Multi-scale predictive habitat suitability modeling based on hierarchically delineated patches: An example for yellow-billed cuckoos nesting in riparian forests, California, USA

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RESEARCH ARTICLE

Multi-scale predictive habitat suitability modeling based on hierarchically delineated patches: an example for yellow-billed cuckoos nesting in riparian forests, California, USA

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Abstract The discipline of landscape ecology recognizes the importance of measuring habitat suitability variables at spatial scales relevant to specific organisms. This paper uses a novel multi-scale hierarchical patch delineation method, PatchMorph, to measure landscape patch characteristics at two distinct spatial scales and statistically relate them to the presence of state-listed endangered yellow-billed cuckoos (*Coccyzus americanus occidentalis*) nesting in forest patches along the Sacramento River, California, USA. The landscape patch characteristics calculated were: patch thickness, area of cottonwood forest, area of riparian scrub, area of other mixed riparian forest, and total patch area. A third, regional spatial variable, delineating the north and south portions of study area was also analyzed for the effect of regional processes. Using field surveys, the landscape characteristics were related to patch occupancy by yellow-billed cuckoos. The area of cottonwood forest measured at the finest spatial scale of patches was found to be the most important factor determining yellow-billed cuckoo presence in the forest patches, while no patch characteristics at the larger scale of habitat patches were important. The regional spatial variable was important in two of the three analysis techniques. Model validation using an independent data set of surveys (conducted 1987–1990) found 76–82% model accuracy for all the statistical techniques used. Our results show that the spatial scale at which habitat characteristics are measured influences the suitability of forest patches. This multi-scale patch and model selection approach to habitat suitability analysis can readily be generalized for use with other organisms and systems.

Keywords Geographic information systems (GIS) · Spatial analysis · Landscape ecology · Riparian ecosystems · PatchMorph

Introduction

The science of habitat suitability modeling has evolved from simple expert opinion models (Verner et al. 1986), to more complex multi-scale and statistically based models (Scott et al. 2002). Determining the relevant spatial scale to measure habitat characteristics has become important for modeling species habitat needs at the landscape level (Scott et al. 2002). Habitat features must be measured at spatial and temporal scales which are relevant to the organism or ecological process being modeled,

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because habitat features—such as vegetation community boundaries, animal density, patch geometry, and resource availability—can exhibit changing patterns when measured at different scales (Bissonette 1997; Milne 1997). Depending on the focal organism and system, changing the scale of measurement of a scale-sensitive landscape characteristic can hide, filter, or magnify the effect of the characteristic (Wu and Loucks 1995).

The theory of hierarchical patch dynamics has laid out a framework for how organisms respond to landscape patches at different spatial scales, and how patches might be perceived differently by the same organism at different life history stages or seasons in an annual cycle (Kotliar and Wiens 1990; Wu and Loucks 1995). Although it is known that patch-based habitat suitability modeling should take into account how patches are perceived by different organisms, it has been difficult to model habitat suitability in terms of hierarchically organized patches (Talley 2007). This is in part due to the lack of patch delineation algorithms to create spatially hierarchical patches.

Geographic information system (GIS) analyses have been used to identify habitat effects at different spatial scales. These techniques often used a "moving window analysis" to measure landscape characteristics at a range of focal distances from each point in the landscape (Bailey et al. 2002; Fuhlendorf et al. 2002). Although these techniques can measure landscape characteristics at multiple scales, they do not incorporate information about the hierarchical structure of patches in the landscape, nor do they incorporate how different organisms may perceive landscape patch structure differently from one-another.

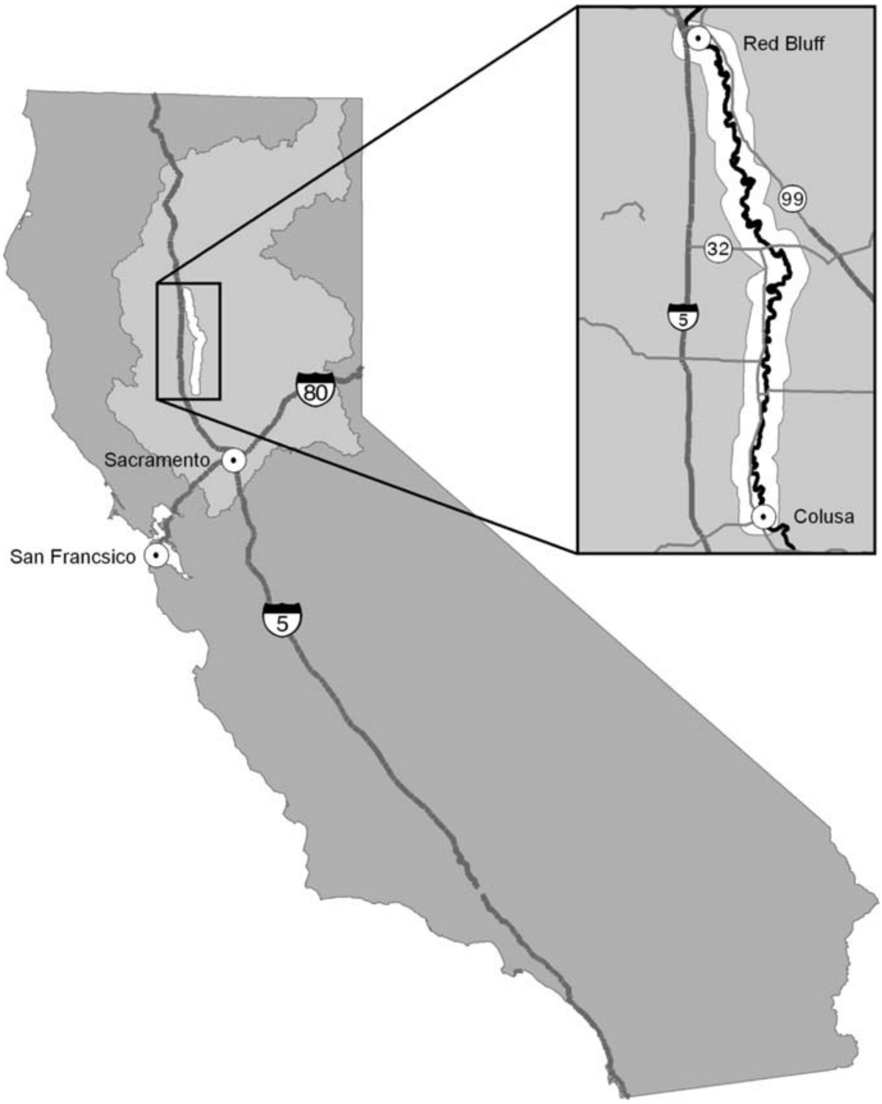
To address this deficit, a novel spatially explicit habitat patch delineation technique was developed, called PatchMorph (Girvetz and Greco 2007). This algorithm delineates patches at multiple spatial scales based on organism-specific thresholds for patch perception and utilization. It is an improvement over using simple rules of contiguity patch delineation methods, which are commonly used to geographically delineate habitat patches. These rules of contiguity define a raster cell of habitat as being in the same patch as an adjacent raster cell if they touch sides in one of the four cardinal directions (the four-cell rule), or if they have a side or a diagonal touching (the eight-cell rule, McGarigal et al. 2002; Turner et al. 2001; With 1997). Rules of contiguity only delineate patches at a single spatial scale, which is determined by the spatial scale or raster cell resolution of the underlying habitat base map. Moreover, it has been well established that what is considered part of a contiguous habitat patch in a heterogeneous landscape will depend on the perception of the organism being studied (Wiens 1976; Kotliar and Wiens 1990; Calabrese and Fagan 2004).

This is the case for the endangered California state-listed western yellow-billed cuckoo (*Coccyzus americanus occidentalis*), whose statewide population was estimated to be 183–202 individuals in 2000, with the largest population located on the Sacramento River (Halterman et al. 2001). This Neotropical migrant songbird species nests in large patches (>5–20 ha) of riparian forests, but is typically not found in parts of the patch less than 100 m thick; however, it will cross gaps in the forest of less than 100 m (Gaines and Laymon 1984; Halterman et al. 2001). Delineating patches using simple rules of contiguity does not fully account for the habitat patch structure relevant to this species. The use of organism-specific patch delineation techniques, such as PatchMorph, can be used to improve the accuracy and realism of habitat suitability models (Girvetz and Greco 2007).

The landscape habitat associations of the yellow-billed cuckoo are of particular interest to conservation and restoration planning. This species once bred abundantly throughout the western United States (Belding 1890), but has experienced declining populations (first noted by Grinnell and Miller 1944) generally thought to be caused by habitat loss from the conversion of riparian habitats into agriculture (Gaines and Laymon 1984; Laymon and Halterman 1989). It is has been reported that the preferred habitat type for this species is a mosaic of riparian vegetation consisting of willow (*Salix* spp.) and cottonwood (*Populus fremontii*) forests (Gaines and Laymon 1984). While the preferred habitat types are generally known, much less is known about how this species interacts with the forest patch landscape structure.

The goal of this paper is to use the PatchMorph algorithm to investigate the spatial scale at which different landscape habitat characteristics affect the presence of western yellow-billed cuckoo nesting in riparian forest patches along the Sacramento River,

Fig. 1 Context map showing the location of the study area within California and the Sacramento River watershed (*lighter gray*)



California, USA (Fig. 1). The Sacramento River is ideal for analyzing habitat use of forest patches by western yellow-billed cuckoos across multiple spatial scales for the following reasons: (1) there is empirical evidence that this subspecies has strong patch-based habitat associations (Laymon and Halterman 1989); (2) comprehensive surveys of habitat patch occupancy of this bird species are available for the entire study area; and (3) fine-scale geographic habitat data of the riparian forests along this river is also available.

We investigate how yellow-billed cuckoos respond to habitat patch characteristics at various spatial scales along a 100 river-mile reach of the Sacramento River. Patches were delineated at two spatially hierarchical scales using the PatchMorph GIS algorithm (Girvetz and Greco 2007), and habitat characteristics of these patches were measured from fine scale GIS land cover maps. A regional spatial variable representing whether the patch is in the northern or southern portion of the study area was also included in the analysis to account for processes that may be acting at a more regional and spatially extensive scale. Statistical inferences were then drawn from these data to identify the most important patch characteristics in determining yellow-billed cuckoo presence, and a set of predictive models were built then validated against western yellow-billed cuckoo surveys.

Methods

Yellow-billed cuckoo surveys and land cover maps

Surveys of yellow-billed cuckoo nesting pair presence in riparian forest patches along the main river channel of the Sacramento River were conducted using a protocol developed by Johnson et al. (1981) and Gaines and Laymon (1984) that utilizes a call-back tape played from a boat or land within or near riparian habitat at intervals of 100 m. The surveys were conducted during the summers of 1999 and 2000 (Halterman et al. 2001) and the summers of 1987–1990 (Halterman 1991). The more recent set of surveys used GPS to locate the survey sites, while the locations of the earlier surveys were identified by river mile, and were manually digitized into a GIS dataset using ArcGIS 8.3 (ESRI 2003). We defined yellow-billed cuckoo "presence" in a patch as constituting one or more pair of yellow-billed cuckoos detected (by sight or sound) in proximity to that patch. There were a total of 162 breeding pairs observed in the 5 years of surveys (average of 27 per year).

GIS datasets of land cover polygons within the study area were digitized from aerial photography taken in 1997 (Greco et al. 2003) and 1999 (Nelson 2000). These datasets distinguished among areas of cottonwood forest, riparian scrub, other mixed riparian forest (including restored forests), oak woodlands, annual grassland, agricultural land, disturbed areas, and various types of open water. The mapping precision of these datasets is 10 m.

Hierarchical patch delineation

Two nested hierarchical levels of western yellow-billed cuckoo nesting habitat patches were delineated from the GIS dataset of land cover polygons using the patch delineation algorithm PatchMorph (Girvetz and Greco 2007). For this analysis, cottonwood forest, riparian scrub, and other riparian forest, were considered suitable habitat types, while all other land cover types were considered unsuitable. The PatchMorph algorithm delineates patches based on two main parameters: (1) the maximum *gap* threshold for patch thickness, defined as the maximum distance across non-suitable habitat that an organism will readily move without the gap of non-suitable habitat being a barrier to the organism's movement; and (2) the minimum *spur* threshold, defined as the minimum thickness of suitable habitat that an organism will readily move into or utilize, before it becomes so narrow that it is unsuitable for the organism. Patches were delineated from the map of suitable land cover using gap and spur values of 100 m (Figs. 2, 3), because western yellow-billed cuckoos have been

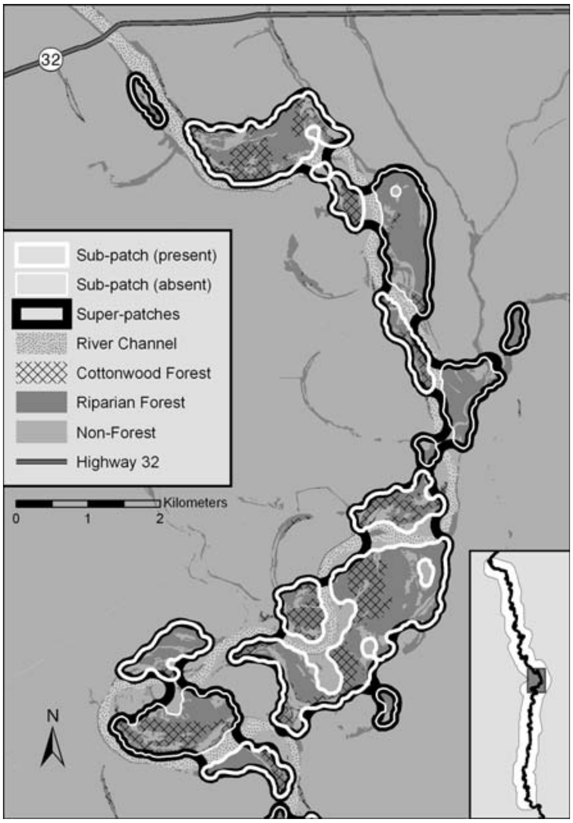


Fig. 2 Riparian forest habitat patches modeled at two spatial scales (*sub-patches* and *super-patches*) using the PatchMorph algorithm based on patch threshold parameters specific to the yellow-billed cuckoo within a small portion of the study area along the Sacramento River. The presence (*thick white lines*) and absence (*thin white lines*) of yellow-billed cuckoos are shown for each of the sub-patches. The distribution of cottonwood forests are shown as a *cross-hatched* overlay for reference

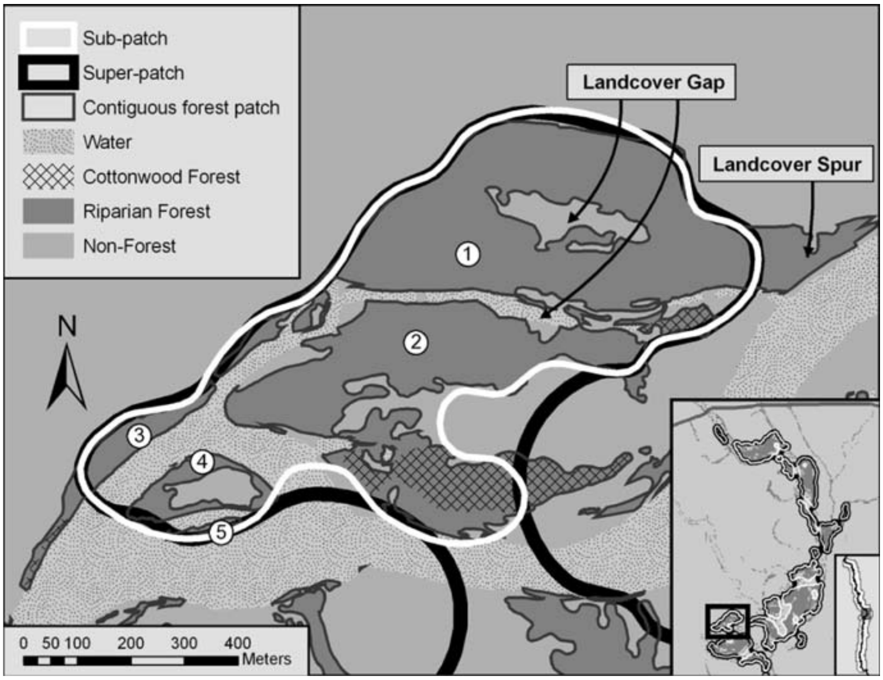


Fig. 3 Close-up map of one forest sub-patch in the study area delineated using the PatchMorph algorithm that would have been delineated as five separate forest patches (*numbered*) using rules of contiguity shown with *circled* numbers. Note that even though water is not considered when delineated the forest patches using the PatchMorph algorithm, the patches delineated patches end up containing some water if it is less than the threshold of 100 m wide and is surrounded by a sufficient amount of suitable forest habitat

observed to generally not to utilize patches of forest <100 m wide, but can cross gaps of <100 m thick (Halterman et al. 2001). In addition, disturbed areas and the main river channel were designated as a hard barrier, preventing them from being part of any patch at this scale. Only patches greater than 5 ha were retained for further analyses. The patches delineated using these PatchMorph parameters are hereafter referred to as “sub-patches”. A second hierarchical level of patches—referred to hereafter as “super-patches”—were then delineated by re-running PatchMorph using the sub-patches as the input land cover surface, and changing the *gap* and *spur* threshold values each to 300 m. These threshold values were used because it has been observed that when nesting, these birds will occasionally move over non-forested areas up to 300 m wide (Gaines and Laymon 1984; Halterman et al. 2001). Super-patch boundaries were allowed to cross the river channel and disturbed areas. Only patches within 100 m of the river channel were included in subsequent analyses because the yellow-billed cuckoo surveys were conducted from along the main river, and birds in patches further from the river channel would not have been observed.

Patch characteristics

Patch metrics were calculated for both sub-patches and super-patches by intersecting the sub-patches and super-patches with the land cover dataset using ArcGIS 8.3 (ESRI 2003). For each patch, the area of cottonwood forest, area of riparian scrub, area of other mixed riparian forest, and patch thickness were calculated. In this case, patch “thickness” is measured as the diameter of the largest circle that can be inscribed within a delineated patch (ESRI 2003). The patch characteristics measured at the super-patch scale were attributed to sub-patches that were nested inside of each super-patch. In order to make these distributions approximately normal, we transformed all patch parameters using the natural log (ln) for all the statistical analyses. In addition, a binary spatial variable denoting the spatial location along the river (north/south) relative to the highway 32 crossing (RM 198) was attributed to each patch (Figs. 1, 4) to represent ecological processes acting at a more regional scale of the landscape. The western yellow-billed cuckoo survey data for all years collected were attributed to the sub-patches.

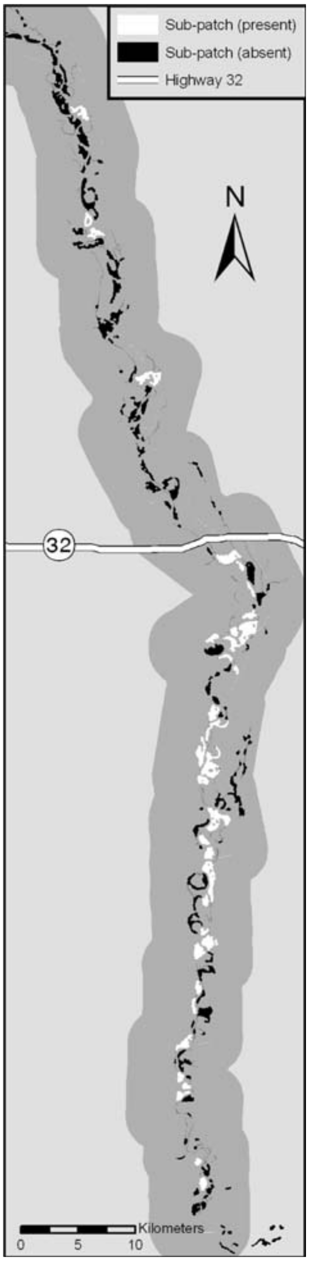


Fig. 4 The distribution of yellow-billed cuckoo presence (*white polygons*) and absence (*black polygons*) in the modeled habitat sub-patches for the entire study area along the Sacramento River. Note the much higher occupancy in habitat patches located south of highway 32 as compared with those located to the north

Statistical analyses

A multiple logistic regression analysis was used to relate cuckoo presence in sub-patches from the survey data for 1999–2000, to the other patch characteristics measured at the three spatial scales. The global logistic regression model used for the analysis was:

$$\ln\left(\frac{P}{1-P}\right) = \beta_0 + \beta_1 \ln(thk_{sub}) + \beta_2 \ln(cwf_{sub}) + \beta_3 \ln(rs_{sub}) + \beta_4 \ln(mrf_{sub}) + \beta_5 \ln(area_{sub}) + \beta_6 \ln(thk_{sup}) + \beta_7 \ln(cwf_{sup}) + \beta_8 \ln(rs_{sup}) + \beta_9 \ln(mrf_{sup}) + \beta_{10} \ln(area_{sup}) + \beta_{11} loc_{reg} + \varepsilon \quad (1)$$

where P is the probability that a given sub-patch patch has a yellow-billed cuckoo nesting pair present, the β_i values are the regression parameter coefficients, *thk* is the patch thickness, *cwf* is the area of cottonwood forest within the patch, *rs* is the area of riparian scrub, *mrf* is the area of other mixed riparian forest, and *area* is the total area of the delineated patch. The subscripts refer to which hierarchical spatial scale the characteristic was measured at, sub-patch (*sub*), or super-patch (*sup*). In addition, a regional scale spatial variable (loc_{reg}) is a boolean variable representing whether the habitat patch is north or south of highway 32 (Figs. 1, 4).

These analyses tested logistic regression models with all possible combinations of the 11 variables ($2^{11} = 2048$ models) for two main goals: (1) to draw inferences about which patch characteristics measured at what spatial scales are the best predictors of yellow-billed cuckoo presence, and (2) find one or a few best models that balance explanatory power (i.e., fit to the data) with parsimony (i.e., fewest explanatory variables). Both goals were accomplished using a combination of statistical techniques including hierarchical partitioning of the models, model selection based on the corrected Akaike information criterion (AIC$_c$), and classification and regression tree analysis (CART).

The AIC$_c$ was calculated for all 2048 (2^{11}) possible nested sub-models of the global model (Eq. 1), and Akaike weights were calculated. A suite of "best models"—with AIC$_c$ values within 2.0 AIC$_c$ points of the model with lowest AIC$_c$—were analyzed in detail. An accuracy assessment was performed for these models, where the logistic regression equation was back transformed and used to estimate the probability that the patch is occupied (P). For each model, an error matrix comparing modeled to observed (during

1987–1990) yellow-billed cuckoo occupancy for each sub-patch, from which the percent accuracy was calculated, and the number of omission errors, commission errors, and kappa value were calculated.

A hierarchical partitioning statistical approach was used to partition the variance explained by each variable (calculated as proportion deviance explained) into the portion the variable explains independently of all other variables, as well as the portion it explains jointly with the other variables (Mac Nally 2000, 2002). The "hier.part" contributed package to the statistical program R was used for this analysis (R-project 2006). A standardized logistic regression was also run for the global model that includes all variables. This analysis was used to draw inferences about the magnitude and direction of the effect on nesting probability for each explanatory variable. The standardized beta values were reported for all eleven explanatory variables from this global logistic regression model.

A classification and regression tree analysis (CART, Breiman et al. 1984) was conducted using the "rpart" contributed package to the statistical program R (R-project 2006) to develop and test predictive models of patch nesting suitability using combinations of the 11 explanatory variables. To prevent over fitting of the model, the minimum number of observations needed to allow a split in the classification tree was set to 20. The resulting classification tree was used to predict presence and absence of yellow-billed cuckoos. Patches were considered to be modeled as occupied if $P \geq 0.5$. An accuracy assessment was performed for the CART model, by creating an error matrix comparing the CART model predicted occupancy to observed yellow-billed cuckoo occupancy during 1987–1990 for each sub-patch. From this error matrix, the percent accuracy, number of omission errors (observed present, but modeled absent), number of commission errors (observed absent, but modeled present), and kappa statistic of agreement were calculated (Agresti 2002).

Results

Nesting occupancy and land cover characteristics of habitat patches

The PatchMorph patch delineation algorithm identified 102 sub-patches and 44 super-patches located within 100 m of the Sacramento River (river miles 143–244). Of the 102 sub-patches, 34 were occupied by a yellow-billed cuckoo nesting pair during 1999–2000, with 23 of the patches being occupied during 1999, and 28 being occupied during 2000. During 1987–1990, 35 of the patches were found to be occupied, with 13–18 being occupied in any single year. When all of the survey data were pooled together, 41 of the patches were occupied during at least one of the surveyed years.

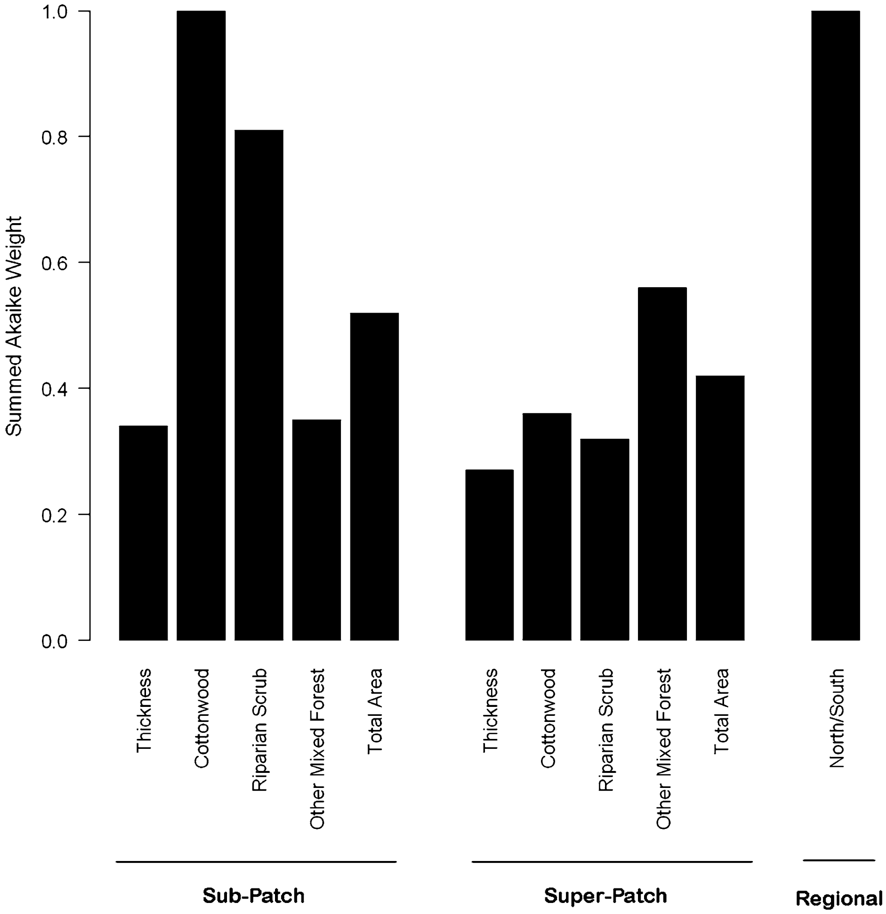
The average size of sub-patches was 59 ha, ranging from 6 to 269 ha. These patches contained an average of 31 ha (range of 1–142 ha) of mixed riparian forest, 15 ha (range of 0–72 ha) contained cottonwood forest, 2 ha (range of 0–15 ha) of open water, and had an average thickness of 233 m (range of 84–517 m). The mean size of the modeled super-patches was 177 ha (range of 6–1074 ha). These patches contained an average of 78 ha (range of 1–487 ha) of mixed riparian forest, 35 ha (range of 0–182 ha) of cottonwood forest, 6 ha (range of 0–60 ha) of open water, and had an average thickness of 298 m (range of 78–733 m).

Splitting the study area into northern and southern sections at highway 32 led to more patches in the southern section occupied than in the northern section (Fig. 4). For 1999–2000, only 4 of the 41 patches (10%) were occupied in the north, compared to 30 of 61 patches (50%) in the south. Similarly during 1987–1990 only 2 of the 31 patches (6%) were occupied in the north, while 28 of the 41 patches (68%) were occupied in the southern section.

Statistical analyses: inference

The area of cottonwood forest measured at the sub-patch scale was the single most important variable identified by all statistical analyses for predicting yellow-billed cuckoo occupancy. It was shown to have a positive effect on nesting probability in all cases. The summed Akaike weight of 1.0 shows that this variable had a 100% likelihood of being a part of the "best model" (Fig. 5). All of the top ranked models identified by the AIC_c analysis included this variable (Table 1). Similarly, the hierarchical partitioning analysis showed that area of cottonwood forest measured at the sub-patch scale explains the most variance of any variable, both independently of other variables (8%) and jointly with other variables

Fig. 5 Summed Akaike weights for the five habitat variables (patch thickness, area of cottonwood forest, area of riparian scrub, area of other mixed riparian forest, total patch area) measured at two spatial scales of patches (*sub-patch* and *super-patch*), and a regional spatial variable indicating if the patch is in the northern or southern portion of the study area. The sum of the Akaike weights can be interpreted as the probability that the habitat variable is part of the "best model" for predicting yellow-billed cuckoo occupancy during 1999–2000



(16.2%, Fig. 6). In addition, the logistic regression analysis of the global model shows that this variable is highly important, having a standardized beta value of 2.33 (Fig. 7). Moreover, the CART analysis found this variable to be the most important variable for predicting nesting presence in forest patches, with it having a positive effect on the probability (Fig. 8).

The regional variable (i.e., north vs. south of highway 32) was also identified by both of the two general linear modeling-based analyses (AIC and hierarchical partitioning) as having a large influence on nesting probability. It also had a summed Akaike weight of 1.0 (Fig. 7), and all top models include this regional variable (Table 1). The hierarchical partitioning analysis found this regional spatial variable explained 7.2% of the total variance independently of other variables, and 9.6% jointly with other variables (Fig. 6). In addition, the logistic regression analysis of the global model showed that this variable is highly important, having a standardized beta value of 2.89 (Fig. 7). In contrast, the CART analysis did not find this regional spatial variable to be important.

The area of riparian scrub measured at the sub-patch scale had a moderate negative effect on nesting presence. It had an Akaike weight of 0.81 (Fig. 5), and was included in all of the "best models" as having a negative effect. The hierarchical partitioning analysis did not find this variable to explain a relatively high proportion of the total variance independent of other variables. However, the analysis did find that this variable explains a negative amount of variance jointly with other variables, suggesting that it is a suppressor variable (Fig. 6). In addition, the CART graph found area of riparian scrub has a negative effect but only for patches that had between 2.65 and 3.85 ha of cottonwood forest (Fig. 8). The logistic regression analysis of the global model shows

Table 1 The top eight models selected from the Akaike Information Criterion analysis for predicting yellow-billed cuckoo occupancy in habitat patches based on the habitat variables—patch thickness (*thk*), area of cottonwood forest (*cf*), area of riparian scrub (*rs*), area of mixed riparian forest (*mrf*), total patch area (*area*)—measured at two spatial scales of patches—sub-patch (*sub*) and super-patch (*sup*)—and the regional spatial variable (Reg. N/S) indicating northern (N) versus southern (S) location in the study area

Model rank	*Sub. thk*	*Sub. cf*	*Sub. rs*	*Sub. mrf*	*Sub. area*	*Sup. thk*	*Sup. cf*	*Sup. rs*	*Sup. mf*	*Sup. area*	Reg. N/S	AICc	*w*(*i*)	# Var.	Percent correct	Omission errors	Commission errors	Kappa	r^2
1	0	+	−	0	+	0	0	0	+	0	S	72.4	0.037	5	82%	8	10	0.58	0.47
2	0	+	−	0	+	0	0	0	0	+	S	73.5	0.021	5	81%	8	11	0.56	0.46
3	0	+	−	0	+	0	−	0	+	0	S	73.7	0.019	6	80%	8	12	0.55	0.48
4	0	+	−	0	+	0	−	0	0	+	S	73.8	0.018	6	80%	8	12	0.55	0.47
5	0	+	−	+	0	0	0	0	+	0	S	74.0	0.016	5	81%	8	11	0.56	0.46
6	0	+	−	0	+	0	0	0	+	−	S	74.1	0.015	6	80%	8	12	0.55	0.49
7	+	+	−	0	0	0	0	0	+	0	S	74.3	0.014	5	81%	9	10	0.56	0.46
8	0	+	−	0	+	0	0	+	0	0	S	74.3	0.014	5	81%	8	11	0.56	0.46

Shaded boxes represent the variables included in each model while the plus or minus sign represents the direction of effect of the variable on patch occupancy. Note that included in every top model is sub-patch area of cottonwood forest with a positive relation, sub-patch area riparian scrub patch, and the regional spatial variable. Area of sub-patch is in six of the eight models, and super-patch area of other mixed riparian forest is in five of the eight models

that this variable is moderately important, having a standardized beta value of −1.5 (Fig. 7).

Area of other mixed riparian forest measured at the super-patch scale was another possibly important variable. The Akaike weight analysis shows it has a 56% likelihood of being in the best model (Fig. 5). Similarly, the hierarchical partitioning analysis shows this variable explains 4.2% of the total variance independently of other variables, and 7.8% jointly with other variables (Fig. 6). Similarly, the logistic regression analysis of the global model shows that this variable is moderately important, having a standardized beta value of 1.53 (Fig. 7).

Statistical analysis: prediction

A suite of eight "best models" were identified that were within two $\mathrm{AIC_c}$ points of the single "best model" (Table 1). All of these "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). These models were validated for accuracy against surveys of yellow-billed cuckoo occupancy conducted in these same patches during 1987–1990. The range of prediction accuracy was 80–82%, with 8–9 omission errors and 10–12 commission errors, resulting in kappa values ranging from 0.55 to 0.58 (Table 1). The number of variables in these models ranged from 5 to 6 and model r^2 ranged from 0.46 to 0.49 (Table 1). When the $\mathrm{AIC_c}$ single "best model" was compared with the CART analysis for predictive accuracy, the $\mathrm{AIC_c}$ "best model" performed slightly better, with an accuracy of 82%, and a kappa statistic of 0.58, while, the CART analysis had an accuracy of 76% and a kappa of 0.47.

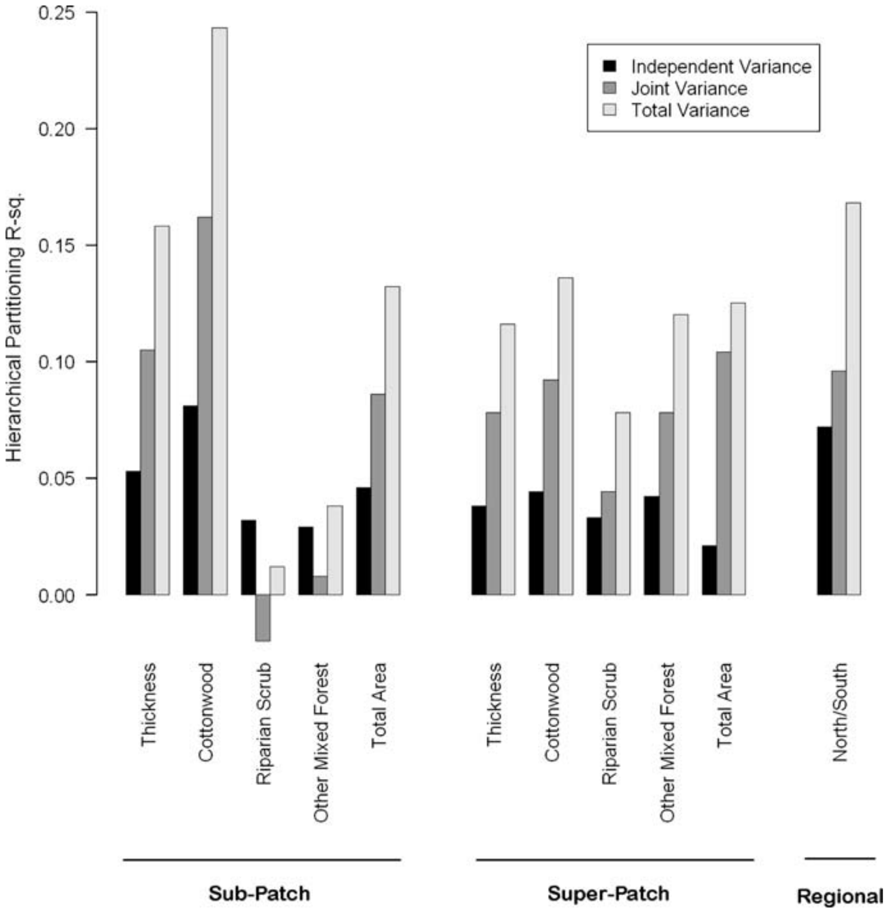


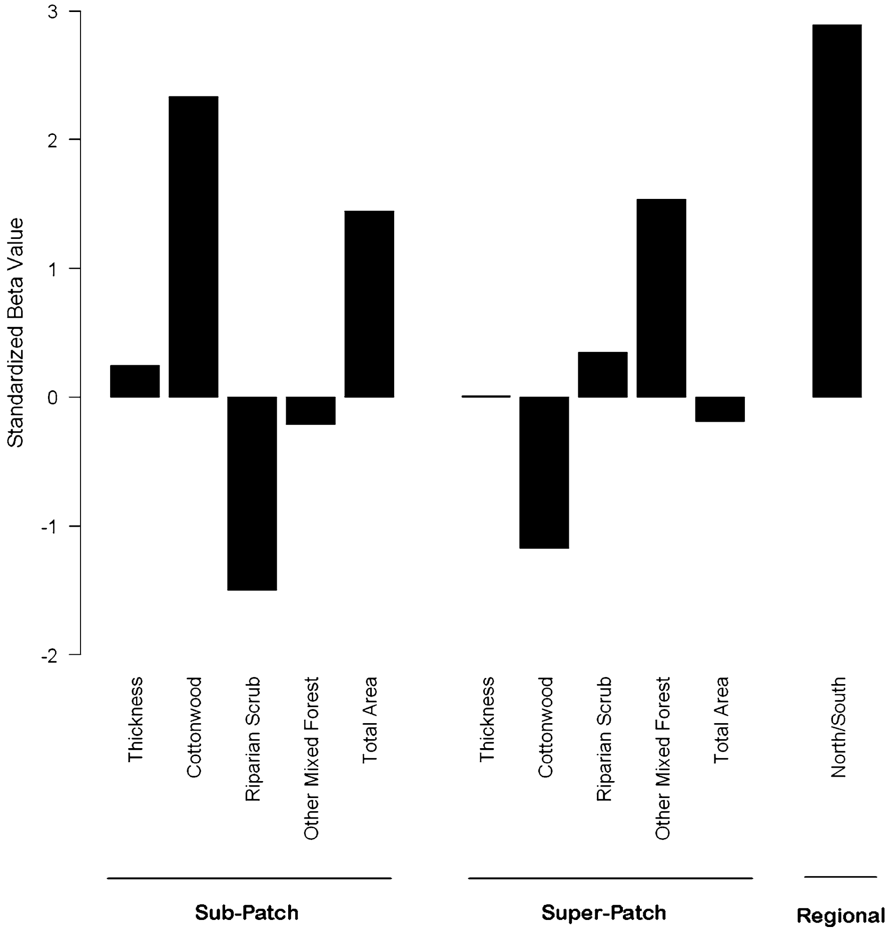
Fig. 6 Results from the logistic regression hierarchical portioning analysis showing the variance explained (r^2) in yellow-billed cuckoo occupancy in habitat patches during 1999–2000 by the five habitat variables (patch thickness, area of cottonwood forest, area of riparian scrub, area of other mixed riparian forest, total patch area) measured at two spatial scales of patches (*sub-patch* and *super-patch*), and a regional spatial variable indicating if the patch is in the northern or southern portion of the study area. For each explanatory variable, the graph shows the proportion of the overall variance explained by that variable independently of, and jointly with the other variables, as well as the total proportion of variance explained by that variable

Discussion

This analysis has shown how land cover characteristics affect habitat suitability at specific spatial scales of the landscape habitat patch structure. For the yellow-billed cuckoo, the area of cottonwood forest measured at the sub-patch scale was found to be the most important factor determining the presence of nesting in forest patches. These results agree with observational studies in California that show cuckoos inhabit wide patches of riparian forest with willow and cottonwood trees (Halterman 1991; Laymon 1980). Cottonwood forests provide the best foraging areas for yellow-billed cuckoo (Gaines and Laymon 1984; Laymon 1980), which is likely why they are the most important factor determining patch occupancy. Cottonwood forests are highly dependent on river flooding, flow recession rate, and seasonal timing for their establishment and maintenance in the riparian community (Bradley and Smith 1986). This suggests that the hydro-geomorphic processes that drive cottonwood recruitment at the sub-patch scale (see Mahoney and Rood 1998) are important factors affecting the future population viability of cuckoos. As such, management of a more natural river flow dynamics (Poff et al. 1997) could promote cottonwood forest establishment, and in turn restore yellow-billed cuckoo habitat (Rood et al. 2005).

The regional variable representing the spatial relation to highway 32 (north/south in the study area) was found to be very important in determining nesting probability in all statistical analyses, except for the CART analysis. The AIC$_c$, hierarchical partitioning, and standardized beta values analyses found that the patches south of highway 32, are colonized by the yellow-billed cuckoo more often, even when accounting for differences in patch characteristics at both spatial scales of patches (sub-patch and super-patch). All of these statistical analysis approaches are based on parametric general

Fig. 7 Standardized beta values from a logistic regression analysis run with all variables included. This graph shows the magnitude and direction of the effect that each variable has on yellow-billed cuckoo nesting probability



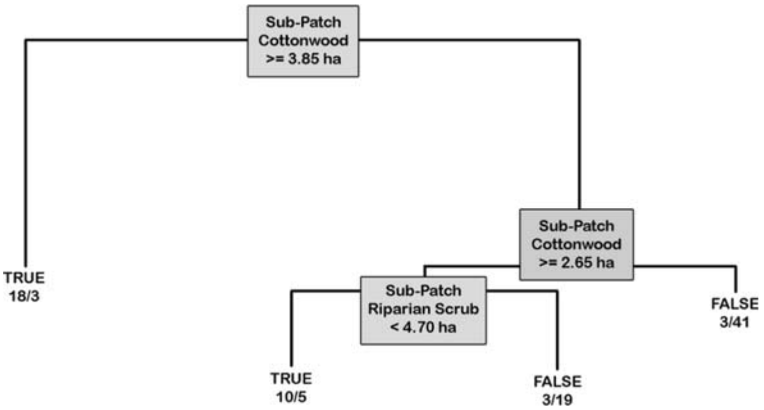


Fig. 8 Classification and regression tree analysis *CART* results showing that cottonwood forest measured at the sub-patch scale has the strongest positive effect on yellow-billed cuckoo nesting probability. The first and second splits of this graph shows that 18 of 21 patches with more than 3.85 ha of sub-patch cottonwood forest were occupied, while 3 of 41 patches with less than 2.65 ha of sub-patch cottonwood forest were not occupied. The third level split show that of the patches with sub-patch cottonwood levels in between, a *negative* relationship with riparian scrub partitioned the two groups the best

linear modeling. In contrast, this regional spatial variable was not found to be important by the CART. This may be because CART is a non-parametric statistical analysis technique that partitions data based on thresholds, and will be sensitive to different aspects of the data than will linear parametric approaches. Needless to say, there certainly is a striking difference in occupancy between the northern and southern portions of the study area (Fig. 4). As such, the effect of this regional variable should not be disregarded, but deserves further investigation.

There could be many reasons to explain why the regional spatial variable may be important. One could speculate that highway 32 acts as a habitat barrier to the northerly migration of this species. When looking at the study area from the regional scale, there is an obvious break in the contiguity of habitat patches immediately north of highway 32, which fragments the study area into northern and southern sections (Fig. 4). This may seem unlikely that the highway would act as a barrier considering that the birds traverse long distance migration from South America where they have crossed many roads larger than highway 32. However, by this point in their migration, the individuals are selecting a suitable location for nesting and mating. The highway and break in habitat may act as a barrier because the individuals are flying and exploring at lower altitudes and are more responsive to habitat fragmentation, rather than flying higher as they would during the other parts of their migration. In addition the southern section may be more colonized simply because it gets colonized first as the birds migrate north, and the population is not large enough that birds would “spillover” into the northern section.

The findings presented here corroborate with other multi-scale habitat suitability analyses. Buler et al. (2007) found that hardwood forest measured within a 5 km radius was the best predictor of the presence of migratory birds along the US gulf coast. This radius is approximately an order of magnitude larger than the average movement range of species on the ground, suggesting it may be a scale that the birds perceive as they adjust their flight path to select a suitable nesting habitat (Buler et al. 2007). That study also found that at the finer-scale of forest patches, food abundance factors were the most important. This is similar to results in our study, as cottonwood forests tend to support more preferred prey species for the yellow-billed cuckoo, than do other types of forest. Also, a study of forest grouse in the Swiss Alps showed that the best correlating habitat factors with bird presence were measured at a scale of 250 ha, approximately the home range size of this grouse. The home range of the yellow-billed cuckoo on the Sacramento River is on the order of spatial scale of sub-patches (Laymon 1980), which is probably why that scale showed the best relation to patch occupancy. Also, a study of bird communities in cottonwood forests along the Snake River, Idaho, showed that the distribution of breeding birds correlated with habitat factors at a range of spatial scales depending on the species analyzed (Saab 1999). That analysis showed core specialist species tended to be associated with large cottonwood patches with less edge, while the opposite was found for edge specialists. Similarly, the yellow-billed cuckoo is a core-dwelling species and has been observed to prefer larger patches of cottonwood forest (Gaines and Laymon 1984).

Yellow-billed cuckoo patch occupancy did not respond strongly to habitat characteristics measured at the super-patch scale. Although general linear modeling approaches found that area of other mixed riparian forest measured at the super-patch scale may have a moderate level of importance in predicting yellow-billed cuckoo presence, this was not a strong finding. This is a spatial scale that the yellow-billed cuckoo is probably not responding to because it is intermediate between processes acting at the more regional scale related to migration, and processes acting at the finer sub-patch scale related to nesting and food availability.

The use of multiple statistical analysis techniques was useful for identifying how riparian scrub (that contains *Salix exigua* as a common dominant willow species) measured at the sub-patch scale may be affecting patch occupancy. The AIC$_c$ multi-model analysis showed that all of the “best models” included this variable, but that it had a negative effect. The hierarchical partitioning analysis shows that although this variable does not explain a large portion of variance it is acting to suppress the variance explained by other variables, through its negative effect. Moreover, the CART analysis shows that this variable is only important for discriminating patches that have between 2.65 and 3.85 ha of cottonwood forest. Without further data and analysis it is difficult to explain this finding since cuckoos have been observed to utilize this habitat type. However, we can speculate that the absence of riparian scrub is negatively correlated to some other habitat factor that influences yellow-billed cuckoo habitat suitability in a positive way.

Patch dynamics

The riparian system on the middle Sacramento River is inherently dynamic, exhibiting substantial changes over time (Greco and Plant 2003). The principal agents of change for vegetation patches are flooding, geomorphological, and successional dynamics (Greco et al. 2007), though fires and other anthropogenic effects are known to occur in localized areas. However, rock revetment installed on the river over the past half-century for erosion control has dampened the rate of hydro-geomorphological change and forest patch genesis. A study by Greco et al. (2002) showed on a 37 km reach (a subset of this paper's study area) that total area of suitable habitat patches for yellow-billed cuckoos changed on a multi-decadal scale between 1938 and 1976, ranging from about 200–350 ha, however, between 1987 and 1997 total suitable habitat showed little change, ranging from about 450–500 ha. This suggests that patch dynamics did not change the forest patch structure substantially during the time frame our study (e.g., between the calibration and validation data sets).

This research can be built upon to investigate the temporal patch dynamics of this system both retrospectively and prospectively. Historical changes in the forest patch structure could be investigated by using land cover maps derived from historical aerial imagery (e.g., Greco and Plant 2003). Future projected changes to the patch structure could be investigated using river meander migration models (Larsen et al. 2006) in conjunction with vegetation succession models.

Conclusion

By combining high quality geographic habitat data and systematic field surveys with multi-scale patch delineation and statistical modeling, this paper showed that the yellow-billed cuckoo responded strongly to landscape patch habitat characteristics at the sub-patch scale. Our results also show that the cuckoos may also be responding to landscape characteristics at a broad regional scale (north/south in the study area), but that it did not respond strongly to characteristics at a third intermediate spatial scale (super-patch). This demonstrates the importance of conducting analyses at appropriate spatial scales, and provides additional support for the need of habitat suitability models to account for the spatial scale at which landscape characteristics are measured.

Landscape ecological theory states that the levels of organization of the patch hierarchy should be extracted *a posteriori* from empirically derived data, and should represent entities relevant to the ecological system and organisms of focus (King 1997). The PatchMorph algorithm used in this analysis does this by delineating habitat patches at multiple spatial scales from the underlying structure of the landscape heterogeneity. The PatchMorph algorithm could be used to model patches relevant to other patch-dependent organisms and to identify the habitat characteristics at specific spatial scales to which those organisms are responding.

The ability to identify important habitat characteristics at specific spatial scales will help habitat conservation and land use planning efforts target specific restoration and management actions for promoting the recovery of the western yellow-billed cuckoo. In this case, promoting the natural recruitment of cottonwood should be considered a primary management objective by conservation and restoration practitioners working on the recovery this endangered population (Greco 2008). This analysis also showed that there are likely other factors acting at a range of spatial scales, particularly at the regional spatial scale. Just focusing on one factor or one spatial scale may not be sufficient for understanding the habitat suitability requirements of this and other organisms.

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