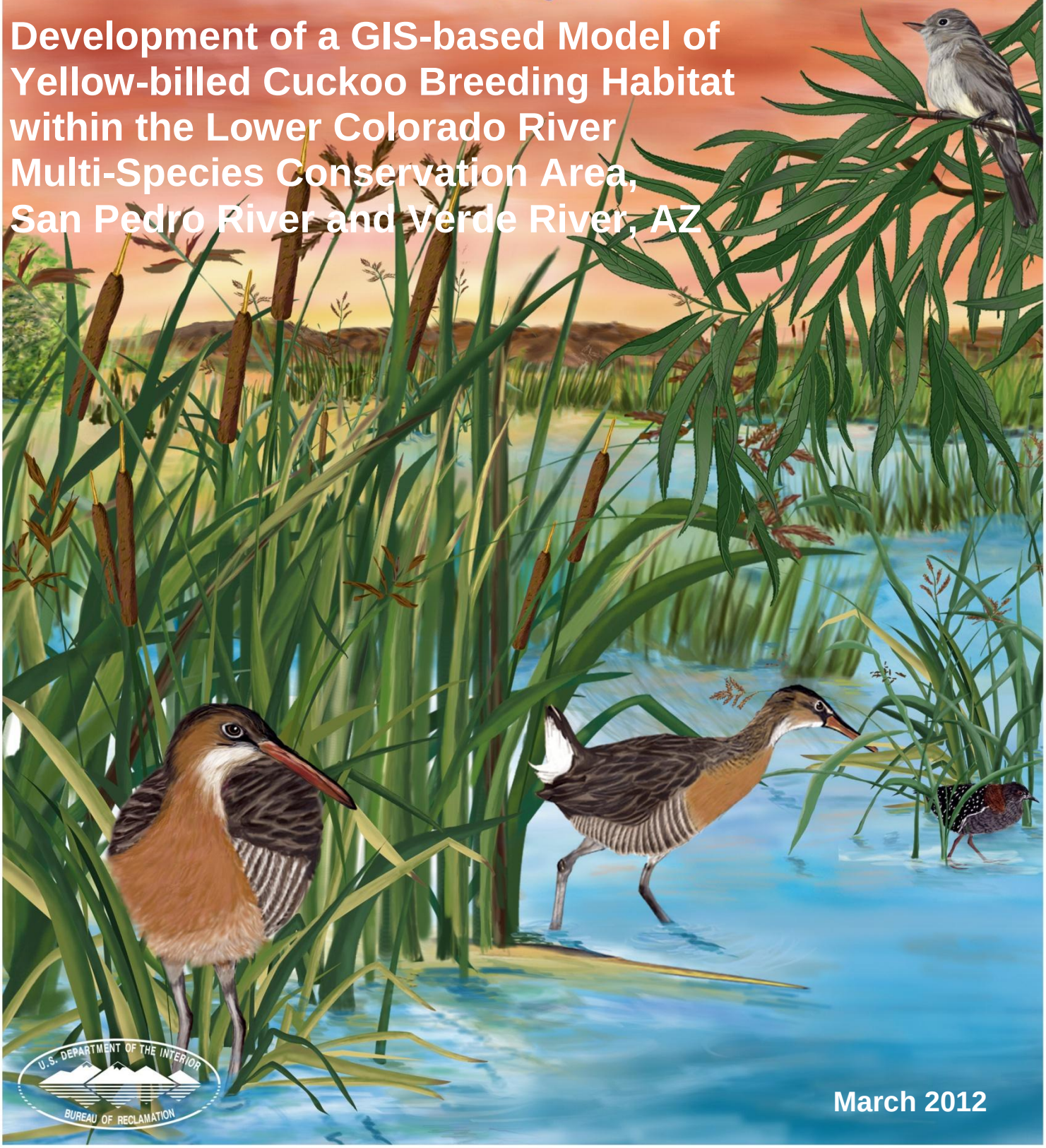
Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

Development of a GIS-based Model of Yellow-billed Cuckoo Breeding Habitat within the Lower Colorado River Multi-Species Conservation Area, San Pedro River and Verde River, AZ



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Lower Colorado River Multi-Species Conservation Program

Development of a GIS-based Model of Yellow-billed Cuckoo Breeding Habitat within the Lower Colorado River Multi-Species Conservation Area, San Pedro River and Verde River, AZ

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EXCUTIVE SUMMARY

This report summarizes the results of the project *Development of a GIS-Based Model of Yellow-billed Cuckoo* (*Coccyzus americanus occidentalis*) *Breeding Habitat within the Lower Colorado River Multi-Species Conservation Area, San Pedro River and Verde River, AZ,* funded by The Lower Colorado River Multi-Species Conservation Program (LCR MSCP 2004). The goal of our project was to provide management agencies with the knowledge necessary to conserve and enhance yellow-billed cuckoo breeding habitat along the Lower Colorado River and its tributaries. Specific objectives to accomplish our goal were: (1) characterize and map yellow-billed cuckoo (hereafter "cuckoo") breeding habitat inside the LCR MSCP boundaries; (2) develop a GIS-based probability model of cuckoo breeding habitat; and (3) extrapolate and verify the cuckoo model inside (LCR MSCP) and outside (Verde and San Pedro rivers) the project area. We hypothesized that cuckoo breeding locations are typically associated with broad floodplains, moderately rough terrain, and large, vigorous riparian vegetation, dominated by cottonwood and/or willow trees.

For habitat characterization and logistic-regression model construction, we used cuckoo breeding locations collected in 2006, as well as vegetation data and floodplain features obtained from satellite imagery, orthorectified digital aerial photography, and a digital elevation model (DEM). We used multivariate logistic regression to identify significant associations among cuckoo occurrences and biophysical features, and to test hypotheses. We tested two different types of models: Satellite-based and Map-based (Aerial). The Satellite model characterized vegetation features surrounding cuckoo breeding locations off of Landsat5 Thematic Mapper imagery, identifying vegetation density and structure with the Normalized Difference Vegetation Index [NDVI]). In contrast the Aerial model characterized vegetation types (aerial cover of species, communities) surrounding cuckoo breeding locations off of a vegetation map obtained from orthorectified digital aerial photography. We examined both techniques because each provided unique information and had different strengths and weaknesses. The Satellite model was presumed to be advantageous because of the remote mapping capability of large tracts of riparian vegetation every 16 days, with near perfect repeatability: however, it lacks the ability to identify specific plant communities. The Aerial model had the advantage of producing relatively accurate vegetation cover maps, but this approach is relatively expensive and difficult to repeat.

We hoped a dual approach to modeling would result in the most useful information for the management and conservation of cuckoo breeding habitat. We tested the accuracy of each model's predictions with an independent set of cuckoo locations obtained the following year (2007).

The Satellite and Aerial models informed us about several important features associated with cuckoo breeding habitat. First, a core area of dense cottonwood/willow within a 120-m radius (4.5 ha) of a location increased the chances of cuckoo occurrence. The likelihood of cuckoo occurrence continued to increase if the core area was surrounded by a large, native forest (480 m radius/72 ha) that contained lots of structural diversity. Third, a landscape of moderate topographic roughness (i.e., the Bill Williams NWR) further increased the odds of cuckoo occurrence. The odds of cuckoo occurrence decreased rapidly when too much tamarisk surrounded the site. When we challenged the 2006 model with 2007 data we obtained accuracies between 75 - 80% inside the LCR MSCP boundary. A correlation analysis found the Satellite and Aerial models' predictions were significantly correlated, indicating the Satellite model indirectly characterized structural features and vegetation types important to breeding cuckoos.

An important finding of this project is that there were higher number of cuckoo detections in areas that our habitat models predicted to be most suitable (i.e., higher-probability classes), making them useful to management agencies for conservation and restoration purposes. The Satellite model appeared more accurate on reaches with large floodplains and broad riparian patches, while the Map model produced better results on reaches with smaller floodplains and riparian patches. The accuracy of the Satellite model was mixed and somewhat ambiguous outside the project area, so we recommend it be used with caution outside the LCR MSCP boundary, and only with field verification.

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INTRODUCTION

This report summarizes the results of the project, "*Development of a GIS-Based Model of Yellow-billed cuckoo* (*Coccyzus americanus occidentalis*) *breeding habitat within the Lower Colorado River Multi-Species Conservation area, San Pedro River and Verde River, AZ,*" funded by the Lower Colorado River Multi-Species Conservation Program (LCR MSCP 2004).

The LCR MSCP is a coordinated, long-term, multi-agency effort to conserve native species, work towards the recovery of endangered species, and protect and maintain wildlife habitat on the lower Colorado River. The LCR MSCP Habitat Conservation Plan (HCP) measures are designed to meet the biological goals for 26 covered species, including the western yellow-billed cuckoo. These goals include maintaining important existing habitat areas, and creating and maintaining new habitat. Hence, there is a need to measure and predict yellow-billed cuckoo habitat, to discover areas that might support cuckoos, and to identify areas that may develop into appropriate habitat.

One of the key challenges facing the management and conservation of the yellow-billed cuckoo is that the riparian areas in which the cuckoo nests are dynamic, with individual habitat patches subject to cycles of creation, growth, and loss due to drought, flooding, fire, and other disturbances (Webb et al. 2007). Former breeding patches can lose suitability, and new habitat can develop within a matter of only a few years, especially in reservoir drawdown zones and locations where water is available (Johnson et al. 2008). Therefore, describing and predicting yellow-billed cuckoo habitat - either to discover areas that might support cuckoos, to identify areas that may be developed into appropriate habitat, or to develop criteria for created habitats - requires knowledge of recent/current habitat conditions and an understanding of the factors that determine cuckoo use of riparian sites.

In the past, much of the determination of whether a riparian site is likely to support cuckoos has been based on qualitative criteria (e.g., "dense vegetation" or "large patches"), often by on-the-ground field evaluations by local or regional experts. Information regarding cuckoo habitat requirements is almost entirely limited to descriptions of patch-level vegetation characteristics and composition, generally described as consisting of multi-structured or multi-layered riparian vegetation with substantial canopy cover provided by native riparian trees (Hamilton and Hamilton 1965, Rosenberg et al. 1991, Laymon et al. 1997, Corman and Wise-Gervais 2005, Johnson et al. 2007, 2008, 2010) and patch size (Gaines and Laymon 1984, Laymon and

Halterman 1989, Halterman 1991, Laymon et al. 1997, Holmes et al. 2008). Yet, there is evidence that consideration of patch-level habitat variables alone does not adequately describe yellow-billed cuckoo breeding habitat requirements (Johnson et al. 2007, 2008; Johnson 2009), and the effects of landscape-level habitat characteristics should also be considered in order to understand the factors that affect cuckoo habitat use.

The goal of our project was to provide management agencies with the knowledge necessary to conserve and enhance yellow-billed cuckoo breeding habitat along the Lower Colorado River and its tributaries. Specific objectives in order to accomplish our goal were as follows: (1) characterize and map yellow-billed cuckoo (hereafter "cuckoo") breeding habitat inside the LCR MSCP boundaries; (2) develop a GIS-based probability model of cuckoo breeding habitat; and (3) extrapolate and verify the cuckoo model inside (LCR MSCP) and outside (Verde and San Pedro rivers) the project area.

Spatially explicit habitat suitability models provide powerful tools for identifying habitat requirements of target species at multiple spatial scales. Such models are useful for managers because they increase understanding of the ecology of the target species, while providing site-specific information in the form of GIS habitat maps. They can identify the relative "importance" of individual variables (or combination of variables) in influencing the distribution of a species. In addition, habitat models derived from remote sensing have proven repeatability and usefulness in landscape analyses (Scott et al. 2002, Hatten et al. 2010).

We developed spatially explicit (i.e., GIS-based) models to identify yellow-billed cuckoo breeding habitat within the LCR MSCP boundaries. Using existing data on cuckoo distribution and abundance within the planning area (Johnson et al. 2007, 2008), the Verde River watershed (Holmes et al. 2008), and the San Pedro River (Halterman 2004 and 2005, Johnson et al. 2006), we examined the effects of landscape-scale habitat variables on cuckoo distribution and identified features that constitute high quality cuckoo habitat within the planning area. This information can contribute to increased effectiveness of LCR MSCP actions for the cuckoo and is vital for making informed decisions concerning the selection of areas for habitat conservation, and the assessment of alternative designs and management for riparian restoration to conserve the cuckoo. Thus, this project contributes to meeting the LCR MSCP goal to avoid, minimize, and fully mitigate adverse effects of covered activities and LCR MSCP implementation on the cuckoo.

BACKGROUND

Conservation status

Western yellow-billed cuckoos have historically bred in riparian areas from western Washington to northern Mexico, including Oregon, southwestern Idaho, California, Nevada, Utah, western Colorado, Arizona, New Mexico, and western Texas (American Ornithologists' Union 1983, 1998). Although analysis of population trends is difficult because quantitative data, including historic population estimates, are generally lacking, rough extrapolations of historic and current information suggest that the yellow-billed cuckoo's habitat distribution, range, and population numbers have declined substantially across much of the western United States over the past 50 years (USFWS 1985, USFWS 2002).

Along the lower Colorado River, yellow-billed cuckoos were once considered abundant throughout the riparian floodplain (Stephens 1903, Grinnell and Miller 1944). A substantial population of cuckoos was detected north of Laguna Dam during the 1960s and 1970s (Hamilton and Hamilton 1965, Gaines and Laymon 1984). During surveys in the 1970s and 1980s a dramatic decline of the species was noted along the lower Colorado River. In 1976–77, the lower Colorado River and its tributaries in both Arizona and California supported an estimated 180–240 pairs, a number that had declined by an estimated 80–93 percent by 1986 (Laymon and Halterman 1987a, Rosenberg et al. 1991), coinciding with habitat loss from high water levels of long duration in 1983–84 and 1986 (Laymon and Halterman 1987b, Ohmart et al. 1988, Rosenberg et al. 1991). In 1998, no pairs were found in California west of the Colorado River that had been occupied in 1976–77 (Halterman 1998). Losses have been greatest at lower elevations, below 900 m (3000 ft) along the lower Colorado River and its major tributaries, which have been strongly affected by upstream dams, flow alterations, channel modifications, and clearing of land for agriculture (Groschupf 1987).

Since the 1960s, the largest known population of yellow-billed cuckoos in the region has been located along the lower Bill Williams River, a tributary of the Lower Colorado River. The riparian habitat within the Bill Williams River National Wildlife Refuge is the most continuous, unfragmented habitat of its kind in the lower Colorado River Basin and recent surveys (Johnson et al. 2007 and 2008) confirm that it continues to have the largest yellow-billed cuckoo population along the Lower Colorado River.

On 25 July 2001, findings by the U.S. Fish & Wildlife Service (USFWS) determined that the western yellow-billed cuckoo (i.e., populations west of the continental divide) represents a distinct population segment and warrants protection under the Endangered Species Act as "threatened," but that listing of the cuckoo was precluded by other higher priority listing actions (USFWS 2002). Probable factors believed to have contributed to population declines in the West are the loss, fragmentation, and alteration of native riparian breeding habitat, the possible loss of wintering habitat, and pesticide use on breeding and wintering grounds (Gaines and Laymon 1984, Franzreb 1987, Laymon and Halterman 1987a, Hughes 1999).

Cuckoo surveys

The USFWS initiated statewide yellow-billed cuckoo surveys in Arizona, in 1998. Cuckoos were documented along 25 drainages. The primary concentrations in Arizona were along the Agua Fria, San Pedro, and Verde rivers, Cienega and Sonoita creeks, and the Bill Williams River within the lower Colorado River region (Johnson et al. 2010). Surveys for cuckoos were conducted in the Verde River watershed in 2004 and 2005, and cuckoos were detected at 59% (n=37) of the sites surveyed, in riparian habitat dominated by native tree species (Holmes et al. 2008). Areas along the San Pedro River were surveyed by M. Halterman (Halterman 2004 and 2005) and M. Johnson (Johnson et al. 2006a). Cuckoos were found to be relatively common in riparian habitats along the San Pedro River, where substantial amounts of riparian habitat, including large mesquite bosques exist.

The survey data we used for modeling are from surveys conducted in 2006 and 2007 by M. Johnson and others of the USGS, under the LCR MSCP (Johnson et al. 2007, 2008). These surveys were part of a project to document western yellow-billed cuckoo distribution, abundance, and habitat use throughout the LCR MSCP boundary area. Surveys employed the use of playback recordings of cuckoo calls; this method is used because it increases the number of detections of this secretive, elusive species. When a cuckoo was detected during a survey, the UTM coordinates of the survey point, the estimated number of individual cuckoos detected, and the estimated distance and direction (i.e., the compass bearing) from the surveyor to the detected cuckoo were recorded (Halterman et al. 2006). Cuckoo locations were subsequently mapped in a geographic information system (GIS).

In 2006, yellow-billed cuckoos were surveyed at 55 sites in the LCR MSCP area, between 11 June and 13 September. Cuckoos were detected at 27 of the 55 sites, primarily at the Bill Williams River National Wildlife Refuge (NWR) sites (n = 117 detections) and the Grand Canyon National Park–Lake Mead National Recreation Area delta sites (n = 29 detections). In 2007, cuckoo surveys were conducted at 40 sites between 11 June and 9 September. Cuckoos were detected at 25 of the 40 sites, primarily at the Bill Williams River NWR study area (n = 139 detections; 85 percent of all detections).

Survey data used in model verification were acquired in 2005 for the Verde River (*n* = 88; Holmes et al. 2008). Survey data used in model verification along the San Pedro River (*n* = 281) were collected by M. Halterman (Halterman 2004, 2005) and M. Johnson (Johnson et al. 2006a).

METHODS

Modeling Overview

We started our modeling project by developing a conceptual model of yellow-billed cuckoo breeding-habitat selection (**Figure** 1)**.** Embedded in the conceptual model is a set of hypotheses that we tested with multivariate logistic regression (Hosmer and Lemeshow 1989). We hypothesized that selection of breeding habitat would be influenced by riparian patch size, vegetation density, structure and community, habitat fragmentation, and patch location in relation to land use/cover (e.g., agriculture, urban development, water) on habitat selection. We tested our hypotheses with two classes of models: (1) Satellite models, which characterized vegetation from Landsat Thematic Mapper (TM) imagery; and (2) Aerial models, which characterized vegetation from orthorectified digital aerial photography. The major difference between these two techniques was resolution - Landsat TM imagery has 30 X 30-m pixel-to-ground resolution, while the aerial photography used to create vegetation maps had a 3 X 3-m pixel-to-ground resolution. We used Landsat TM imagery to provide coarse-scale information about riparian vegetation features such as structure, lushness, and spatial arrangement. In contrast, we used maps of vegetation cover types created from the aerial photography to identify vegetation species and patch extents. The Aerial-model vegetation map for the Lower Colorado River was created by Bio-west, Inc. (2006), and we created the Bill Williams River vegetation map.

Satellite and Aerial model development and testing followed a 6-step process. First, we created a yellow-billed cuckoo use/nonuse map of the project area for the 2006 breeding season.

Second, we developed a spatial database of vegetation and floodplain features that were extracted from Landsat Thematic Mapper (TM) imagery or maps created from the digital aerial photography. Third, we used logistic regression to test a set of hypotheses, identify significant associations between cuckoos and biophysical variables, and to build and test predictive models. Fourth, we created a probability map that depicts the likelihood of cuckoo habitat based upon a specific logistic-regression equation. Fifth, we tested (i.e., challenged) the spatial model(s) with a set of cuckoo locations obtained on the LCR the following year (2007). Sixth, we extrapolated the Satellite model (but not the Aerial model) to reaches of the Verde and San Pedro rivers. Extrapolation and testing of the Satellite model outside the project area was straightforward since we had the Landsat imagery and cuckoo surveys. Unfortunately, we were unable to extrapolate or test the Aerial model outside the project area due to a lack of vegetation maps created with the same techniques or dates as this study.

Cuckoo Use/Nonuse Map

Creating spatial models of cuckoo breeding habitat required that we develop an accurate map of all cuckoo use/nonuse (i.e., presence/absence, suitable/unsuitable) areas inside the project area. Specifically, we buffered the cuckoo presence locations (point locations from 2006 surveys by Johnson et al.) by 200 m; any cell (30x30 m) within the 200-m buffer was considered cuckoo use areas (i.e., cuckoo presence, suitable habitat). We considered 200 m to be a conservative estimate of the minimum distance a cuckoo moves, based on field observations. Next, we buffered the absence locations (point locations from 2006 surveys by Johnson et al.) by 200 m; any cell within the absence buffer was considered unsuitable (i.e., a nonuse area). Wherever a use polygon overlapped a nonuse polygon, due to the sample locations being closer than 400 m, the use polygon took precedence. Thus, all cells that fell within the use buffers were considered suitable habitat, even if a subsequent survey in the same season found it to be empty. We used a GIS to randomly generate hundreds of use and nonuse sampling points throughout the project area, split equally between groups, with no more than one point per cell. Our sampling approach resulted in 148 random points; 73 points fell inside nonuse areas (i.e., cells) and 75 fell inside use areas.

Biophysical Database

Satellite Vegetation maps

Following an approach that was developed for southwestern willow flycatcher (Hatten and Paradzick 2003), we created a biophysical dataset for modeling from Landsat Thematic Mapper (TM) imagery and a digital elevation model (DEM). By stitching together multiple Landsat Thematic Mapper images and DEMs, we covered the entire LCR MSCP boundaries (**Figure 2**). Specifically, we extracted vegetation characteristics (vegetation quantity and density) from the Landsat TM data, and floodplain characteristics (width, aspect, roughness) off of the DEM. We characterized vegetation density in each 30x30 m cell with the Normalized Difference Vegetation Index (NDVI [band 3 – band 4 / band 3 + band 4]). NDVI values range from -1 to 1; cells that contain small values (i.e., < 0) have little or no vegetation, whereas cells with large NDVI values contain dense, green vegetation (**Figure 3**). This approach allowed us to characterize the relative lushness and density of riparian vegetation throughout the project area.

Aerial vegetation maps

In addition to the models derived from remote sensing data, we wanted to assess yellow-billed cuckoo use of different vegetation types or communities for breeding. To classify vegetation within our study area, we initially used a vegetation map developed by Bio-West, Inc. for the Bureau of Reclamation (Bio-West, Inc. 2006). They classified riparian and marsh vegetation using 2004 color infrared (CIR) orthophotography as the base layer and used the Anderson-Ohmart method of classification (Anderson and Ohmart 1976) to classify vegetation along the lower Colorado, Virgin, Bill Williams, and Gila Rivers. This classification system identifies community and structural type classes. In addition to the Anderson-Ohmart community-structural classes, they added classes to capture non-riparian features (e.g., agriculture, open water). They classified vegetation into 41 community-structural classes (**Appendix 1**). Their accuracy assessment indicated a community level overall accuracy of 72%, while their accuracy for the cottonwood-willow community was 61%. At the structural-type level, their classification accuracy was 37% (Bio-West, Inc. 2006). The vegetation map produced by Bio-West, Inc. was used for most of the project area, but field surveys found it highly inaccurate in the Bill Williams River NWR area (M. Johnson, unpublished data), where the cottonwood-willow class was misclassified. Fortunately, an alternative vegetation map produced

by the U.S. Geological Survey (P. Shafroth, in prep.) was available, and with minimal reclassification effort it was made compatible with the Bio-West, Inc (2006) map (**Appendix 2**).

Floodplain maps

We generated slope and aspect values for each cell within the project area directly off of a 30-m resolution DEM. In order to assess habitat relationships at multiple spatial scales, we used a GIS and moving windows to characterize the amount of floodplain or flat area inside of concentric circles (60 – 900 m; Hatten et al. 2010), and in the creation of a terrain ruggedness index (TRI; Riley et al. 1999) inside a 1600-m radius.

Satellite NDVI variables

We used a GIS to create a secondary (derivative) set of spatial variables extracted from NDVI layers. Each NDVI variable was developed to test a specific hypothesis embedded in the conceptual model. All of the NDVI variables are grids comprised of 30x30 m cells (0.09 ha), because that is the resolution of TM data. For our initial model testing, we developed over a dozen spatial variables (**Table 1**) to characterize vegetation density at multiple spatial scales: (1) within a grid cell (30x30 m, 0.09 ha), (2) inside concentric circles (60 m to 480 m radius, ~1 – 72 ha), or (3) within irregularly shaped patches (~ 1 – 250 ha).

By categorizing vegetation at different NDVI thresholds, we were able to determine riparian patch boundaries and size of riparian patches (Paxton et al. 2007, Hatten et al. 2010). Use of fragmentation software enabled us to characterize the fragmentation and connectivity in the vegetation (McGarigal and Marks 1995). In order to develop as specific a model as possible, we applied a NDVI mask to eliminate all cells that were not comprised of riparian vegetation, i.e., with NDVI values less than 0.126 (Hatten and Paradzick 2003). This cutpoint ensured that randomly generated sample locations did not fall outside of riparian vegetation. To ensure that agricultural fields did not get spectrally confused with riparian vegetation, we applied an agricultural mask that was developed in 1993 for a statewide riparian study (Valencia et al. 1993). We updated the mask by screening out new agricultural fields and urban areas that developed since 1993.

Aerial vegetation variables

Forty-one community-structural classes was an unrealistic number for logistic modeling given the modest number of cuckoo presences observed during 2006 or 2007 in the project area. To prevent over-fitting a logistic regression model, at least 10 presences (cuckoo occurrences)

are required for each covariate in the model, including the constant (Peduzzi et al. 1996). Thus we combined Anderson and Ohmart's vegetation classes into fewer, broader categories, based upon our knowledge of yellow-billed cuckoo ecology and the lower Colorado River ecosystem (**Appendix 1**). The resultant polygon map was converted into a raster dataset with 30x30 m cells represented by the seven reclassified community-vegetation types.

This approach allowed us to characterize vegetation types at the same resolution as the Satellite variables, and conduct analogous analyses. We used a GIS and moving windows to create variables of (1) the amount of each vegetation type, (2) the major, or dominant, vegetation type, (3) the variety (number) of vegetation types, and (4) the heterogeneity of vegetation types, inside of concentric circles (60 m to 480 m radius, ~1 – 72 ha). Each variable was developed to test a specific hypothesis embedded in the conceptual model. For our initial model testing, we developed eleven types of spatial variables (**Table 2**) to characterize vegetation type(s) at multiple scales: (1) within a grid cell (30x30 m, 0.09 ha), (2) inside concentric circles (60 – 480 m radius, ~1 – 72 ha).

Model Construction and Hypothesis Testing

Spatially Explicit Modeling

Logistic regression allowed us to determine what vegetation characteristics and patch configurations (e.g., size or fragmentation) were important to breeding cuckoos. We used GIS to attribute the use and nonuse random points with their respective vegetation and floodplain characteristics that were stored in our spatial database. Thus, for each set of models, all locations contained a common set of attributes that described a set of conditions (e.g., patch size, vegetation heterogeneity, floodplain size, area of vegetation-cover type within a specified neighborhood). We used backwards stepping and the likelihood-ratio test (*G*) to determine what covariates were significant in the model under consideration (Hosmer and Lemeshow 1989) and to test hypotheses. Covariates with the largest *G* values had the greatest influence on the model's log-likelihood and the tightest association with cuckoo presence.

We used Arc/Info® GRID (ESRI 1992) to calculate and map the relative quality of breeding habitat within 0.09 ha (30x30 m) cells. We calculated the relative quality of breeding habitat (P) with the following equation:

$$\mathbf{P_i = e^{g(x)} / 1 + e^{g(x)}} \qquad \textbf{(equation 1)}$$

where g(x) is the linear combination of parameter estimates obtained from the logistic regression (Hosmer and Lemeshow 1989, Keating and Cherry 2004). In equation 1, the relative quality of cuckoo breeding habitat is linked to the model probability based on the logistic regression under consideration. Each model's probabilities were stored in a unique grid; cell probabilities ranged from ~ 0 - 99%.

Model Calibration and Accuracy

To assist in model evaluation and selection (2006 data), and verification (2007 data), we examined model accuracies with four techniques. First, we used classification tables that were automatically generated by SPSS for each model-run, quantifying omission (false negatives), commission (false positives), and overall classification (Story and Congalton 1986). Second, we generated Receiver Operator Characteristic (ROC) Area-Under-the-Curves (AUC) to graphically and quantitatively sum errors at all possible thresholds. Third, we calculated the density of cuckoos observed in 5 model probability classes (20% intervals). Fourth we created binary habitat-suitability maps (suitable or unsuitable) through the application of a single probability threshold. For example, at a 50% threshold, cells with a model probability greater than 50% were considered suitable (habitat), while cells under the threshold were considered unsuitable (not habitat).

For verification, we tested the Satellite and Aerial models with cuckoo locations collected in 2007, which required that we populate the 2006 Satellite model with vegetation features extracted from 2007 satellite imagery. For the Aerial model, we had one species-vegetation map produced in 2004, so we examined cuckoo distribution and accuracy on this map for both 2006 and 2007. In addition, we extrapolated the Satellite model (but not the Aerial model) to reaches along the Verde and San Pedro rivers, overlaid survey data, and calculated model accuracies. To aid in the interpretation of results within and among each test area (Lower Colorado, Verde, or San Pedro), we generated box-and-whisker plots that displayed the range of biophysical variables at cuckoo locations.

RESULTS

Multiple Logistic Regression

Satellite model

We developed multiple models of yellow-billed cuckoo breeding habitat that were comprised of unique combinations of explanatory variables (see **Table 1**), but here we report on the top 2 Satellite models (**Table 3**). Satellite model 1 contained three variables: (1) terrain ruggedness (TRI), (2) heterogeneity in vegetation density in a 480-m radius (ND_SD480), and (3) amount of dense vegetation (NDVI > 0.41) inside a 120-m radius (ND_BEST120). Satellite model 2 contained the same 2 vegetation variables as model 1, but omitted TRI. Most variables listed in **Table 1** were significant in various candidate models, but they lowered model fit when entered into our top two models.

There was considerable contrast between the biophysical values found at presence versus absence locations, with higher median values at presence locations (**Figure 3**, left panel). Backwards stepping and the likelihood-ratio test revealed that terrain ruggedness had the tightest association with cuckoos in the project area (**Table 4**). Broken into increasing levels of terrain roughness (i.e., flat, low, moderate, high), the odds ratios informed us that classes two (low) and four (high) were approximately four times as likely to contain cuckoos as class one (flat), while class three (intermediate roughness) was ~26 times as likely. The amount of dense vegetation (NDVI > 0.41) within a 120-m radius patch (ND_BEST120) was the second most significant covariate in Satellite model 1. The odds ratio informed us that for each 10% increase in dense vegetation inside a 120-m circle, the odds of cuckoo use increased approximately 15%. The heterogeneity in riparian density inside a 480-m radius patch (ND_SD480) was only slightly less influential than ND_BEST120, with the odds ratio informing us that for each 1 SD increase in vegetation-density heterogeneity, the likelihood of cuckoo use increased by 68%. For model 2, the ND_SD480 variable was slightly more influential than ND_BEST120, but both were highly significant.

Aerial Model

Using the Aerial data, we developed multiple models of yellow-billed cuckoo breeding habitat that were comprised of unique combinations of explanatory variables (see **Table 2**), but here we report on the top model (**Table 5**). The top model contained six variables: (1) amount of

saltcedar within a 480 m radius (SC_480), a negative relationship, (2) amount of cottonwood-willow within a 120 m radius (CW_120), a positive relationship, (3) amount of cottonwood-willow within a 480 m radius (CW_480), a negative relationship, (4) amount of open or structured open water within a 480 m radius (OW_480), (5) amount of "other" vegetation types (see **Table 5**) within a 480 m radius (OT_480), a negative relationship, and (6) the standard deviation of the variety (number of) vegetation types surrounding each 30x30 m cell within a 480 m radius (SD_Var480), a negative relationship. This model obtained the best overall classification and model-fit statistics. Other variables listed in **Table 2** were considered and found significant in various candidate models, but produced lower classification and model-fit statistics than our top model.

The odds ratios (**Table 5**) informed us that for each 1 ha increase in the area of saltcedar vegetation type inside a 480 m radius circle, the odds of cuckoo use decreased by 8%. The amount of cottonwood-willow vegetation type within a 120 m radius (CW_120) was also a significant covariate in our model. The odds ratio informed us that for each 1 ha increase in area of cottonwood-willow within a 120 m radius (4.5 ha), the likelihood of cuckoo use increased by approximately 109%. The heterogeneity of vegetation types within a 480 m radius (VEGSD_480) was negatively associated with cuckoo presence. The odds ratios informed us that for each 1 SD increase in the heterogeneity in number of vegetation types within a 480 m radius circle, the likelihood of cuckoo use decreased by 92%. Area of open water was negatively associated with cuckoo use. Similarly, the likelihood of a cuckoo decreased with increasing area of other-vegetation types (e.g., shrubs and bare ground; see **Appendix 1**) within a 480 m radius.

The area of cottonwood-willow vegetation type within a 480 m radius (CW_480) and the area of other-vegetation types within a 480 m radius (OT_480) were the least significant in the model. The odds of a cuckoo decreased as the area of cottonwood within a 480 m radius increased. An examination of the mean proportion of cottonwood-willow vegetation type within progressively larger concentric circles, in use and nonuse areas showed that, in use areas, the proportion of cottonwood willow decreased as the distance from the use point (the radius) increased. Conversely, in nonuse areas, the proportion of cottonwood-willow vegetation type increased slightly farther away from the non-use point. Backwards stepping and the likelihood-ratio test revealed that the amount of saltcedar within a 480 m radius (SC_480) had the tightest

association, a negative association, with cuckoos in the project area (**Table 6**), while the amount of cottonwood-willow inside a 480-m radius had the weakest association.

Model Accuracy

Comparison of model distributions

The distribution of model probabilities for the two model types was remarkably similar (**Figure 5A**) considering that the Satellite model used vegetation structure (NDVI) obtained from a satellite, while the Aerial model used vegetation maps of community types obtained from high-resolution digital orthophotography. The Satellite and Aerial model distributions remained similar again when challenged with 2007 presence/absence data (**Figure 5B**). The Satellite model produced a narrower range of probabilities (i.e., tighter niche) than the Aerial model when predicting absences, while the Aerial model produced a narrower range when predicting presence locations. The median values were more similar between the Satellite and Aerial models in 2006 than 2007, possibly because the Aerial model was using the same static vegetation map that was produced in 2004, while the Satellite model used up-to-date imagery.

Lower Colorado River

Following application of agriculture and urban masks, and an NDVI mask (values <0.126 = non-riparian), we created habitat suitability maps for cuckoos through the reclassification of model probabilities into 5 classes (20% intervals), or binary reclassification, through the application of a probability threshold. Application of a 50% probability threshold resulted in 1,926 ha of predicted cuckoo habitat in 2006, or 5.1% of all riparian vegetation considered by our Satellite model (38,122 ha). Application of the Satellite model in 2007 produced 1,984 ha of predicted habitat, or 5.6% of the total riparian vegetation considered in 2007 (35,133 ha). In contrast, application of the Aerial model from 2004 - at a 50% threshold - resulted in 2,778 ha, or 8.9% of all riparian vegetation considered by the model (31,360 ha).

Using 2006 cuckoo locations for Satellite-model calibration and fit, Model 1 obtained 76% overall accuracy, with 25% omission and 23% commission error at a 50% probability cutpoint. Model 2 accuracy declined to 61% when TRI was removed from the model. The Aerial model preformed slightly better with 76% overall accuracy, with 16% omission error, and 33% commission error. An ROC curve (**Figure 6A**) shows classification performance of the Satellite

model across all probability cutpoints, with an AUC of 0.83 (an AUC value of 1 is perfect classification; an AUC of 0.5 is no better than random). When the TRI variable was removed from the model, AUC dropped to 0.69 (model 2). When we challenged the Satellite model with 2007 data, AUC increased to 0.88 (**Figure 6B**). The Aerial model produced a remarkably similar ROC curve for 2006, with an AUC score of 0.88. The ROC curves for 2007 were also similar, but there was a distinct departure in classification accuracy after 80% sensitivity was achieved by both models, with the Aerial model obtaining a 0.91 AUC score. The ROC curves indicate that the Satellite model was slightly more accurate at classification accuracy where model probabilities ranged from 0 – 80%, but became less accurate than the Aerial model above 80% sensitivity.

The Satellite models produced a stair-stepped (model 1) or exponential (model 2) relationship between the density of cuckoo detections and each model's five probability classes, with higher probability classes containing larger densities of detections than lower classes (**Figure 7A**). The Aerial model produced roughly similar cuckoo detection densities in the 5 probability classes as Satellite model 1, achieving greater detection densities in classes 1 and 2, lower detection densities in classes 3 and 4, and greater in class 5. The Aerial model also achieved greater detection densities in all five probability classes than Satellite model 2, with a pronounced exponential relationship. Of all three models, the Aerial model achieved the greatest density of cuckoo detections, in class 5, indicating that it did the best job of identifying the highest quality yellow-billed cuckoo habitat.

Satellite model accuracy: Verde and San Pedro rivers

Graphical results from applying the Satellite models for the Verde, upper San Pedro, and lower San Pedro are displayed on **Figures 8, 9, and 10**, respectively. Satellite model accuracy along the Verde and San Pedro rivers was mixed, depending on the reach, model, or probability threshold. However, in both systems, the lower the probability threshold we selected to create a binary habitat map, the higher the accuracy (i.e., correctly identifying cuckoo breeding sites), since more of the riparian landscape was considered suitable. Along the Verde River (**Figure 11A**), the density of cuckoo detections increased slightly in the first four probability classes, but jumped up in the 5th class. For model 2, there was a dramatic increase in the first 3 probability classes, but classes 4 and 5 contained no cuckoo detections. The increase in cuckoo density by probability class indicates that there was a correlation between model probability and cuckoo

occurrence. However, the relationship between model probabilities and cuckoo occurrence was different along the Lower Colorado River, with a much lower threshold required to obtain similar classification accuracy. Nevertheless, cuckoos were clumped in distribution and tended to fall within areas with more predicted habitat.

The Satellite models did not perform as expected along the San Pedro River (**Figure 11B, C**), with lower-probability classes containing a higher density of cuckoos than higher-probability classes. This response indicates a lack of discrimination in habitat selection in relation to the model probabilities. An examination of accuracy in relation to different probability thresholds revealed that model 1 could barely achieve 20% classification accuracy at a low threshold (10%). In contrast, model 2 was much more sensitive, achieving 80% classification accuracy at a 10% threshold. The large difference in performance in model 1 compared to model 2 indicates that terrain ruggedness, which is in model 1 and not model 2, negatively affected the performance of model 1.

An aerial perspective of the upper San Pedro River shows a fairly narrow corridor of riparian vegetation, while the lower San Pedro had a broader and more contiguous riparian forest, with more abundant amounts of higher-probability habitat. There were relatively few detections of cuckoos in the lower San Pedro, which was due to limited access to survey sites. However, their distribution was clumped, as was observed in the Verde and Lower Colorado River, with higher-probability classes containing greater densities of cuckoos.

Landscape Comparison

Comparison of the biophysical conditions among the three study sites revealed considerable contrast in the range of biophysical conditions cuckoos experienced, with some very distinct patterns (**Figure 12**). Specifically, the median values of the three biophysical variables that were important in the Satellite models were substantially larger in the Lower Colorado River, lowest along the San Pedro, and intermediate in the Verde. These differences appear to reflect the underlying topography and abundance and distribution of vegetation along the floodplains. On the Lower Colorado River and its tributaries, floodplains were larger and vegetation patches were correspondingly bigger, and topographic contrast was largest. Along the Verde River, flows were smaller than the Lower Colorado River, resulting in smaller vegetation patches and a decrease in vegetation-density heterogeneity. Along the San Pedro, which had the

flattest topography, the amount and heterogeneity in vegetation density was the smallest of the three sites. In fact, 50% of the sites along the San Pedro had little to no dense vegetation (NDVI > 0.41) within the 120-m core radius of cuckoo locations, representing a serious (and unexplained) mismatch of model predictions.

DISCUSSION

Vegetation Associations

There were two spatial scales of vegetation characteristics that were significantly associated with cuckoo breeding habitat selection in the Satellite and Aerial models. At the finest scale (120 m radius; 4.5 ha patch), two vegetation variables (ND_BEST120 and CW_120) characterized a core area surrounding a cuckoo location, comprised of dense cottonwood-willow. At a coarse scale (480 m radius; 72 ha patch), there were five variables in the Satellite and Aerial models that characterized important vegetation features around a cuckoo location (ND_SD480, SC_480, CW_480, OT_480, VEGSD_480), but only ND_SD480 was positively associated. ND_SD480 is a measure of the heterogeneity in the density of riparian vegetation within a 72 ha patch, and may act as a measure of vegetation structural diversity within the patch, positively associated with cuckoo use. Cuckoos were negatively associated with diversity of vegetation cover types (VegSD_480), a measure of habitat fragmentation. This variable had the strongest influence in the Aerial model, and the higher the diversity of cover types (i.e., the standard deviation of the number of vegetation types within a 72 ha patch), the less likely it was to be cuckoo habitat. The amount of saltcedar within a 480 m radius was also a negative association, and as the amount of saltcedar cover increased within a 72 ha patch, the odds of cuckoo use decreased.

The ND_BEST120 variable has been identified in previous research as an important feature of southwestern willow flycatcher breeding habitat (Hatten and Paradzick 2003, Hatten et al. 2010), but to our knowledge the remaining variables in our habitat models are unique. A major difference between the cuckoo and flycatcher satellite models is the scale of analysis. In the flycatcher model, the ND_BEST120 variable was the most important patch-scale examined, while our models indicate that cuckoos require a much larger patch for breeding habitat (72 ha; 480-m radius), an order of magnitude larger. The different patch-size preference is likely due to the differences in natural history traits of the two species. Western yellow-billed cuckoos are non-territorial and breed in large patches (10 to 40 ha) of riparian vegetation (Gaines 1974, Ehrlich et al. 1988, Laymon 1997, USFWS 2002), while southwestern willow flycatchers are

territorial, requiring between 0.24 and 4.5 ha (Sedgwick and Knopf 1992, Hatten and Paradzick 2003, Paxton et al. 2007, Hatten et al. 2010). A yellow-billed cuckoo's breeding cycle is also extremely rapid and they depend on abundant large prey items, including cicadas, katydids, and caterpillars to nest (Hamilton and Hamilton 1965, Rosenberg et al. 1982, Hughes 1999). Larger patches of riparian vegetation likely provide more abundant and larger prey items.

Landscape Associations

The terrain ruggedness variable (TRI) proved to be our most important variable in the best-performing Satellite model. Broken out into four roughness classes, going from flat to extremely rugged, this variable is likely a surrogate for multiple biophysical factors that the Satellite model could not capture directly. This observation is supported by the fact that TRI was not retained in the Aerial model, which had vegetation-species information. In the Satellite model, the odds ratios informed us that areas of low and high ruggedness were approximately 3 times more likely to contain a cuckoo, when compared to flat terrain. However, the intermediate class of ruggedness (class 3) was approximately25 times more likely to contain a cuckoo, when compared to flat terrain. This pattern reflected the fact that the majority of presence locations, located in the lower Bill Williams River and lower Grand Canyon above Lake Mead's delta, were in intermediately rough areas. In contrast, many of the nonuse sites in our analysis were immediately adjacent to the Colorado River, or along reservoirs, areas which were relatively flat. It appears likely that the TRI variable was a surrogate for where the best cottonwood-willow patches were located in the project area, which also contained the most cuckoos.

In the West, cuckoos nest almost exclusively near water and many researchers have hypothesized that the species might be restricted to moist river bottoms because of humidity requirements for successful breeding (Hamilton and Hamilton 1965, Rosenberg et al. 1991, Johnson et al 2007). Our Satellite model did not find distance to water to be a significant variable, while the Aerial model found the amount of open or structured-open water was negatively associated with cuckoo presence. These results are likely due to the fact that all of our sample locations (use/nonuse) were within 2 km of water, which lacked the contrast necessary for this analysis. If this analysis were performed over a larger landscape, with more absence locations found along intermittent or ephemeral channels, the distance to water variable would surely be important. Thus, scale is an important factor to consider when testing hypotheses.

Model Accuracy

The Satellite and Aerial models performed similarly when classification tables or ROC were examined, or when the distributions of their model probabilities were plotted. Curiously, the Satellite model did a better job of correctly identifying cuckoo absences, while the Aerial model was better at predicting cuckoo presences. The box-plots revealed that there was a smaller spread in the model probabilities for each best-performing situation described, meaning the Satellite model identified a smaller niche for absence locations, while the Aerial model produced a tighter niche for presence locations. Another interesting pattern we observed was that the Satellite models did a better job of habitat classification where there were wider floodplains and larger vegetation patches (i.e., Bill Williams NWR, or above the Lake Mead inlet), while the Aerial model appeared to perform better in smaller floodplain habitats (i.e., the Colorado River near the Gila River confluence, or Yuma). Such patterns indicate that a one-size-fits-all model is probably not desirable or achievable, and provides evidence that both approaches have merit under different conditions.

Satellite-model 1's probability classes contained higher numbers of cuckoo detections than model 2 along the Lower Colorado River because it contained the terrain ruggedness variable and was more specific (i.e., it predicted less habitat). A comparison of model 1 and 2 revealed the importance of terrain ruggedness in model fit (i.e., AIC, R^2) and classification accuracy (i.e., ROC, classification table). When terrain ruggedness was removed from model 1, there were significant decreases in accuracy along the Lower Colorado River. However, we did not find this to be the case along the Verde and San Pedro rivers. In fact, model 2 performed better along both reaches when we overlaid and compared verification data obtained in 2005. Cuckoos more frequently occupied floodplains with flatter surroundings on the Verde and San Pedro rivers than the Lower Colorado River, resulting in greater accuracy with model 2.

It is interesting to note that the Satellite model's probability thresholds used to create binary-habitat maps produced very different accuracy results in the three systems. On the Lower Colorado River, probability thresholds of 0.4 – 0.5 produced accuracies of 65-80%, depending on the model employed. In contrast, the same probability thresholds produced ~10-30% accuracy along the Verde and San Pedro rivers. Not until we selected a probability threshold of 0.1 were comparable accuracies obtained along the Verde or San Pedro rivers. These disparate results indicate that the habitats cuckoos utilized along the Verde and San Pedro rivers were

significantly different than along the Lower Colorado River. Yellow-billed cuckoos were once considered abundant throughout the riparian floodplain along the Lower Colorado River. The effects of upstream dams, flow alterations, channel modifications, and clearing of land for agriculture, has especially affected the vegetation immediately adjacent to the Colorado River, and along reservoirs, areas which were relatively flat. Cuckoos were absent from these areas during our surveys; the majority of our cuckoo presence locations were located in the lower Bill Williams River and lower Grand Canyon above Lake Mead's delta, where riparian habitat is the most continuous, unfragmented habitat of its kind in the Lower Colorado River Basin.

Along the San Pedro, there were 288 yellow-billed cuckoo detections in 2005: 15 were on the lower (northern) San Pedro, the remainder along the upper (southern) San Pedro. The northern locations were more likely to be correctly classified than the southern locations using either model, indicating that there were differences in habitat selection patterns within the San Pedro. The large number of locations along the upper San Pedro that contained little to no dense vegetation (NDVI > 0.41) within a 120-m radius of a site indicates that habitat preferences of cuckoos were different along this reach compared to the lower San Pedro, Verde, or Lower Colorado River. A second characteristic of the upper San Pedro cuckoo locations was the apparent uniformity in the spatial distribution along the river, without distinct clumping of cuckoos. The relatively uniform distribution suggests that there was little difference in the underlying quality of habitat, but the model probabilities showed a fairly broad distribution available, suggesting that there were different habitat selection patterns on the upper San Pedro. The upper San Pedro is unique in that its riparian habitat includes considerable areas of mesquite woodlands adjacent to cottonwood-willow patches, and cuckoos forage and sometimes nest in these areas (Halterman 2004, 2005). These mesquite areas may have NDVI signatures less than 0.41, the threshold of a key variable in the models. It may be that applying a lower NDVI threshold along this reach may improve classification accuracy, but additional research is needed on this topic.

Comparisons with other Yellow-billed Cuckoo Habitat Models

We conducted a literature review and summarized the results of habitat models for western yellow-billed cuckoos found in the literature (**Appendix 3**). Models have been developed to describe and predict western yellow-billed cuckoo breeding habitat, mainly along

the Sacramento River, California, dating back to 1974. The first habitat model, developed by Gaines (1974), for the yellow-billed cuckoo in the Sacramento Valley, found that patch size was a primary determinant of cuckoo use, and that occupied riparian habitat patches were at least 61 ha (25 acres) in size, 100.5 m (330 ft) wide, 302 m (990 ft) long, within 100.5 m (330 ft) of surface water, and dominated by cottonwood/willow gallery forest with high-humidity microclimate. Other models (Laymon and Halterman 1989, Greco et al. 2002, Galbraith et al. 2004, Girvetz and Greco 2009) had similar results. Patch sizes ranged from 41 to 81 ha, with "optimal' patch size of 80 ha or larger (Laymon and Halterman 1989, Greco et al. 2002, Girvetz and Greco 2009). In addition, area of cottonwood-willow vegetation was found to be an important component of cuckoo habitat (Laymon and Halterman 1989, Greco et al. 2002, Galbraith et al. 2004, Girvetz and Greco 2009).

Some of our model covariates have similarities to those identified in the literature. We found that cottonwood-willow vegetation and vegetation density are important within a core area of 4.5 ha, the amount of scrubby vegetation has a negative association with cuckoo use. But our models contributed new, unique information on yellow-billed cuckoo habitat use along the Lower Colorado River. Specifically, cuckoo habitat quality declined as the amount of saltcedar increased within a 72 ha patch (Aerial model), but increased in areas of moderate terrain ruggedness (Satellite model). Heterogeneity in the density of riparian vegetation, or structural diversity, was important within a 72 ha area. Conversely, heterogeneity in vegetation cover types, with greater heterogeneity representing greater fragmentation of vegetation cover types, including cottonwood-willow, was negatively associated with cuckoo use.

Future Modeling Efforts for Yellow-billed Cuckoo and other Wildlife Species

Vegetation structure is a key factor underlying avian habitat selection and an important consideration in the development of bird–habitat models. Though we incorporated information on vegetation structure in our Satellite models with NDVI, a measure of vegetation lushness and greenness, we lacked information regarding vegetation height, an important feature of breeding habitat (Johnson et al. 2007, Johnson 2009). Unfortunately, manual surveys of vegetation structure become prohibitive in terms of time and cost if sampling needs require fine-grained characterization at a landscape extent. Thus, future efforts to model yellow-billed cuckoo or other wildlife habitat may want to consider the use of Airborne Light Detection and Ranging (LiDAR), a remote sensing technique that can capture information on the height of vegetation

(Lefsky et al. 2002, Bradbury et al. 2005) over larger spatial extents than is practical through field surveys.

An important aspect of our Satellite models is their proven repeatability, at low cost, making them useful in analyzing landscape-level changes in cuckoo habitat over time. Given that the principle sensor used by our Satellite model (Landsat5 TM) operated continuously from 1984 until November 2011 (Landsat 5 has just been declared inoperative), it provides a unique opportunity to retroactively explore the underlying causes of habitat formation and destruction, and habitat-density relationships, similar to temporal-habitat analyses conducted for the southwestern willow flycatcher in Arizona (Paxton et al. 2007, Hatten et al. 2010). Much could be learned by creating videos of habitat formation and destruction through repeat images that are acquired at the same location and date each year. The modeling procedures performed in this study are of special significance for establishing habitat requirements for yellow-billed cuckoo along the lower Colorado River. Our process of model development and testing could also be used to examine the effects of landscape-scale habitat variables on the distribution of other covered wildlife species, and to identify features that constitute high quality habitat for those species within the planning area.

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TABLES 1-6

Table 1. List of variables examined in a multivariate logistic regression analysis of yellow-billed cuckoo breeding habitat. We also examined whether probability grids output from a Southwestern Willow Flycatcher model (Hatten and Paradzick 2003) were significant in the cuckoo model (WIFL prefix).

Variable	**Description**
TRI	Terrain ruggedness index - SD of elevation within 1.6-km radius of river
**AGDIST	Distance from agriculture or urban areas
FLOOD12	Amount of floodplain or flat area within a 41-ha neighborhood
**H20DIST	Distance from water observable from Landsat5 satellite imagery
*ND_BEST	Amount of vegetation with NDVI values > 0.41
ND_RAP	Density of vegetation (determined from NDVI) in a 30X30-m cell
*ND_SD	Heterogeneity in vegetation density (determined from NDVI)
ND_BEST33	Cells with NDVI >0.33 were coded 1 (binary) in a 30X30-m cell
ND_BEST120	Amount of dense vegetation (NDVI >0.41) inside a 120-m radius (4.5 ha)
**PATCHDIST	Distance from patch interior to exterior boundary
*PATCHSIZE	Size of patch – # contiguous cells with NDVI >0.41
WIFL_50	Southwestern willow flycatcher (SWFL) habitat
WIFL_PROB	SWFL model probabilities
WIFL_5CL	SWFL model probabilities in 5 classes (0-20%; 21-40%, etc)

*Variable examined at multiple scales (e.g.., 30-, 60-, 90-m radius)

**Scalar variable (value varies depending on location)

Table 2. Variables derived from maps of vegetation type. Variables, derived from maps of vegetation type, we examined in a multivariate logistic regression analysis of yellow-billed cuckoo breeding habitat.

Variable*	**Description**
CW	Amount of cottonwood-willow vegetation type inside concentric circles (60 – 480 m radius, ~1 – 72 ha) around each 30x30 m cell
SC	Amount of salt cedar vegetation type inside concentric circles (60 – 480 m radius, ~1 – 72 ha) around each 30x30 m cell
SM	Amount of salt cedar-mesquite vegetation type
ME	Amount of mesquite vegetation type inside concentric circles (60 – 480 m radius, ~1 – 72 ha) around each 30x30 m cell
MA	Amount of marsh vegetation type inside concentric circles (60 – 480 m radius, ~1 – 72 ha) around each 30x30 m cell
AG	Amount of agriculture vegetation type inside concentric circles (60 – 480 m radius, ~1 – 72 ha) around each 30x30 m cell
OW	Amount of open water and structured open water inside concentric circles (60 – 480 m radius, ~1 – 72 ha) around each 30x30 m cell
OT	Amount of other vegetation type inside concentric circles (60 – 480 m radius, ~1 – 72 ha) around each 30x30 m cell
Majority	Measures the dominant vegetation type. Determines the vegetation type that comprises the majority of the area inside concentric circles (60 – 480 m radius, ~1 – 72 ha) around each 30x30 m cell
Variety	Measures the fragmentation of vegetation types. Determines the number of vegetation types that occur inside concentric circles (60 – 480 m radius, ~1 – 72 ha) around each 30x30 m cell
VEGSD	Measures vegetation heterogeneity. Finds the standard deviation of the Variety values for each 30x30 m cell within concentric circles (60 – 480 m radius, ~1 – 72 ha) around each 30x30 m cell
TRI	Terrain ruggedness index (SD of elevation within 1.6-km radius of river)

*All variables were examined at multiple scales (e.g., 60-, 90-, 120-, 180-, 240-, 300-, 360-, 420-, 480-, and 540-m radius circles around each 30m x30m cell).

Table 3. Two multivariate Satellite models of yellow-billed cuckoo breeding habitat (*n* = 148). See Table 1 for variable definitions. Model 1: Nagelkerke pseudo R^2 = 0.39; $\hat{C}$ = 0.69. TRI (terrain ruggedness index) characterized ruggedness in four classes (1 = flat, 2 = low, 3 = moderate, 4 = high). Model 2: same as model but without the terrain ruggedness (TRI) variable (R^2 = 0.163; $\hat{C}$ = 0.49).

Predictor		**B**	**S.E.**	**Wald**	**df**	**Sig.**	**Exp(B)**	**95.0% C.I. for EXP(B)**	
Model 1								**Lower**	**Upper**
	ND_BEST120	.029	.013	4.759	1	.029	1.030	1.003	1.057
	TRI			23.752	3	.000			
	TRI(2)	1.418	.577	6.045	1	.014	4.127	1.333	12.777
	TRI(3)	3.277	.676	23.472	1	.000	26.509	7.040	99.822
	TRI(4)	1.292	.589	4.801	1	.028	3.638	1.146	11.552
	ND_SD480	.519	.281	3.417	1	.065	1.680	.969	2.912
	Constant	-4.405	1.387	10.080	1	.001	.012		
Model 2									
	ND_BEST120	.031	.012	6.223	1	.013	1.031	1.007	1.057
	ND_SD480	.62	.245	6.408	1	.011	1.86	1.15	3.006
	Constant	-3.408	1.132	9.058	1	.003	.033		

Table 4. Satellite model's log-likelihoods. The change in -2 times model log-likelihoods (G statistic) when a variable was removed from the model. In Model 1, TRI had the largest influence on the model's log-likelihood, followed by ND_BEST120, and last by ND_SD480. In model 2, ND_SD480 had the larger influence on the model followed by ND_BEST120.

Variable		**Model Log Likelihood**	**Change in -2 Log Likelihood (*G*)**	**df**	**Sig. of the Change**
Model 1					
	ND_BEST120	-79.301	4.849	1	.028
	TRI	-92.942	32.132	3	.000
	ND_SD480	-78.704	3.655	1	.056
Model 2					
	ND_BEST120	-96.083	6.281	1	.012
	ND_SD480	-96.466	7.046	1	.008

Table 5. The Aerial multivariate model of yellow-billed cuckoo breeding habitat (n = 148). See Table 2 for variable definitions.

Predictor	B	S.E.	Wald	df	Sig.	Exp(B)	95.0% C.I. for EXP(B)	
							Lower	Upper
VEGSD_480	-2.485	0.996	6.228	1	.013	.083	.012	.587
CW_120	.738	0.286	6.667	1	.010	2.092	1.195	3.664
CW_480	-.048	0.025	3.722	1	.054	.953	.908	1.001
SC_480	-.080	0.023	12.155	1	.000	.923	.882	.966
OW_480	.178	0.080	4.943	1	.026	.837	.715	.979
OT_480	-.060	0.027	5.087	1	.024	.942	.894	.992
Constant	2.736	0.718	14.510	1	.000	15.425		

Table 6. Aerial model log-likelihoods. The change in -2 times model log-likelihoods (G statistic) when a variable was removed from the model. The amount of Salt cedar inside a 480-m radius was the most influential variable in the model, while amount of cottonwood-willow inside a 480 m radius was the least influential.

Variable	**Model Log Likelihood**	**Change in -2 Log Likelihood (*G*)**	**df**	**Sig. of the Change**
VEGSD_480	-79.965	6.859	1	.009
CW_120	-80.144	7.217	1	.007
CW_480	-78.481	3.892	1	.049
SC_480	-84.009	14.947	1	.000
OW_480	-80.992	8.913	1	.003
OT_480	-79.165	5.260	1	.022

FIGURES 1-24

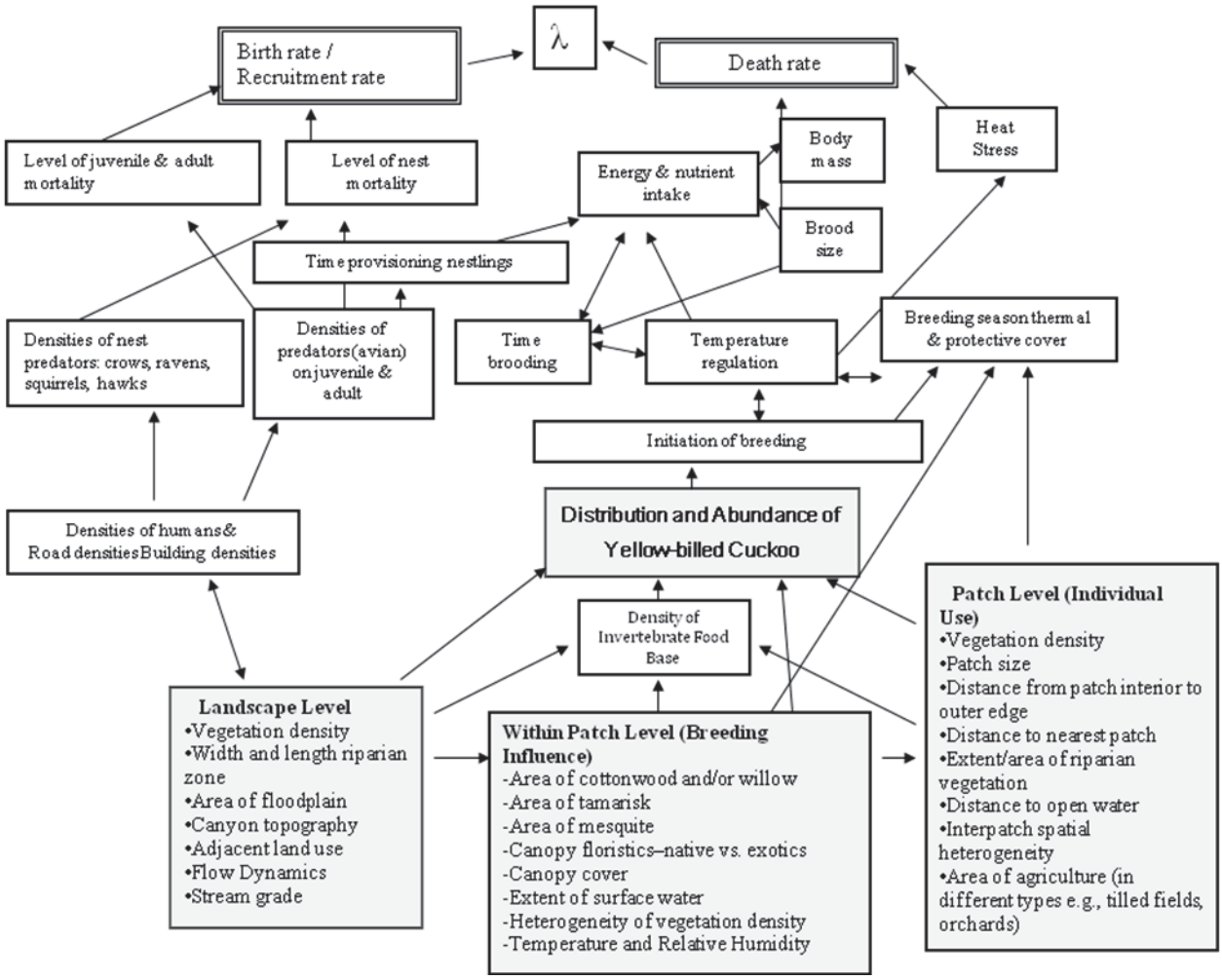


Figure 1. Conceptual model of factors that affect yellow-billed cuckoo habitat selection along the Lower Colorado River, Verde River Watershed and San Pedro River.

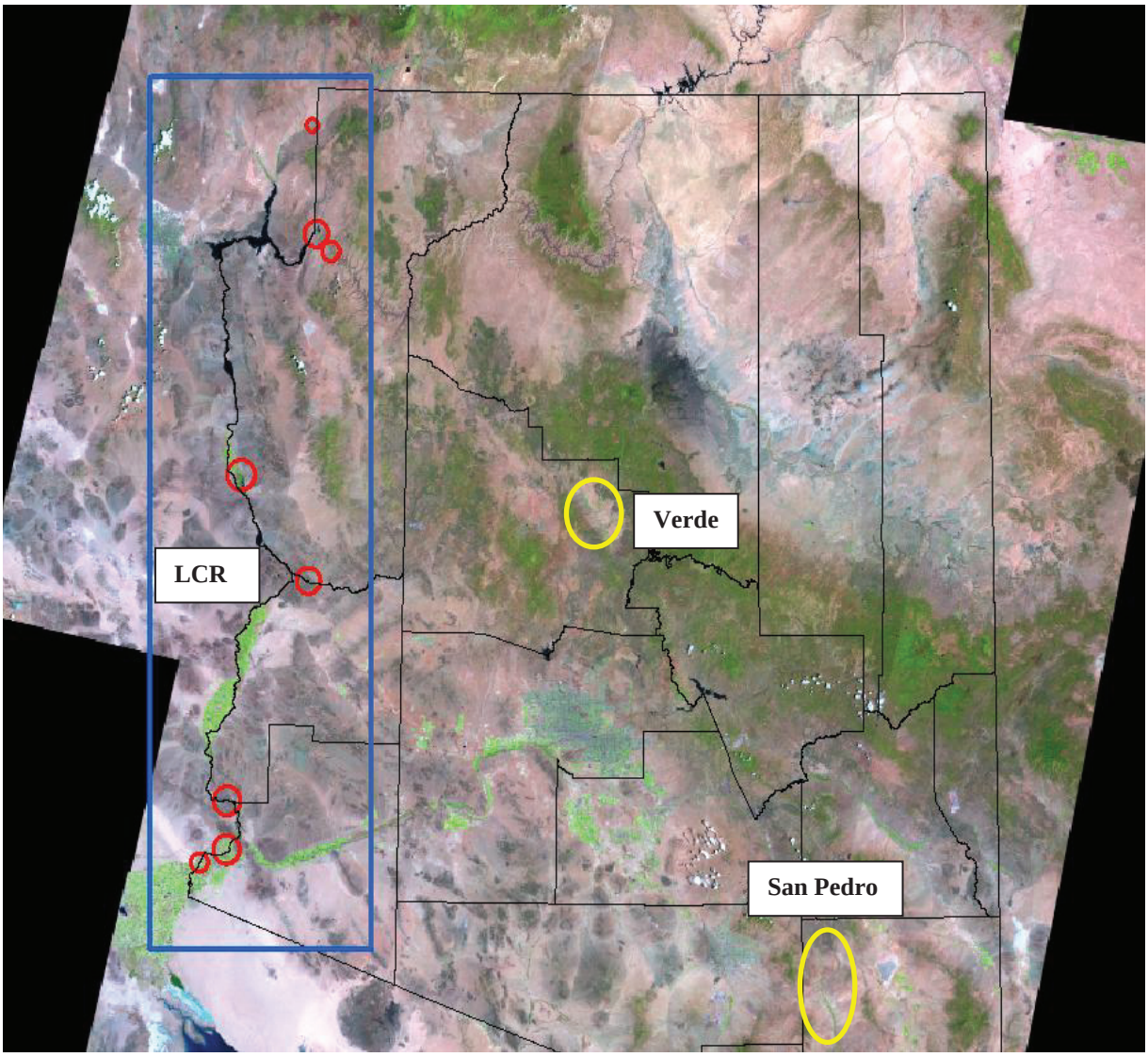


Figure 2. The project area (Lower Colorado River - LCR) overlays a Landsat Thematic Mapper image that was acquired during June, 2006. The red circles along the LCR overlay areas where yellow-billed cuckoos were observed during the 2006 breeding season. Yellow polygons depict reaches along the Verde and San Pedro Rivers where the Satellite model was tested outside the project area. Arizona's county boundaries are outlined in black.

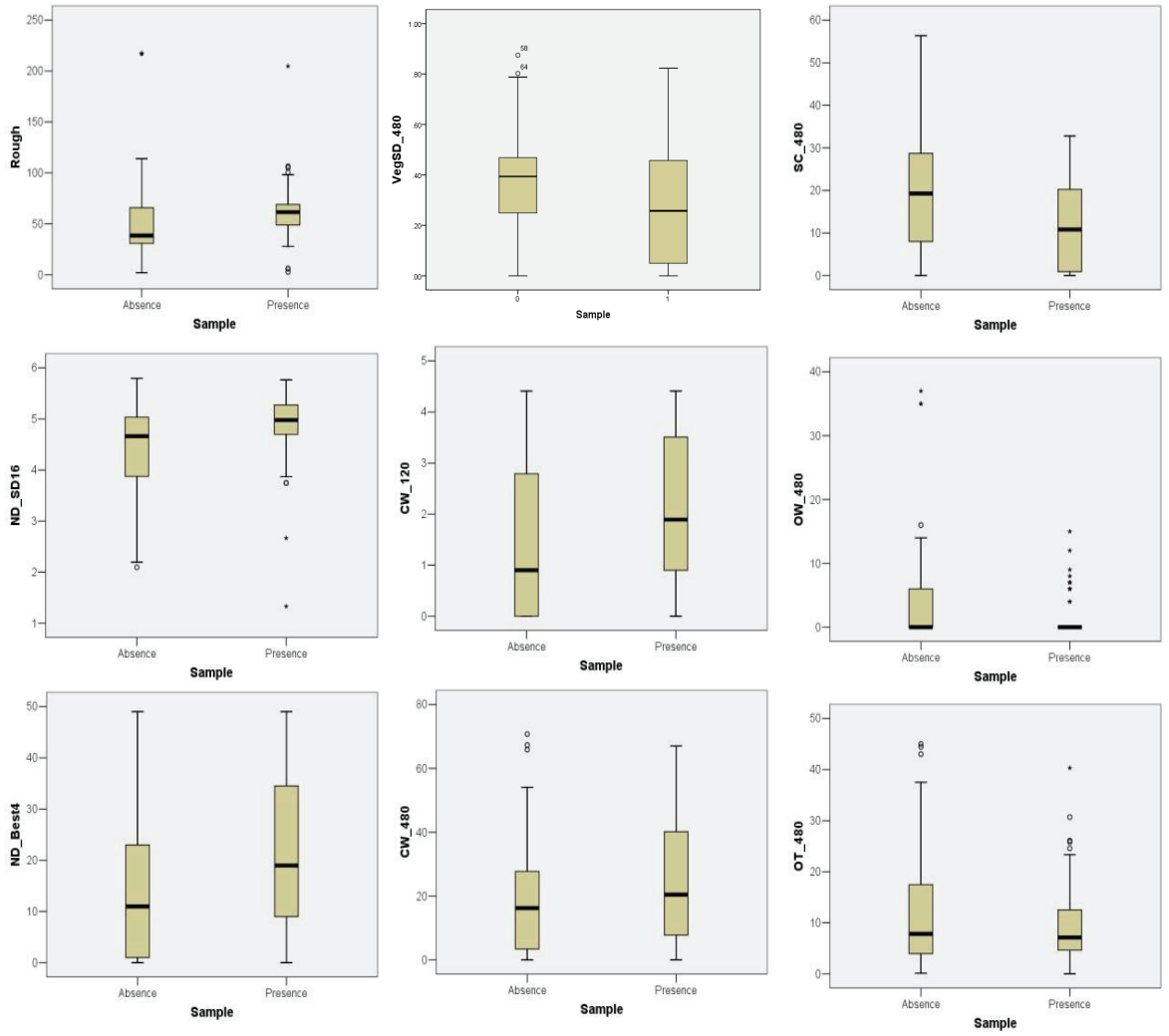


Figure 3. Box-and-whisker plots display the range of biophysical values for each covariate, output by the Satellite models (left panel) or Aerial model (middle and right panels), at presence and absence locations. The box boundaries depict the quartiles of the biophysical values; the whiskers portray the largest and smallest observed values that are not outliers (outliers are shown as circles).

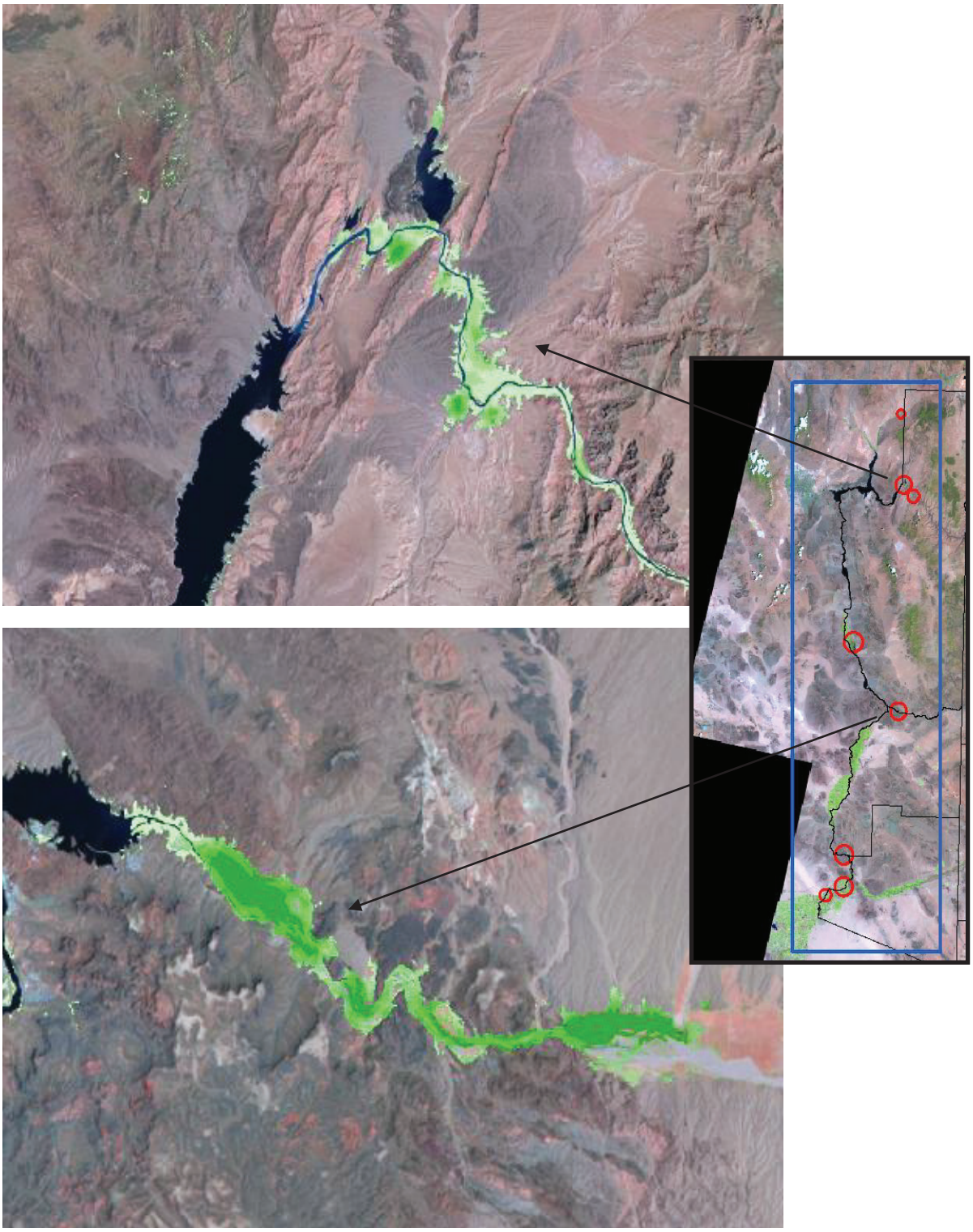


Figure 4. Five model probability classes output by model 1 along Lake Mead's delta (top panel) and the Bill Williams River (bottom panel). Model 1 outputs are presented in 5 discrete classes: the darker the shade of green, the higher the model probability class (i.e., higher likelihood of cuckoo use).

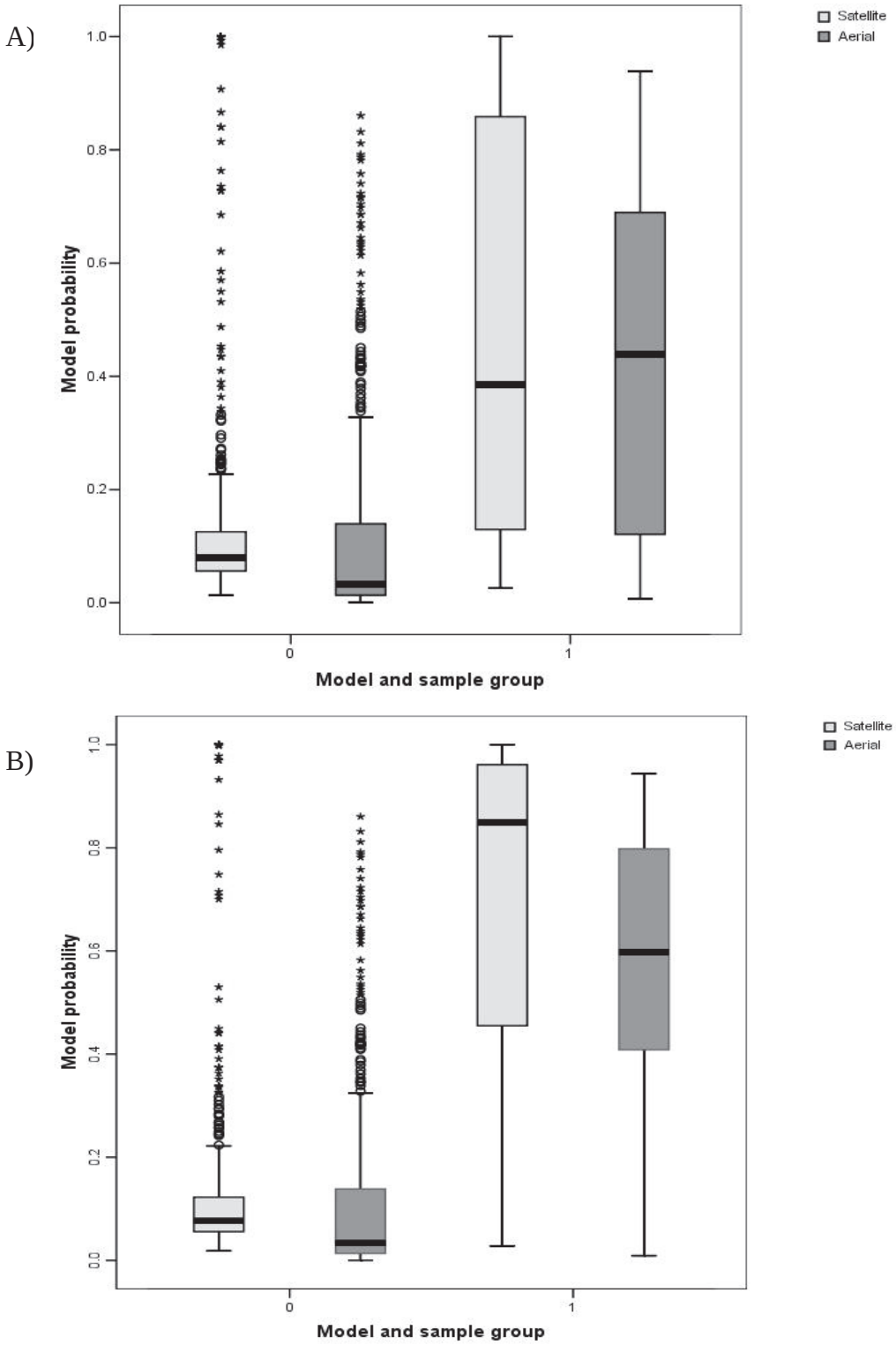
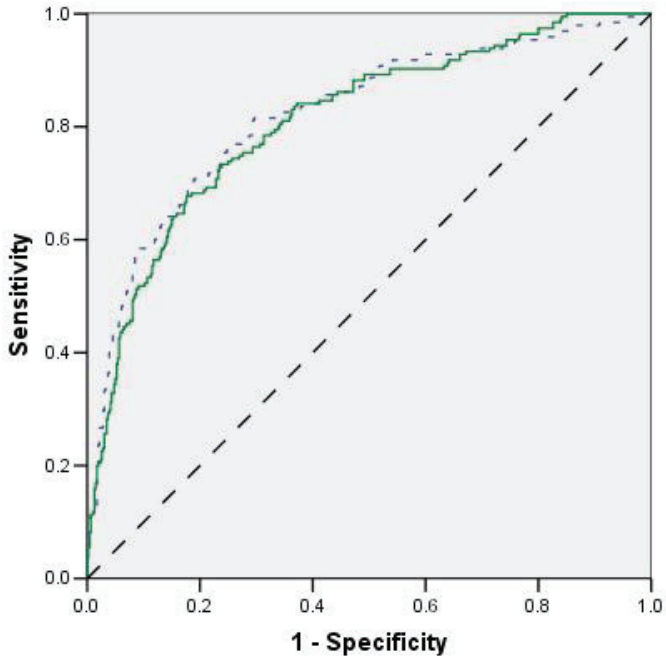


Figure 5. Distribution of model probabilities for 2006 and 2007. (A) Box-and-whisker plots display the distribution of model probabilities for 2006 (A) and 2007 (B) observed in nonuse (sample = 0) and use (sample = 1) areas for project area. The box boundaries depict the quartiles (25th and 75th) of the model probability values; the whiskers portray the largest and smallest observed values that are not outliers (outliers are shown as circles and stars). The median value is the thick bar between the 25th and 75th quartiles.

A)



B)

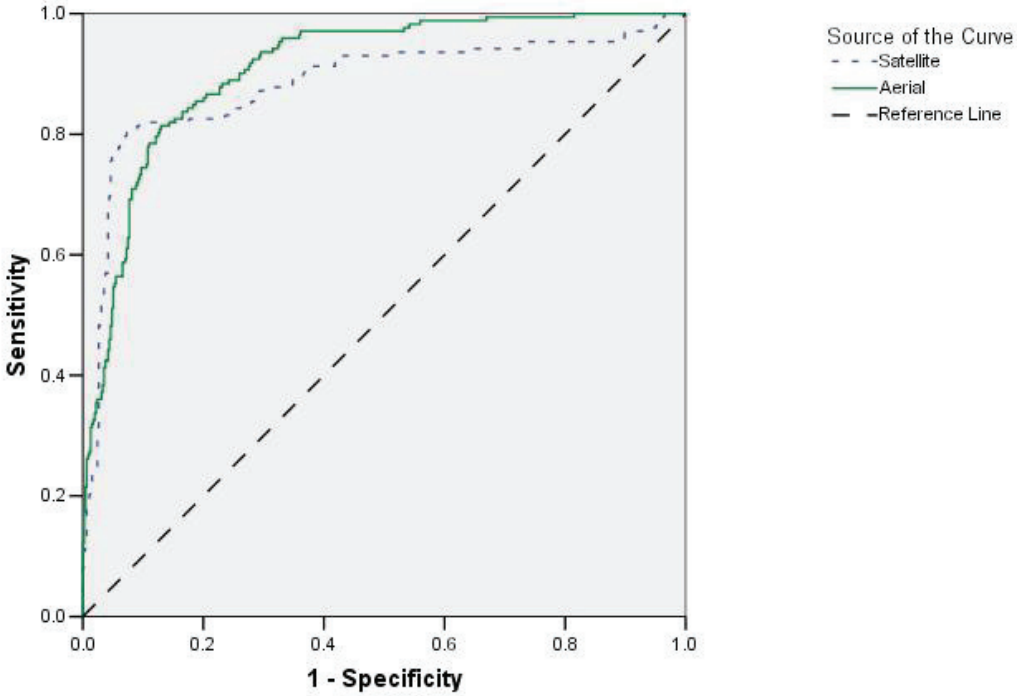


Figure 6. Yellow-billed cuckoo habitat classification results (AUC) in (A) 2006 and (B) 2007 for the Satellite and Aerial models. The X axis displays commission error (false positives), while the Y axis shows classification accuracy of presence locations (1 – omission error). The diagonal axis is a reference line that is no better than an average (random) classification. The closer the two model results are to the left and top axis, the better the overall classification.

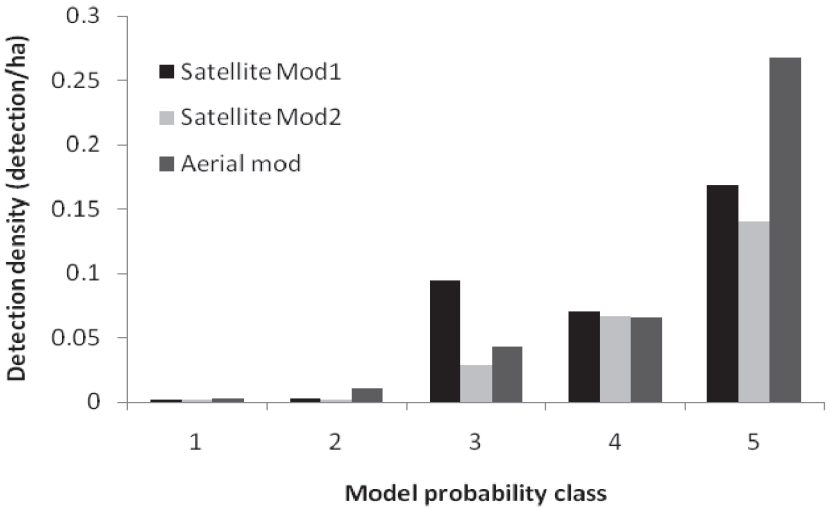


Figure 7. The relationship between the Satellite and Aerial models' probability classes and the density of cuckoo detections in each class along the Lower Colorado River in 2007 (*n* = 383). The density of cuckoo detections increased in either a stair-step or exponential fashion, with lower-probability classes generally containing lower densities of cuckoo detections than higher-probability classes.

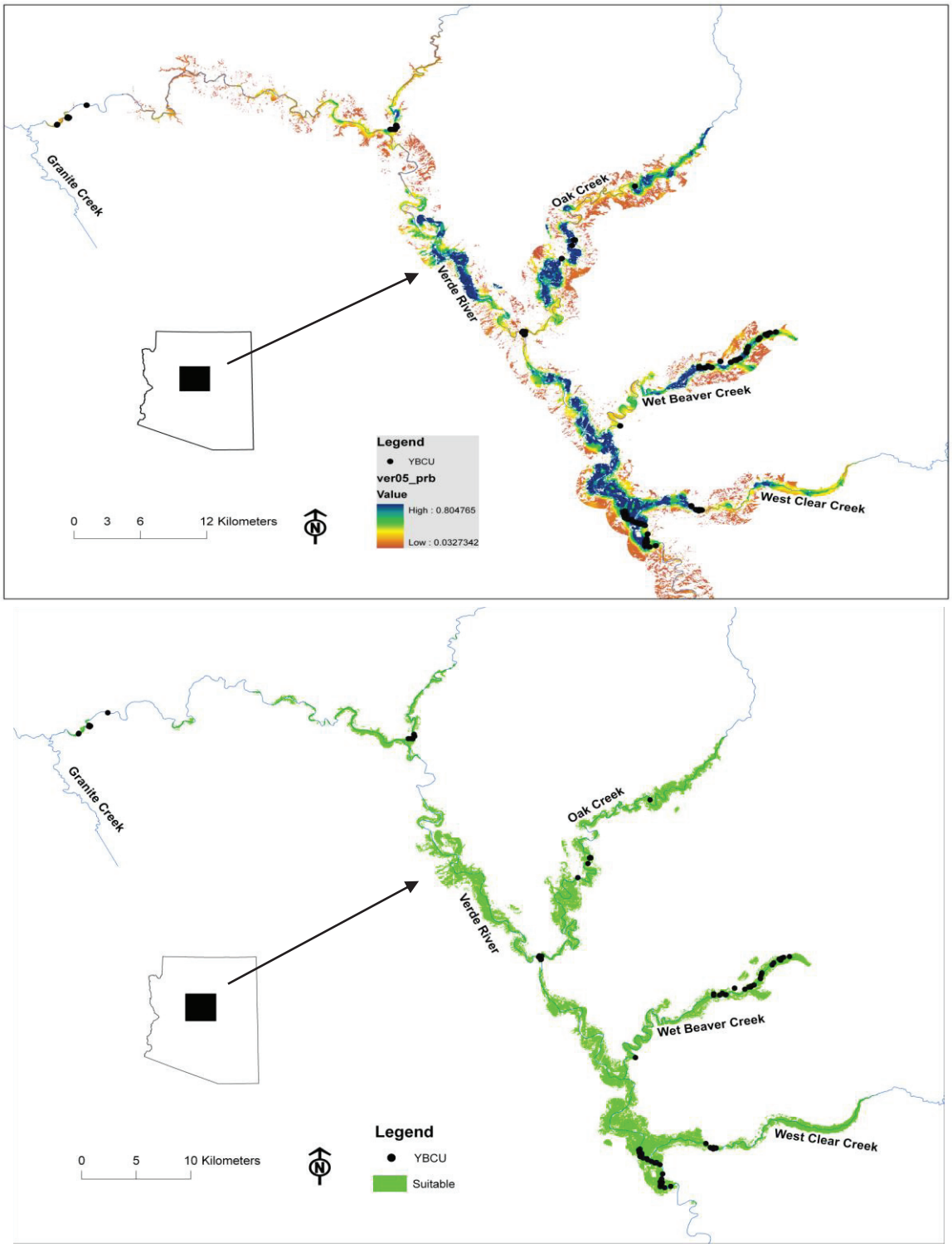


Figure 8. Yellow-billed cuckoo habitat along the Verde River Watershed was output from model 2 as a continuous probability surface (top panel), and as a binary habitat map (bottom panel) created from a 10% probability threshold. The cuckoo locations and satellite imagery used by the model were obtained in the summer of 2005. An elevation mask was applied so only cells with an elevation less than 1290 m were considered in this analysis.

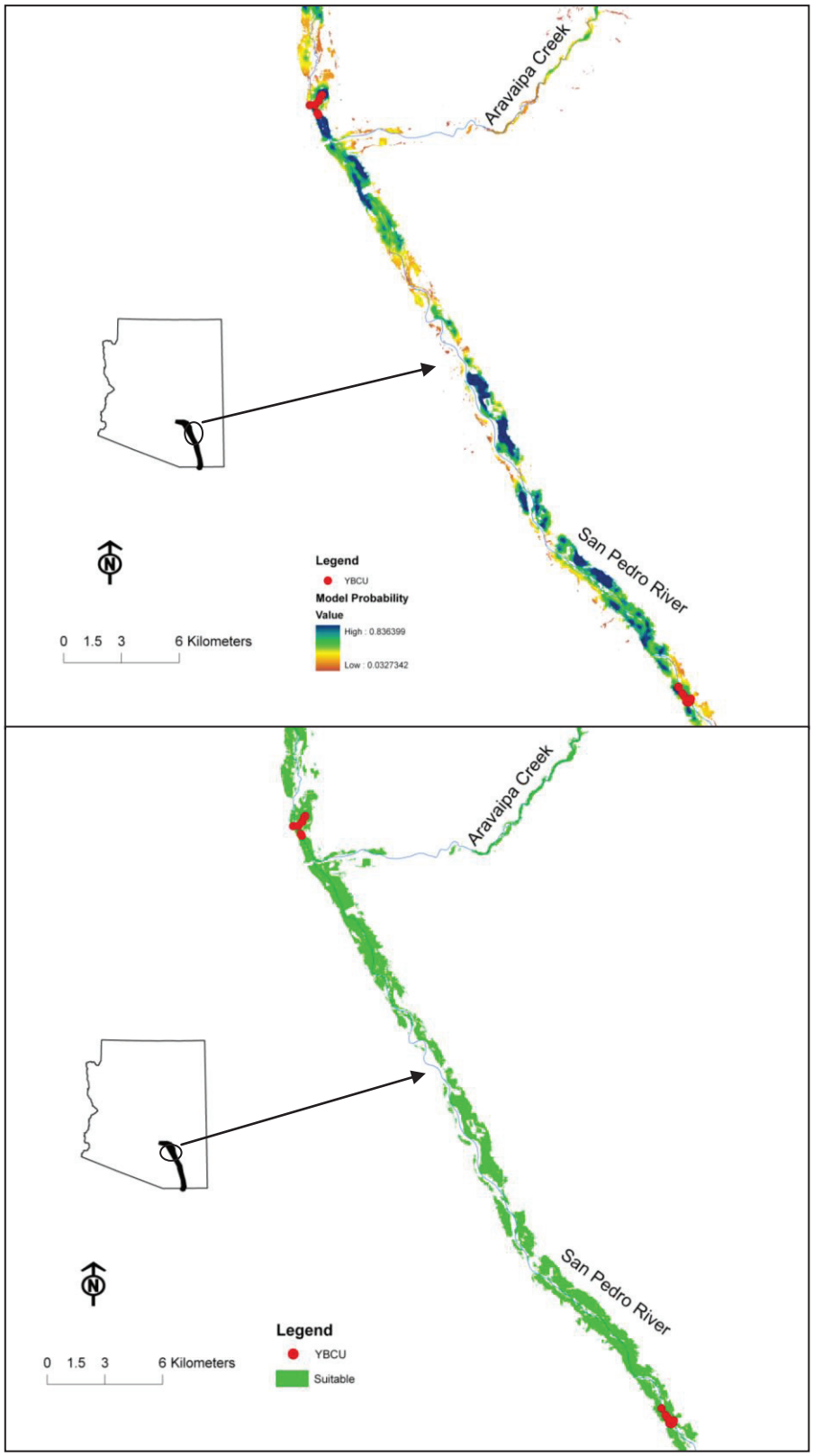


Figure 9. Cuckoo habitat for the lower San Pedro River was output from model 2 as a continuous probability (top), and as a binary habitat map (bottom) that was derived from a 10% probability threshold. The cuckoo locations and satellite imagery used by the model are from the summer of 2005.

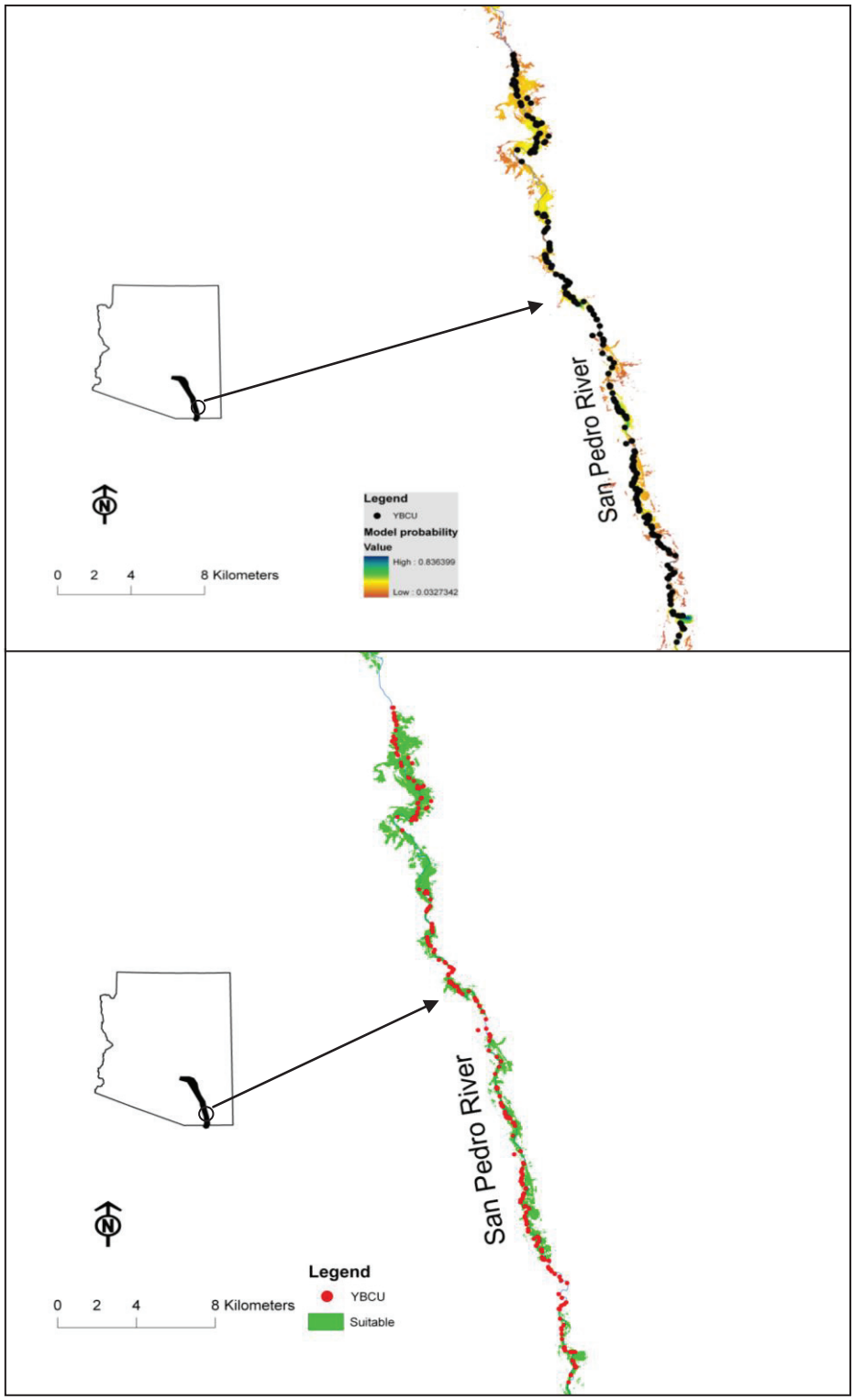


Figure 10. Cuckoo habitat along the upper San Pedro River was output from model 2 as a continuous probability (top panel), and as a binary habitat map (bottom panel) that was derived from a 10% probability threshold. The cuckoo locations and satellite imagery used by the model are from the summer of 2005.

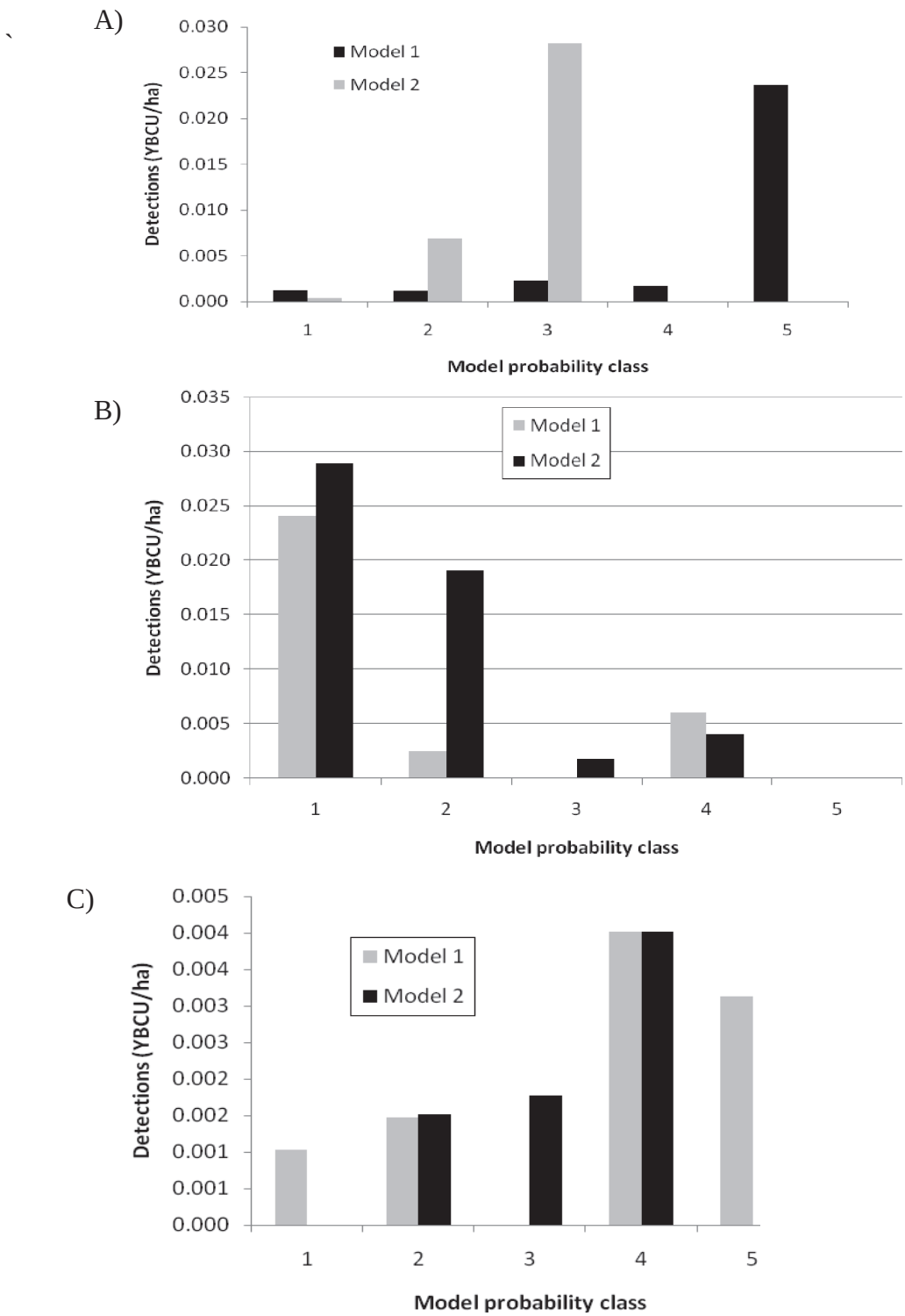


Figure 11. (**A**) Densities of cuckoo detections within 5 model-probability classes along the Verde River in 2005 (*n* = 88 detections), as output by the Satellite models; (**B**) the upper and lower San Pedro River, and (**C**) the lower San Pedro River (using just Johnson et al. 2006; n = 15). The probability classes are in 20% increments (i.e., class 1 = 1 – 20%, class 2 = 21 – 40%, class 3 = 41 – 60%). For model 1, there were no cuckoos detected in class 3; for model 2, there were no cuckoos detected in classes 1 or 5.

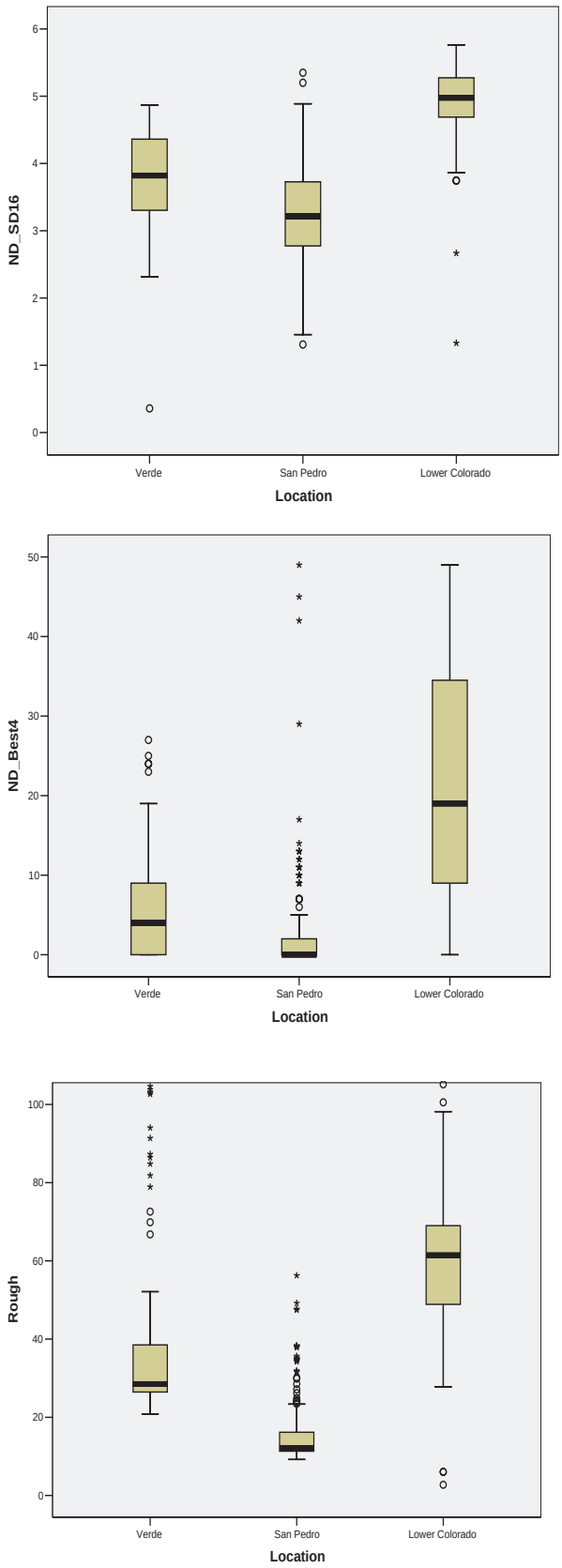


Figure 12. Box-and-whisker plots display the range of environmental values for each variable in Satellite models 1 and 2, for Verde, San Pedro, and Lower Colorado rivers.

Appendix 1. Vegetation and other classifications used in modeling yellow-billed cuckoo habitat. The table shows our classifications and the corresponding Anderson and Ohmart vegetation classes (1976) and other classes used by Bio-West, Inc. (2006).

Our Classification	**Anderson-Ohmart/Bio-West, Inc. Classification**		
Vegetation/other Class	**Community name**	**Community**	**Structural Type**
Cottonwood - Willow	Cottonwood - Willow	CW	IV
	Cottonwood - Willow	CW	V
	Cottonwood - Willow	CW	VI
	Cottonwood - Willow	CW	I
	Cottonwood - Willow	CW	II
	Cottonwood - Willow	CW	III
Saltcedar	Saltcedar	SC	I
	Saltcedar	SC	II
	Saltcedar	SC	II
	Saltcedar	SC	III
	Saltcedar	SC	IV
	Saltcedar	SC	V
	Saltcedar	SC	VI
Saltcedar-Mesquite	Saltcedar - Honey mesquite	SH	I
	Saltcedar - Honey mesquite	SH	III
	Saltcedar - Honey mesquite	SH	IV
	Saltcedar - Honey mesquite	SH	V
	Saltcedar - Honey mesquite	SH	VI
	Saltcedar - Screwbean mesquite	SM	III
	Saltcedar - Screwbean mesquite	SM	IV
	Saltcedar - Screwbean mesquite	SM	V
	Saltcedar - Screwbean mesquite	SM	VI
Mesquite	Honey mesquite	HM	III
	Honey mesquite	HM	IV
	Honey mesquite	HM	V
	Honey mesquite	HM	VI
Marsh	Marsh	MA	1
	Marsh	MA	1
	Marsh	MA	2
	Marsh	MA	3
	Marsh	MA	4
	Marsh	MA	5
	Marsh	MA	6
	Marsh	MA	7
Agriculture	Agriculture	AG	
Open Water	Open Water	OW	
	Structured Open Water	SOW	

Appendix 1 cont.

Our Classification	Anderson-Ohmart/Bio-West, Inc. Classification		
Other	Artiplex - saltbrush	ATX	
	Arrowweed	AW	
	Backwater	BW	
	Creosote	CR	
	No Classification	NC	
	No Classification	NC	IV
	No Classification	NC	II
	No Classification	NC	V
	Undeveloped Bare Ground	UD	

Appendix 2. Vegetation and other classifications used in modeling yellow-billed cuckoo habitat, and the corresponding vegetation categories used on the Bill Williams River NWR (Shafroth, In prep.).

Our Classification	**Shafroth Category Description**
Cottonwood-Willow	Woody vegetation on flood plain surface. Total cover 2-50%, with cottonwood and/or willow dominant and other woody species subdominant
	Woody vegetation on flood plain surface. Total cover > 50%, with cottonwood and/or willow dominant and other woody species subdominant
Saltcedar	Woody vegetation on flood plain surface. Total cover 2-50%, with saltcedar dominant and other woody species subdominant
	Woody vegetation on flood plain surface. Total cover > 50%, with saltcedar dominant and other woody species subdominant
Saltcedar-Mesquite	Not applicable
Mesquite	Woody vegetation on high flood plain or terrace. Total cover 2-50% with mesquite dominant
	Woody vegetation on high flood plain or terrace. Total cover >50% with mesquite dominant
Marsh	Deltaic marshland
Agriculture	Cultivated land.
Open Water	Not applicable
Other	Woody vegetation on high flood plain or terrace. Total cover 2-50% with low shrub species (e.g., *Hymenoclea salsola*, *Tessaria sericea*, *Atriplex* sp., *Lycium* sp.)
	Woody vegetation on high flood plain or terrace. Total cover >50% with low shrub species (e.g., *Hymenoclea salsola*, *Tessaria sericea*, *Atriplex* sp., *Lycium* sp.) dominant
	Low flood plain surface. Total cover >2% with small woody plants dominant
	Low flow channel, mostly open water but including vegetated channel margins and islands
	Essentially bare sediment (< 2% vegetated) within flood plain
	Essentially bare sediment (<2% vegetated) on terrace
	Dry wash vegetation or upland vegetation
	Rock outcrop

Appendix 3. Summary of a review of published western yellow-billed cuckoo models with the area studied, and the variables that influenced cuckoo habitat use.

Author	River, State	Yellow-billed Cuckoo Model Description and Results
Gaines 1974	Sacramento River, CA	Minimum patch size is 61 ha (25 acres), minimum patch width of 105 (330 ft.); minimum patch length is 302 m (990 ft), dominated by cottonwood/willow forest. Microclimate within the patch was high-humidity.
Laymon and Halterman 1989	Lower Colorado, River, CA and AZ	Patch size ranged from 41- 81 ha (102- 200 acres), patch width ranged from 201-603 m (660-1980 ft). Habitat was dominated by cottonwood/willow forest. Smaller patches were unsuitable. Away from the Colorado River, a relationship was found between size of habitat patch and the proportion of patches that are occupied by either pairs or unmated males. Of the 21 sites 20 - 40 ha in extent, only 2 were occupied (9.5%), while of the 17 sites 41 - 80 ha in extent, 10 were occupied (58.8%), and of the 7 sites >80 ha 100% were occupied. This trend towards increased occupancy with increased size was significant ($t=3.63$, $p<0.001$). Along the Colorado River, of the 13 sites 20 - 40 ha in extent, 6 were occupied (46.2%), and the only site >80 ha was occupied.
Greco et al. 2002	Sacramento River, CA	The purpose of this model was to identify potential suitable or optimal habitat patches (using characteristics, such as patch size, and vegetation type, determined to be suitable in previous studies) within the extent of the study river reach, over time. Found that optimal yellow-billed cuckoo habitat (patch area = >80 ha; patch width = 600 m; distance to water = <100 m; tree height) formation can occur in a nine year time span within this specific reach along the Sacramento River, CA. The structure of the riparian landscape, the suitability or quality of habitat with respect to the potential value for nesting and foraging, can change rapidly through time, forming a shifting mosaic of habitat patches that can vary in a particular river reach.
Galbraith et al. 2004	San Pedro River, AZ	Cottonwood-willow dominated (51-100%) patches contribute to cuckoo habitat. Shrub cover, saltcedar, and/or mesquite did not contribute to cuckoo habitat. High canopy >15 m and mid-level (10-15 m) canopy cover contribute to cuckoo habitat.

Appendix 3 cont.

Girvetz and Greco 2009	Sacramento River, CA	Used a multi-scale hierarchical patch delineation method, PatchMorph, to measure landscape patch characteristics at two distinct spatial scales: (1) sub-patches, averaging 59 ha in size, with 15 ha of cottonwood-willow, and (2) super-patches, averaging 177 ha, with 35 ha of cottonwood-willow, and statistically relate them to the presence of cuckoos. The area of cottonwood forest measured at the sub-patch scale (15 ha average, range of 0-72 ha) was found to be the most important factor determining the presence of nesting in forest patches. All of the ‘‘best models’’ contained area of cottonwood measured at the sub-patch scale (positive effect), area of riparian scrub measured at the sub-patch scale (negative effect), and the regional spatial variable of being south of Highway 32 (positive effect).