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Modeling the dynamic habitat and breeding population of Southwestern Willow Flycatcher

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ABSTRACT

To aid in the management and conservation of Southwestern Willow Flycatcher (*Empidonax traillii extimus*, hereafter “Flycatcher”), we developed numerous models of flycatcher breeding habitat at Roosevelt Lake, AZ. For model development and testing, we compiled 10 years of flycatcher territory data that were obtained from intensive fieldwork between 1996 and 2005. We identified riparian vegetation annually in the project area from Landsat Thematic Mapper images, and extracted floodplain features from a digital elevation model. We created a novel class of temporal (i.e., multiyear) variables by characterizing the stability and variability in breeding habitat over a 6-year time interval. We used logistic regression to determine associations between environmental variables and flycatcher territory occurrence, and to test specific hypotheses. We mapped the probability of territory occurrence with a GIS and determined model accuracies with a classification table and a 10-year population database. Environmental features that were associated with breeding flycatchers included floodplain size, proximity to water, and the density, heterogeneity, age and stability of riparian vegetation. Our best model explained 79% of the variability in the flycatcher breeding population at Roosevelt Lake. The majority of predicted flycatcher habitat formed between 1996 and 2004 on an exposed lakebed ~3 years after water levels receded during a prolonged drought. A high correlation between annual reservoir levels and predicted breeding habitat ($r = -0.82$) indicates that we can create and manage habitat for conservation purposes. Our predictive models quantify and assess the relative quality of flycatcher breeding habitat remotely, and can be used to evaluate the effectiveness of habitat restoration activities. Numerous techniques we developed can be used to characterize riparian vegetation and patch dynamics directly off of satellite imagery, thereby increasing its utility for conservation purposes.

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1. Introduction

Riparian habitats in the southwestern United States are disproportionately important for wildlife. For example, over 50% of Southwestern birds are directly dependent on riparian habitat while it only covers about 1% of the landscape (Knopf et al., 1988; Skagen et al., 1998). Unfortunately, riparian habitat has declined by as much as 90% in historic times, and is generally considered a habitat of great conservation and management concern (Busch and Smith, 1995; Comer et al., 2003; Turner et al., 2003; Rich et al., 2004). Many stressors have contributed to the decline of riparian habitat, but one of the most wide-scale stressors to riparian systems is due to dams (Graf, 2006). Dams disrupt the natural flood cycle that riparian systems have adapted to, creating rivers that flood infrequently, lose their meanders, and generally become more channelized (Graf, 2006; Webb and Leake, 2006). However, while much attention has been directed at the down-stream effects of dams, reservoirs can allow for rich riparian habitat to exist along their up-stream fringes. In the U.S. Southwest, many reservoirs fluctuate depending on regional patterns of precipitation, and given the right geomorphology of a reservoir basin, large tracts of riparian habitat can form in the reservoir beds and fringes, especially near inflows. Lowering reservoir levels expose soil that is rich in nutrients, cleansed of salts, and free of existing vegetation that allows for rapid growth of riparian vegetation. Conversely, rising reservoir levels destroy this habitat, setting the stage for a repeat during the next drawdown.

The cycle of creation–destruction caused by fluctuating reservoir levels, reminiscent of the once-frequent scouring flood events of major rivers in pre-dam times, can create large swaths of dense riparian habitat at relatively young successional stages. When this occurs, the riparian habitat is quickly colonized by wildlife, particularly vagile species such as birds, and can become important habitat for the period of time that it exists. One species of great

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conservation and management concern that has come to utilize these reservoir-created riparian woodlands is the Southwestern Willow Flycatcher (*Empidonax traillii extimus*). Declared an endangered species in 1995 (USFWS, 1995), the flycatcher is dependent on riparian habitat for breeding and its decline has been linked to the loss of riparian habitats (Unitt, 1987). While most flycatcher breeding locations are along rivers, some of the most important breeding sites for flycatcher occur in reservoir basins, including Lake Isabella, CA, Lake Mead, NV, Roosevelt Lake, AZ, and Elephant Butte, NM (Durst et al., 2005).

Roosevelt Lake, a reservoir, supports one of the largest breeding populations of Southwestern Willow Flycatcher in the Southwest. Formed in 1911 after construction of Roosevelt Dam, Roosevelt Lake serves primarily to impound water for the greater Phoenix metropolitan area. In an effort to increase storage capacity, Roosevelt Dam was raised 24 m between 1992 and 1994. Because the dam's primary purpose is water storage, the reservoir fluctuates freely depending on input, primarily winter precipitation and water demand. From 1996 to 2004, a decadal drought in the Southwest U.S. led to a steady decline in the reservoir levels at Roosevelt Lake. This decline exposed large areas of reservoir bed that were colonized by riparian vegetation and subsequently breeding flycatchers. Flycatcher breeding was documented in 23 patches that comprised 242 ha of riparian habitat, although the number of patches and amount of habitat changed every year. Our goal was to understand the complex relationships between environmental variables, habitat availability, and the fluctuating population of breeding flycatchers at Roosevelt Lake between 1996 and 2004. Underlying our goal was a hypothesis that habitat availability limits the flycatcher population. Information from our analysis will provide wildlife managers with a better understanding of the biophysical features that create flycatcher habitat, environmental conditions that limit its formation, and the likely response of a flycatcher population to environmental conditions through time.

2. Methods

2.1. Study area

Roosevelt Lake, located in central Arizona at an elevation of 655 m (33°39′N, 110°58′W), is over 30 km in length (Fig. 1). The primary source of water inflow is the Salt River to the southeast of the reservoir, supplemented by Tonto Creek from the northwest. The Salt River Project (SRP) and Army Corp of Engineers manage the reservoir for two primary purposes: water storage and flood control. Below 655 m SRP operates the reservoir primarily for water storage and as part of SRP's overall system storage on both the Salt and Verde Rivers. Above 655 m, the reservoir enters flood control space and operations to evacuate the control space over a designated time period are set by the Army Corp of Engineers. Roosevelt Lake's water level fluctuates up and down on a monthly and annual basis, but the overall trend between 1995 and 2004 was downward due to a long-term drought. As the reservoir receded, riparian habitat quickly established and grew on the exposed lakebed. Following an unusually wet winter and spring in 2005, the reservoir refilled to a historic high-water mark due to the increased dam height (Fig. 1B). Readers can view the dynamic fluctuations in lake level during the breeding season at either Salt River or Tonto Creek inflows, between 1994 and 2005, by viewing the videos we made from Landsat Thematic Mapper imagery (see Supplementary materials).

The vegetation at Roosevelt Lake is categorized as Sonoran Desert Riparian habitat (Brown, 1994), with flycatchers occupying a heterogeneous mosaic of discreet riparian forest patches of varying ages and vegetation compositions, ranging from 0.2 to 43 ha in size. Both native and exotic vegetation were present at the study site. Native habitat is characterized by Goodings willow (*Salix gooddingii*) and Fremont cottonwood (*Populus fremontii*), whereas exotic habitat is dominated by tamarisk (saltcedar; *Tamarix* spp.). The understory vegetation is made up of a variety of grasses, forbs, and shrubs (mesquite [*Prosopis* spp.], coyote willow [*Salix exigua*], tamarisk, cocklebur [*Xanthium strumarium*], and *Baccharis* spp.). Surrounding uplands are characterized as Sonoran Desert Uplands.

2.2. Flycatcher surveys

Southwestern Willow Flycatcher breeding surveys were conducted from 1996 to 2005 along the Salt River and Tonto Creek following a standardized presence/absence survey protocol (Sogge et al., 1997). Potential breeding habitat was surveyed using tape playback at least three times a season, and territory locations were recorded using GPS units. Due to intensive survey efforts each year (Paxton et al., 2007; Ellis et al., 2009), little potential breeding habitat was left unsurveyed and we believe that no breeding patches went undetected within the study area during the study period. We defined a breeding site as any location that contained an active flycatcher territory, while a nonuse site referred to any location that did not contain a flycatcher territory. Once a flycatcher was detected, intensive searching was conducted to document breeding status, locate nests, and monitor productivity (Ellis et al., 2009). For database construction and spatial analyses, a spatial location was recorded for each territory.

2.3. Modeling overview

We used a five-step process to model the fluctuations in flycatcher breeding habitat and population size at Roosevelt Lake (Fig. 2). First, we developed a conceptual model of flycatcher breeding habitat (Fig. 3) based upon knowledge derived from previous studies that found flycatchers select wide floodplains with large patches of dense, young, heterogeneous riparian vegetation (Hatten and Paradzick, 2003; Paradzick, 2005; Brodhead, 2005), and display annual fidelity to their breeding grounds (Paxton et al., 2007). Second, we characterized the environmental conditions where flycatchers bred with Landsat Thematic Mapper imagery, a digital elevation model, and GIS. Third, we used logistic regression to identify significant associations between flycatcher territories and biophysical variables, and to construct cell-based probabilistic models of flycatcher breeding habitat. Fourth, we quantified and mapped breeding habitat at Roosevelt Lake between 1985 and 2005. Fifth, we explored correlations among predicted flycatcher breeding habitat, environmental variables, and the size of the flycatcher breeding population. For additional details related to our modeling approach, refer to Appendix A.

2.4. Spatial variables

For modeling and hypothesis testing, we developed a set of spatial predictor variables with fine resolution and broad scope to characterize vegetation and floodplain features at multiple scales (Table 1). Vegetation and floodplain features were characterized in discrete 30 m × 30 m (0.09 ha) cells obtained from TM imagery or a USGS DEM, respectively. We focused upon predictor variables extractable from TM or DEM data because they could be created for any part of the project area, or throughout the flycatcher's breeding range. We examined vegetation density, edge habitat, proximity to patch boundaries or water, because they are thought to be important to flycatchers (Sogge et al., 1997; Sogge and Marshall, 2000), and width of floodplain because it can influence riparian plant community establishment and persistence (Szaro, 1990; Stromberg, 1993). We did not directly examine vegetation species or seral

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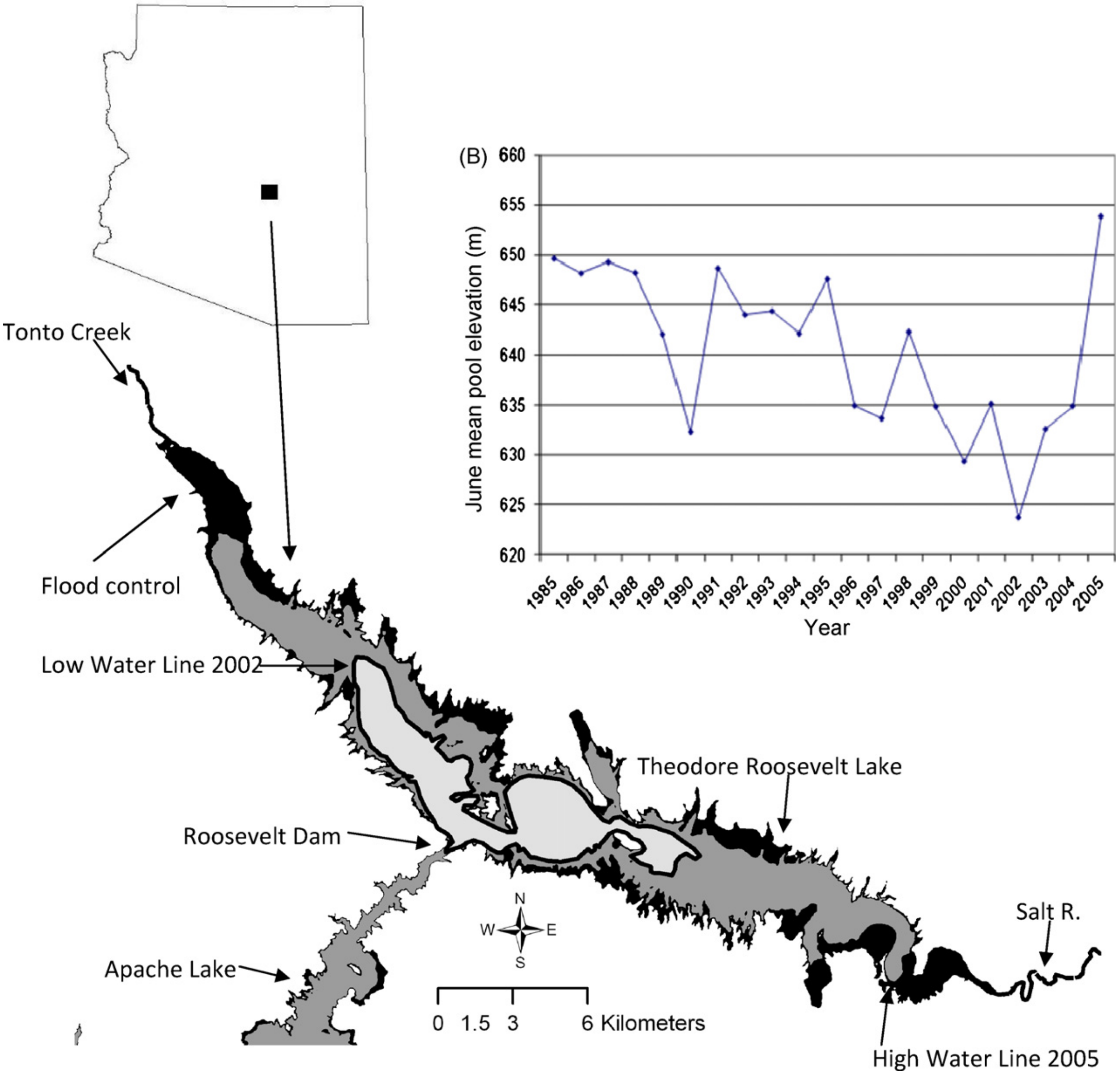

Fig. 1. (A) A map of the project area in south-central Arizona and with the mean-June monthly water-surface elevation at Roosevelt Lake between 1985 and 2005 (B). Three different water levels are shown for Roosevelt Lake; the low-water line that occurred in 2002 (~624 m); the conservation pool height (655 m), which was also the project's high-water line; and the flood-management zone (655–676 m). Tonto Creek and Salt River flow into Roosevelt Lake; the only outlet is the spillway located at Roosevelt Dam.

stage, two variables which may influence habitat selection (Sogge et al., 1997; Sogge and Marshall, 2000), because they could not be accurately extracted from TM imagery.

In addition to the spatial variables that we created from a single year of vegetation data (i.e., a snapshot in time, a single image date), we created a novel class of temporal variables (i.e., obtained from multiple dates and satellite scenes) to characterize the stability and variability of flycatcher breeding habitat resulting from lake fluctuations, drought, or geographic location (e.g., close or far from lake, patch interior). We characterized the stability and variability in predicted breeding habitat with descriptive statistics (e.g., mean or SD, respectively), over a 6-year time interval, with GIS functions. We rationalized that vegetation that was exposed to lake drawdowns, flooding, or drought would have a lower mean NDVI signature and a higher SD in NDVI due to stress and phenological differences. Alternatively, vegetation that was not exposed to such catastrophic events would have a higher mean NDVI value and a lower SD. A 6-year time interval was long enough for the lake to cycle up and down and for vegetation of a suitable age to emerge. For additional information related to our spatial database, refer to Appendix B.

2.5. Statistical design

We developed an environmental dataset for spatial modeling by employing a case–control sampling design (Keating and Cherry, 2004) at Roosevelt Lake in 2004 ($n = 215$). Specifically, we compared a set of randomly selected territory locations ($n = 107$) with a set of absence locations ($n = 108$) that were randomly generated in areas that had been searched and found to be empty during the 2004 breeding season. We reserved an equal number of presence/absence locations ($n = 215$) that were not used in model construction for model verification. To create the most specific models possible, we excluded non-riparian and marginal riparian vegetation from our modeling by only sampling and modeling riparian areas (cells) where NDVI values exceeded 0.126 (Hatten and Paradzick, 2003). Retrospective sampling provided a practical way to examine our survey data and is well suited for animals

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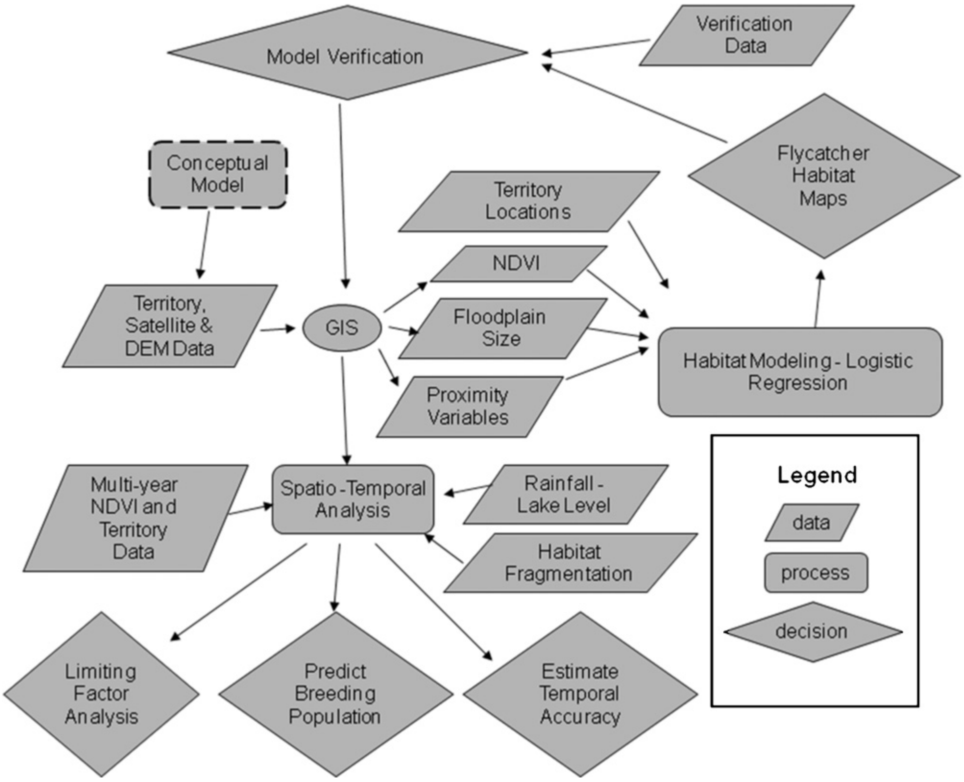

Fig. 2. A flowchart depicts the steps and processes we undertook to create and test a spatial model of Southwestern Willow Flycatcher breeding habitat at Roosevelt Lake, examine factors that limit formation of habitat, and to estimate the flycatcher breeding population.

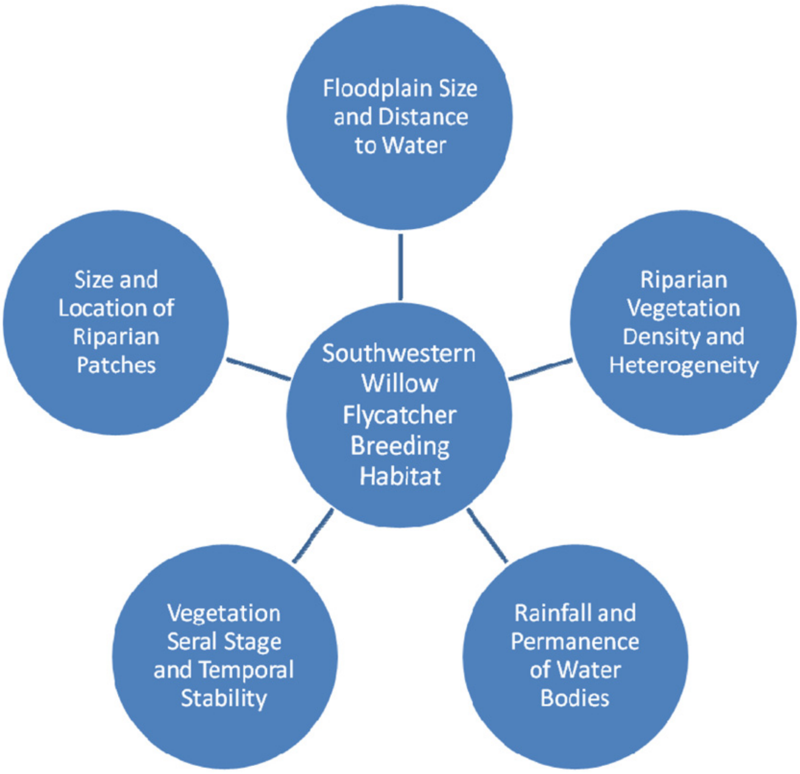

Fig. 3. A conceptual diagram of Southwestern Willow Flycatcher breeding habitat. Habitat features thought to be important included size of floodplain, distance to water, density and heterogeneity in riparian vegetation, vegetation seral stage, and size and shape of vegetation patches.

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Table 1
Ten predictor variables used to characterize vegetation density or stability, and floodplain size, at Southwestern Willow Flycatcher use/nonuse sites in south-central Arizona (Roosevelt Lake). Some variables were examined at multiple scales and NDVI thresholds (those listed below are representative of a larger set). Additional details about predictor variables can be obtained from Appendix B.

Variable	Description
LAKEDIST	Distance from lake surface in June or July
CREEKDIST	Distance to perennial/intermittent stream
EDGEDIST-33[a]	Distance from patch interior to outer edge (patch defined with an NDVI threshold > 0.33)
ND_BEST4[a]	Amount (i.e., number) of cells with NDVI values >0.41 within a 120-m radius
ND_TOP3[a]	Binary (cells with NDVI > 0.33 = 1; NDVI < 0.33 = 0)
ND_SD4[b]	Variability (SD) in NDVI within a 120-m radius
Flood30[b]	Amount of floodplain or flat area within a 360-m radius (as determined from a 30-m DEM)
PATCHSIZE-41[a]	Size of patch (number of contiguous cells with NDVI values > 0.41)
MOD_SD6	Variability (SD; 6-year) in probability classes (i.e., habitat stability)
MOD_MN6	Mean (6-year interval) probability class (i.e., habitat quality)

[a] Variable was examined at multiple NDVI thresholds (i.e., different densities).
[b] Variable was examined at multiple scales (i.e., different-sized moving windows).

that exhibit preferences for rare habitat types (Ramsey et al., 1994). Additional details about our statistical sampling design can be found in Appendix C.

2.6. Spatially explicit modeling

We used binary logistic regression to identify habitat associations and to develop equations useful for spatially explicit (GIS-based) habitat models, considering both univariate and multivariate models. Logistic regression is ideal for evaluating relationships between predictor variables and flycatcher territory occurrence because presence/absence data are binary. We used Arc/Info® GRID (ESRI, 1992) to calculate and map the relative quality of breeding habitat within 0.09-ha (30 m × 30 m) cells. We calculated the relative quality of breeding habitat (P) with the following equation:

$$P = \frac{e^{g(x)}}{1 + e^{g(x)}} \qquad (1)$$

where $g(x)$ is the linear combination of parameter estimates obtained from the logistic regression (Hosmer and Lemeshow, 1989; Keating and Cherry, 2004). In Eq. (1), the relative quality of flycatcher breeding habitat is linked to the probability of a flycatcher territory occurring based on the logistic regression under consideration. Each model assigned cells a probability between 1 and 98%, which we reclassified into 1 of 5 probability classes: (1) 1–20%, (2) 21–40%, (3) 41–60%, (4) 61–80%, and (5) 81–98%. Larger probability classes have been found to contain higher densities of breeding flycatchers in Arizona and New Mexico (Hatten and Paradzick, 2003; Hatten and Sogge, 2007).

2.7. Multivariate model selection

We evaluated over a dozen multivariate models in our analysis, using multiple tests to judge how well the models fit the verification dataset. Multiple tests were performed for each candidate model because the models and the system modeled are complex. We assessed model fit with Akaike's Information Criterion (AIC [Burnham and Anderson, 2002]), Hosmer–Lemeshow goodness-of-fit test ($\hat{C}$; [Hosmer and Lemeshow, 1989]), Nagelkerke's pseudo R^2 (Nagelkerke, 1991), and area under the curve (AUC [Egan, 1975; Fawcett, 2004]). We evaluated the significance of each covariate with the G-statistic, produced from backwards stepping and a log-likelihood ratio test (Hosmer and Lemeshow, 1989). The G-statistic and Nagelkerke R^2 are roughly equivalent to the F and R^2 statistics, respectively, in linear regression. We checked for linearity between the logit and the continuous variables with the Box–Tidwell test (Box and Tidwell, 1962). When nonlinearity was observed, we transformed the covariate (e.g., squared, categorical, exponential) and reassessed model fit. Lastly, we checked for interactions between the covariates.

We were very interested in model performance over space (year 2004) and through time (1996–2004), so we gave extra weight to models that performed well in both domains. In addition, we focused upon models that had a relatively clear biological interpretation in regard to a specific set of variables. We compared all candidate models to model 1, which was constructed from a set of variables found to be important to flycatchers in riverine and lake habitats in Arizona (Hatten and Paradzick, 2003) and New Mexico (Hatten and Sogge, 2007). For brevity sake, we presented a subset of models that achieved the best combination of spatial and temporal accuracies, and were the most interpretable from an ecological perspective.

2.8. Model verification

We assessed the spatial accuracies of our logistic-regression models with an independent dataset (i.e., territories not used in model development). Model accuracies depended upon a movable probability cutpoint used to delineate (extract) suitable versus unsuitable breeding locations (i.e., cells) from the probability grid. For our analyses, we set the probability cutpoint at 50%; cells with probabilities ≤50% were classified unsuitable; cells with probabilities >50% were classified suitable. Model accuracies were calculated as model sensitivity (1 − omission error), specificity (1 − commission), and overall accuracy (sensitivity + specificity/2). Breeding territories that fell outside of predicted habitat were counted as an omission error (Story and Congalton, 1986), whereas cells that were predicted suitable but found to be empty were counted as a commission error. We assessed each model's fit by calculating the density of territories inside each of the five probability classes with the verification dataset. We assessed the temporal fit of our models with linear regression, regressing predicted habitat output from a specific logistic-regression model on the number of flycatcher territories observed between 1996 and 2004 ($n = 9$). This technique required that we populate each model with vegetation characteristics specific to a given year and TM scene.

2.9. Relationships among environment, predicted habitat and breeding population

We examined the relationships between environment variables, predicted habitat, and the flycatcher breeding population in two steps with linear regression. First, we identified factors that appeared to limit the quantity of flycatcher breeding habitat over time. For this we treated predicted habitat as a response variable, regressing the amount of predicted habitat output from our logistic-regression models annually on hydrologic and meteorological data obtained between 1985 and 2005. Specifically, we focused upon the mean-June lake elevation and rainfall data that were summarized by different monthly combinations (e.g., October–April; January–April). Secondly, we predicted, or hindcasted, the flycatcher breeding population between 1996 and 2004 by treating predicted habitat as an explanatory (i.e., predictor) variable. Specifically, we regressed predicted habitat output from our logistic-regression models for each year on the flycatcher breeding population, plus hydrologic and meteorological variables. In addition, we examined whether fragmentation metrics (e.g., patch size,

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Table 2
Univariate logistic-regression results for Roosevelt Lake ($n = 215$). The test statistic (G) is calculated as −2 (change in log-likelihood) for the constant only model versus the full model (constant and predictor variable). Larger G values indicate a stronger association between the predictor and response variable (presence of territories). Refer to Table 1 for variable definitions, and Appendices B and C for more details about how the spatial variables were created.

Variable	β	G	P
LAKEDIST	−0.001	59.6	<0.001
MOD_MN6	0.918	59.1	<0.001
ND_TOP3	2.622	53.2	<0.001
MOD_SD6	1.306	33.9	<0.001
ND_BEST4	0.048	33.2	<0.001
PATCHSIZE-41	0.015	24.78	<0.001
EDGEDIST-33	0.006	13.28	<0.001
FLOOD30	0.046	12.4	0.002
CREEKDIST	−0.002	7.71	0.005
ND_SD4	64.0	0.7	0.38

number of patches, length of edges) were associated with the flycatcher breeding population. The reader may refer to Appendices A–C for more specific details on our modeling.

3. Results

3.1. Univariate analysis

Ranked by G-statistic values (Table 2), the top 3 predictor variables were distance from lake (LAKEDIST), mean habitat quality over a 6-year period (MOD_MN6), and density of vegetation at a fine scale (0.09 ha; ND_TOP3). Thus, proximity to water, habitat persistence, and vegetation density within a cell (30 m × 30 m) were the most significant univariates. Interpretation of the odds ratios, obtained by exponentiating the coefficient (Table 2) (Hosmer and Lemeshow, 1989) provided additional information about the strength of the associations between flycatcher territories and biophysical variables. For example, the odds of a flycatcher territory being present in a location (i.e., cell) with high vegetation density (NDVI values >0.33; ND_TOP3) were ~14 times that of an area with an NDVI value ≤ 0.33 (i.e., exp (2.622)). Similarly, the odds of territory occurrence increased ~27% for each 10% increase in amount of densest vegetation (ND_BEST4) inside a 120-m radius of a cell (note that 49 cells are found within a 120-m radius: exp (0.048 × 4.9 cells)). Some negative relationships (i.e., a decreased probability of territory occurrence) included distance from the lake (LAKEDIST), or distance from a river or creek (CREEKDIST). The most powerful univariate was LAKEDIST; interpretation of the odds ratio revealed that for each 100-m increase away from the lake, the odds of territory occurrence decreased ~10%. Additionally, for each 100 m increase away from Salt River or Tonto Creek, the odds of a territory decreased ~18%.

3.2. Multivariate model selection and verification

Evaluating our top 4 multivariate models with different model-fit statistics produced mixed results depending on the statistic we focused upon (Table 3). For example, model 3 performed the best when evaluated with goodness-of-fit statistics (AIC, ROC, R^2) or a classification table, and was the most specific (i.e., it predicted the lease amount of habitat). However, it had the worst $\hat{C}$ and $10R^2$ statistics, indicating that is was least able to distinguish between poor, fair, or good habitat (i.e., low $\hat{C}$), and it had the weakest temporal fit (i.e., lowest $10R^2$) to flycatcher territories between 1996 and 2004 ($n = 9$). Collectively, this indicates that model 3 was overfit to environmental conditions found in 2004, making it too specific in both time and space to be useful. From a temporal perspective, models 1, 2 and 4 performed markedly better, explaining between 60 and 79% of the variability in territory numbers between 1996 and 2004. Our top models were highly correlated with one another ($r > 0.9$), enabling us to focus on various aspects of each model due to their unique combinations of explanatory variables.

Model 2 contained four covariates found to be important in a previous study (Hatten and Paradzick, 2003), plus a distance-to-creek variable (Table 4). The G and WALD statistics indicated that vegetation density at the site (ND_TOP3) was the most influential covariate, followed by floodplain size (FLOOD30), distance to creek (CREEKDIST), and amount and variability in dense vegetation in a 120-m radius (ND_BEST4 and ND_SD4, respectively). In contrast, model 4 contained two variables that were found to be important in model 2 (ND_TOP3 and ND_SD4), plus 2 spatiotemporal variables that characterized the quality (MOD_MN6) and stability (MOD_SD6) of flycatcher breeding habitat over a 6-year period (1999–2004). While model 4 was unremarkable in its classification and model-fitting performance in 2004, it obtained exceptional temporal accuracy (79%) between 1996 and 2004. When we rendered the model probabilities as grids, distinct differences emerged as to where the most suitable breeding habitat was located. For example, model 2 (Fig. 4A) primarily emphasized vegetation closest to the river, while model 4 (Fig. 4B) also emphasized locations far from the river channel. Despite these differences, both models produced a high correlation between their 5 probability classes (e.g., 0–20%, 21–40%) and territory densities within those classes ($r = 0.98$ and 0.95, respectively), demonstrating an excellent fit to

Table 3
Results of a multivariate logistic-regression analysis at Roosevelt Lake ($n = 215$). Model 1 was obtained by fitting a set of covariates found to be important in a previous model of flycatcher habitat (Hatten and Paradzick, 2003). To calculate classification accuracy for these models, we set the probability cutpoint at 50% (cells with a probability value ≤50% were considered unsuitable for breeding, values >50% were considered suitable). Models 1–3 are spatial models that characterize environmental conditions in 2004. In contrast, model 4 is a spatiotemporal model because it contains variables that characterize 6 years of environmental conditions (1999–2004). See Table 4 for model parameters.

Model[a]	$R^{2\,b}$	$\hat{C}$ [c]	Pres[d]	Ab[e]	All[f]	ROC[g]	AIC[h]	$10R^{2\,i}$	Predicted[j]
1	0.43	0.74	88.9	54.2	71.6	0.83	223.1	0.60	671.6
2	0.47	0.34	80.6	72.0	76.3	0.85	215.5	0.69	483.3
3	0.53	0.01	84.2	72.0	78.1	0.87	198.7	0.25	403.6
4	0.51	0.73	65.7	71.0	68.4	0.86	204.7	0.79	551.2

[a] Refer to Table 4 for model parameters.
[b] Nagelkerke pseudo R^2 statistic.
[c] Hosmer–Lemeshow goodness-of-fit test ($\hat{C}$).
[d] Percent of presence sites correctly classified (sensitivity).
[e] Percent of absence sites correctly classified (specificity).
[f] Overall model accuracy (sensitivity + specificity)/2.
[g] Receiver operating characteristic (ROC) test (area under the curve).
[h] Akaike's Information Criterion.
[i] Explained variability in inter-annual fluctuations in SWFL territories (1995–2004).
[j] Amount of predicted breeding habitat (ha) in 2004 at a 50% cutpoint.

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Table 4
Model parameters of four multivariate logistic-regression models developed and tested for Roosevelt Lake ($n = 215$). Refer to Table 1 for variable definitions; see Appendices B and C for additional details on spatial variables.

Model	Variable	β	SE	Wald	Df	P	Exp(β)
1	ND_TOP3	2.035	0.59	11.901	1	0.001	7.649
	ND_SD4	0.547	0.144	14.516	1	0	1.729
	FLOOD30	0.06	0.018	11.448	1	0.001	1.062
	ND_BEST4	0.056	0.021	7.213	1	0.007	1.057
	Constant	−7.288	1.284	32.225	1	0	0.001
2	ND_TOP3	2.032	0.594	11.723	1	0.001	7.631
	ND_SD4	0.387	0.154	6.276	1	0.012	1.472
	FLOOD30	0.057	0.018	10.583	1	0.001	1.059
	ND_BEST4	0.058	0.021	7.539	1	0.006	1.060
	CREEKDIST	−0.003	0.001	8.627	1	0.003	0.997
	Constant	−6.046	1.309	21.321	1	0.000	0.002
3	ND_TOP3	2.608	0.508	26.320	1	0.000	13.575
	FLOOD30	0.055	0.018	8.913	1	0.003	1.056
	CREEKDIST[a]	−3.235	0.809	16.010	1	0.000	0.039
	LAKEDIST[a]	−0.402	0.091	19.589	1	0.000	0.669
	Constant	−2.348	1.000	5.508	1	0.019	0.096
4	ND_TOP3	1.327	0.568	5.460	1	0.019	3.769
	ND_SD4	0.235	0.097	5.906	1	0.015	1.265
	MOD_MN6	0.893	0.182	24.104	1	0.000	2.443
	MOD_SD6	1.512	0.327	21.388	1	0.000	4.534
	Constant	−5.386	0.863	38.952	1	0.000	0.005

[a] Distance was converted from meters to km.

the verification dataset (Fig. 4C). We did not detect any significant interactions, nonlinearity or collinearity in either model.

3.3. Habitat limiting factors

The amount of predicted habitat between 1985 and 2005 changed markedly, though not necessarily progressively, at Roosevelt Lake (Fig. 5A). Specifically, there was a general increase in predicted habitat from 1985 to 2004, particularly between 1995 and 2004, but the amount of predicted habitat fluctuated along with the mean-June water levels. Most noticeable was the drop in predicted habitat in 2005 when the reservoir rose to a record high level following dam modification in 1995. The large reduction in predicted habitat in 2005 resulted from inundation of riparian vegetation during the flood, as well as the model having difficulty predicting semi-inundated habitat due to saturation of the vegetations' spectral signatures from the surrounding water. The amount of predicted habitat varied based upon which model we used and what cutpoint was selected, but all models were highly correlated to one another ($r > 0.9$). Generally, the spatiotemporal model (not shown in Fig. 5) predicted more habitat than the best spatial model (model 2), but less than model 1 (not shown in Fig. 5). Readers can view the dynamic fluctuations in predicted habitat between 1994 and 2005 (as output by model 2) at either Salt River or Tonto Creek inflows by viewing the videos in Supplementary materials section.

We found through linear regression that Roosevelt Lake's mean-June water-surface elevation strongly influenced the amount of predicted habitat output by our logistic-regression models. Recall that Roosevelt Lake's mean-June water level hovered between 648 and 650 m from 1985 to 1988, then fluctuated greatly between 1989 and 2005 (624–654 m). In concert with the water-level fluctuations, there was a general downward pattern in water-surface elevations between 1995 and 2004, before filling up again in 2005. The correlation between mean-June-water level and predicted breeding habitat between 1985 and 2005 was strong (model 2; $r = -0.81$; $P = 0.001$; $n = 21$), indicating that low reservoir levels produced more habitat for flycatchers than high reservoir levels. The smallest amounts of predicted breeding habitat occurred in the highest water years of 1985 and 2005, while the greatest amounts occurred in the lowest water years between 2000 and 2004. Using predicted habitat (ha) from model 2, the following linear regression explained 66.5% of the variability in predicted flycatcher breeding habitat at Roosevelt Lake (Fig. 5B):

$$H = 8221.085 - 12.462(X) \tag{2}$$

(95% CI = 16.712–8.212, $n = 21$, $P < 0.001$), where H = predicted habitat (ha) and X = mean lake elevation (m) in June. The incorporation of rainfall data, summarized in different monthly intervals, by year, did not improve the statistical relationship in Eq. (2) but it was a significant predictor when modeled alone. Thus, the mean-June lake level overshadowed the influence of rainfall in Eq. (2).

3.4. Relationship between predicted habitat and breeding-flycatcher population

We found a strong relationship between the size of the flycatcher breeding population at Roosevelt Lake and the amount of predicted habitat between 1996 and 2004 (Fig. 6A). Through linear regression we explained 69% of the variability in flycatcher territory numbers at Roosevelt Lake with the following equation:

$$T = -106.95 + 0.603(X) \tag{3}$$

where T = number of flycatcher territories, and X = predicted habitat (ha) output from model 2 [$P = 0.006$, $t = 3.89$, 95% CI = 0.244–0.957; $R^2 = 0.69$]. We improved upon the explanatory power of Eq. (3) by 14.5% when we regressed predicted habitat output from model 4 on territory numbers with the following equation (Fig. 6B):

$$T = -145.646 + 0.595(X) \tag{4}$$

($P = 0.001$, $t = 5.182$, 95% CI = 0.324–0.867; $R^2 = 0.79$). We omitted 2005 from the breeding-population analysis due to the extreme flood event that resulted from high spring runoff and the increased spill-crest height at Roosevelt dam. The increase in explanatory power using model 4 indicated that spatially explicit knowledge of the quality and variability of habitat proceeding territory selection improved the temporal performance of the model. The mean-June lake level, rainfall, and fragmentation metrics did not contribute significantly to Eq. (3) or (4). However, both rainfall and lake level were significant predictors of the flycatcher population when modeled singularly. A curvilinear analysis found a linear fit was best for these regressions.

4. Discussion

4.1. Habitat selection patterns

NDVI-based variables that describe vegetation density were dominant in our models, reaffirming the importance of dense, vigorous riparian vegetation as a major selection criterion for breeding flycatchers (Sogge and Marshall, 2000; Hatten and Paradzick, 2003; Paradzick, 2005). The NDVI variable that summarized vegetation density at the finest scale (ND_TOP3; ∼17-m radius) was the most influential covariate in two of our featured models. Dense vegetation provides many advantages to flycatchers including refuge, cooling, and nesting habitat (Allison et al., 2003). Floodplain size (FLOOD30) was influential in the three spatial models, but it was not influential in the spatial-temporal model. Floodplain (FLOOD30) was our only geomorphic, coarse-scale variable (360-m radius; ∼72 ha), providing information about an area that is substantially larger than a flycatcher territory (i.e., ∼1–4.5 ha; Hatten and Paradzick, 2003; Brodhead, 2005; Cardinal and Paxton, 2005). Floodplain size appears important in that it provides an opportunity for larger stands of riparian vegetation to form and persist (Szaro, 1990; Stromberg, 1993), thereby providing increased nesting opportunities to flycatchers. In areas where the floodplain is

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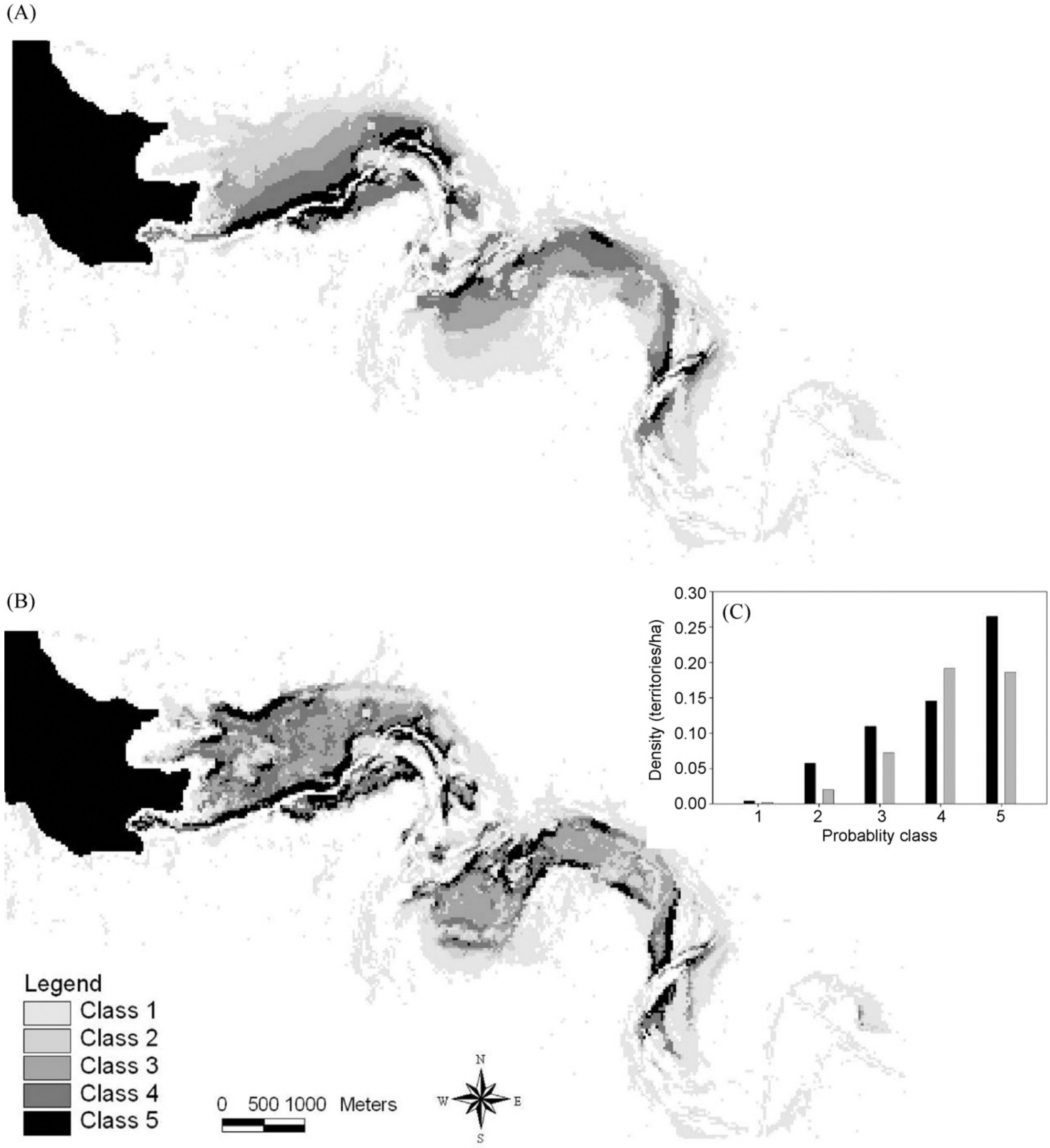

Fig. 4. Spatially explicit maps of Southwestern Willow Flycatcher breeding habitat at the Salt River inflow to Roosevelt Lake (June 2004), as predicted by models 2 (A) and 4 (B). Model probabilities were reclassified into 5 probability classes that are known to be important to flycatchers (Hatten and Paradzick, 2003): (1) 1–20%, (2) 21–40%, (3) 41–60%, (4) 61–80%, and (5) 81–98%. The density of flycatcher territories ($n = 107$) found within the 5 probability classes output from models 2 (black bars) and 4 (gray bars) at Roosevelt Lake are also displayed (C). Territory densities were obtained by dividing the number of flycatcher territories (from a verification dataset) by the area contained within each probability class. Actual territory densities would have been two times greater if we had used the full dataset instead of the verification dataset (a random subset of the total dataset).

restricted, flycatchers are rarely observed (Hatten and Paradzick, 2003).

Distance-to-water variables (i.e., CREEKDIST, LAKEDIST) were very important in models 2 and 3, representing new additions to the original flycatcher model (see Hatten and Paradzick, 2003). Both are continuous variables without a fixed scale. Flycatchers at Roosevelt Lake quickly colonized emergent riparian vegetation close to the receding lake (e.g., Gooding willow and tamarisk) when the vegetation was as young as 3–4 years of age. Simultaneously, flycatchers slowly abandoned seemingly adequate, albeit older, vegetation above high-water levels, but reoccupied many of these older vegetation patches that they had previously abandoned in favor of younger vegetation when the younger habitat was inundated (Paxton et al., 2007). Thus, the distance-to-water variables identified a zone in which riparian vegetation had the physical and biological attributes heavily favored by breeding flycatchers, and may have indirectly informed the model of vegetation seral stage. Lastly, the strong inverse relationship between Roosevelt Lake's water-surface elevation and amount of predicted breeding habitat suggests that more habitat becomes available when the lake draws down. However, a dropping lake level will eventually result in patches becoming farther removed from the water table or the lake's surface, resulting in a loss of vegetation density and vigor, and decreased suitability for flycatchers (Paradzick, 2005; Paxton et al.,

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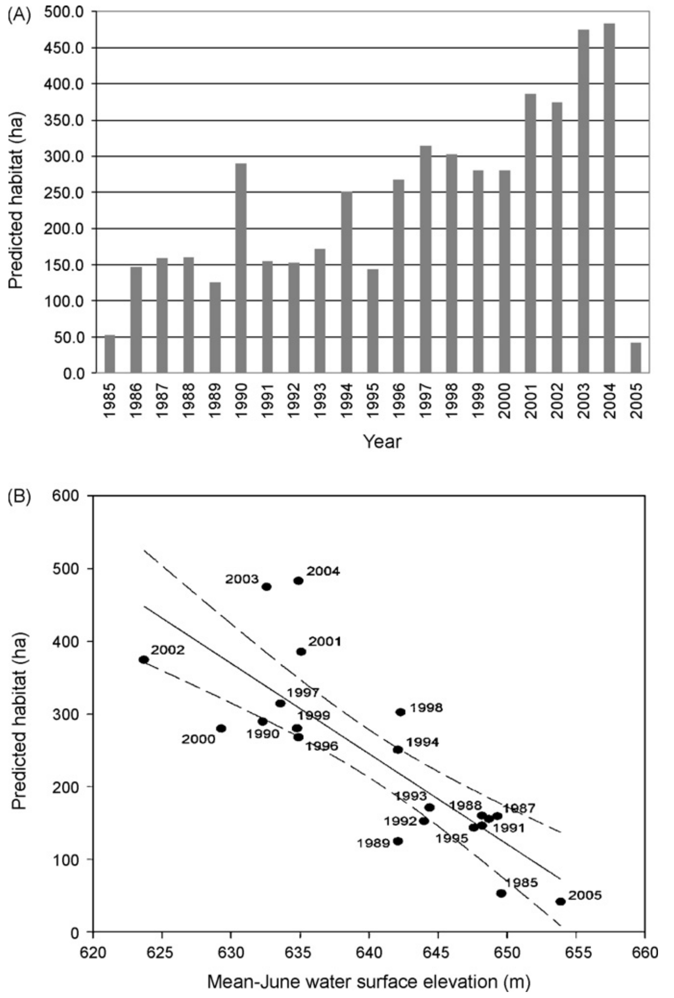

Fig. 5. Amount of predicted flycatcher breeding habitat output by model 2 at Roosevelt Lake between 1985 and 2005 (A). We created the graph by populating model 2 with a new TM scene each year to characterize the annual-specific vegetation characteristics. We set the model's probability cutpoint at 50%; cells with a probability ≤50% were coded unsuitable, cells with a probability >50% were coded suitable. Also displayed is the linear relationship between the mean–June water–surface elevation and predicted breeding habitat, as output by model 2, at Roosevelt Lake between 1985 and 2005 (B).

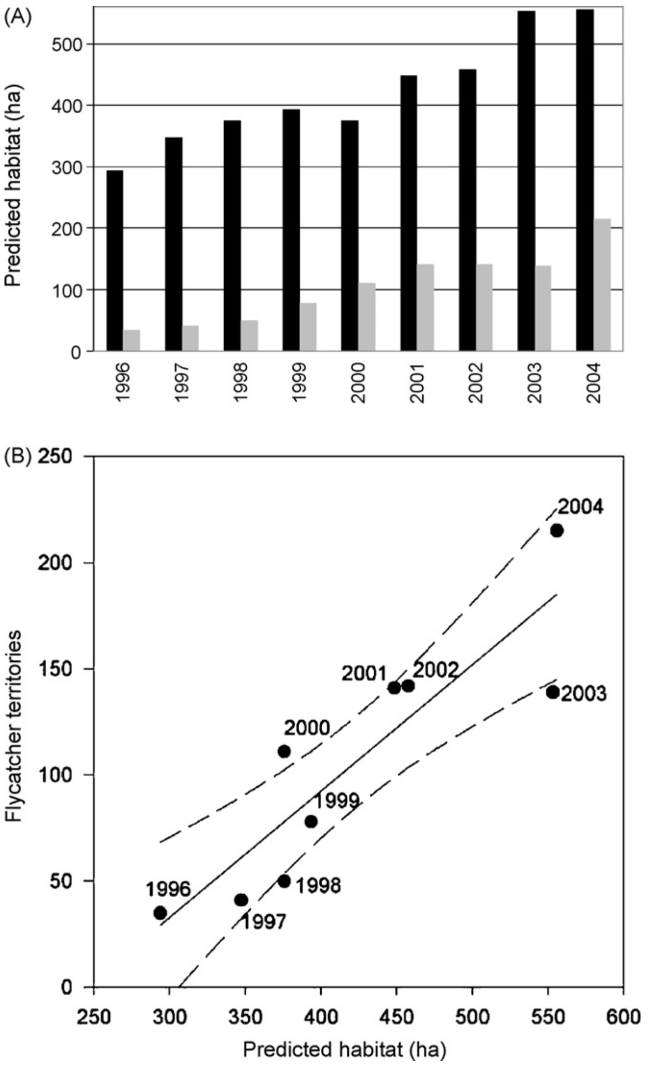

Fig. 6. Amount of predicted flycatcher breeding habitat output by model 4 between 1996 and 2004 (black bars) and number of flycatcher territories (gray bars) (A). Also displayed is the linear relationship between amount of predicted breeding habitat and flycatcher territories at Roosevelt Lake, as output from model 4, between 1996 and 2004 (B).

2007). Thus, it is the cyclic filling and emptying of the reservoir that creates high quality habitat for the flycatcher.

Two covariates (ND_SD4 and ND_BEST4) of intermediate scale (120-m radius; 4.5 ha) were found to be important in three of our models. With a scale that corresponds to the upper size range of a flycatcher territory (Cardinal and Paxton, 2005), they likely characterized canopy roughness, patchiness, habitat mosaics, openings, and different vegetation types. Found to be important in previous studies (Hatten and Paradzick, 2003; Paradzick, 2005), they suggest that beyond dense riparian vegetation, flycatchers choose habitat that is heterogeneous in structure. This may be related to the availability of exposed song perches (Sedgwick and Knopf, 1992) or foraging openings in the vegetation (Barlow and McGillivray, 1983; Sedgwick, 2000; Sogge, 2000).

4.2. Spatiotemporal modeling

The spatiotemporal model (model 4) obtained the best fit to the flycatcher breeding population between 1996 and 2004, underscoring the importance of capturing dynamic growth patterns in riparian vegetation when modeling flycatcher habitat. Although there is evidence that flycatchers will visit young habitat in a year or two preceding being occupied (Paxton et al., 2007), it is likely that flycatchers determine suitability in the year that they settle into a territory. Therefore, the temporal aspects of the model may be a surrogate for features that the model cannot measure directly but that flycatchers use to determine age and suitability. For example, vegetation density can be inferred from NDVI, but multiple years of high NDVI values in the same place may reflect a more static, homogeneous, mature vegetation structure.

The spatiotemporal model included a 6-year mean (MOD_MN6) and SD (MOD_SD6) of model probabilities, enabling it to more fully identify vegetation of the right age, size and structural diversity that breeding flycatchers preferred. Specifically, the temporal variables captured the stochastic water-level fluctuations at Roosevelt Lake over a range of years (1999–2004) compared to model 3, which characterized distance to water for a single year (2004). The ability to discriminate the age of the vegetation was particularly important near the water's edge where young vegetation sprouted up repeatedly as the water level fluctuated seasonally. Young vegetation close to the water's edge provides strong NDVI signatures that can confound our models, because flycatchers do not occupy the vegetation until it is 3 or 4 years of age (Hatten and Paradzick, 2003;

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Paradzick and Hatten, 2004). The spatiotemporal model was able to partially overcome the age misclassification problem, thereby making it more specific and accurate from a temporal scale. However, model specificity often comes at a cost, and model 4 appears to have achieved a better temporal accuracy at a cost to model sensitivity (i.e., higher omission error) in 2004 (see Table 3). Therefore, the questions being asked should drive the models used, with full awareness of the tradeoff between accuracy in a given place and time, versus generality.

Clearly, the dynamic habitat that flycatchers prefer is best described by models that characterize temporal changes in vegetation. While a temporal characterization of NDVI has been found to be important in a range of vegetation studies that classify vegetation based upon productivity or phenology (Moody and Johnson, 2001; Morisette et al., 2006; Baker et al., 2006), to our knowledge this is the first time our NDVI-based approach has been used to characterize avian breeding habitat. Although Greco et al. (2002) characterized yellow-billed cuckoo (*Coccyzus americanus*) patch dynamics over a period of decades with aerial photography and a vegetation classification, their approach required considerable digitizing and photo-interpretation to implement. The strength of our approach is that it can be automated to characterize important characteristics of riparian vegetation and to characterize the temporal dynamics of patch habitat directly off of Landsat Thematic Mapper imagery. Our approach might also be used to distinguish different tree species that exhibit unique phenologies as a result of changing seasons (Morisette et al., 2006) through the incorporation of late-season imagery, versus same-date imagery in different years. A multi-season approach might also help us to incorporate species-specific information about riparian vegetation that we currently lack, such as species or seral stage.

4.3. Breeding habitat and population size

From 1996 to 2004 the size of the breeding-flycatcher population at Roosevelt Lake increased nearly an order of magnitude (Ellis et al., 2009), while predicted habitat nearly doubled. We found the flycatcher breeding population was highly correlated with the amount of predicted habitat ($r = 0.89$; $P < 0.001$), suggesting that habitat availability was a dominant controlling factor. A lack of an inflection in Fig. 6B indicates that the flycatcher population had not yet reached carrying capacity, suggesting Roosevelt Lake's deltas can likely support more territories. While the overall relationship was linear, the year-to-year tracking of the flycatcher population in relation to predicted habitat suggests that the population spurted and lagged. For example, predicted habitat showed a rapid increase in available habitat from 1996 to 1999 (Fig. 6A) before leveling off in 2000, but the flycatcher population lagged before increasing rapidly to occupy the new habitat (Fig. 6B). The amount of predicted habitat increased again from 2000 to 2002, but a severe drought in 2002 (Paxton et al., 2007; Ellis et al., 2009) reduced the number of breeding flycatchers, and greatly reduced productivity, such that the 2003 population declined slightly. Favorable environmental conditions returned in 2003 which allowed the flycatcher population to increase rapidly in 2004 (Ellis et al., 2009). Thus, while the amount of available habitat may set an upper limit to the size of the population, the actual population size in a given year depends on the amount of habitat and population dynamics.

Our modeling suggests that in the most favorable year (2004) there was 553 ha of predicted habitat, as output from model 4, and 215 flycatcher territories, which equals ∼2.6 ha/territory. Other flycatcher studies that have used different models and techniques have found habitat requirements of ∼0.5–4.5 ha/territory (Hatten and Paradzick, 2003; Brodhead, 2005; Cardinal and Paxton, 2005). Flycatcher territory densities were lowest in 1996 and 1997 (∼0.11–0.25/ha) when our study began and the reservoir was near capacity and population sizes were small, and greatest in 2004 (0.3–0.4/ha) after a prolonged reservoir drawdown and rapid increase in both habitat and number of breeding flycatchers. Thus, even for the same location, the exact relationship between the amounts of habitat (in ha) needed per flycatcher will vary depending on a number of complex factors.

Predicting an exact amount of breeding habitat for flycatchers is difficult and the amount of predicted habitat can vary for three important model-based reasons. First, while we have a very strong relationship between the increase in predicted habitat and the flycatcher population size at Roosevelt Lake between 1996 and 2004, our model was fitted to a time period when the lake's water level was descending, albeit unsteadily (see Fig. 1B). However, it is uncertain how well our model's predictive power would be during a period when the lake level is ascending. We can say that higher water levels restricted the amount of predicted flycatcher habitat at Roosevelt Lake to between 70 and 185 ha since 2005 (on the 2006–2009 post-flood era, unpublished data), which greatly reduced the flycatcher breeding population (Ellis et al., 2008b, 2009). Second, different models based on different combinations of variables will vary in the amount of predicted habitat. Third, all of our models produced suitability probabilities per spatial cell that ranged from ∼0 to 98%. While flycatchers are more likely to be found in high-probability areas, some were found in low-probability areas. To predict flycatcher habitat, a cutpoint or probability threshold needs to be chosen at which high-probability habitat is dichotomously distinguished from low-probability habitat. For all models, the lower the probability cutpoint that was used, the greater the amount of predicted habitat and the more sensitive the performance, but at a cost of lower specificity. Inversely, as the cutpoint was increased, model sensitivity decreased while model specificity increased. This is an issue inherent with all models of this kind and there is no perfect cutpoint.

4.4. Management implications

We identified important relationships among predicted flycatcher breeding habitat, Roosevelt Lake's mean-June water-surface elevation, and the breeding population through time (1996–2004). This information could prove useful in water-management plans at Roosevelt Lake in order to insure the flycatchers' long-term survival. While not our goal, the probabilistic models we developed could be used to develop a decision support system (DSS) that balances water demands of metropolitan areas with habitat availability for flycatchers, or other riparian obligate species. Our approach could be applied to other reservoir systems as well, but the models ideally should be customized (i.e., refit) for each system to account for differences in topography, hydrology, and the ecology of the target species. Specifically, our models suggests that careful manipulation of lake levels at the right time of the year, over a period of years, could result in the creation and maintenance of critical habitat necessary to sustain flycatcher populations. The ability to create and manage riparian habitat for populations of flycatchers and other riparian obligate species will become increasingly important if predictions of climate change do result in a drier, hotter climate in the Southwest (Seager et al., 2007) and reduced stream flows (Ellis et al., 2008a). Our models can also be used to prioritize flycatcher survey efforts, or for planning restoration and enhancement activities. Using the GIS models for restoration activities could allow for adaptive restoration efforts, where different treatments are tracked and judged by the models, and future restoration efforts adjusted according to response of riparian habitat.

We explained 79% of the variability in the flycatcher breeding population at Roosevelt Lake with a spatiotemporal model, demonstrating that habitat availability and persistence are strong

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limiting factors. Some of the modeling techniques featured in this paper can be utilized by scientists and managers to gain further insight into single- or multiyear relationships between a target species and its habitat. Of particular importance is that we derived these models from data extracted from DEMs and Landsat Thematic Mapper scenes without relying on a preexisting land-cover classification map. Our approach eliminated the cost associated with producing a land-cover classification, is consistently repeatable, and broadly applicable to other areas and ecosystems. Coupling videography obtained from repeat Landsat imagery (see attached videos in Appendix D) to probabilistic models enabled us to see patterns in habitat selection, creation, persistence, and destruction that would have been difficult to visualize or comprehend otherwise. Once expensive, the USGS EROS Data Center now provides Landsat TM imagery free of charge. We encourage managers and scientists to consider an approach similar to ours when investigating complex, dynamic systems that change frequently, such as riparian ecosystems.

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Appendix A. Modeling overview (continued)

Using flycatcher presence/absence data obtained between 1996 and 2005, we built and tested multiple models of flycatcher breeding habitat at Roosevelt Lake. We used logistic regression to determine the associations between environmental variables and flycatcher territory occurrence, and a GIS to map the probability of territory occurrences for each model tested. We developed two kinds of multivariate logistic-regression models, spatial and spatiotemporal. We created spatial models by fitting territory locations to a single season of habitat data (2004) that was obtained during the period that breeding occurred (late June). In contrast, we created spatiotemporal models by fitting flycatcher territory locations to temporal variables that described the stability and variability in riparian vegetation over multiple breeding seasons (i.e., 6 years). We accomplished this with a GIS by running a spatial model (usually model 1) repeatedly on the same time period (late June), over multiple years, and summarizing the stability and variability in predicted habitat with descriptive statistics (i.e., mean, SD). A temporal analysis of a species' habitat is important for understanding processes within a system (Henebry and Merchant, 2002; MacKenzie et al., 2006), such as patch dynamics (Greco et al., 2002). A temporal profile of NDVI can also provide useful information for discriminating vegetation classes based on their phenology (Moody and Johnson, 2001; Morisette et al., 2006).

We compared the spatial and temporal fit of both types of models with a classification table and a 10-year breeding-flycatcher population database, respectively. The classification table contained a set of presence/absence sites that was not used in model development in order to test model accuracy. We used the best performing models to quantify the amount of predicted breeding habitat between 1985 and 2005 inside the project area. Quantifying predicted breeding habitat with multiple models allowed us to visually and quantitatively assess uncertainty in our estimates.

We used linear regression to identify factors that limited the amount of flycatcher breeding habitat that formed between 1985 and 2005. For this analysis, we focused upon Roosevelt Lake's mean-June water-surface elevations during the breeding season (June) and the amount of rainfall that occurred during the proceeding fall, winter and spring periods (October–April). We focused upon water-surface elevation because it has been shown to influence the amount of flycatcher breeding habitat at Roosevelt Lake due to floodplain inundation (Paradzick and Hatten, 2004). We examined rainfall because it strongly influences lushness and vigor of vegetation, i.e., NDVI (Hess et al., 1996; Moody and Johnson, 2001), an important characteristic of flycatcher breeding habitat (Hatten and Paradzick, 2003; Paxton et al., 2007).

We used linear regression to examine the fit of each models' output (i.e., amount of predicted habitat) to breeding-flycatcher population estimates between 1996 and 2004 ($n = 9$), equating the breeding population to the number of flycatcher territories each year. In addition to the quantity of predicted habitat, we examined the influence of the mean-June water-surface elevation, rainfall (same as above), and habitat fragmentation. We characterized the degree of fragmentation in predicted habitat over the entire project area (i.e., the landscape) with FRAGSTATS (McGarigal and Marks, 1995), a software program that calculates over 100 fragmentation metrics. Some of the fragmentation metrics we examined were number and average size of patches, variation in patch size, total length of edges, cohesion, dispersion, average distance between patches, and a landscape shape index (McGarigal and Marks, 1995).

Appendix B. Spatial variables (continued)

We created riparian-vegetation density grids (0.09 ha cells) for the project area with TM imagery and ERDAS® Imagine software (Atlanta, GA). We selected TM images (path 36, row 37) that were acquired during cloud-free periods inside the months of June or July 1985–2005. The TM images were radiometrically and geometrically corrected by EROS Data Center (USGS) for maximum accuracy and change detection. We created riparian-vegetation density variables (i.e., grids) in a manner similar to Hatten and Paradzick (2003): (1) we calculated the Normalized Difference Vegetation Index (NDVI), which correlates with relative density and biomass of green vegetation (Avery and Berlin, 1992), within approximately 1.6 km of perennial/intermittent waters; (2) we distinguished riparian vegetation from non-riparian vegetation by selecting NDVI values > 0.126; and (3) we created two additional riparian-vegetation density variables found to be important by selecting NDVI values > 0.336, or >0.413 (Table 1).

We characterized vegetation and floodplain features at multiple spatial scales (0.09–72 ha) with circular moving windows (i.e., neighborhood functions) and stored results from each operation in a separate grid (ESRI, 1992). We calculated the proportion of neighborhood covered in dense vegetation (NDVI > 0.33 or 0.41) off of TM imagery, and size of floodplain off a DEM with a GIS. We identified distances between riparian and non-riparian features, such as from the center of a patch to its exterior edge, or to water. We extracted the lake's water-surface boundary off of a TM image each year by selecting an NDVI value < −0.20 because reflected infrared (TM band 4) is absorbed by water, resulting in very low NDVI values (Avery and Berlin, 1992). To calculate the distance of a flycatcher

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territory to the river channel, we digitized the Salt and Tonto channels off of a 2002 TM image in June when the lake reached its lowest level of our study (∼624 m). This technique was sufficient for temporal analyses because the river channels did not migrate between 1985 and 2005. We characterized heterogeneity in vegetation density with a moving window, calculating the standard deviation among 12 NDVI classes (Hatten and Paradzick, 2003). We examined the influence of various habitat fragmentation metrics (e.g., calculating the number and size of patches in the study area) on flycatcher occurrence with GIS and FRAGSTATS software (McGarigal and Marks, 1995). We calculated patches, which are distinct, contiguous areas (i.e., polygons), from a vegetation grid (NDVI > 0.413) because it has been shown to be highly influential in territory selection (Hatten and Paradzick, 2003).

We created our spatiotemporal variables in several steps. First, we ran a spatial model (model 1; Table 4) in successive years, populating it with vegetation characteristics specific to each year with a TM scene. Second, we calculated five probability classes for each year modeled with predefined probability thresholds (e.g., 0–20%, 21–40%) because higher probability classes are known to contain greater densities of flycatchers (Hatten and Paradzick, 2003; Hatten and Sogge, 2007). Third, we characterized whether the quality of flycatcher breeding habitat increased or decreased by subtracting the 5 probability classes between years. This technique results in an interval-scale change-detection variable (grid) that contains values from −5 to 5 (Paradzick and Hatten, 2004). A negative value indicates a decrease in habitat quality, while a positive value indicates an improvement. Statistical GIS functions (e.g., FOCALMEAN, FOCALSTD) were used to characterize the stability or variability of habitat within each cell (ESRI, 1992). A larger mean indicates that the flycatcher habitat was of higher sustained quality over the time interval examined. Conversely, a bigger SD indicates that there was more variability in habitat quality over the time interval examined.

Appendix C. Statistical design (continued)

To examine habitat associations at multiple spatial scales (Ripple et al., 1991), we characterized vegetation and floodplain features within different-size neighborhoods of breeding and nonuse locations. We characterized variables at multiple scales (0.3–72 ha) within concentric circles (e.g., amount of densest vegetation) or within irregularly shaped contiguous patches (i.e., patch size) that could be any size. We defined fine scale as 0.09–1.1 ha, with 0.09 ha equal to the 30-m resolution of TM imagery, and 1.1 ha corresponding to the upper end of flycatcher territory size (Cardinal and Paxton, 2005). We selected intermediate (2.5–28 ha) and coarse scales (>41 ha) to characterize riparian forest patches and floodplains, respectively (Hatten and Paradzick, 2003).

We adjusted our database to minimize the effects of temporal and spatial autocorrelation (Legendre, 1993) because breeding flycatchers have high patch fidelity (up to 78%) between years (Luff et al., 2000) and are tightly clustered (Hatten and Paradzick, 2003). At Roosevelt Lake, the mean nearest neighbor (MNN) distance between territories was ∼59 m. We reduced clustering in the data by randomly removing 50% of territories, resulting in a MNN of ∼103 m. All territories that were withheld from model development stage were used for model verification. We reduced temporal correlation (i.e., site fidelity) in the data by only using a single season of breeding territories (2004) when constructing the model. The adequacy of this approach was tested with multiple years of data (i.e., linear regression). To reduce the chance of producing overfit models resulting from too many variables (i.e., too few events per variable [EPV]), we maintained an EPV ≥ 10 (Peduzzi et al., 1996). Thus, we limited the number of covariates in each model to ≤10.

Appendix D. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2010.03.026.

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