Identifying western yellow-billed cuckoo breeding habitat with a dual modelling approach

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Abbreviations: BWR, Bill Williams River; LCR, Lower Colorado River; LCR MSCP, Lower Colorado River Multi-Species Conservation Program; NDVI, Normalized Difference Vegetation Index; SD, standard deviation; SDM, species distribution model; TRI, terrain ruggedness index; USFWS, U.S. Fish and Wildlife Service

Abstract

The western population of the yellow-billed cuckoo (*Coccyzus americanus*) was recently listed as threatened under the federal Endangered Species Act. Yellow-billed cuckoo conservation efforts require the identification of features and area requirements associated with high quality, riparian forest habitat at spatial scales that range from nest microhabitat to landscape, as well as lower-suitability areas that can be enhanced or restored. Spatially explicit models inform conservation efforts by increasing ecological understanding of a target species, especially at landscape scales. Previous yellow-billed cuckoo modelling efforts derived plant-community maps from aerial photography, an expensive and oftentimes inconsistent approach. Satellite models can remotely map vegetation features (e.g., vegetation density, heterogeneity in vegetation density or structure) across large areas with near perfect repeatability, but they usually cannot identify plant communities. We used aerial photos and satellite imagery, and a hierarchical spatial scale approach, to identify yellow-billed cuckoo breeding habitat along the Lower Colorado River and its tributaries. Aerial-photo and satellite models identified several key features associated with yellow-billed cuckoo breeding locations: (1) a 4.5 ha core area of dense cottonwood-willow vegetation, (2) a large native, heterogeneously dense forest (72 ha) around the core area, and (3) moderately rough topography. The odds of yellow-billed cuckoo occurrence decreased rapidly as the amount of tamarisk cover increased or when cottonwood-willow vegetation was limited. We achieved model accuracies of 75 - 80% in the project area the following year after updating the imagery and location data. The two model types had very similar probability maps, largely predicting the same areas as high quality habitat. While each model provided unique information, a dual-modelling approach provided a more complete

picture of yellow-billed cuckoo habitat requirements and will be useful for management and conservation activities.

1. Introduction

The western population of the yellow-billed cuckoo (*Coccyzus americanus*) (hereafter “cuckoo”) is a species of conservation concern and was recently listed as threatened under the federal Endangered Species Act (U.S. Fish and Wildlife Service [USFWS], 2014). The cuckoo is a Neotropical migrant that breeds in the western portions of the United States, Canada, and Mexico, where it nests in low to moderate elevation (328 to 6,902 ft; 100 to 2,104 m) riparian woodlands (Hughes, 1999). The riparian habitats upon which they depend are dynamic and can undergo repeated cycles of establishment, growth, and destruction (Paxton et al. 2007). Anthropogenic alterations of watersheds and riparian systems are degrading and destroying its habitat range-wide, while habitat fragmentation results in small isolated populations of cuckoos that contribute to its vulnerability. The cuckoo is included in several habitat conservation plans, including the Lower Colorado River Multi-Species Conservation Program’s (LCR MSCP; LCR MSCP, 2004), which aims to minimize and mitigate the effects of projects or actions on cuckoos.

Conservation of the cuckoo requires detailed information about its breeding habitat requirements at multiple spatial scales. Currently, most information indicates the importance of specific, finite, patch-level vegetation-community composition and structure, generally consisting of multi-structured or multi-layered riparian vegetation with substantial canopy cover provided by native riparian trees, particularly willows (*Salix* spp.) and cottonwoods (*Populus* spp.; Corman and Wise-Gervais, 2005; Girvetz and Greco, 2009; Johnson et al., 2010). There is evidence that consideration of patch-level habitat variables alone does not adequately describe cuckoo breeding habitat nor the potential effects of landscape-level habitat characteristics and

processes (Girvetz and Greco, 2009; Greco, 2013; Johnson, 2009). Habitat features such as vegetation communities boundaries, patch size, patch shape, patch fragmentation and patch connectivity can have different influences when measured at different scales (Bissonnette, 1997; Girvetz and Greco, 2009).

Understanding the spatial scales at which organisms respond to environmental factors and processes is especially essential for sustaining species of conservation concern and threatened habitats. Recognizing the need for assessing species' habitat needs at multiple spatial scales, in conjunction with the availability of remotely sensed measures of vegetation and landscape composition, has prompted ecologists to model habitat associations with hierarchical approaches that incorporate predictor variables measured at multiple spatial scales (Girvetz and Greco, 2009; Meyer and Thuiller, 2006; Saab, 1999; Scott et al., 2002; Wiens 1989). These approaches often combine variables of vegetation structure or composition that are measured at a relatively fine scale (e.g. <1 ha), and landscape variables (e.g. percent cover within a given area or patch configuration) measured at considerably broader spatial scales (e.g. entire watershed; Meyer and Thuiller, 2006). Comparing the relative strength of predictor variables measured at different spatial scales may be one tool for understanding the appropriate scale of measurement (Holland et al., 2004) and, ultimately, management actions. Through the identification of habitat features at multiple spatial scales, spatially explicit models increase our ecological understanding of a target species while providing site-specific habitat maps (Hatten and Paradzick, 2003; Paxton et al., 2007).

Previous efforts to spatially model cuckoo habitat used maps of vegetation communities obtained from orthorectified aerial photography (hereafter “aerial-photo models”). While aerial-photo models are comparatively easy to interpret, they are expensive to obtain and difficult to

accurately reproduce due to classification errors, subjectivity, and the lack of standardized methods (Cherrill and McClean, 1995; Hearn et al., 2011). In contrast, vegetation maps created from Landsat imagery (hereafter “satellite models”) can characterize vegetation features across broad areas with the normalized difference vegetation index [NDVI]) with near perfect repeatability (Hatten et al., 2010). However, satellite models usually lack the ability to identify specific plant communities and can be difficult to translate into target habitat conditions for conservation purposes (Paxton et al., 2007). Thus, the goal of the project is an important consideration when selecting imagery for classification purposes. When projecting habitat models across very large geographic areas, Landsat imagery is ideal (Hatten, 2016); when classifying vegetation at species or community levels, higher resolution imagery is preferred (Carter et al., 2009; Xun and Wang, 2015).

The goal of our study was to characterize and map cuckoo breeding habitat along the Lower Colorado River (LCR) with a dual modeling approach, at multiple spatial scales. We used aerial-photo and satellite models to accomplish five objectives; (1) identify factors associated with high-quality habitat, (2) develop species distribution models, (3) map habitat quality throughout the study area, (4) identify areas where habitat restoration will be most effective, and (5) increase our understanding of cuckoo breeding habitat by comparing and contrasting the two modelling techniques. To facilitate the modelling process, we developed a conceptual model of cuckoo breeding habitat that identified habitat features hypothesized to be important (Fig. 1). Specifically, we hypothesized that cuckoo habitat selection is influenced by riparian patch size and fragmentation, vegetation density and structure, and plant community and patch location in relation to land cover (e.g. agriculture, urban development, surface water).

2. Materials and methods

2.1. Study Area

The study area consists of riparian habitats within the LCR MSCP boundaries, which we refer to as the LCR. It includes areas up to and including the full-pool elevations of Lake Mead, Lake Mohave, Lake Havasu, and the historical floodplain of the Colorado River from Lake Mead to the United States–Mexico Southerly International Boundary, a distance of about 644 river km (400 mi; Fig. 2). Yellow-billed cuckoos were once considered abundant throughout the study area's riparian floodplain (Grinnell and Miller, 1944; Stephens, 1903), when the Colorado River flowed unimpeded and was a highly dynamic system. Since the late 1800s, the riparian ecosystem of the LCR has undergone dramatic changes. Dam construction and irrigation practices between 1909 and 1966 inundated floodplains and altered hydrology, resulting in destruction and modification of native riparian woodland. Dams also enabled the conversion of floodplains to agricultural uses and dam operations contributed to the replacement of native riparian vegetation with non-native plants, most notably tamarisk (*Tamarix* spp.; Ohmart et al., 1988; Rosenberg et al., 1991; and Shafroth et al., 2002).

The LCR in Arizona and California supported an estimated 180–240 yellow-billed cuckoo pairs in 1976–77, a number that declined by an estimated 80–93% by 1986 (Laymon and Halterman, 1987a; Rosenberg et al., 1991). In 1998, no cuckoos were found in California on the southwestern portion of the study area in sites that were occupied in 1976–77 (Halterman, 1998). Declines in cuckoo abundance coincided with habitat loss due to high water levels and inundation of long duration in 1983–84, and 1986 (Laymon and Halterman, 1987b, Ohmart et al., 1988, and Rosenberg et al., 1991).

The Bill Williams River (BWR) is a tributary of the Colorado River, and due to water releases from Alamo Dam ~60 km upstream of its confluence with the Colorado River, the BWR has had the most continuous, native-dominated riparian habitat along the LCR. Since the 1960s, the largest known population of cuckoos has been in the BWR and our surveys confirmed that it continued to support the largest cuckoo population in the LCR (Johnson et al., 2007, 2008; Rosenberg et al., 1991). More recently, surveys have shown that cuckoos continue to be more abundant in the native-dominated habitat of the BWR, in addition to LCR MSCP restoration habitat (McNeil et al., 2013).

2.2. Modelling Overview

The major difference between the satellite and aerial-photo models was resolution – the satellite model used Landsat Thematic Mapper (TM) imagery, which has 30x30 m pixel-to-ground resolution, while the aerial-photo model used imagery with a 3x3 m pixel-to-ground resolution, to create land cover maps. We used Landsat TM imagery to provide coarse-scale information about riparian vegetation features such as structure, lushness, and spatial arrangement (Hatten et al., 2010). In contrast, we used higher resolution digital ortho-photos to identify vegetation types and patch extents. Examining the effectiveness of habitat models developed with different variable resolutions and sensors enabled us to compare their ability to correctly identify features of cuckoo habitat at multiple locations (Carter et al., 2009; Hatten, 2016; and Xun and Wang, 2015).

We created species distribution models (SDMs) from Landsat imagery and digital ortho-photos in a five-step process. First, we created a cuckoo use/nonuse map of the project area for the 2006 breeding season. Second, we developed spatial databases of vegetation and floodplain features that were extracted from Landsat TM imagery, digital elevation models, and digital

ortho-photos. Third, we used logistic regression to test a set of hypotheses, identify significant associations between cuckoos and biophysical variables, and build and test predictive models (Hosmer and Lemeshow, 1989). Fourth, we created probability maps that depicted cuckoo habitat suitability based upon specific logistic-regression equations. Fifth, we tested (i.e. challenged) the spatial models with a set of cuckoo locations obtained on the LCR the following year (2007).

2.3. Yellow-billed Cuckoo Location Data

Data on cuckoo locations in the LCR were obtained from breeding-season surveys conducted in 2006 and 2007 (Johnson et al., 2007, 2008) with a standardized methodology (Haltermann et al., 2015). All cuckoo locations were subsequently mapped in a geographic information system (GIS). In 2006, cuckoos were surveyed at 55 sites within the LCR study area, between 11 June and 13 September. Cuckoos were detected at 27 of the 55 sites, primarily at the BWR (n = 117 detections) and Lake Mead inlet (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 BWR (n = 139 detections; 85 percent of all detections).

2.4. Cuckoo Use/Nonuse Map

Creating unbiased spatial models of cuckoo breeding habitat required that we develop an accurate map of all cuckoo use/nonuse (i.e., presence/absence) sites inside the study area, with minimal pseudo replication and spatial autocorrelation (Legendre, 1993). We accomplished this task in several steps. First, 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. Second, we buffered cuckoo presence locations (Johnson et al., 2006, 2007, 2008) by 200 m since this is the minimum distance cuckoos move inside a core breeding area (Johnson

et al., 2008), and to avoid classifying nonuse areas as use areas. Third, we buffered absence locations by 200 m, thus any cell within an absence buffer was considered a nonuse area. Wherever a use polygon overlapped a nonuse polygon, due to sample locations 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 had no cuckoo detections. Our sampling approach resulted in 148 random points; 73 points fell inside nonuse areas (i.e. 30x30 m cells) and 75 fell inside use areas.

2.5. Satellite Vegetation and Floodplain Explanatory Variables

Following a published modelling approach (Hatten and Paradzick, 2003) for southwestern willow flycatcher (*Empidonax traillii extimus*), we created a biophysical dataset for modelling from Landsat Thematic Mapper (TM) imagery and a digital elevation model (DEM). By stitching together multiple TM images and DEMs, we covered the entire study area (Fig. 2). Specifically, we extracted vegetation characteristics (vegetation quantity and density) from the TM data, and floodplain characteristics (width, aspect, terrain ruggedness) from a DEM. We characterized vegetation density in each 30x30 m cell (0.09 ha) with the 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. This approach allowed us to characterize the relative lushness and density of riparian vegetation throughout the project area. Also, in order to develop as specific an SDM as possible, we applied an NDVI mask to eliminate all cells that were not comprised of riparian vegetation ($NDVI < 0.126$; Hatten and Paradzick, 2003). This cutpoint ensured that randomly generated sample locations did not fall outside of riparian vegetation. To ensure agricultural fields were not 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.

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 were grids comprised of 30x30 m cells. To create our SDMs, 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 (30 m increments, from 60 m to 540 m radius, ~1 – 92 ha), or (3) within irregularly shaped patches (~1 – 250 ha). We developed riparian-patch variables through the identification of patch boundaries and patch size (patches were defined using contiguous raster cells), categorizing vegetation at different NDVI thresholds (Hatten et al., 2010; Paxton et al., 2007).

We characterized the fragmentation and connectivity in riparian vegetation with fragmentation software (FRAGSTATS; McGarigal and Marks, 1995), examining the influence of patch size, distance between patches, and amount of patch edge, at the patch level of analysis. 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. The TRI variable was considered as a direct parameter of habitat suitability, and also as an indicator of land use and dominate vegetation, since flat areas are more subject to anthropogenic factors than moderate or high ruggedness areas, and are more often dominated by saltcedar.

Lastly, given that the study area is within the Bureau of Reclamation's multispecies conservation plan, we tested whether any of the predictor variables or habitat layers output by the southwestern willow flycatcher (hereafter "flycatcher") model (Hatten and Paradzick, 2003) were significant predictors in the cuckoo model. Specifically, 7 of 14 variables listed in Table 1 were obtained from the Hatten and Paradzick modeling effort: 4 are predictor variables (FLOOD12, ND_BEST, ND_BEST33, ND_BEST120) while three are habitat predictions (WIFL_50, WIFL_PROB, WIFL_5CL).

2.6. Aerial-Photo Vegetation and Land Cover Explanatory Variables

In addition to variables and models derived from remote sensing data, we wanted to assess cuckoo use of different vegetation-community or land cover types for breeding. To classify vegetation within our study area, we initially used a land cover map developed by Bio-West, Inc, and GEO/Graphics, Inc. for the Bureau of Reclamation (Bio-West, Inc. and GEO/Graphics, Inc., 2006). They classified riparian and marsh vegetation using 2004 color infrared (CIR) orthophotography as the base layer and used the Anderson-Ohmart classification system (Anderson and Ohmart, 1976) to identify vegetation community and structural-type classes, with a minimum mapping unit of 1 acre (0.40 ha). In addition to the Anderson-Ohmart vegetation community-structural classes, they added classes to capture non-riparian land cover (e.g., agriculture, open water), for a total of 41 land cover classes. The land cover map produced by Bio-West, Inc. and GEO/Graphics, Inc. was used for most of the project area, but field surveys found it to be inaccurate in the BWR area (M. Johnson, unpublished data), where the cottonwood-willow class was misclassified. To remedy this, we created a detailed vegetation map of the BWR by interpreting orthorectified color-infrared photos from September 2005 (scale 1:15,840), using methods and identifying 13 cover classes described in Shafroth et al. (2002).

With minimal reclassification effort, we made it compatible with the Bio-West, Inc. and GEO/Graphics, Inc. (2006) map.

Forty-one land cover classes was an unrealistic number for logistic modelling given the modest number of cuckoo presences observed during 2006 or 2007 in the study 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 (1976) vegetation classes into fewer, broader categories, based upon our knowledge of yellow-billed cuckoo ecology and the LCR ecosystem (see Table 2). The resultant polygon map was converted into a raster dataset, using “center of the cell” method, with 30x30 m cells represented by the reclassified land cover types.

Our dual modelling approach allowed us to characterize vegetation-community and land cover types at the same resolution as the satellite variables. We used a GIS and moving windows to create variables of (1) the area of each vegetation-community type, (2) the major, or dominant, vegetation-community type, (3) the variety (number) of vegetation-community types, and (4) the heterogeneity of vegetation-community types. We developed eleven types of spatial variables (Table 2) to characterize vegetation-community and other land-cover types at multiple scales: (1) within a grid cell (30x30 m, 0.09 ha), (2) inside concentric circles (30 m increments, from 60 – 480 m radius, ~1 – 72 ha).

2.7. SDM Construction and Hypothesis Testing

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 use and nonuse locations with their respective vegetation and floodplain characteristics stored in a spatial database. Thus, for each set of models, all locations contained a common set of

attributes describing background conditions they experienced (e.g. area of vegetation-community type within a specified neighborhood, patch size, heterogeneity in vegetation density, floodplain size). We identified and eliminated highly correlated variables before using backward 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 loglikelihood 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:

$$P_i = e^{g(x)} / 1 + e^{g(x)} \quad (1)$$

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 or suitability 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%.

To assist in model evaluation, 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 (Chicago, Ill) 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 cuckoo detections 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 equal or greater than 50% were considered suitable (habitat), while cells under the threshold were considered unsuitable (not habitat). For verification purposes, we tested the satellite and aerial-photo models with cuckoo locations collected in 2007 within the LCR, requiring we populate the 2006 satellite models with vegetation features extracted from 2007 Landsat imagery. For the aerial-photo model, we had one vegetation-community land cover map produced in 2004 and 2005, so we examined cuckoo distribution and accuracy on this map for both 2006 and 2007.

3. Results

3.1. Yellow-billed Cuckoo Satellite Model

We developed multiple satellite models of yellow-billed cuckoo breeding habitat that were comprised of unique combinations of explanatory variables (Table 1); we present the top two model performers in Table 3. Satellite model 1 contained three variables (all positive coefficients): (1) terrain ruggedness (TRI) broken into four classes of ruggedness (flat, low, moderate, high), (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 two vegetation-density variables as model 1, but without TRI. Most of the variables listed in Table 1 were significant in one model or another, but they were not significant in the top two satellite models. There was considerable contrast between the biophysical values found at yellow-billed cuckoo presence versus cuckoo absence sites, with higher median values at presence sites (Fig. 3, left panel). Backwards stepping and the likelihood-ratio test (equivalent to the F -test in linear regression) revealed that terrain ruggedness (TRI) had the tightest association with cuckoos in the project area in satellite model 1 and the

largest influence on the model's log-likelihood, followed in decreasing order by ND_BEST120 and ND_SD480 (Table 4). In satellite model 2, ND_SD480 had the larger influence on the model's log-likelihood followed by ND_BEST120 (G statistic of 7.046 versus 6.281), but both were highly significant (Table 4).

Broken into increasing levels of terrain roughness (i.e., flat, low, moderate, high), the odds ratios (Table 3) 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 ~25.5 times as likely (Table 3). In satellite model 1, a 1 ha increase in dense vegetation (ND_BEST120) within a 120-m-radius neighborhood (~4.5 ha) increased the odds of a cuckoo occurring by ~38% (Table 3), with the odds ratio obtained as follows: exponentiate the coefficient ($\exp(0.324)$), subtract 1, and multiply by 100 (e.g., $1.382 - 1 = 0.382 * 100 = 38.2\%$). The heterogeneity in riparian density inside a 480-m radius, or 72-ha patch (ND_SD480), was only slightly less influential than ND_BEST120, with the odds ratio informing us that for each one standard deviation (SD) increase in vegetation-density heterogeneity, the likelihood of a cuckoo increased by 68% (Table 3).

3.2. Yellow-billed Cuckoo Aerial-photo Model

Using aerial-photo vegetation and landcover data, we developed multiple aerial-photo models of yellow-billed cuckoo breeding habitat containing varying combinations of explanatory variables (see Table 2), but we focused on the best model (Table 5). The top model contained six variables: (1) amount of tamarisk cover within a 480-m radius (SC_480), a negative relationship, (2) amount of cottonwood-willow cover within a 120-m radius (CW_120), a positive relationship, (3) amount of cottonwood-willow cover 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), a positive relationship, (5) amount of “other” vegetation-community cover types (see Table 2) within a 480- m radius (OT_480), a negative relationship, and (6) the standard deviation of the variety (number) of vegetation-community cover types surrounding each 30x30-m cell within a 480-m radius (SD_Var480), a negative relationship (Table 5). 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. There was considerable contrast between the amount of vegetation/land cover types at cuckoo presence versus absence sites, with more cottonwood-willow cover (CW_120 and CW_480), and less tamarisk cover (SC_480) at presence sites (Fig. 3, middle and right panels). Backwards stepping and the likelihood-ratio test revealed that the amount of tamarisk cover within a 480-m radius (SC_480) had the tightest association (negative) with cuckoos in the project area, while the amount of cottonwood-willow cover inside a 480-m radius had the weakest association (see *G* statistic, Table 6).

The odds ratios informed us that for each 1 ha increase in the area of tamarisk cover inside a 480-m radius circle, or 72 ha (SC_480), the odds of cuckoo use decreased by ~8%. The amount of cottonwood-willow cover within 4.5 ha, or 120-m radius (CW_120), was also a significant covariate, with the odds ratio showing that for each 1 ha increase in area of cottonwood-willow cover within 4.5 ha, the likelihood of cuckoo use increased by approximately 109%. The heterogeneity of vegetation-community types within a 480-m radius (VEGSD_480) was negatively associated with cuckoo presence, with the odds ratio revealing for each 1-SD increase in heterogeneity in number of vegetation-community types within a 480-m radius circle (72 ha), likelihood of cuckoo use decreased 92%. Area of open water was also negatively associated

with cuckoo use. Similarly, the likelihood of a cuckoo decreased with increasing area of other land cover types (shrubby-vegetation communities and bare ground) within a 480-m radius.

The area of cottonwood-willow cover within a 480-m radius (CW_480) and the area of other-vegetation-community types within a 480-m radius (OT_480) were the least significant in the model. The odds of cuckoo occurrence decreased as the area of cottonwood-willow cover within a 480-m radius increased. An examination of the mean proportion of cottonwood-willow cover 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 as the distance from the non-use point (the radius) increased.

3.3. Model Performance and Comparison of Satellite and Aerial-photo Model Distributions

Following application of agriculture, urban, and NDVI masks ($\text{NDVI} < 0.126$ = 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 (see Fig. 4). 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 1 (38,122 ha). Application of the satellite model in 2007 produced 1,984 ha of predicted habitat, or 5.6% of total riparian vegetation considered in 2007 (35,133 ha). In contrast, application of the aerial-photo model that used 2004-2005 vegetation and land cover data, at a 50% threshold, resulted in 2,778 ha of predicted cuckoo habitat, or 8.9% of all riparian vegetation considered by the model (31,360 ha).

Using year 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-photo model performed slightly better with 76% overall accuracy, with 16% omission error and 33% commission error. An ROC curve (Fig. 5A) shows classification performance of satellite model 1 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 satellite model 1 with 2007 data, AUC increased to 0.88 (Fig. 5B). The aerial-photo model produced a remarkably similar ROC curve for year 2006, with an AUC score of 0.88 (Fig. 5A). The ROC curves for year 2007 were also similar, but there was a distinct departure in classification accuracy after 80% sensitivity was achieved by both models (Fig. 5B), with the aerial-photo model obtaining a 0.91 AUC score. Thus, the satellite model 1 was slightly more accurate when model probabilities ranged from 0 – 80%, but less accurate than the aerial-photo 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 (Fig. 6). The aerial-photo model produced roughly similar cuckoo detection densities in the five 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-photo model achieved greater detection densities in all five probability classes than satellite model 2, with a pronounced exponential relationship. Of all three models, the aerial-photo 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 (Fig. 6).

The distribution of model probabilities for the two model types was very similar (Fig. 7A). The satellite model 1 and aerial-photo models' distributions remained similar again when challenged with 2007 cuckoo presence/absence data (Fig. 7B). Satellite model 1 produced a narrower range of probabilities (i.e. tighter niche) than the aerial-photo model when predicting absences, while the aerial-photo model produced a narrower range when predicting presence locations. The median values were more similar between the satellite and aerial-photo models in 2006 than 2007, possibly because the aerial-photo model was using the same static land-cover map that was produced in 2004 and 2005, while the satellite model used up-to-date imagery.

4. Discussion

Our dual modelling approach leveraged the advantages of fine- and coarse-scale data extracted from digital ortho-photos or Landsat imagery, respectively. The satellite maps can be produced quickly and efficiently, applied across large areas (e.g. drainages, regions), and produce replicable results. The weakness of the satellite model is its inability to distinguish vegetation communities, something we did achieve with the aerial-photo model. Thus, combining them produced the most interpretable and useful results. Both modelling approaches assessed factors using a hierarchical spatial scale and both found the 120 m radius/4.5 ha (core breeding area) and the 480 m radius/72 ha (larger patch) scales to be the most influential spatial scales. In addition, the two model types had very similar probability maps, largely predicting the same areas as high quality habitat. The challenge of the aerial-photo model approach is the availability or creation of vegetation-community or land cover maps that utilize standardized classification criteria, so replicable results can be produced. While the dual modelling approach added another layer of complexity, it can provide key information on habitat requirements at

multiple spatial scales and generate detailed habitat maps of cuckoo breeding habitat in complex riparian systems.

4.1. Yellow-billed Cuckoo and Vegetation Associations

Some of our models' vegetation covariates had similarities to those identified in previous studies. Gaines (1974) found cuckoos inhabited patches greater than 60 ha dominated by cottonwood-willow gallery forest in the Sacramento Valley. Others found patch sizes ranging from 41 to 81 ha with abundant cottonwood-willow vegetation (Girvetz and Greco, 2009; Greco et al., 2002; Halterman, 1991; Laymon and Halterman, 1989). We found that cottonwood-willow cover and vegetation density are important within a core area of 4.5 ha, and the amount of scrubby vegetation had a negative association with cuckoo use at the larger, 72 ha scale. Furthermore, our models contributed new, unique information on cuckoo vegetation associations in the LCR. Specifically, cuckoo habitat quality declined as the amount of tamarisk vegetation increased within a 72 ha patch, and heterogeneity in density of riparian vegetation, or structural diversity, was important within a 72 ha area. Heterogeneity in the density of riparian vegetation likely corresponds to the heterogeneity in canopy closure that typically occurs in riparian areas subject to natural flow dynamics and episodic regeneration of cottonwood and willow trees. Conversely, heterogeneity in vegetation-community cover types, with greater heterogeneity representing greater fragmentation, was negatively associated with cuckoo use.

One of the variables we found important in the satellite models was ND_BEST120, representing the amount of dense vegetation within a 120-m radius (4.5 ha) of a given location. This variable is also an important feature of breeding habitat of southwestern willow flycatcher

(Hatten and Paradzick, 2003), an endangered riparian bird. However, a major difference between the cuckoo and flycatcher satellite models is the spatial scale of habitat characteristics. In the flycatcher model, a 120-m-radius (4.5 ha) patch variable is the most important covariate, while our models indicated cuckoos require a 480-m-radius patch (72 ha), an order of magnitude larger. The difference in patch-size preference is likely due to different natural history traits. Western yellow-billed cuckoos are non-territorial and breed in large patches (between 15 and 80 ha or more in extent; Laymon and Halterman, 1989; USFWS, 2014) of riparian vegetation with native riparian trees, while southwestern willow flycatchers use a variety of riparian habitats, and are territorial, requiring between 0.24 and 4.5 ha (Paxton et al., 2007; Sedgwick and Knopf, 1992). A yellow-billed cuckoo's breeding cycle is also extremely rapid and during breeding they depend on abundant, large prey items, including cicadas, katydids, and caterpillars gleaned from foliage (Hamilton and Hamilton, 1965; Hughes, 1999; Rosenberg et al., 1982). Larger patches of riparian vegetation may provide more abundant and diverse large prey items.

4.2. Yellow-billed Cuckoo and Landscape Associations

The terrain ruggedness variable (TRI) proved to be our most important variable in the best-performing satellite model within the LCR. Broken out into four roughness classes, going from flat to extremely rugged, TRI was a surrogate for multiple biophysical factors the satellite model could not capture directly. This observation was supported by the fact that TRI was not retained in the aerial-photo model, which contained species-specific vegetation information. In the satellite model, the odds ratios informed us that areas of low and high ruggedness were approximately three times more likely to contain a cuckoo when compared to flat terrain. However, the intermediate class of ruggedness (class 3) was approximately 25.5 times more likely to contain a cuckoo, when compared to flat terrain. This pattern reflected the fact that the

majority of presence locations, located along the lower BWR and lower Grand Canyon above the Lake Mead inlet, were in intermediately rough areas. In contrast, many of the nonuse sites in our analysis were immediately adjacent to the Colorado River in the larger floodplain along the mainstem, 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, yellow-billed cuckoo's 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; Johnson et al., 2007, 2008; Rosenberg et al., 1991). Our satellite models did not find distance to water to be a significant variable, while the aerial-photo model found the amount of open or structured-open water was negatively associated with cuckoo presence. These results are likely due to the majority of sample locations (use and nonuse) occurring within two km of water, which lacked the contrast necessary for this analysis. If our analysis were repeated over a larger landscape where more absence locations occurred along intermittent or ephemeral channels, the distance-to-water variable would likely be important.

Within the LCR, cuckoos were once considered abundant throughout the riparian floodplain along the LCR, where cottonwood and willow was the dominant vegetation (Grinnell and Miller 1944). The effects of upstream dams, flow alterations, channel modifications, and land clearing for agriculture, has especially affected the vegetation immediately adjacent to the Colorado River and along reservoirs, areas which have relatively flat, wide floodplains where tamarisk is now the dominant vegetation (Johnson et al., 2007, 2008). Cuckoos were absent from these areas during our surveys; the majority of our cuckoo presences were located in the lower Bill Williams

River and lower Grand Canyon above the Lake Mead inlet, where the terrain is moderately rugged, riparian habitat is primarily comprised of native vegetation, and is the most continuous, unfragmented habitat of its kind in the LCR.

4.3. *Model Accuracy*

The satellite and aerial-photo models performed similarly when classification tables or ROC were examined, and when the distributions of their model probabilities were plotted.

Interestingly, the satellite model did a better job of correctly identifying cuckoo absences, while the aerial-photo 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 or nonuse areas, while the aerial-photo model produced a tighter niche for presence locations or use areas. Another interesting pattern we observed was the satellite models did a better job of habitat classification where there were larger vegetation patches (BWR, and above the Lake Mead inlet), while the aerial-photo model appeared to perform better in smaller vegetation patches (the Colorado River near the Gila River confluence, and the Yuma area). 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 probability classes contained higher density of cuckoo detections than satellite model 2 along the LCR because it contained the terrain ruggedness variable and was more specific (it predicted less habitat). A comparison of satellite models 1 and 2 revealed the importance of terrain ruggedness in model fit (R^2) and classification accuracy (ROC and

classification table). When terrain ruggedness was removed from model 1, there were significant decreases in accuracy along the LCR.

4.4. Yellow-billed Cuckoo Breeding Habitat and Conservation Implications

We characterized and mapped cuckoo breeding habitat within the LCR to provide information relevant the LCR MSCP Habitat Conservation Plan. Under this plan, the Bureau of Reclamation is maintaining existing habitat and implementing the restoration of 5,940 acres of cottonwood–willow habitat, including 4,050 acres specifically for the cuckoo (LCR MSCP, 2004). Our spatially explicit models mapped the relative quality of cuckoo habitat throughout the LCR and thus identified areas of high quality habitat for maintaining and areas of moderate-quality habitat for restoration.

Conservation of the cuckoo requires detailed information about its breeding habitat requirements and our models allowed us to determine key habitat characteristics for breeding cuckoos, including vegetation and patch characteristics. Specifically, the models indicated that efforts to conserve and restore high quality cuckoo breeding habitat should include conserving and creating habitat patches that are at least 480-m-radius (72 ha) with a core area of at least 120-m-radius (4.5 ha). The core area should be comprised of dense cottonwood-willow vegetation with a surrounding habitat patch created to minimize or eliminate tamarisk cover, minimize dense shrubby cover, minimize the number of vegetation cover types (i.e. minimize fragmentation), and have heterogeneity in canopy closure and vegetation density. The latter criterion could be met by planting cottonwood and willow in a manner that mimics the pattern of alternating, arcuate bands of dense cottonwood-willow patches of different ages and more open areas that are typically produced by natural flow dynamics and episodic regeneration of these tree species.

The riparian habitat patches that cuckoos depend on are both spatially and temporally dynamic and conservation of the yellow-billed cuckoo requires conservation and restoration of the natural processes that create and maintain its habitat (Greco, 2013), and/or long-term restoration that ensures the availability of high quality habitat. The impacts of dams, diversion structures, canals, groundwater management, urban wastewater, channelization and levees have introduced numerous modifications to the hydrography of southwestern rivers. Reductions in streamflow or groundwater levels can cause plants to undergo physiological stress and lose productivity, with adverse implications for riparian habitat (Graf et al., 2002), while flooding is the primary natural disturbance that enhances riparian ecosystems (Poff et al., 1997; Stromberg et al., 2007). Restoration and maintenance of yellow-bill cuckoo habitat is severely limited without process-based management approaches (Beechie et al., 2010).

Managing streamflow downstream of dams is a process-based approach that has been implemented on the BWR, where cuckoos have persisted and where our model predicts high quality cuckoo breeding habitat. Since the early 1990s and especially since 2004, several experimental flow releases have been implemented generally to further understanding of how operation of Alamo Dam affects ecosystems downstream, and specifically to promote establishment and maintenance of riparian forest dominated by cottonwood-willow, while limiting non-native tamarisk (Shafroth et al., 2010). Management of flows downstream of Alamo Dam has shown the potential to promote cottonwood and willow forest regeneration (Shafroth et al., 1998), maintain this native habitat (Shafroth et al., 2002), and disfavor tamarisk (Johnson et al., 2008; Wilcox and Shafroth, 2013). These changes in tamarisk and willow density correspond with the results of our yellow-billed cuckoo modelling that demonstrated a greater chance a cuckoo will occupy a site when dense tamarisk is limited and native species such as cottonwood

and willow are predominant within a core patch of 4.5 ha and within a surrounding larger patch of 72 ha.

5. Conclusion

Spatially explicit models are valuable tools when assessing the quantity and quality of avian breeding habitat. The dual modelling approach that we used provided us with information that individual modelling approaches could not. The aerial-photo model provided detailed vegetation maps that informed us about species-specific plant associations with breeding cuckoos, but acquiring vegetation cover data for such models is expensive, difficult to repeat, and poorly suited for tracking changes over time. 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. Another advantage of the satellite models is the image archive that dates back to 1984, providing 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 (Hatten et al., 2010). Much could be learned by creating and analyzing spatial datasets of habitat formation and destruction through repeat images acquired at the same location and date each year.

Vegetation structure is a key factor underlying avian habitat selection and an important consideration in the development of bird–habitat models that identify habitat features with conservation implications. 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 cuckoo breeding habitat (Johnson, 2009; Johnson et al., 2007). 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 (Bradbury et al., 2005; Lefsky et al., 2002) over larger spatial extents than is practical through field surveys. The modelling procedures performed in this study are of special significance for establishing habitat requirements for yellow-billed cuckoo along the LCR. 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 study area.

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TABLES 1-6

Table 1. List of satellite-based variables and DEM variables examined in a multivariate logistic regression analysis of yellow-billed cuckoo breeding habitat. Included in the list are predictor grids used to create a southwestern willow flycatcher model and habitat maps (WIFL_prefix) output from the model (Hatten and Paradzick, 2003).

Variable	Description
TRI	Terrain ruggedness index - SD of elevation within 1.6 km radius of river, broken into four categories of roughness: (1 = flat, 2 = low, 3 = moderate, 4 = high)
^b AGDIST	Distance from agriculture or urban areas
^c FLOOD12	Amount of floodplain or flat area within a 41-ha neighborhood
^b H20DIST	Distance from water observable from Landsat5 satellite imagery
^{a,c} ND_BEST	Amount of vegetation with NDVI values > 0.41 inside a 30x30-m cell; variable rescaled into 1 ha units (0 – 4.5 ha)
ND_RAP	Density of vegetation (determined from NDVI) in a 30x30-m cell
^{a,c} ND_SD	Heterogeneity in vegetation density (determined from NDVI); variable scaled from 0 – 6.
^c ND_BEST33	Cells with NDVI >0.33 were coded 1 (binary) in a 30x30-m cell
^c ND_BEST120	Amount of dense vegetation (NDVI >0.41) inside a 120-m radius (4.5 ha)
^b PATCHDIST	Distance from patch interior to exterior boundary
^b PATCHSIZE	Size of patch – # contiguous cells with NDVI >0.41
^c WIFL_50	Southwestern willow flycatcher (SWFL) habitat - binary at 50% threshold
^c WIFL_PROB	SWFL model probabilities (continuous)
^c WIFL_5CL	SWFL model probabilities in 5 classes (0-20%; 21-40%, etc.)

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

^bScalar variable (value varies depending on location)

^cVariable also used in the southwestern willow flycatcher model (Hatten and Paradzick, 2003)

Table 2. List of aerial-photo-based variables derived from maps of vegetation type, 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 – 540 m radius, ~1 – 92 ha) around each 30x30 m cell
SC	Amount of salt cedar vegetation type inside concentric circles (60 – 540 m radius, ~1 – 92 ha) around each 30x30 m cell
SM	Amount of salt cedar-mesquite vegetation type
ME	Amount of mesquite vegetation type inside concentric circles (60 – 540 m radius, ~1 – 92 ha) around each 30x30 m cell
MA	Amount of marsh vegetation type inside concentric circles (60 – 540 m radius, ~1 – 92 ha) around each 30x30 m cell
AG	Amount of agriculture vegetation type inside concentric circles (60 – 540 m radius, ~1 – 92 ha) around each 30x30 m cell
OW	Amount of open water and structured open water inside concentric circles (60 – 540 m radius, ~1 – 92 ha) around each 30x30 m cell
OT	Amount of other vegetation type (shrubby vegetation types and bare ground) inside concentric circles (60 – 540 m radius, ~1 – 92 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 – 540 m radius, ~1 – 92 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 – 540 m radius, ~1 – 92 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 – 540 m radius, ~1 – 92 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 (i.e., 30 m increments, from 60 to 540-m radius circles around each 30x30 m 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 $R^2 = 0.39$; Hosmer and Lemeshow Goodness-of-Fit test ($\hat{C}$) = 0.69. TRI (terrain ruggedness index) characterized ruggedness in four classes (1 = flat, 2 = low, 3 = moderate, 4 = high). Model 2: same as model 1 but without the terrain ruggedness (TRI) variable (Nagelkerke pseudo $R^2 = 0.163$; $\hat{C} = 0.49$). Interpreting the odds ratios [Exp(B)] for model 1, the odds of a cuckoo increased ~38% for each ha of dense vegetation inside a 120-m radius core area (ND_BEST120 is scaled from 0 – 4.5). The odds of a cuckoo occurring in TRI class 2 were ~3 times greater than class 1 (e.g., 4.127 – 1), ~25.5 times greater in class 3, and ~2.6 times greater in class 4 (TRI was broken into 4 classes, with class 1 the reference category). The odds of a cuckoo increased ~ 68% for each 1-unit increase in standard deviation of NDVI (ND_SD480) within a 480-m radius (scaled from 0 – 6).

Variable	B	S.E.	Wald	df	Sig.	Exp(B)	95.0% C.I.for EXP(B)	
							Lower	Upper
Model 1								
ND_BEST120	0.324	0.148	4.759	1	0.029	1.382	1.033	1.848
TRI_1			23.752	3	0			
TRI_2	1.418	0.577	6.045	1	0.014	4.127	1.333	12.777
TRI_3	3.277	0.676	23.472	1	0	26.509	7.04	99.822
TRI_4	1.292	0.589	4.801	1	0.028	3.638	1.146	11.552
ND_SD480	0.519	0.281	3.417	1	0.065	1.68	0.969	2.912
Constant	-4.405	1.387	10.08	1	0.001	0.012		
Model 2								
ND_BEST120	0.343	0.137	6.223	1	0.013	1.409	1.076	1.845
ND_SD480	0.62	0.245	6.408	1	0.011	1.86	1.15	3.006
Constant	-3.408	1.132	9.058	1	0.003	0.033		

B, coefficient for the constant; S.E., standard error around the coefficient for the constant; Wald, Wald chi-square statistic; df, degrees of freedom for the Wald chi-square test; Sig., p-value for the Wald chi-square test; Exp(B), the exponentiation of the B coefficient; 95.0% C.I. for EXP (B), the 95.0% confidence interval for the exponentiation of the B coefficient. The coefficient for ND_BEST120 (model 1) is 0.029 when analyzed at the 30-m pixel resolution (versus 0.324 at 1-ha resolution); The coefficient for ND_BEST120 (model 2) is 0.031 when analyzed at the 30-m pixel resolution (versus 0.343 at 1-ha resolution);

Table 4. Satellite models' log-likelihoods. The change in -2 times model log-likelihoods (G statistic) when a variable was removed from the model.

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-photo multivariate model of yellow-billed cuckoo breeding habitat (n = 148). See Table 2 for variable definitions. The scale of measurement for each predictor variable was in hectares, except for VEGSD_480, which was in decimal format (0.0001 to 0.9999). Interpreting the odds ratio, a 1 unit (e.g., 1 ha) increase in cottonwood-willow (CW_120) within a 120-m-radius neighborhood (4.5 ha) increased the odds of a cuckoo occurring by 109%. See section 3.1 for how odds ratios were calculated.

Predictor	B	S.E.	Wald	df	Sig.	Exp(B) - Odds ratio	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		

B, coefficient for the constant; S.E., standard error around the coefficient for the constant; Wald, Wald chi-square statistic; df, degrees of freedom for the Wald chi-square test; Sig., p-value for the Wald chi-square test; Exp(B), the exponentiation of the B coefficient; 95.0% C.I. for EXP (B), the 95.0% confidence interval for the exponentiation of the B coefficient.

Table 6. Aerial-photo model log-likelihoods. The change in -2 times model log-likelihoods (G statistic) when a variable was removed from the model. The amount of tamarisk (salt cedar) inside a 480-m radius (SC_480) was the most influential variable in the model, while amount of cottonwood-willow inside a 480 m radius (CW_480) 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 1-7

Figure 1. Conceptual model of factors that may affect yellow-billed cuckoo breeding habitat selection at different spatial scales: nest site (small circle), riparian patch (large circle), and landscape scales, along the Lower Colorado 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 indicate areas where yellow-billed cuckoos were observed during the 2006 breeding season. Arizona's county boundaries are outlined in black. Sizes of red circles are stylistic and do not represent numerical values.

Figure 3. Box-and-whisker plots display the range of biophysical values for each covariate, output by the satellite models (left panel) or aerial-photo 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 satellite model 1 along Lake Mead's delta (A) and the Bill Williams River (B), summer 2006. Model 1 outputs are presented in 5 discrete probability classes (20% increments): the darker the shade of green, the higher the model probability class (i.e., higher likelihood of cuckoo use).

Figure 5. 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 6. The relationship between the satellite and aerial models' probability classes (1=0–20%, 2=21–40%, 3=41–60%, 4=61–80%, 5=81–100% probability) 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 7. Satellite model 1 and aerial-photo model distribution of model probabilities for 2006 and 2007. 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.