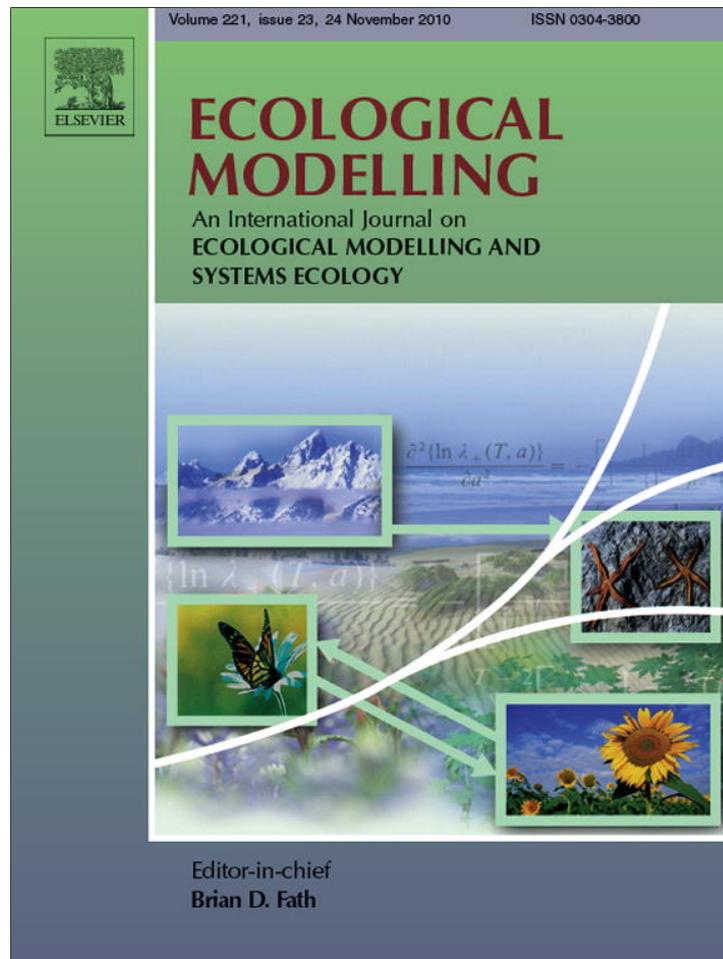


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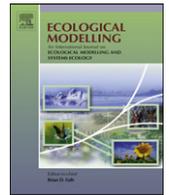
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Accuracy of gap analysis habitat models in predicting physical features for wildlife-habitat associations in the southwest U.S.

Kenneth G. Boykin^{a,*}, Bruce C. Thompson^{b,1}, Suzanne Propeck-Gray^{a,2}

^a New Mexico Cooperative Fish and Wildlife Research Unit and Department of Fish, Wildlife, and Conservation Ecology, P.O. Box 30003, MSC 4901, New Mexico State University, Las Cruces, NM 88003, USA

^b U.S. Geological Survey, New Mexico Cooperative Fish and Wildlife Research Unit, P.O. Box 30003, MSC 4901, Las Cruces, NM 88003, USA

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ABSTRACT

Despite widespread and long-standing efforts to model wildlife-habitat associations using remotely sensed and other spatially explicit data, there are relatively few evaluations of the performance of variables included in predictive models relative to actual features on the landscape. As part of the National Gap Analysis Program, we specifically examined physical site features at randomly selected sample locations in the Southwestern U.S. to assess degree of concordance with predicted features used in modeling vertebrate habitat distribution. Our analysis considered hypotheses about relative accuracy with respect to 30 vertebrate species selected to represent the spectrum of habitat generalist to specialist and categorization of site by relative degree of conservation emphasis accorded to the site. Overall comparison of 19 variables observed at 382 sample sites indicated $\geq 60\%$ concordance for 12 variables. Directly measured or observed variables (slope, soil composition, rock outcrop) generally displayed high concordance, while variables that required judgments regarding descriptive categories (aspect, ecological system, landform) were less concordant. There were no differences detected in concordance among taxa groups, degree of specialization or generalization of selected taxa, or land conservation categorization of sample sites with respect to all sites. We found no support for the hypothesis that accuracy of habitat models is inversely related to degree of taxa specialization when model features for a habitat specialist could be more difficult to represent spatially. Likewise, we did not find support for the hypothesis that physical features will be predicted with higher accuracy on lands with greater dedication to biodiversity conservation than on other lands because of relative differences regarding available information. Accuracy generally was similar ($>60\%$) to that observed for land cover mapping at the ecological system level. These patterns demonstrate resilience of gap analysis deductive model processes to the type of remotely sensed or interpreted data used in habitat feature predictions.

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1. Introduction

Wildlife-habitat modeling has evolved greatly since 1980. Modeling trends have shifted from species- and site-specific predictions to multi-species models applicable to large regions. These trends represent 3 main time frames: early to mid 1980s, late 1980s to mid-1990s, and late 1990s to the present.

The 1980s were years of prolific model development. Most wildlife-habitat models of the period were species-specific, such as the model developed by Mosher et al. (1986) to predict nesting habitat for broad-winged hawks (*Buteo platypterus*) and red-

shouldered hawks (*Buteo lineatus*), or the model to predict breeding densities of ruffed grouse (*Bonasa umbellus*) by Hammill and Moran (1986). Researchers often overlooked effects of spatial scale and applied models developed from local data over broad areas (Wiens, 1981) or applied multivariate approaches in sometimes questionable ways (Capen, 1981). Models were rarely tested for accuracy (Berry, 1986), as was the case with Habitat Suitability Index models (Cole and Smith, 1983). When new models were introduced, the general tendency among scientists was to spend more time applying them in research and less time evaluating circumstances where models were most useful (Stauffer, 2002). Only after much time had passed were limitations sufficiently comprehended to allow models to be applied more fittingly, if less often (Stauffer, 2002).

The latter part of the 1980s through the mid-1990s encompassed the transition of research focus from single-species models to multi-species models (either simultaneous models or multiple species model overlays). Single-species models were still frequently used, but limitations to their applicability were recognized.

* Corresponding author. Tel.: +1 575 646 6303; fax: +1 575 646 1281.

E-mail address: kboykin@nmsu.edu (K.G. Boykin).

¹ Present address: Energy, Minerals and Natural Resources Dept., 1220 South St. Francis Drive, Santa Fe, NM 87505, USA.

² Present address: 12621 Sunset Drive, St. Louis, MO 63128, USA.

With advances in knowledge about remote sensing and geographic information systems (GIS), multi-species models became common and were applied over large land areas (Morrison et al., 1998). One such modeling approach developed during this period was gap analysis (Scott et al., 1993), which has been used to perform statewide or broader analyses (Gap Analysis Handbook via Internet at <<http://www.gap.uidaho.edu/handbook>>). The amount of verifications and accuracy assessments performed on wildlife-habitat models also increased during this timeframe (Fielding and Haworth, 1995; Edwards et al., 1996; Fielding and Bell, 1997).

From the late 1990s to the present, deductive and inductive GIS-based wildlife-habitat models have become mainstream (Scott et al., 2002; Guisan and Thuiller, 2005). Deductive models use literature and expert opinion to identify suitable habitat features based on environmental variable associations. Gap analysis models are common among these models. The tenet that vegetation/land cover and related physical feature maps generally predict distribution of suitable vertebrate habitat is the basis of gap analysis habitat predictions (Edwards et al., 1996). Inductive modeling uses algorithms (e.g. GARP, Maximum Entropy), species occurrence points, and environmental variables to determine the probability of suitable habitat (Peterson et al., 2002; Phillips et al., 2006). Accuracy assessments have not been performed routinely on habitat models, including gap analysis models, to assess their usefulness to depict presence of actual habitat characteristics, but are essential to demonstrate reliability (Williams, 1996).

Model accuracy can be poor if the features a specialist species is associated with have a lower resolution than the land cover map, are included as part of a different vegetation class, or are difficult to identify via remote sensing (Edwards et al., 1996). Information gathered to create a predictive habitat model imparts a strong influence on the map derived from the model (Garrison and Lupo, 2002; Austin, 2007). Edwards et al. (1996), in assessing models relative to species occurrence data, found the accuracy of their habitat models to be proportional to amount of park area, possibly because large parks tend to have more complete species inventories that would reduce commission errors. Garrison and Lupo (2002) found that model-based map accuracy was lower regarding species that are not territorial, are fewer in number, have small ranges, and utilize aquatic habitats. Small colonial specialist species that need restricted microhabitats may be expected to have poorer model performance because microhabitat features are less frequently mapped over large areas. However, most assessments have been based on measures of species occurrence, which is highly variable in detection among taxa (Kery, 2002). Further, there is value in validation of model application by a user versus verification of general performance of a model approach (Rykiel, 1996).

Models that help delineate possible effects of and alternatives to management actions and that apply to large areas are necessary to overcome challenges faced by resource managers (Stauffer, 2002). Knowledge of the predictive accuracy of habitat distribution models is necessary for effective conservation planning (Edwards et al., 1996; Boone and Krohn, 1999). Virtually all wildlife-habitat models in the past have been tested by evaluating species occurrence in the predicted areas, whether by comparing model predictions to documented lists of species in the area or by trapping or observing species in the field. This method of accuracy assessment has limitations and could be misleading because species lists may be outdated, suitable habitats are not occupied at all times and/or may not be used by a species during field sampling (Greco et al., 2002; Kery, 2002), or a species is not detected despite being present (Mackenzie et al., 2002; Stauffer et al., 2002). Most habitat models do not predict the actual occurrence of a species in an area; instead they use a suite of modeled physical characteristics of habitat (e.g. land cover) to forecast the likelihood of suitable habitat presence. Habitat models that predict where a combination of habi-

tat features are likely to be suitable for a certain species should be evaluated on the basis of what they are actually forecasting: where the suitable habitat features combinations are not the presence of the species. We assessed accuracy of Southwest Regional Gap Analysis Project (SWReGAP) habitat models in predicting the location of appropriate habitat features (Boykin et al., 2007). We further examined the degree to which concordance between predicted and field data indicated whether predictive capability was different among specialist versus generalist species and among land areas considered to have lesser or greater likelihood of management to conserve biodiversity. Specifically, we hypothesized that accuracy of SWReGAP habitat models is inversely related to degree of taxa specialization because physical features in a model of a habitat specialist are suspected to be more difficult to represent spatially. We also hypothesized that modeled physical features will be predicted with higher accuracy on lands with greater dedication to biodiversity conservation than on other lands because more physical and ecological information has been collected and is available spatially regarding lands devoted to conservation.

2. Study area

The study area constituted all area encompassed by the ecological regions defined by SWReGAP as occurring in New Mexico and extending into surrounding parts of Arizona, Colorado, and Utah (Fig. 1). The study area was defined by ecological features and related land cover mapping prepared for our specific project, not by any specific political boundary. Within the study area, specific sample sites were distributed randomly and proportionally among the 10 ecoregions.

3. Methods

3.1. Comparative predictive data

The datasets incorporated in the SWReGAP wildlife-habitat models are described in detail by Prior-Magee et al. (2007). The SWReGAP project created a 125-class land cover dataset for the states of Arizona, Colorado, Nevada, New Mexico, and Utah. This dataset included 109 ecological systems and 16 other land cover/land use classes (e.g. agriculture). Land relief variables were extracted from the National Elevation Dataset (<http://ned.usgs.gov/>) and included elevation, slope, aspect, and a 10-class land-form coverage (Prior-Magee et al., 2007). Presence of soil texture classes (clay, loam, sand, etc.), rockiness, and rock outcrop percent were extracted from the State Soil Geographic database (STATSGO) available from the USDA Natural Resources Conservation Service (<http://www.ncgc.nrcs.usda.gov/products/datasets/statsgo/>). Data collected from each sample site corresponded to variables used in the SWReGAP wildlife-habitat models and were separated into categories for analysis (Table 1).

3.2. Taxa specialization and land status

We examined degree of taxa specialization relative to model performance for species previously identified for conservation focus because of limited presumed occurrence on conserved lands. Using the original New Mexico Gap Analysis Project (Thompson et al., 1996), we identified species that had less than 10% of their distribution predicted to occur on Status 1 and 2 lands. GAP uses a categorical scale of 1 to 4 to identify the degree of maintenance of biodiversity (Prior-Magee et al., 1998, 2007). Examples of these categories include research natural areas (Status 1), wilderness areas (Status 2), multiple use lands (Status 3), and private lands with unknown management intent (Status 4) (Prior-Magee et al., 1998,

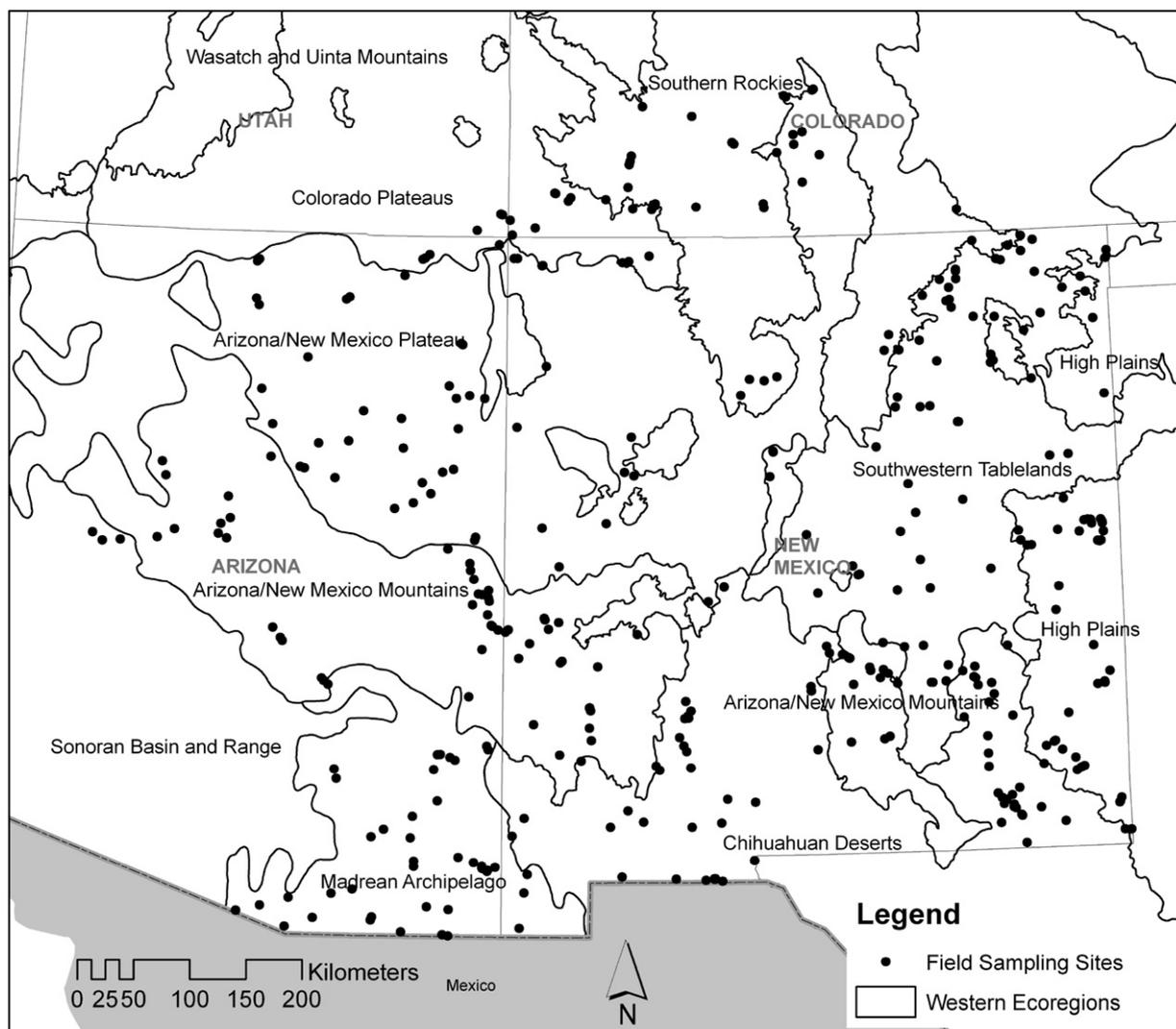


Fig. 1. Map of study area showing distribution of 382 sample sites among 10 ecological regions in Arizona, Colorado, New Mexico, and Utah to assess physical feature characteristics for habitat modeling in gap analysis.

2007). A status category of “1” identifies the highest, most permanent level of conservation, with a “4” representing the lowest level of biodiversity management, protection, or unknown status where information was not available to assign a different rating (Scott et al., 1993).

We selected 14 birds, 10 mammals, 4 amphibians, and 2 reptiles to use in sample site selection to provide for analysis of effects of specialization (Table 2). The number of species in each group approximated the percentage of that taxa group in the SWReGAP species list. Species were picked at random to represent a variety of habitat types, distribution, and specialization. Subsequent selection of sample sites represented distributions of these species (see below).

Land status categorization followed Prior-Magee et al. (1998), and specifically related to degree of active management to provide for biological diversity and land area protection. Every sample site was labeled as to its land status category in the SWReGAP data set for subsequent analyses.

3.3. Site selection and data collection

A double blind approach was used to select and examine field sampling sites to minimize bias. We randomly selected 382 points

within 1 km of a road to facilitate sampling access and adequately represent ecological landscapes throughout New Mexico and bordering areas of Arizona, Utah, and Colorado. Field sites were selected such that there were at least 10 sites within the predicted modeled distribution of each taxa selected to represent habitat specialists and generalists.

All sites were examined by the same person (SPG) during July 2003–July 2005. The observer drove as close as possible and then walked to each sample site defined as 0.81 ha (equivalent of a 3×3 pixel area) and located the center point using a GPS unit accurate to within 15 m (<9% of sample unit size). The physical and vegetation/land form features at the sites were examined and recorded. Digital images were taken of each for later reference as needed to clarify descriptive assignments. Habitat features from the SWReGAP habitat models that were observed and recorded included slope, aspect, hydrology type (stream, wetland, etc.), distance to water, patch size, land cover, soil type, percent rock outcrop, and landform (valley, hill, cliff, etc.). Slope and aspect values for entire site were measured at the center of site using a clinometer and compass. Hydrology type, percent rock outcrop, and landform values were ocular estimates. Land cover was based on predominant vegetation and classified into ecological systems. Distance to hydrology and patch size were calculated from contemporary aerial photogra-

Table 1
Summary of physical features recorded at 382 sample sites in Southwest U.S. for comparison to features predicted from gap analysis modeling of wildlife-habitat.

Variable	Descriptions	Values
Slope (degrees)	6 categories from 0 to 90	0–15, 16–30, 31–45, 46–60, 61–75, 76–90
Aspect	16 categories with specific azimuth ranges	N (348.75–11.25), NNE (11.25–33.75), NE (33.75–56.25), ENE (56.25–78.25), E (78.75–101.25), ESE (101.25–123.75), SE (123.75–146.25), SSE (146.25–168.75), S (168.75–191.25), SSW (191.25–213.75), SW (213.75–236.25), WSW (236.25–258.75), W (258.75–281.25), WNW (281.25–303.75), NW (303.75–326.25), NNW (326.25–348.75)
Distance to Water (m)	6 categories from 0 to beyond 1000	<50, 50–<100, 100–<250, 250–<500, 500–1000, >1000
Land cover	Dominant vegetation species observed	Later matched to an alliance from the National Vegetation Classification System
Soil type	9 categories particle size and texture	Clay, Silt, Sand, Loam, Gravel, Cobble, Stone, Boulder, Rocky
Rock outcrop (%)	4 categories of area covered by rock outcrop	<15, 15–30, 31–65, >65
Landform	10 categories of slope and basin site	Valley flats: floodplains, basin floors (alluvial, lacustrine) [0–2.9 slope] Toe slopes, bottoms, and swales: riparian and semi-riparian, moist lower slopes and bottoms (fluvial/alluvial, colluvial, glacial) [3–9.9 slope] Gently sloping ridges, fans, and hills: ridges and moderately dry hills and moraines (residual, glacial, other) [3–9.9 slope] Nearly level plateaus and terraces: upland or terrace flats (residual, alluvial) [0–2.9 slope] Very moist steep slopes: lower north facing valley and mountain sideslopes [10–35 slope] Moderately moist steep slopes: northerly facing valley and mountain sideslopes [10–35 slope] Moderately dry steep slopes: southerly facing valley and mountain sideslopes [10–35 slope] Very dry steep slopes: upper southwest facing valley and mountain sideslopes [10–35 slope] Cool aspects cliffs, scarps, cirques: over-steepened, northerly slopes [>35 slope] Hot aspects cliffs, scarps, cirques: over-steepened, southerly slopes [>35 slope]

Table 2
List of 30 animal species and degree of habitat specialization used to analyze concordance of gap analysis predictions of habitat features with observed features on 382 sample sites in Southwest U.S., 2003–2005.

Species	Classified as	
	Generalist	Specialist
Great Plains toad (<i>Bufo cognatus</i>)		×
Southwestern toad (<i>Bufo microscaphus</i>)		×
Barking frog (<i>Eleutherodactylus augusti</i>)		×
Bullfrog (<i>Rana catesbeiana</i>)		×
Checkered whiptail (<i>Cnemidophorus tesselatus</i>)	×	
Smooth green snake (<i>Ophedrys vernalis</i>)		×
Grasshopper sparrow (<i>Ammodramus savannarum</i>)		×
Black-throated sparrow (<i>Amphispiza bilineata</i>)		×
Mallard (<i>Anas platyrhynchos</i>)		×
Black-chinned hummingbird (<i>Archilochus alexandri</i>)		×
Western sandpiper (<i>Calidris mauri</i>)		×
Northern flicker (<i>Colaptes auratus</i>)		×
American crow (<i>Corvus brachyrhynchos</i>)	×	
Townsend's solitaire (<i>Myadestes townsendi</i>)		×
Painted redstart (<i>Myioborus pictus</i>)		×
Western screech-owl (<i>Otus kennicottii</i>)	×	
Rock wren (<i>Salpinctes obsoletus</i>)		×
Pygmy nuthatch (<i>Sitta pygmaea</i>)		×
Tennessee warbler (<i>Vermivora peregrina</i>)	×	
Yellow-headed blackbird (<i>Xanthocephalus xanthocephalus</i>)		×
American beaver (<i>Castor canadensis</i>)		×
Yellow-faced pocket gopher (<i>Cratogeomys castanops</i>)		×
Gunnison's prairie dog (<i>Cynomys gunnisoni</i>)		×
Allen's big-eared bat (<i>Idionycteris phyllotis</i>)		×
Prairie vole (<i>Microtus ochrogaster</i>)		×
White-tailed deer (<i>Odocoileus virginianus</i>)	×	
White-ankled mouse (<i>Peromyscus pectoralis</i>)		×
Pinon mouse (<i>Peromyscus truei</i>)		×
Arizona gray squirrel (<i>Sciurus arizonensis</i>)		×
Mountain cottontail (<i>Sylvilagus nuttalli</i>)	×	

phy. Soil composition and texture were determined at each sample site using texture by feel analysis (Thien, 1979). Hydrology, land cover class, percent rock outcrop, and landform were observed visually.

3.4. Analysis

Field site data (actual habitat features) and SWReGAP predictions of suitable habitat features were compiled in independent spreadsheets and then subjected to a concordance assignment based on value or category assignments to all variables for all sites. The resulting concordance table was then converted to a frequency tabulation for all variables. The frequency table was used to perform a series of goodness of fit tests regarding taxa category and conservation categorization relative to concordance of predicted and observed data for all sites. These concordance analyses were performed to assess the relative degree of similarity of model-predicted features to features on the ground as well as to assess the 2 specific hypotheses about how taxa life history and knowledge about lands may affect predictive performance.

4. Results

Overall comparison of 19 variables observed at the 382 sample sites relative to SWReGAP predicted values indicated ≥60% concordance (59.7% rounded to 60%) for 12 of the 19 variables (63%) examined (Table 3: All sites column). Directly measured or observed variables (slope, soil composition, rock outcrop) generally displayed high concordance, while variables that required judgments relative to descriptive categories (aspect, ecological system, landform) were less concordant. Aspect was a directly measured variable that required a preliminary judgment about presence and direction of slope, which could vary across a sample unit.

Moreover, there were no differences detected in concordance regarding taxa groups, degree of specialization/generalization of selected taxa, or land conservation categorization of sample sites with respect to all sites (Table 3). There also was inde-

Table 3

Percentage concordance among 19 physical factors evaluated at 382 field sample sites as compared to predicted factor values from Southwest Regional Gap Analysis Project data used for predicting likelihood of wildlife-habitat features in Arizona, Utah, Colorado, and New Mexico, 2003–2005.

Factor ^a	All sites	Specialist only sites	Generalist only sites	Specialist sites total	Generalist sites total	Amphibians	Birds	Mammals	Reptiles	Steward 1&2	Steward 3&4
N	382	36	18	355	337	130	265	336	77	16	366
Slope	92.1	94.4	100.0	91.8	92.0	96.9	90.2	92.3	92.2	100.0	91.8
Aspect	27.0	19.4	38.9	26.8	28.2	28.5	26.8	28.6	35.1	31.3	26.8
Distance–Water	64.4	83.3	44.4	65.1	62.0	65.4	57.4	64.9	71.4	56.3	64.8
Ecol. System	39.8	52.8	55.6	39.7	39.2	31.5	41.5	38.1	37.7	25.0	40.4
Land cover–Gen	63.9	83.3	77.8	64.2	62.9	60.8	63.8	64.0	58.4	43.8	64.8
Clay	45.8	33.3	50.0	44.8	46.3	36.2	47.5	43.5	29.9	37.5	46.2
Silt	64.4	72.2	50.0	64.8	63.2	68.5	64.2	63.1	58.4	56.3	64.8
Sand	49.7	41.7	38.9	49.6	49.9	55.4	50.6	50.0	53.2	56.3	49.5
Loam	26.4	25.0	5.6	28.2	27.3	27.7	29.8	27.7	24.7	18.8	26.8
Gravel	75.9	75.0	77.8	75.8	76.0	80.8	73.2	76.5	77.9	81.3	75.7
Cobble	64.9	61.1	66.7	64.5	65.0	70.0	63.0	66.4	71.4	68.8	64.8
Stone	81.4	88.9	88.9	81.4	81.0	84.6	81.1	81.8	87.0	68.8	82.0
Boulder	96.3	97.2	100.0	96.1	96.1	95.4	95.8	96.7	98.7	87.5	96.7
Rocky	32.7	27.8	16.7	34.1	33.8	33.8	37.0	34.5	33.8	25.0	33.1
Outcrop <15	59.7	58.3	55.6	60.0	59.9	56.2	60.8	60.7	51.9	87.5	58.5
Outcrop 15–30	75.9	77.8	83.3	76.1	76.3	80.0	76.2	76.5	79.2	81.3	75.7
Outcrop 30–65	89.8	86.1	94.4	89.9	90.5	90.8	89.4	89.6	92.2	100.0	89.3
Outcrop >65	98.4	97.2	100.0	98.6	98.8	97.7	98.5	98.8	100.0	100.0	98.4
Land Form	16.8	13.9	27.8	16.1	16.9	14.6	15.5	17.0	13.0	0.0	17.5
Goodness of fit relative to all sites	–	21.889	14.970	9.89	11.99	9.06	5.911	1.786	10.189	8.33	0.38
<i>P</i> (df = 18)		0.237	0.664	0.935	0.847	0.958	0.997	1.00	0.926	0.973	1.00

^a Values in table are percentages except for values of N.

pendence among all taxa groups relative to each other (test values = 7.69–14.97, $P = 0.664$ – 0.848 , $df = 18$) and for Status 1 and 2 sites compared to Status 3 and 4 sites (test value = 8.71, $P = 0.966$).

Despite the relative strength of relationships between predictions and field site observations overall and for most variables, 8 of the variables displayed low concordance. These specific variables indicated types of factors that warrant specific evaluation for possible error propagation effects that were not detected in these analyses but could affect other applications.

We found no support for the hypothesis that accuracy of SWReGAP habitat models is inversely related to degree of taxa specialization that outcome refuted a presumption that features in a model for a habitat specialist are more difficult to represent spatially. Likewise, we did not find support for the hypothesis that physical features will be predicted with higher accuracy on lands with greater dedication to biodiversity conservation than on other lands because of relative differences regarding available information. These patterns demonstrated resilience of gap analysis predictive processes to the type of remotely sensed or interpreted data used in habitat feature predictions.

5. Discussion

Relatively low accuracy for aspect, ecological system, and land-form variables in this analysis appeared to result from greater likelihood of limitations in correctly assigning those values on site versus actual inaccuracy in gap analysis predictions. This is suggested because independently evaluated accuracy of SWReGAP land cover predictions has shown >60% accuracy for most land cover assignments within the overall ecological system classification (Lowry et al., 2007; Prior-Magee et al., 2007). Variation on the ground and gradations of landcover likely contribute to the discordance with remotely sensed data models. This interpretation is supported by increased concordance associated with aggregation of the land cover dataset (Land Cover versus Ecological System in Table 3). LaBram et al. (2007) reported similar accuracy using species occurrence monitoring to assess gap analysis predictive

models. Austin (2007) discussed and emphasized how variables used can affect relative performance of modeling methods.

Field data indicated that the observer experienced some difficulty distinguishing near-zero slope and no slope from areas with greater slope, thus making directional aspect assignments to no slope sites predicted from DEM data used in gap analysis. Based on review of all slope and aspect assignments, the tendency in the field was to indicate there was no discernible aspect at relatively flat sites and to indicate slope was >15% when it was actually less. These situations contributed about 38% discordance for the aspect variable. Computer derived aspect for each pixel is calculated based on the direction of the 8 adjacent neighborhood pixels. Observers likely mentally average these variables using the overall area and may over-emphasize small portions that may not dominate the area but focus observer attention.

With respect to land form, most variation was attributed to mixed attributions among valley flats, bottoms and swales, and nearly level plateaus and terraces. Inspection of data indicated that the majority of discordant sites predicted were mixed among those 3 categories in field assignments relative to how these categories were distributed in model predictions. The intermixing of assignments of valley flats versus nearly level plateaus and terraces contributed 53% of the discordance. Similar to aspect, field determination of these land form types likely focuses on either a more broad interpretation of the descriptions than provided by a strict model code or focus on small areas that dominate visual appearance but not the landscape. Strauss and Biedermann (2007) observed that vegetation structure variables related to species occurrence were more general than the specificity of landscape context variables, a pattern consistent with our analyses.

Distance to water displayed relatively high concordance despite substantial variation across the landscape regarding substance and specificity in mapping wetland and riparian areas. Spatial hydrology data are known for having errors associated with seasonality of surface water and extent of that surface water. This is understandable in arid and semi-arid areas where surface water discharge is directly tied to recent precipitation. The high concordance corre-

sponds more closely to riparian vegetation that, though influenced by recent precipitation, is less affected by varying precipitation changes.

Our results highlight the differences between field inspection and computer generated habitat modeling. In the field, animals (and biologists) observe fine grained natural gradients on the landscape. Habitat models use data (categorical and continuous) that limit these gradients in both space and time. Despite the limitations of input variables and assumptions of species association based on limited knowledge, habitat models still provide a useful tool for conservation managers (Edwards et al., 1996).

Our evaluation used data collected completely independent from data used to prepare the models and further examined model performance among species life histories. Pearce and Ferrier (2000) stressed the importance of using independent data to evaluate predictive performance, and Hernandez et al. (2006) emphasized the importance of applying multiple evaluation measures to assess model accuracy. Further, we did not detect appreciable difference in model performance among taxa groups or specialists versus generalists, a pattern similar to that reported by Hopkins and Burr (2009). However, greater accuracy has been reported for species with smaller geographic ranges and limited environmental tolerance (Hernandez et al., 2006). Our sampling targeted toward species life history was consistent with suggestions of Meynard and Quinn (2007) who suggested that models for species with low prevalence can be improved through targeted sampling. Importantly, we examined specific features that are predicted by predictive models, and provided analytical outcomes stated directly about those features rather than indirectly as suggestions about species occurrence.

6. Habitat modeling implications

The relative uniformity of concordance patterns across comparison categories suggested that SWReGAP predictions are generally robust for vertebrate life history aspects and landscape categorization on biological or social factors that have been a part of gap analysis to date. Moreover, these analyses suggest that most variables used in SWReGAP habitat modeling perform well in describing actual landscape features. This corroboration indicates that modeling approaches in place as part of the overall Gap Analysis Program have prospect for accurately modeling habitat features as long as the association between physical features and species habitat are adequately interpreted. Current efforts to refine these models by using demography, interspecific competition, and microhabitat features should provide more accurate and useful models for conservation managers.

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References

Austin, M., 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological Modelling* 200, 1–19.
 Berry, K.H., 1986. Introduction: development, testing, and application of wildlife-habitat models. In: Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. The University of Wisconsin Press, Madison, pp. 3–4.
 Boone, R.B., Krohn, W.B., 1999. Modeling the occurrence of bird species: are the errors predictable? *Ecological Applications* 9, 835–848.

Boykin, K.G., Thompson, B.C., Deitner, R.A., Schrupp, D., Bradford, D., Lee O'Brien, et al., 2007. Predicted animal habitat distributions and species richness. In: Prior-Magee, J.S., Prior-Magee, J.S., Boykin, K.G., Bradford, D.F., Kepner, W.G., Lowry, J.H., Schrupp, D.L., Thomas, K.A., Thompson, B.C. (Eds.), *Southwest Regional Gap Analysis Final Report*. U.S. Geological Survey, Gap Analysis Program, Moscow, ID, pp. 39–78.
 Capen, D.E., editor. 1981. The use of multivariate statistics in studies of wildlife habitat. U.S. Dept. of Agriculture, Rocky Mountain Forest and Range Experiment Station Gen. Tech. Report RM-87.
 Cole, C.A., Smith, R.L., 1983. Habitat suitability indices for monitoring wildlife populations—an evaluation. *Transactions of the North American Wildlife and Natural Resources Conference* 48, 367–375.
 Edwards Jr., T.C., Deshler, E.T., Foster, D., Moisen, G.G., 1996. Adequacy of wildlife habitat relation models for estimating spatial distributions of terrestrial vertebrates. *Conservation Biology* 10, 263–270.
 Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24, 38–49.
 Fielding, A.H., Haworth, P.F., 1995. Testing the generality of bird–habitat models. *Conservation Biology* 9, 1466–1481.
 Garrison, B.A., Lupo, T., 2002. Accuracy of bird range maps based on habitat maps and habitat relationship models. In: Scott, J.M.P.J., Heglund, M.L., Morrison, J.B., Haufler, M.G., Raphael, W.A., Wall, F.B., Samson (Eds.), *Predicting Species Occurrences: Issues of Accuracy and Scale*. Washington, DC, Island Press, pp. 367–375.
 Greco, S.E., Plant, R.E., Barrett, R.H., 2002. Geographic modeling of temporal variability in habitat quality of the yellow-billed cuckoo on the Sacramento river, miles 196–219, California. In: Scott, J.M.P.J., Heglund, M.L., Morrison, J.B., Haufler, M.G., Raphael, W.A., Wall, F.B., Samson (Eds.), *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Washington, DC, pp. 183–195.
 Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8, 993–1009.
 Hammill, J.H., Moran, R.J., 1986. A habitat model for ruffed grouse in Michigan. In: Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. The University of Wisconsin Press, Madison, pp. 15–18.
 Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L., 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29, 773–785.
 Hopkins, R.L., Burr, B.M., 2009. Modeling freshwater fish distributions using multiscale landscape data: a case study of six narrow range endemics. *Ecological Modelling* 220, 2024–2034.
 Kery, M., 2002. Inferring the absence of a species—a case study of snakes. *Journal of Wildlife Management* 66, 330–338.
 LaBram, J.A., Peck, A.E., Allen, C.R., 2007. Monitoring-based assessment of gap-analysis models. *Southeastern Naturalist* 6, 633–656.
 Lowry, J.R., Ramsey, K., Thomas, D., Schrupp, T., Sajwaj, J., Kirby, et al., 2007. Mapping moderate-scale land-cover over very large geographic areas within a collaborative framework: a case study of the southwest regional gap analysis project (SWReGAP). *Remote Sensing and the Environment* 108, 59–73.
 Mackenzie, D.L., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
 Meynard, C.N., Quinn, J.F., 2007. Predicting species distributions: a critical comparison of the most common statistical models using artificial species. *Journal of Biogeography* 34, 1455–1469.
 Morrison, M.L., Marcot, B.G., Mannan, R.W., 1998. *Wildlife–Habitat Relationships: Concepts and Applications*. The University of Wisconsin Press, Madison.
 Mosher, J.A., Titus, K., Fuller, M.R., 1986. Developing a practical model to predict nesting habitat of woodland hawks. In: Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. The University of Wisconsin Press, Madison, pp. 31–35.
 Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* 133, 225–245.
 Peterson, A.T., Sánchez-Cordero, V., Beard, C.B., Ramsey, J.M., 2002. Ecologic niche modeling and potential reservoirs for Chagas disease, Mexico. *Emerging Infectious Diseases* 8, 662–667.
 Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modeling* 190, 231–259.
 Prior-Magee, J.S., Boykin, K.G., Bradford, D.F., Kepner, W.G., Lowry, J.H., Schrupp, D.L., Thomas, K.A., Thompson, B.C. (Eds.), 2007. *Southwest Regional Gap Analysis Project Final Report*. U.S. Geological Survey, Gap Analysis Program, Moscow, ID.
 Prior-Magee, J.S., Thompson, B.C., Daniel, D., 1998. Evaluating consistency of categorizing biodiversity management status relative to land stewardship in the gap analysis program. *Journal of Environmental Planning and Management* 41, 209–216.
 Rykiel Jr., E.J., 1996. Testing ecological models: the meaning of validation. *Ecological Modeling* 90, 229–244.
 Scott, J.M., Davis, F., Scuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'Erchia, F., Edwards Jr., T.C., Ulliman, J., Wright, R.G., 1993. Gap analysis: a geographic approach to protection of biological diversity. *Wildlife Monographs* 123, 1–41.
 Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A., Samson, F.B. (Eds.), 2002. *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Washington, DC.

- Stauffer, D.F., 2002. Linking populations and habitats: where have we been? Where are we going? In: Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A., Samson, F.B. (Eds.), *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Washington, DC, pp. 53–61.
- Stauffer, H.B., Ralph, C.J., Miller, S.L., 2002. Incorporating detection uncertainty into presence–absence surveys for marbled murrelet. In: Scott, J.M.P.J., Heglund, M.L., Morrison, J.B., Haufler, M.G., Raphael, W.A., Wall, F.B., Samson (Eds.), *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Washington, DC, pp. 357–365.
- Strauss, B., Biedermann, R., 2007. Evaluating temporal and spatial generality: how valid are species-habitat relationship models? *Ecological Modelling* 204, 104–114.
- Thien, S.J., 1979. A flow diagram for teaching texture-by-feel analysis. *Journal of Agronomic Education* 8, 54–55.
- Thompson, B.C., Crist, P.J., Prior-Magee, J.S., Deitner, R.A., Garber, D.L., and Hughes M.A. 1996. Gap analysis of biological diversity conservation in New Mexico using geographic information systems. Research Completion Report to U.S. Geological Survey-Biological Resources Division, Research Work Order No. 13, New Mexico Cooperative Fish and Wildlife Research Unit, Las Cruces, NM.
- Wiens, J.A., 1981. Scale problems in avian censusing. *Studies in Avian Biology* 6, 513–521.
- Williams, B.K., 1996. Assessment of accuracy in the mapping of vertebrate biodiversity. *Journal of Environmental Management* 47, 269–282.