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Predicting breeding habitat for amphibians: a spatiotemporal analysis across Yellowstone National Park

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Abstract. The ability to predict amphibian breeding across landscapes is important for informing land management decisions and helping biologists better understand and remediate factors contributing to declines in amphibian populations. We built geospatial models of likely breeding habitats for each of four amphibian species that breed in Yellowstone National Park (YNP). We used field data collected in 2000–2002 from 497 sites among 16 basins and predictor variables from geospatial models produced from remotely sensed data (e.g., digital elevation model, complex topographic index, landform data, wetland probability, and vegetative cover). Except for 31 sites in one basin that were surveyed in both 2000 and 2002, all sites were surveyed once. We used polytomous regression to build statistical models for each species of amphibian from (1) field survey site data only, (2) field data combined with data from geospatial models, and (3) data from geospatial models only. Based on measures of receiver operating characteristic (ROC) scores, models of the second type best explained likely breeding habitat because they contained the most information (ROC values ranged from 0.70 to 0.88). However, models of the third type could be applied to the entire YNP landscape and produced maps that could be verified with reserve field data. Accuracy rates for models built for single years were highly variable, ranging from 0.30 to 0.78. Accuracy rates for models built with data combined from multiple years were higher and less variable, ranging from 0.60 to 0.80. Combining results from the geospatial multiyear models yielded maps of "core" breeding areas (areas with high probability values for all three years) surrounded by areas that scored high for only one or two years, providing an estimate of variability among years. Such information can highlight landscape options for amphibian conservation. For example, our models identify alternative areas that could be protected for each species, including 6828–10 764 ha for tiger salamanders, 971–3017 ha for western toads, 4732–16 696 ha for boreal chorus frogs, and 4940–19 690 ha for Columbia spotted frogs.

Key words: amphibian conservation; amphibian habitat models; boreal chorus frog, Pseudacris maculata; *breeding habitat; Columbia spotted frog,* Rana luteiventris; *geospatial models; polytomous regression models; tiger salamander,* Ambystoma mavortium; *western toad,* Anaxyrus boreas; *Yellowstone National Park, USA.*

Introduction

Many factors have contributed to amphibian population declines, but habitat loss and alteration continue to be considered major causes (Alford and Richards 1999, Collins and Storfer 2003, Halliday 2005). One of the most effective approaches to combat declines in wildlife populations is to identify and protect breeding habitats, because successful reproduction is critical for the persistence of any species. However, conducting field surveys across entire landscapes to identify species-specific breeding habitat is often time and cost prohibitive. Using remotely sensed data in combination with field data to build predictive models across entire landscapes is an effective way to identify these critical areas (Scott et al. 2002).

Habitat models historically have focused on birds, mammals, and fish (e.g., Manly et al. 2002, Scott et al. 2002, Torgersen and Close 2004), and applications for amphibians are relatively recent (Porter and Mitchell 2006, Bartelt et al. 2010). Among approaches are those that are statistical, geospatial, and combinations of both. Some statistical methods are better for understanding aspects of species–environment relations than for predicting species occurrence or the availability of potential habitat in the landscape. For example, ordination techniques organize data on species occurrence along axes in multidimensional numeric space that, ideally, can be correlated with environmental variables or gradients. Results can shed light on patterns

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of species distributions or habitat use with respect to those variables (e.g., Strijbosch 1979, Owen and Dixon 1989), but do not lend themselves to generating a ready tool (e.g., a predictive map) for a land manager.

Other statistical methods (e.g., regression-based methods) provide the means to build predictive models. In theory, these models could be used to generate maps of species occurrence or the availability of potential habitat, but typically this is not within the scope of the research efforts. For some cases, this is because model inputs require data that are available only at specific field sites or that are time sensitive (e.g., Joly et al. 2001, Bartelt et al. 2004, Egan and Paton 2004). There are, however, efforts that have implemented this predictive mapping step (e.g., Mladenoff et al. 1995, Mace et al. 1999). Over time, particularly in the last decade, digital maps have become available for an increasing array of environmental variables (e.g., land cover, spatially interpolated weather, and geology), improving the opportunity to build statistical habitat models that can be translated into geospatial predictions for use by investigators and land managers (e.g., Welsh et al. 2006).

Predicting potential habitat for amphibians is complicated by temporal changes in habitat conditions. Ponds suitable for breeding in wet years may be unsuitable in normal years or disappear in dry years. This variation can have a considerable influence on the annual distribution of breeding populations (Pechmann and Wilbur 1994). A common source of information on wetland distributions in the conterminous United States is the National Wetlands Inventory, NWI (Cowardin et al. 1979; NWI *available online*).[5] A major limitation in using these maps to model amphibian breeding habitat is that they depict a static set of wetland boundaries. We expect habitat models based on information representing seasonal variation to be more realistic and to provide better models than those based on static wetland maps.

Another challenge to modeling habitat is selecting appropriate spatial and informational resolutions for the models (Wiens 1989, Wiens et al. 1993, Scott et al. 2002). The appropriate resolution depends on the vagility of the animals being modeled. Amphibians have relatively limited vagility, and many habitat features, such as breeding ponds, are quite small. Thus, data of relatively high spatial resolution are needed. In addition, amphibians can display selection not only for the type of wetland in which they breed, but also for specific locations within a wetland (Egan and Paton 2004). For some species, particular water depths, assemblages and/or shapes of emergent plant stems, exposure to sunlight, or composition of the substrate can be very important for providing necessary amounts of thermal energy, oxygen, and other factors (for a review, see Wells 2007). A combination of fine spatial and informational resolution better represents such variations across a wetland.

Our objective was to build species-specific predictive models of amphibian breeding habitat within Yellowstone National Park (YNP) that also addressed the temporal changes in wetlands at as fine a resolution as source data would support and that would be of use to YNP managers. Building habitat models in an area with limited anthropogenic activity (such as YNP) provides good baseline models to help us better understand how habitat change might affect amphibians in highly disturbed areas outside YNP. We developed regression models based on landscape characteristics associated with the breeding habitat requirements for the four species of amphibians that inhabit YNP: tiger salamanders (*Ambystoma mavortium*), western toads (*Anaxyrus boreas*), boreal chorus frogs (*Pseudacris maculata*), and Columbia spotted frogs (*Rana luteiventris*) (Koch and Peterson 1995).

We expected these habitat models to reflect variations in use that we have observed over many years of field observations. We expect that these species generally select exposed ponds (i.e., away from the shade of forest cover) occurring in wetter regions of YNP with finer grained sediments. We have found that western toads associate more with thermally influenced wetlands, ponds with open aquatic beds, and overflow pools along rivers and streams. Chorus frogs and spotted frogs tend to associate more with ponds supporting greater amounts of graminoid emergent vegetation.

We included predictor variables that reflected our assumptions and incorporated local to broad scales, because amphibian species may respond to environmental heterogeneity at different spatial scales (Johnson et al. 2002). To address the effects of temporal variation of wetlands on amphibians, we developed separate models for each species for years of available field survey data (2000–2002), extracting data on location and breeding status of amphibians to train and validate models.

We evaluated three approaches: (1) using variables collected at sites surveyed for amphibian presence, (2) augmenting these site variables with information extracted from geographic information system (GIS) layers, and (3) using information provided only from GIS layers. These approaches offered different potential benefits. Site variables represent the conditions in the field at the time of the surveys; models based on these data target local-scale conditions (air and water temperature, wetland vegetation, surface area of standing water, water chemistry, and so forth) that might be linked strongly to habitat use. Environmental information extracted from GIS layers provide additional model variables representing broader-scale temporal (e.g., long-term weather variables) and landscape features (e.g., landform type) that might explain distributions of breeding sites. Unlike the first two approaches that relied on site-level conditions at the time of survey, the third approach relied entirely on GIS variables that

[5] ⟨http://www.fws.gov/nwi⟩

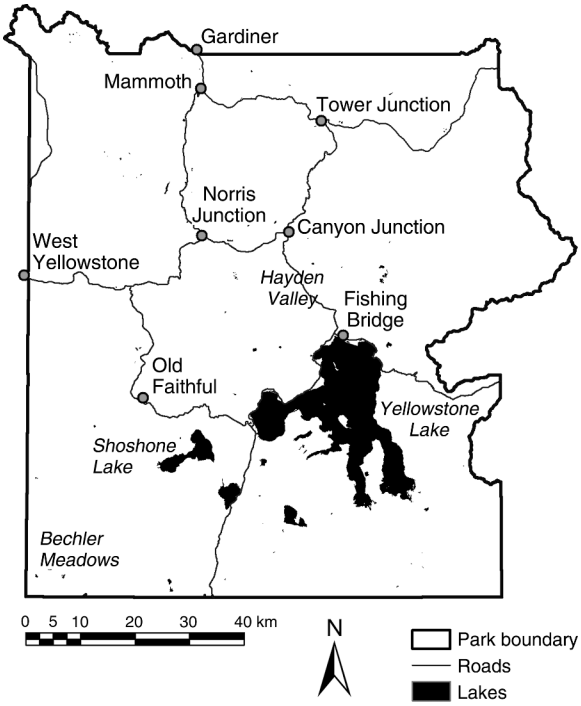

FIG. 1. Major landmarks of Yellowstone National Park, USA.

provide complete spatial coverage across the YNP, enabling us to generate predictive surfaces across the landscape.

METHODS

Study area

YNP encompasses ~900 000 ha in northwestern Wyoming and small amounts of land in the adjoining states of Montana and Idaho, USA (Fig. 1). Wetlands comprise 10.3% of YNP and most wetlands occur in three primary landforms: fluvium, glaciofluvium, and alluvium (Elliott and Hektner 2000). Palustrine wetlands are, by far, the prevalent wetland type in the YNP and include vernal pools, permanent ponds with relatively shallow shores and emergent vegetation, and areas of persistent wetland vegetation within floodplains along rivers or adjacent to open water within lake basins (Wright and Gallant 2007). The upland landscape is dominated by montane forests of pine (e.g., *Pinus contorta* and *P. albicaulis*), spruce (e.g., *Picea engelmanni*), and fir (e.g., *Abies lasiocarpa*), intermixed with sagebrush (*Artemesia* spp.) shrublands and grassy meadows (Despain 1990). YNP receives over three million visitors each year, although human use is highly concentrated in relatively few areas, such as along major roads and scattered tourist attractions and services. Some of these areas, however, have had considerable impacts on local amphibian populations and their habitat (Koch and Peterson 1995, Patla 1997).

Species use of breeding habitat

Breeding amphibians in YNP use a variety of lentic water bodies, including seasonal pools, permanent ponds, small lakes, river oxbows and backwaters, and streams impounded by beaver dams. Thermal features are common in YNP, and water bodies with a mild thermal influence also are used for breeding. Breeding site occupancy, adjusted for detectability based on estimates from other surveys conducted in YNP and adjacent Grand Teton National Park, was ~38% for boreal chorus frogs, 20% for Columbia spotted frogs, 21% for tiger salamanders, and <4% for western toads (Corn et al. 2005). These data suggest that boreal chorus frog breeding is widespread in YNP wetlands; Columbia spotted frogs and tiger salamanders are more selective or limited in terms of breeding sites; and western toads are most restricted in both distribution and use of breeding sites.

Data sources and preparation

Multiple factors interact at landscape and local scales to affect wetland habitat conditions, and therefore our choice of variables for the current study reflects a range of spatial and temporal scales for features that we anticipated to be useful for predicting the occurrence of breeding habitat (Table 1).

Field survey data.—Data on amphibian occurrence used for this modeling project were collected during three years, 2000–2002, as a pilot study for implementing a long-term amphibian monitoring program in YNP. This study targeted potential amphibian breeding sites within the boundaries of a subset of drainage basins (seventh-level hydrologic units) randomly selected from the 464 basins within YNP. These basins range in size from about 86 to 9700 ha, with a mean size of 1926 ha (SE = 60 ha), and median size of 1627 ha. Broad geographic coverage was achieved by selecting one basin from every third square in a grid of 10×10 km squares covering YNP. We selected a total of 30 basins, expecting the work to take 4–6 years for completion. By the end of the 2002, we conducted surveys in 16 of the selected basins (Fig. 2) and at 497 sites (102, 231, and 164 sites in 2000, 2001, and 2002, respectively). Each basin was selected by the method described in Peterson et al. (2005) and was surveyed one year only, except for the basin in Hayden Valley, which was surveyed two years (42 sites surveyed in 2000 and 49 sites in 2002; 31 of these sites were surveyed in both of these years).

We identified potential amphibian breeding habitat (ponds, small lakes, and other wetlands) within the selected basins using NWI and topographic maps. Field crews visited these pre-identified potential habitat areas during the period when larvae were expected to be present, and conducted surveys where suitable surface water was found, as well as at any other suitable sites encountered incidentally. Types of wetlands deemed unsuitable included ephemeral or seasonal wetlands lacking pooled surface water, rapidly flowing water

TABLE 1. Data variables used to model amphibian breeding habitats in Yellowstone National Park, USA.

Variable	Abbreviation	Definition
A) Field site descriptors (observer estimated)		
Permanence	Perm	likelihood of drying by end of season
Connectivity	Connect	isolated from other wetlands "permanently" or "seasonally"
pH	pH	hydronium ion concentration
Conductivity	Cond	total concentration of ions
Distance to forest	DistFor	estimated distance (m) from forest cover
Average site length	Length	estimated length (m) of longest axis
Ratio of site length/site width	L:W	estimated width (m) divided by length (m)
Site area	Area	estimated area (m^2)
Percentage of shoreline with emergent vegetation	%EVeg	estimated area (e.g., 1–25%) of shoreline supporting emergent vegetation
Percentage of shoreline with submerged vegetation	%SubVeg	estimated area (e.g., 1–25%) of shoreline supporting submergent vegetation
Maximum water depth	MaxDepth	estimated maximum depth (m) of wetland
Percentage of shoreline <50 cm deep	% <50 cm	quartile estimated percentage of shoreline that was shallow
Most abundant aquatic vegetation	AbundVeg	abundance of woody or herbaceous vegetation
Primary pond substrate	Substrate	most abundant type of wetland substrate
B) GIS thematic variables (50-m resolution)[1]		
Geology	Geol	
Landform	Lndfrm	any recognizable form/surface feature, compiled from 1:62 500 map
Surface materials	SurfMat	primary materials of landform surface, compiled from 1:62 500 map
Vegetation cover type	CovType	dominant vegetation prior to 1988 fire, compiled from 1:15 840 maps
Wetlands	NWI	National Wetland Inventory, compiled from 1:58 000–1:80 000 maps
Patterns of annual moisture		
Average annual precipitation	Ppt	annual or monthly (e.g., "mayppt")
Average annual snow depth	Snow	
C) GIS continuous variables (30-m resolution)		
Digital elevation model[2]	DEM	digital form of topographic map
Wetland probability models[3]	Wet	likelihood that wetland is classified as palustrine
Aquatic bed submodel	Aquabed	maximum likelihood wetland has open water
Unconsolidated shore submodel	Unshore	maximum likelihood wetland has unconsolidated shoreline
Emergent vegetation submodel	EVeg	maximum likelihood wetland has emergent vegetation
Forest submodel	Forest	maximum likelihood wetland is shaded by forest
Shrub submodel	Shrub	maximum likelihood wetland contains scrub/shrub
Cover density model[4]	CovDen	percent cover of forest canopy
Compound topographic index[4]	CTI	likelihood for surface water accumulation

Note: Data sources (superscript numbers): 1, U.S. National Park Service's Natural Resource Information Portal ⟨https://nrinfo.nps.gov/Home.mvc⟩; 2, Gesch et al. (2002); 3, Wright and Gallant (2007); 4, USGS Earth Resources Observation and Science Center, Sioux Falls, South Dakota, USA.

(streams and rivers), deep water bodies (>1 m) lacking shallower edges or portions, and hot thermal wetlands.

Using visual surveys and dip nets (Thoms et al. 1997), field personnel recorded observations of adult amphibians, eggs, larvae, and recently metamorphosed juveniles, permitting us to classify surveyed sites as having species breeding (eggs, larvae, or recent metamorphs detected), species present but not breeding (adults or subadults only), or species not detected. Habitat data collected included instrument measurements and ocular estimates of site characteristics (Table 1). Conductivity and pH were measured with handheld meters (Oakton Instruments, Vernon Hills, Illinois, USA). To reduce observer variability, ocular estimates of vegetation, and so forth were rule-based and were recorded within broad categories (e.g., 1–25%, 25–50%). All surveys were conducted when evidence of breeding could be detected: about 95% were conducted in June and July, when breeding was most active; about 2% were conducted in May when breeding began; the remaining 3% were conducted in August when metamorphs began leaving the ponds.

GIS layers.—We used a mix of thematic and continuous variables (Table 1). Because the spatial resolution of the thematic layers was 50 m, we converted and/or resampled all GIS layers to raster data of 30-m cell size. We incorporated information from hand-drawn field maps created during the surveys with 1-m resolution digital orthophoto quarter quadrangles to create a raster map of 30-m resolution field survey sites for each year. All sites were labeled by species occurrence and breeding status (i.e., present and breeding, present but not breeding, or not detected). For "present and breeding" sites, when possible, the specific wetland raster cells in which evidence of

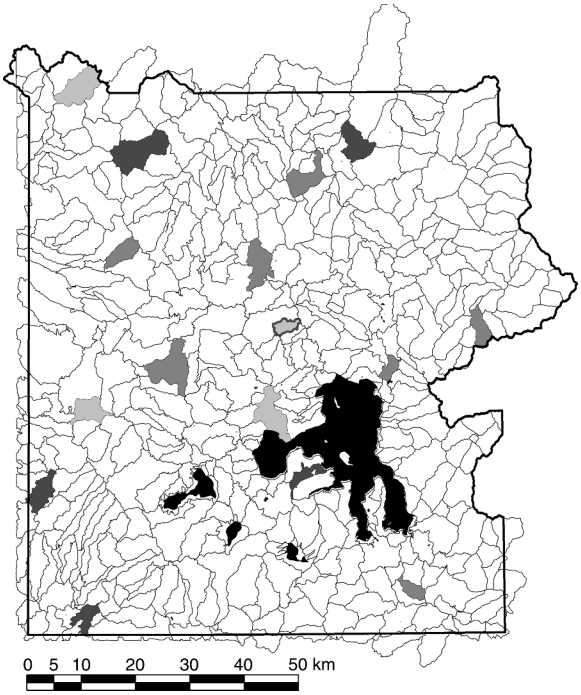

FIG. 2. Distribution of basins (by year) surveyed for amphibians in Yellowstone National Park (light gray, 2000; medium gray, 2001; dark gray, 2002; black, lakes). One basin (within Hayden Valley, near center of map) was surveyed both in 2000 and 2002.

breeding occurred were identified; the remaining wetland cells at these sites were classified as "present and not breeding."

We used a set of annual wetland predictive layers (Wright and Gallant 2007) to address temporal variability in the availability of breeding habitat. These layers were developed using mid- to long-term environmental variables related to hydrogeologic settings associated with wetland development (e.g., climate, terrain and substrate, climax vegetation) and satellite data to capture seasonal conditions in water and vegetation. The maps represented the probability of finding a moist palustrine wetland within a 30-m cell for a given year (2000–2002). We also used layers that provided predictions to the level of palustrine class (aquatic bed, unconsolidated shore, emergent, forested, and scrub/shrub; Wright and Gallant 2007).

Model development

We analyzed data for each species separately for each year and computed the distribution of variable use to estimate which variables were most important to each species. All models were built with polytomous regression (Ashby et al. 1986), using non-collinear variables, as determined by the COLLIN option of PROC REG in SAS v9.1 (SAS Institute, Cary, North Carolina, USA). The response variable had three levels: present and breeding, present and not breeding, and not detected. Because we were primarily interested in identifying breeding sites, we used the first of these levels as the reference level. When applying the best models to build breeding probability maps, we always used the intercept calculated for "present and breeding."

We pursued three general modeling approaches. Our first approach relied solely on site data collected in the field. Regression models developed from these data would enable someone to visually assess (in the field) whether amphibians might breed at specific sites. Our second approach incorporated data from a broader scale, adding GIS thematic (categorical) and continuous variables to the field-based survey data. We extracted information on terrain (geological features), land cover, climate, and wetland probability (Table 1) from raster layers for cells corresponding with the locations of field survey sites. Many of the survey sites extended over multiple cells (41% had 2–10 cells, 12% had 10–50 cells, four sites had 55, 62, 78, or 280 cells) for a given GIS layer, but we needed a single value or class to represent a survey site. For thematic variables (e.g., landform, surface materials), we developed class assignment rules based on results from a contingency analysis that identified variables most associated with breeding habitat. If a category identified as important for breeding occurred in >10% of the total number of cells for a field site, we assigned that category to represent the site; otherwise, the modal category was used. For continuous variables (e.g., digital elevation model [DEM], cover density model), we calculated the mean value across a site to represent the site. Like the first approach, this approach included site-specific field data and therefore could not be used to generate predictive maps identifying additional breeding habitat locations. However, results could help us to determine if supplementing field data with GIS variables improved habitat predictions.

We based our third approach solely on GIS variables. Because these data covered the entire YNP, regression models generated using GIS variables could be implemented to generate predictive maps. Within this (GIS only) approach, we selected at random 80% of survey sites to build the models and used the reserved data to validate the predictions. We defined four methods (annual variation, multiyear variation, maximum wetland probability, and maximum breeding probability) to incorporate yearly variation in conditions into breeding habitat predictions (Table 2, Fig. 3, and Appendix: Fig. A1).

Model selection and validation

We applied results from the distribution of variables previously mentioned to a total of 102 a priori models (18 for tiger salamanders, 10 for western toads, 32 for chorus frogs, and 42 for spotted frogs) using polytomous regression (Appendix: Table A1); we evaluated an additional 33 posterior models (Burnham and Anderson 2002), and 36 more were questionable or invalid (not

TABLE 2. Utility and application of different approaches for modeling amphibian breeding habitat in Yellowstone National Park using only GIS data.

Model building	Model application	Rationale for approach
Annual variation models (single-year field data + single-year wetlands)	Generates one breeding probability surface per year.	Highlights annual fluctuation in conditions (variance embedded within approaches C and D). Can help to understand population/metapopulation dynamics for amphibians. Can be used to help planning for surveys. Should yield the most conservative amount of area identified as breeding habitat.
B) Multiyear variation models (multiyear training data + multiyear wetlands)	Generates one breeding probability surface per year.	Provides a composite perspective of the landscape to assist conservation and planning decisions. Composites the information representing the "best conditions" from all the years. Accumulation of more years of data should illuminate increasingly more habitat suitable for breeding. Should yield the maximum amount of area identified as breeding habitat.
C) Maximum wetlands likelihood (multiyear training data + multiyear wetlands)	Generates one breeding probability surface. Annual variation models are composited with a MAX function to yield a single breeding probability surface.	Highlights annual fluctuation in conditions and maximum amount of wetland available wetland for breeding. Can help to understand population/metapopulation dynamics for amphibians. Can be used to help plan for surveys. Differs from approach A because it attempts to overcome the small number of training records available for a single year. It assumes that the components that make for a desired breeding habitat (from the perspective of the amphibian) are constant across years.
D) Maximum breeding likelihood (multiyear training data + wetlands)	Generates one breeding probability surface per year. The annual surfaces are then composited with a MAX function to yield a single multiyear breeding probability surface.	Provides a composite perspective of the landscape to assist conservation and planning decisions. Composites the highest breeding probability predictions for each of the years to generate a maximum probability surface. Should also maximize the amount of area identified as breeding habitat.

included here). When building models with field data only, we used combinations of variables that related to the biology of each species (e.g., pond depth, amounts of emergent vegetation). When GIS layers were included, with some exceptions, we began with a set of coarser-scale categorical variables (e.g., geological features, surface materials) and then added finer scale continuous variables (e.g., wetland models). We selected the best models from each approach using the receiver operating characteristic (ROC; Bradley 1997) and the lowest Akaike information criterion values (AIC; Burnham and Anderson 2002), both of which are available in SAS (Cary, North Carolina, USA). The area under a ROC curve (values ranging from 0–1) provides an overall assessment of a model's strength and predictive ability, with 0.5 indicating a predictive ability no better than classifying by chance, and 1 indicating that the model can distinguish perfectly among breeding sites. We preferred models with ROC values >0.7 (models with values 0.7–0.8 are considered to have acceptable discrimination, while those with values >0.8 are considered to have excellent discrimination; Hosmer and Lemeshow 2000). AIC values rank models according to how well they fit the data by balancing the trade-off of underfitting and overfitting models; best models have the smallest AIC values. To help overcome the small sample sizes associated with tiger salamanders and western toads, we ranked models for these species according to differences in the second-order Akaike's information criterion (ΔAIC_c). We considered $\Delta AIC_c < 2$ to indicate strong support for a model, ΔAIC_c from 2 to 7 to indicate moderate support for a model, and $\Delta AIC_c > 7$ to indicate little support for a model (Burnham and Anderson 2002). Finally, we used Akaike weights (AIC_w), an estimate of the relative strength (on a scale of 0 to 1) of one model over the competing models, to select the best model.

Only models produced with the third approach (GIS data only) could be used to predict breeding habitat across the entire YNP landscape. We applied the best model for each species to map the probability of breeding habitat across YNP and validated the results with data reserved from the survey sites. For sites that extended across multiple cells, the maximum breeding probability among cells was assigned as the probability for the entire site. Selecting minimum probability values to distinguish breeding from nonbreeding sites intentionally biased our results toward errors of commission so as not to overlook potential breeding habitat. We constructed an error matrix for each species and each modeling approach to report omission and commission errors and calculate two classification rates: breeding and overall accuracy. Breeding accuracy is the propor-

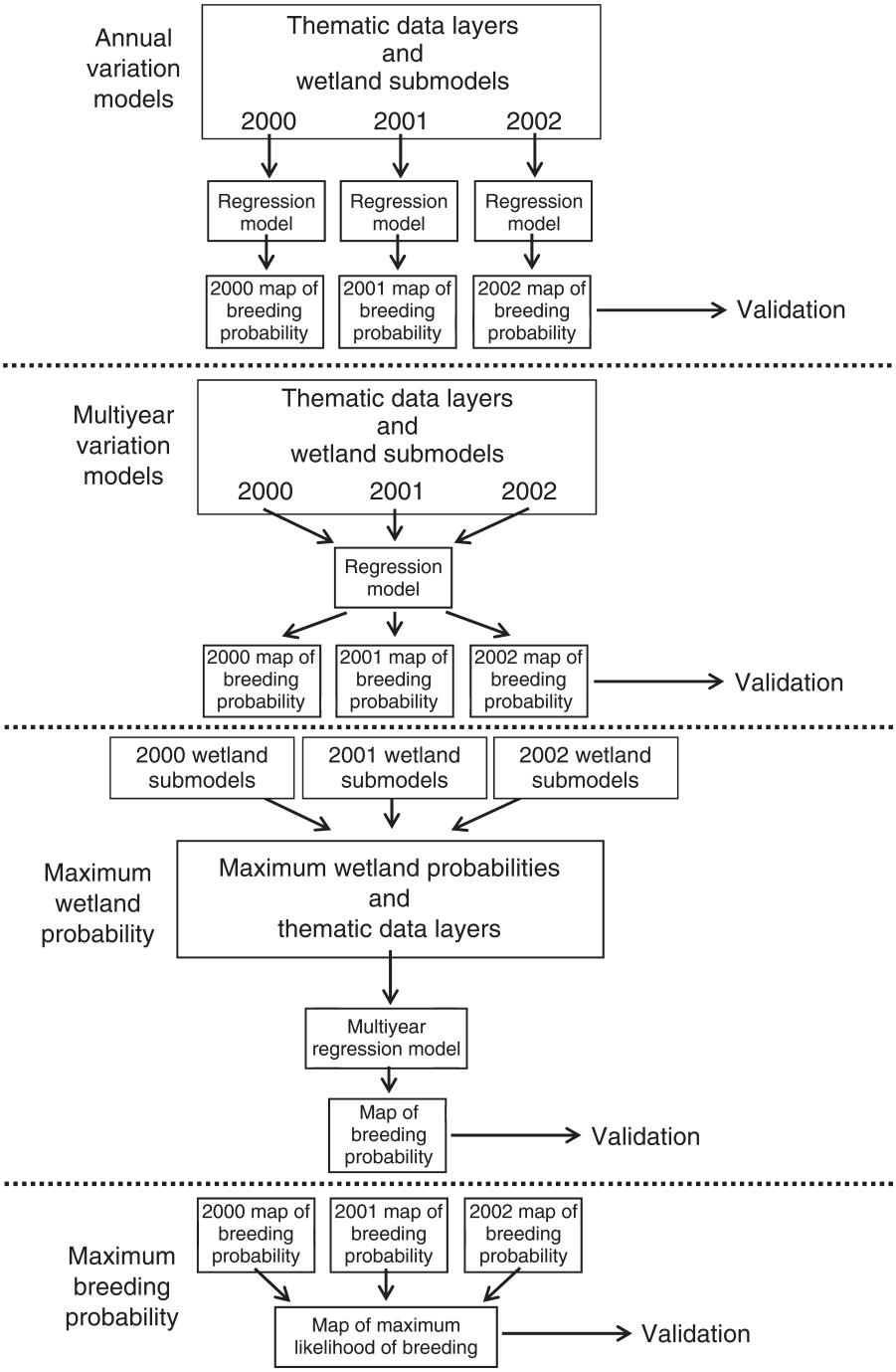

FIG. 3. Four methods used for developing amphibian breeding habitat models from GIS data only. Each of the four methods was applied to each of the four species of amphibians (with the exception of the annual variation models, applied only to Columbia spotted frogs and chorus frogs, which had sufficiently large sample sizes). Each model was built with a random selection of 80% of the survey data, reserving the remaining 20% for model validation. Additional modeling details can be found in the Appendix.

tion of observations correctly classified as breeding vs. the total number of sites where breeding occurred (relates to errors of omission) and overall accuracy is the proportion of observations correctly classified vs. the total number of observations (relates to both errors of omission and commission).

Predicting breeding habitat was contingent upon cells having been classified as $\geq$50% probability of wetland occurrence during the modeling process followed by Wright and Gallant (2007) to develop the wetland layers that we incorporated into the current analysis. This threshold carried over to the development of the wetland

TABLE 3. Sample sizes of survey sites used for building ("Train") and verifying ("Verify") models for each category (breeding, presence, not detected) by species for modeling habitats in Yellowstone National Park.

	Breeding sites		Presence sites		Not-detected sites	
Species	Train	Verify	Train	Verify	Train	Verify
Salamanders	33	6	18	6	347	87
Toads	7	2	16	4	374	94
Chorus frogs	128	38	58	12	212	49
Spotted frogs	65	19	89	22	244	58

class submodels (emergent, forested, shrub/scrub, and so forth), such that cells having <50% probability of containing a wetland were not further classified to the type of palustrine wetland. Field survey data for sites coinciding with cells of <50% wetland probability could not be used to validate model results because the cells automatically were eliminated as potential locations for habitat. This resulted in sample sizes of validation results being smaller than the total number of field sites surveyed.

RESULTS

We used data from 497 survey sample sites to develop and verify breeding habitat models (Table 3). All best breeding models listed and described were built from the "present and breeding" response level. The variation in numbers of wetlands used for breeding among species was large. Breeding of boreal chorus frogs was detected at nearly twice as many sites as for Columbia spotted frogs, almost four times as many as for tiger salamanders, and over 18 times as many as for western toads.

Evaluation of models by approach

Site data only.—The best model for each species was clearly identifiable from the ΔAIC_c and AIC_w values; second-best models all had $\Delta AIC_c \geq 14$. ROC values for the best models ranged between 0.670 and 0.831 (Table 4). The most important variables ($\alpha < 0.05$) for tiger salamanders were the absence of woody emergent vegetation, the presence of submergent vegetation, and distance from forest cover (although its low coefficient value suggests that this variable had little influence). There was no apparent evidence that tiger salamanders selected breeding sites based on levels of water conductivity or size of water body (length of longest axis). The best boreal chorus frog model showed that breeding individuals were associated with ponds of low levels of conductivity and that were relatively permanent and not connected with other wetlands. The best model for Columbia spotted frogs indicated selection for linear-shaped breeding sites offering some emergent vegetation dominated by graminoids, having a weak but significant association with conductivity, and tending to be near other wetlands. There were too few breeding sites encountered for western toads to develop an acceptable model for this species.

Adding GIS data to site data.—This approach offered the greatest number of variables to the regression procedure and resulted in larger and more complex models that yielded higher ROC scores (0.698–0.880) than results from the other two approaches (Table 4). None of the variable parameters for the best model for tiger salamanders were significant at $\alpha < 0.05$, although several were significant at $\alpha < 0.10$ and were generally consistent with those variables in the best "site data only" model. Two exceptions included shape of the wetland (compared to the site-only model, L:W had a reduced and positive effect), and selection for a wetland permanently connected to another was positive. The two best models for chorus frogs were closely ranked ($\Delta AIC_c = 1.884$). Because these two differed by only one variable, we chose the model with the highest ROC score and Akaike weight (AIC_w; Burnham and Anderson 2002). The selection against riverine habitats by chorus frogs was highly significant, as was the selection against alluvium. None of the GIS variables were significant, but results for the other site-specific variables were consistent with those for the "site-only" model. The best model for Columbia spotted frogs suggested that they selected breeding sites that were narrow in shape, located away from forest cover, and had low conductivity but high amounts of herbaceous emergent vegetation.

Using only GIS data.—Sample sizes for tiger salamanders and western toads were too small to produce viable annual variation models, so these models were generated only for chorus frogs and spotted frogs (Table 5). Except for spotted frogs in 2000, these models resulted in ROC values >0.73, and the level and direction of influence of predictive variables varied among years for both species. For example, the only common and significant trend for chorus frogs during all three years was a strong, negative association with ponds that had open water (aquatic bed). This trend was reinforced in the 2001 and 2002 models, with a strong association with ponds having emergent graminoid vegetation; in the 2002 model, this included emergent shrub vegetation. Association with riverine wetlands and regions of YNP with higher amounts of precipitation was reversed between the 2000 and 2002 models, and association with particular landforms was important only in the 2001 model. Similar inconsistencies were apparent in the models for spotted frogs. Categorical wetland variables were important only for 2002; breeding sites were associated with regions of YNP

TABLE 4. Best regression models produced for Yellowstone National Park using site data only and site data plus GIS data.

		Tiger salamander			Boreal chorus frog			Columbia spotted frog		
Variable	Subcat.	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
A) Site data only										
Intercept		−2.6988	1.792	0.174	−0.6884	0.338	0.394	−1.9876	2.294	0.584
Conduct		0.00374	0.004	0.082	−2.7236	0.905	0.003	0.00224	0.001	0.042
Length		−0.0009	0.001	0.062				0.0072	0.003	0.222
L:W		−3.1614	2.924	0.056				−0.1277	0.034	0.03
Connect	Perm.	−0.3439	0.001	0.06	0.7923	0.173	0.001	−0.2397	0.115	0.061
	Isolated				−0.3595	0.114	0.002			
Perm	Season.				−0.4107	0.134	0.002	0.0382	0.02	0.108
DistFor		0.00094	0.137	0.049				1.0626	0.61	0.3
% <50 cm	51–75	−1.3009	0.981	0.082						
%EVeg	26–50	0.5571	0.441	0.062						
	51–75	0.3243	0.311	0.091						
AbundVeg	Woody	−0.5528	0.282	0.032						
	Herb.	0.6081	0.711	0.231				0.6651	0.321	0.003
%SubVeg	11–50	0.022	0.011	0.05						
B) Site data + GIS data										
Intercept		−3.6124	5.439	0.762	−3.1728	1.265	0.014	−2.7392	0.196	0.851
Conduct		0.0088	0.009	0.073	−0.0192	0.006	0.052	−0.0069	0.003	0.049
Length		−0.009	0.005	0.092	−0.0011	0.001	0.183	0.00657	0.006	0.304
L:W		0.0112	0.006	0.088	−0.3626	0.321	0.293	−0.1861	0.631	0.006
Connect	Perm.	0.2223	0.099	0.052	0.4072	0.31	0.117	−0.219	0.101	0.058
Perm	Season.	0.6603	0.718	0.11	−0.0437	0.187	0.761	−0.1955	0.146	0.124
DistFor		0.0887	0.031	0.173	−0.0012	0.003	0.993	0.7592	0.225	0.006
CovDen		−0.211	0.361	0.254				−0.4065	0.163	0.04
% <50cm	<26				0.0413	0.236	0.864			
	51–75	−0.2476	0.117	0.063						
%EVeg	>75	−0.0717	0.185	0.157	−0.3357	0.224	0.073			
AbundVeg	Sedge	−1.1068	2.629	0.433						
	Herb.							1.1719	0.342	0.004
Landform	Alluv.				−1.889	0.761	0.01	−0.4464	0.569	0.598
NWI	River				−1.4826	0.226	<0.0001	0.579	0.435	0.774
	Lacus.							−0.2748	0.484	0.209
CTI		0.0377	0.011	0.075				2.1402	3.11	0.788
Wetland models	Wet	1.3015	4.682	0.761						
	EVeg				0.1506	0.816	0.711			
	Forest	−3.9689	4.118	0.36	−1.3686	1.241	0.148			
	Shrub	−5.2691	3.742	0.069	−1.1001	2.078	0.419			
Precip	<20							−0.4264	0.753	0.642
Nonforest	Moist							0.1716	0.106	0.03

Notes: Refer to Table 1 for variable abbreviations. The "connected" subcategories are: Perm., permanently connected to another water body; Isolated, water body isolated from other sources of water; and Season., water body may be connected for part of the year. For variable Perm, the subcategory "Season" indicates that the water body may dry out in some years. Subcategories "<26" and "51–75" of "% <50 cm" indicate the amount of shallow shoreline: <26% or 51–75% of the pond is <50 cm deep. For "%EVeg," subcategories indicate that 26–50%, 51–75%, or >75% of the water body supports emergent vegetation. For "%SubVeg" 11–50% of the water body contains submergent vegetation. "Precip <20" refers to areas of YNP that receive <20 cm precipitation/year. Akaike weight (AIC_w) and receiver operator curve (ROC) values are estimates of the strength of the model relative to other models tested. All models are built from the "present and breeding" level of response. For tiger salamanders, AIC_w values are 0.99 with site data only (A) and 0.96 with site data + GIS data (B); ROC values for (A) and (B) are 0.831 and 0.86, respectively. For the boreal chorus frog, $AIC_w = 0.91$ (A) and 0.72 (B); ROC = 0.724 (A) and 0.88 (B). For the Columbia spotted frog, $AIC_w = 0.97$ (A) and 0.86 (B); ROC = 0.67 (A) and 0.698 (B).

having greater amounts of precipitation in 2001. Spotted frog breeding habitats were positively associated with wetter sites in 2002, but negatively associated in 2000. They were positively associated with ponds having emergent vegetation in 2000 and 2001, and negatively associated with shrub wetlands in 2002.

Multiyear variation models generally were more complex than annual models (Table 6). Except for spotted frogs, ROC scores for models were ≥0.700. The best model for tiger salamanders showed breeding habitat strongly associated with ponds occurring on alluvium and glacial uplands, in regions of YNP receiving lesser amounts of precipitation, and associated with shrub cover. The best model for western toads showed a negative association with palustrine wetlands in general, but when they used these wetlands, they chose ponds positively associated with open water and unconsolidated shoreline, and with lesser amounts of tree cover. There were no particular landform features that described breeding sites preferred by western toads.

Two models for chorus frogs were closely ranked ($\Delta AIC_c < 2$). We chose the model with the lower AIC value and higher accuracy to be the best model. It showed a negative association with ponds on glacial–

TABLE 5. Best annual variation models produced for Yellowstone National Park using GIS data only, for the years 2000–2002.

Variable	Subcat.	2000 Estimate	2000 SE	2000 *P*	2001 Estimate	2001 SE	2001 *P*	2002 Estimate	2002 SE	2002 *P*
A) Boreal chorus frog										
Intercept		5.3166	0.679	<0.0001	−1.1646	0.397	0.003	−0.8742	0.344	0.011
Landform	Alluv.				−0.3448	0.117	0.003			
	Glac/flu				−1.0307	0.117	<0.0001			
NWI	Riverine	−0.6318	0.163	0.0001	−0.1132	0.081	0.161	0.232	0.086	0.007
	Aquabed	0.4857	0.174	0.005	−0.3918	0.11	<0.001	−0.5644	0.147	<0.001
Precip.		0.1458	0.007	<0.0001	−0.0044	0.004	0.672	0.047	0.004	<0.0001
Wetland models	EVeg.	0.0549	0.388	0.888	1.186	0.212	<0.0001	1.0595	0.227	<0.0001
	Forest	−0.9385	0.621	0.131	−0.7232	0.324	0.026	−0.5372	0.394	0.173
	Shrub	−1.5986	1.602	0.318	−0.8236	0.619	0.183	−0.9366	0.97	<0.0001
B) Columbia spotted frog										
Intercept		4.19	1.05	<0.0001	−1.064	0.343	0.002	−1.082	0.563	0.055
Landform	Flu.upland	−0.907	0.214	<0.0001	1.064	0.12	<0.0001	1.063	0.171	<0.0001
	Gla.upland				0.612	0.113	<0.0001	0.102	0.106	0.336
	Gla.cirque	−0.408	0.215	0.058	0.804	0.116	<0.0001			
NWI	Riverine							−0.02	0.005	0.945
	Aquabed							−0.901	0.194	<0.0001
Precip.		−0.009	0.009	0.347	0.037	0.004	<0.0001	0.03	0.005	0.594
Wetland models	Wet	−2.137	0.743	0.004	0.344	0.32	0.282	2.97	0.659	<0.0001
	EVeg	1.128	0.626	0.071	1.529	0.241	<0.0001	−0.499	0.397	0.209
	Forest	1.08	0.772	0.162				−0.792	0.561	0.158
	Shrub	−2.113	1.596	0.186	−0.469	0.395	0.236	−4.674	0.82	<0.0001
	Aquabed	−5.577	1.101	<0.0001	0.177	0.323	0.583			
	Unshore	−0.312	1.538	0.839	−2.461	0.452	0.307			

Notes: Akaike weight (AIC_w) and receiver operator curve (ROC) values are listed as estimates of the relative strength of the model. All models are built from the "present and breeding" level of response. For the boreal chorus frog for 2000, 2001, and 2002, respectively, $AIC_w = 0.98$, 0.99, and 0.99; ROC = 0.774, 0.735, and 0.731. For the Columbia spotted frog for 2000, 2001, and 2002, respectively, $AIC_w = 0.99$, 0.98, and 0.99; ROC = 0.816, 0.709, and 0.75.

fluvial landforms and with rivers. These breeding ponds also supported high graminoid emergent vegetation, but were not associated with shrubs or tree cover. The best model for Columbia spotted frogs indicated that breeding habitat was negatively associated with fluvial or glacial uplands or glacial cirques. They were the only species to associate with lake systems. These ponds, associated with regions of YNP with lesser amounts of precipitation, supported growths of graminoid emergent vegetation.

Validation summaries of GIS models

We applied models based on GIS data only across the entire YNP landscape to estimate probability of breeding by species for each method (Fig. 4a–d). The values listed for these maps are relative, not absolute probabilities. We compared reserved field data with predictions from these maps to validate the models (Table 7).

Annual variation models.—Accuracy rates among the three years were highly variable for both boreal chorus frogs and Columbia spotted frogs. Accuracy rates for prediction of breeding habitat for boreal chorus frogs ranged from 0.38–0.50. Similarly, accuracy rates for Columbia spotted frogs ranged from 0.30–0.80. Accuracy rates for both species were highest in year 2000.

Multiyear variation models.—Accuracy rates for predicting breeding habitat varied among species, ranging from 0.60 for boreal chorus frogs to 0.80 for Columbia spotted frogs (the accuracy rate for western toads was 1.00, but the extremely small sample size for this species made this figure unreliable). Rate of commission errors for breeding habitat was high for all species except boreal chorus frogs. The models for tiger salamanders and boreal chorus frogs failed to predict 33% and 44%, respectively, of the actual breeding sites from the test sample (errors of omission). The model for Columbia spotted frogs failed to predict 20% of the actual breeding sites.

For the Hayden Valley basin, accuracy rates for 2000 and 2002, respectively, for tiger salamanders were 83% and 82%; accuracy rates for chorus frogs were 44% and 50%; accuracy rates for spotted frogs were 84% and 91%; western toads did not breed at any of these sites.

Maximum wetland probabilities.—With this approach, breeding accuracy rates for each species were similar to those in the previous approach (multiyear models), and variation increased in the overall accuracy rates. Although overall accuracy rates for western toad models remained about the same, accuracy rates were slightly diminished for boreal chorus frogs and sharply diminished for tiger salamanders and Columbia spotted frogs.

Maximum breeding probability models.—Breeding accuracy rates for models produced with this approach were similar to those of previous models for all species. Except for the toad models, overall accuracy rates were <0.5 and indicated high commission errors.

TABLE 6. Best multiyear variation models produced for Yellowstone National Park using GIS data only.

		Tiger salamander ($AIC_w = 0.98$, ROC = 0.822)			Western toad ($AIC_w = 0.98$, ROC = 0.712)		
Variable	Subcategory	Estimate	SE	*P*	Estimate	SE	*P*
Intercept		−1.402	0.62	0.024	−1.718	0.75	0.023
Landform	Alluv.	0.7849	0.19	<0.0001			
	Fluv.upl						
	Gla/fluv	−0.185	0.15	0.225			
	Gla.upl	0.9706	0.2	<0.0001			
	Gla.cirque						
	Thermal						
NWI	River						
	Aquabed	−0.9001	0.12	<0.0001			
	Lacus						
Precip.		−0.0174	0.006	0.003	−0.008	0.007	0.283
CovDen		0.00165	0.004	0.702	−0.011	0.005	0.05
Wetland models	Wet	0.00758	0.43	0.98	−1.854	0.462	<0.0001
	EVeg						
	Shrub	−1.5365	0.76	0.04	0.73	1.139	0.521
	Forest	−1.5438	1.16	0.18			
	Aquabed				1.285	0.553	0.02
	Unshore				3.099	0.81	0.0001

Notes: Akaike weight (AIC_w) and receiver operator curve (ROC) values are reported as estimates of the relative strength of the model. All models are built from the "present and breeding" level of response.

Temporal variation

Models produced solely from GIS data provided a range of total area within YNP predicted to be breeding habitat (Fig. 4, Table 8). Multiyear variation models identified those areas most likely to be used for breeding by each species for each of the three years, and areas that were probably suitable breeding sites for one, two, or all three years (Fig. 5, Table 9). Multiyear variation models identified the greatest number of hectares of breeding habitat; maximum breeding probability models identified the fewest. Annual variation models estimated breeding habitat area for boreal chorus frogs and Columbia spotted frogs to be ~75% and 80%, respectively, of that estimated by multiyear variation models. Except for tiger salamanders, breeding habitat area estimated by maximum wetland models was similar to that estimated for multiyear models; the area estimated by maximum wetland models for tiger salamanders was similar to that estimated by maximum breeding models and ~40% of that estimated by multiyear variation models.

DISCUSSION

We present a variety of approaches for modeling amphibian breeding habitats in YNP. Models using site data were the most difficult to evaluate, but produced strong models, based upon ROC scores. Although they provided important information on local characteristics of habitats, these data were time sensitive and/or not available for other areas and could not be applied or validated elsewhere in the landscape. Combining site data with GIS data produced the strongest models of any modeling approach. These models contained the most information at multiple spatial scales, but were the most complex, and this level of complexity also could be considered a weakness. These models, too, were difficult to evaluate for the same reasons as the site-only models.

The GIS data-based models provided advantages over those that included site data. First, they best captured and incorporated the temporal variation expressed in the wetland models. Second, they incorporated data at multiple scales and of varying types and produced relatively moderate to high ROC values. Third, they were the only models that could be applied and validated across the entire YNP landscape. Fourth, except for annual variation models, GIS-based models provided the only approach that produced models for the very limited sample size of western toads. Fifth, they were the most flexible; they produced different maps of breeding probabilities that could be used for different management and research applications, such as locating new breeding sites or selecting particular areas for conservation purposes.

Using a combination of models produced from site data as well as maps produced using GIS data may be a good way to identify new breeding ponds. Results from broader-scale variables and the breeding probability maps could be used to identify new breeding areas in the landscape; then, in the field, the site data models could be used to identify a particular pond (e.g., from a cluster of ponds) that has the best breeding habitat characteristics.

Relating model results to the biology of amphibians in YNP

The collective results of our analyses and models reflect aspects of the breeding biology of these animals. For example, wetlands generally need to provide emergent vegetation and be relatively free of shade from forest cover to be suitable for breeding by

TABLE 6. Extended.

Boreal chorus frog ($AIC_w = 0.56$, ROC = 0.759)			Columbia spotted frog ($AIC_w = 0.97$, ROC = 0.669)		
Estimate	SE	*P*	Estimate	SE	*P*
−0.2117	0.36	0.558	0.914	0.448	0.062
0.0701	0.18	0.69			
			−0.861	0.324	0.007
−0.5851	0.18	0.001			
			−0.773	0.319	0.016
			−0.8	0.332	0.015
0.3591	0.21	0.09			
−0.7092	0.16	<0.001	−0.182	0.165	0.265
−1.0917	0.17	<0.001			
			1.212	0.175	<0.0001
−0.0119	0.003	0.13	−0.043	0.004	<0.0001
			0.464	0.362	0.196
0.7402	0.18	<0.001	0.585	0.238	0.016
−2.0906	0.32	<0.001	0.741	0.452	0.101
−1.366	0.56	<0.001			

amphibians in YNP. Emergent vegetation provides cover and attachment sites for eggs (Koch and Peterson 1995), and exposure to sunlight provides thermal energy for more rapid development (Wells 2007). The strong tendency for breeding sites to have low conductivity values adds strength to our initial assumption that amphibians generally do not use thermally influenced waters, a common feature in parts of YNP. Wetlands used by amphibians for breeding in northern latitudes often are temporary and/or not permanently connected to larger permanent bodies of water, a feature that helps to exclude fish, important predators of amphibians (Lannoo 1996, Pilliod and Peterson 2001). Although temporary, these wetlands need to retain water long enough to allow the development and metamorphosis of larvae; alluvium and similar fine-grained surface materials often provide the necessary water-holding capacity (Lannoo 1996). We frequently find salamanders in areas of YNP supporting willows or other shrubs and in ponds with submergent vegetation, consistent with our models for salamanders.

Western toads may present an exception to some of the patterns just described. For example, toad egg strings often are not associated with emergent vegetation, but are laid atop exposed, dark, substrate in shallower waters, also reflected in the models for toads. Toads commonly breed in overflow pools along streams and rivers in YNP, and in some places also breed in slow moving, thermally influenced streams that support fish. We suspect that the slight thermal influence warms the water sufficiently to allow faster larval development and to allow development to occur longer in the season. The higher conductivity of the water may provide toads with greater resistance against chytridiomycosis (Hawk 2000). R. Klaver, C. R. Peterson, and D. A. Patla (*unpublished data*), in a wider analysis of toad breeding site characteristics, found that waters with high conductivity measures were preferred by toads. Finally, the generally unpalatable nature of toad larvae (Duellman and Trueb 1999) may protect them from fish inhabiting these riverine breeding sites. The parameters in the toad models support these observations, and maps produced by the models show high breeding probabilities in potential overflow areas along streams. Unfortunately, the very small sample size of toad breeding sites available for this study, together with the equally limited scale of breeding probabilities on the predictive maps, greatly constrains our ability to draw conclusions from them. Protection for species with such few breeding populations should rely more on careful, thorough field surveys (and less on habitat models) before any disturbance activities begin.

Conclusions for other species are more reliable. In spring, the calls of boreal chorus frogs so fill the air in portions of YNP that they seem to be present almost anywhere standing, still water can be found (Koch and Peterson 1995). One will not, however, find chorus frog tadpoles in every puddle. Abundant emergent vegetation in sun-exposed sites of relatively shallow shorelines is a typical feature of chorus frog breeding sites, where these frogs attach their egg masses to the stems of vegetation. The parameters for model variables support these observations. Because chorus frogs are so abundant and widespread, we are uncertain why accuracy rates for this species were no higher, but it could be related to specific habitat features not captured by our input data layers (e.g., water depth or their preference for low-conductivity waters).

Columbia spotted frogs also breed in shallow nearshore areas of still bodies of water, often with emergent stems in which their egg masses become entangled (Koch and Peterson 1995). Shade produced by forest cover is not an important feature and our

fieldwork has shown that egg masses often are laid in fully exposed sites. Breeding tiger salamanders commonly use deeper, more permanent ponds with good sun exposure. The parameters for model variables support all of these observations.

Reasons why the parameters for some variables switched between positive and negative influence for the single-year models is unclear, but may reflect differences in the habitat conditions that chorus frogs and spotted frogs used among these years. Weather conditions became drier from 2000 to 2002. If, for example, cumulative drying caused water levels to diminish and relative amounts of emergent graminoids to increase, then this could explain why selection for ponds with greater amounts of emergent vegetation became more important for chorus frogs.

Model utility

The GIS-based breeding models provide predictive surfaces that can be used for a variety of needs and applications. For example, these models can be applied to identify the most likely breeding sites in new areas, improving efficiency of survey efforts to locate breeding habitat across large landscapes. In another and larger study focused specifically on the breeding habitats of boreal chorus frogs, results from our GIS-based models identified previously unknown breeding sites for chorus frogs in YNP watersheds (M. Murphy, *personal communication*). The models correctly identified new breeding sites ~60% of the time, similar to the accuracy rate measured in this study. Our modeling approach also could assist with the efficient planning of surveys on other intermountain western U.S. Department of Interior lands.

Multiyear variation models provide the greatest amount of management planning flexibility by allowing one to apply or combine modeling results in different ways for different management needs. We think that this method can allow us to analyze temporal variation by combining the results of all three years of the multiyear models. For example, by combining the breeding probability surfaces for each of three years (Fig. 4), one can identify "core" areas that have high likelihood of breeding every year and those that have high likelihood only in certain years (e.g., wet years or dry years). However, the best way to capture temporal variation is through annual resurvey of a set of sites. Because so few YNP sites for this study were surveyed more than once, some temporal variation expressed in the annual variation models may have confounded with spatial variation. In principle, repeating this modeling process annually would also help ecologists to monitor temporal changes in suitable breeding habitat to better understand how changes in weather and/or land cover (e.g., road construction) and related hydrologic alterations can affect the quality of breeding habitat across the landscape. Because the three-year survey did not capture much range in weather variation characteristic of YNP, data from additional survey years should be incorporated into model development. By relating these changes to variations in weather conditions, and by including wetland models that simulate drying conditions, one could test scenarios of the effects of climate change on amphibian populations and breeding.

The different methods presented here provide land managers and ecologists with the flexibility often required in making complex management and research decisions. For example, to protect critically threatened populations, a land manager might use the method that minimizes omission errors and maximizes the amount of land to be protected. For a more conservative approach, land managers can identify "core" likely breeding area, using either maximum breeding probability models or multiyear variation models (those areas that score as "likely" for multiple years), and can protect likely breeding areas with high confidence. These areas can then gradually be expanded by identifying additional wetlands with the best accuracy rates from among the methods that progressively reduce omission errors. This approach could be important especially in areas where amphibian populations are declining. These models can help in planning, but should not replace field surveys for site-specific project implementation, and additional field surveys can contribute data to improve the models.

A possible application for these models is to assist planning by the National Park Service's Greater Yellowstone Network, which selected amphibians for inclusion in the Vital Signs monitoring program (amphibians are being monitored as "vital signs" in YNP to help determine trends in the condition of YNP resources). Occupancy data, collected annually, could be used to further refine the habitat models, particularly to improve how wetlands and their capacity to support amphibians may be changing over time. Because YNP amphibian monitoring is designed to provide inference to the entire YNP, this approach would be pertinent to elucidating trends in the condition of wetlands, an important resource that is not otherwise monitored.

Limitations of the models

The accuracy and usefulness of models are dependent on factors such as observer variability, sample size, and the quality of the input data sources. A major limitation of our analyses was the inability to incorporate occupancy and detectability data in our models because sites were surveyed only once per season. Imperfect detection of amphibians creates commission errors for the model when the species actually is present (MacKenzie et al. 2003). Gu and Swihart (2004) demonstrated that incorporating estimates for detectability improves habitat models. Unfortunately, the surveys for this study were conducted before the methods and statistics for calculating occupancy were derived and implemented. To estimate how much observer error may exist in the survey data, we estimated the probability of a site being occupied, given that a species was not detected

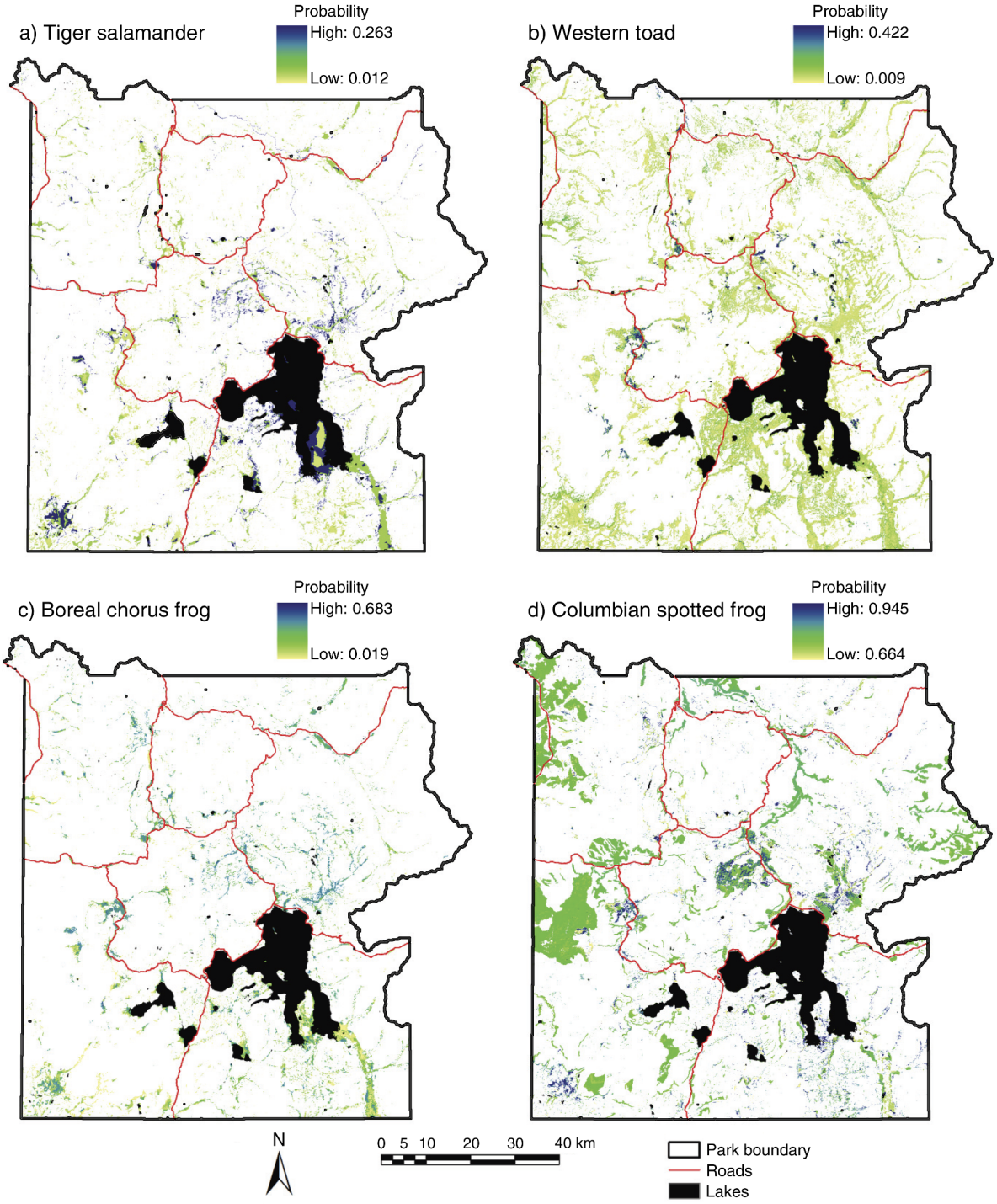

FIG. 4. Potential amphibian breeding habitat in Yellowstone National Park, 2002. Maps were developed using GIS data and the multiyear approach for (a) tiger salamander (*Ambystoma mavortium*), (b) western toad (*Anaxyrus boreas*), (c) boreal chorus frog (*Pseudacris maculata*), and (d) Columbia spotted frog (*Rana luteiventris*).

(MacKenzie et al. 2003). Using the occupancy values and detection rates (83% for spotted frogs and 72% for tiger salamanders; Corn et al. 2005), our calculations suggest that by visiting each of these sites only once, there were 7%, 8%, and 8% chances that observers missed tiger salamanders, chorus frogs, and spotted frogs, respectively (data were insufficient to make this calculation for western toads). Had each pond been surveyed twice, the probabilities for overlooking species would have been reduced to 3%, 1%, and 2%, respectively. Clearly,

TABLE 7. Best accuracy rates for the different approaches and applications for modeling amphibian breeding habitat in Yellowstone National Park.

Modeling method	Accuracy measure	Tiger salamander	Western toad	Chorus frog			Spotted frog		
				2000	2001	2002	2000	2001	2002
Annual variation	breeding	n.a.	n.a.	0.7	0.32	0.5	0.75	0.78	0.8
	overall	n.a.	n.a.	0.69	0.45	0.5	0.65	0.68	0.67
Multiyear variation	breeding	0.67	1.00		0.6			0.8	
	overall	0.81	0.86		0.64			0.53	
Maximum wetlands	breeding	0.6	1.00		0.6			0.8	
	overall	0.3	0.97		0.51			0.37	
Maximum breeding probability	breeding	0.8	1.00		0.52			0.79	
	overall	0.3	0.97		0.34			0.42	

Note: Values for annual variation models are averages for three years. No annual variation models were produced for tiger salamanders or western toads (n.a. means not applicable).

multiple surveys would have improved our training and validation data, but the results reported and validated here demonstrate the approach and utility of the models. Adjusting the occurrence data for detectability probably would have reduced commission errors, particularly for Columbia spotted frogs and tiger salamanders (e.g., Pellet and Schmidt 2005, Smith et al. 2006).

Another limitation is the small number of sites that were resurveyed among years; this limits our ability to address effects of changes in environment from year to year (analysis of temporal changes in breeding habitat patterns). Results from surveying the Hayden Valley basin twice (2000 and 2002) provide some additional measure of the accuracy and reliability of these models. Amphibians did not breed in the same ponds each year; that is, there was little repetition between 2000 and 2002 in the ponds selected for breeding. Of the total 31 ponds surveyed each year, we found evidence that tiger salamanders bred in the same six ponds in both years, chorus frogs bred in 15 ponds in both years, and spotted frogs never used the same pond for both years. Despite this high amount of variation, accuracy rates of the salamander and spotted frog multiyear variation models for this basin was higher than the accuracy rates for these species over entire YNP landscape, suggesting these models incorporate changes in breeding conditions among years. Accuracy rates for chorus frogs for this basin, however, were lower than those for the YNP landscape, perhaps reflecting the difficulty of modeling their generalist habits, or that we failed to capture one or more key breeding habitat variables.

The accuracy and usefulness of models also are dependent on factors such as the quality of the input data sources. In this study, the wetland probability layers greatly influenced the accuracy of breeding models. Breeding models that were restricted to using only the (static) NWI layer had higher AIC_c scores and lower ROC scores than models developed with annual wetland probability layers.

Decision criteria used in the development of the wetland probability layers had a direct effect on our applying them for modeling breeding habitat. The palustrine wetland submodels (scrub/shrub wetlands, emergent vegetation wetlands, and so forth) were developed only for cells that had a probability ≥ 0.5 in the general palustrine model. We eliminated training data for cells not identified as having $\geq$50% probability of occurrence of palustrine wetlands because we lacked associated information on palustrine wetland classes. This contributed to model error rates (omission errors) when field validation sites were located in such cells.

Setting clear definitions for what constitutes a "breeding site" vs. a "sampling site" is imperative for effective interpretation of field results and breeding models. Ambiguity in these definitions can affect all aspects of model construction, from sample size (e.g., are six small ponds spaced 10 m apart considered one "sampling site" or six?) to inconsistencies in data classification and interpretation of results. The defini-

TABLE 8. Total amount of land identified as breeding habitat with four different GIS-based methods of modeling amphibian breeding habitats in Yellowstone National Park.

Species	Identified breeding habitat (ha)			
	Annual variation	Multiyear variation	Maximum wetland	Maximum breeding
Tiger salamander	···	38 840	15 363	14 066
Western toad	···	42 784	43 473	6016
Chorus frog	26 791	36 191	32 175	11 130
Spotted frog	25 424	31 423	28 362	17 459

Note: Amounts for multiyear variation models (GIS data only) were compiled by combining models for all three years for each species; duplicate counts of hectares were removed.

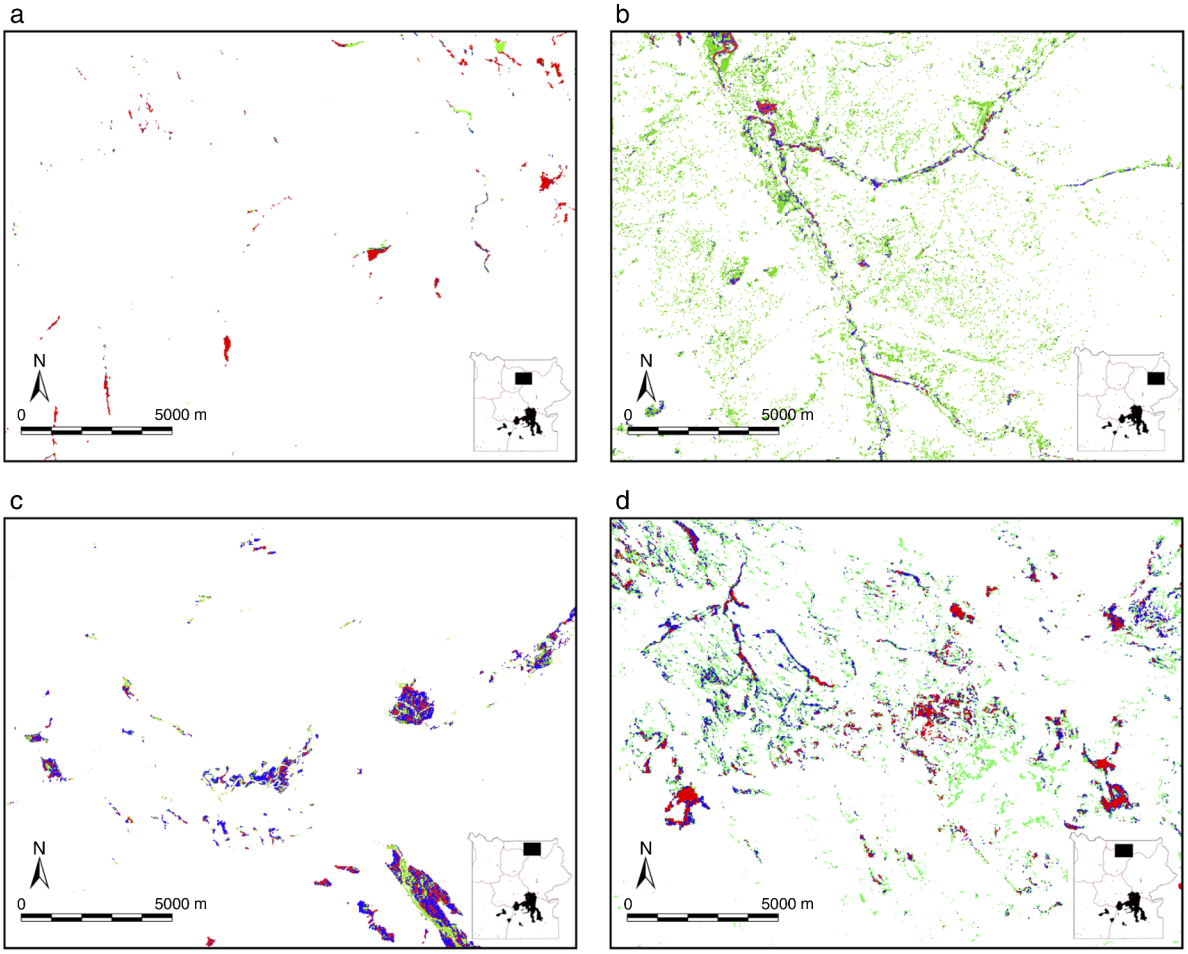

FIG. 5. The number of years (2000, 2001, and 2002) when different areas in Yellowstone National Park (YNP) were predicted to be likely breeding habitat for four species of amphibians: (a) tiger salamander, (b) western toad, (c) boreal chorus frog, and (d) Columbia spotted frog. Each panel represents a small and different portion of YNP. The color key to number of years is: green, one year; blue, two years; red, three years.

tions for these should fit the resolution of the data layers and final breeding models. Setting clear definitions is important because wetland connectivity can change throughout a season and from year to year.

Suggestions for improvement

The breeding models presented here could be refined a number of ways. Larger quantities of data on breeding sites (especially for salamanders and toads) would provide a more robust sample with a greater range of variation. For species that are rare or may be experiencing population declines, however, this simply may not be possible. Resurveying sites within a season and across years would provide detectability coefficients, yield better estimates of occupancy (MacKenzie et al. 2003, MacKenzie and Bailey 2004), and improve the ability of these models to predict breeding sites under different seasonal and annual weather conditions. Future studies will need to balance the extra effort required for resurveying sites with efforts needed to build sample size.

Additional field tests with new sites could have helped to identify particular characteristics to reduce omission or commission errors. For example, M. Murphy (*personal communication*) observed that thermally influenced wetlands may be less suitable for breeding boreal chorus frogs. To test this relation, we reclassified sites in thermal areas as unsuitable for breeding. This reduced

TABLE 9. Amount of land scored as likely breeding habitat in Yellowstone National Park for one, two, or three years.

Species	Likely breeding habitat (ha)		
	1 year	2 years	3 years
Tiger salamander	12 521	13 905	12 414
Western toad	13 667	13 141	15 976
Chorus frog	8986	14 427	12 778
Spotted frog	9402	10 389	11 632

Note: These amounts were derived from multiyear variation models (GIS data only) and represent unique areas that were scored as likely for only one year, for two of the three years, and for all three years.

commission errors by ~12% and increased overall accuracy by ~9%. Additional field studies could test these and other observations, providing better detection of available, suitable breeding habitat.

Because the wetland probability layers were important in constructing these breeding models, altering criteria used for predicting wetlands and wetland types probably would improve the breeding habitat models. One option is to use a lower threshold (<0.5 probability of being a palustrine wetland) for developing the wetland class layers. This would remove the problem caused by field site locations that coincide with map cells classified as "non-wetland." The wetland probability layers were based on procedures that tried to balance errors of omission and commission in wetland prediction (Wright and Gallant 2007), and for amphibian breeding models, it may be more beneficial for the wetland probability layers to emphasize minimizing errors of omission (i.e., it is more desirable to overpredict potential wetlands that might provide breeding habitat than to risk missing them).

The stability of a metapopulation (Hanski and Gilpin 1991) results from a balance between population extinction and colonization rates. Because the proximity of populations is important to the persistence of a metapopulation (Sjogren-Gulve 1994), including data that reflect the distances to other occupied breeding sites as an additional predictor variable may improve the breeding habitat models.

Finally, the accuracy and utility of these breeding models could be improved with information on the configuration of the terrestrial matrix of the landscape. Amphibians forage in terrestrial habitats and move through them to reach other wetlands. Some wetlands may be less accessible than others; they may be remote, located in extremely steep topography, or surrounded by habitats that are especially exposed to drying or are otherwise hostile to amphibians. These or other factors may combine to reduce the likelihood of amphibians using a wetland, even if the habitat in the wetland is conducive to breeding. Incorporating characteristics of the terrestrial matrix can help to determine the accessibility or isolation of wetlands and may improve our ability to predict breeding habitats. Toward this end, landscape genetics studies (e.g., Spear et al. 2005, Storfer et al. 2007) can help to elucidate historical movement patterns, further helping us to evaluate the landscape characteristics that are important not only for predicting breeding habitats under current conditions, but also for maintaining metapopulations subject to a changing climate and landscape.

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APPENDIX

A table listing all models (a priori and posterior) created and evaluated for building amphibian breeding habitat maps in Yellowstone National Park and an expansion of Fig. 3 showing how we integrated different data sets to produce our different modeling approaches using only GIS data (*Ecological Archives* A021-113-A1).

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