Ecological Applications, 19(7), 2009, pp. 1848–1857

Riparian bird response to vegetation structure: a multiscale analysis using LiDAR measurements of canopy height

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Abstract. The ability to measure vegetation structure at spatial scales that are biologically meaningful for wildlife is often limited because information about the spatial scale of habitat selection is lacking and there are logistical constraints to measuring vegetation structure at ever larger spatial scales. To address this challenge, we used LiDAR-derived measurements of vegetation canopy height to quantify habitat associations of riparian birds at the Cosumnes River Preserve in central California, USA. Our objectives were (1) to evaluate the utility of LiDAR (light detection and ranging) measurements for describing habitat associations of riparian passerine birds, and (2) to capitalize on the ease with which LiDAR measurements can be summarized at multiple spatial scales to evaluate the predictive performance of vegetation measurements across spatial scales from 0.2 to 50 ha. At each location where we conducted point-count surveys of the avian community, we summarized the mean and coefficient of variation of canopy height measured at five spatial scales (0.2, 0.8, 3.1, 12.6, and 50.2 ha). For each of these spatial scales, we used stepwise model selection to identify the best logistic-regression model describing patterns of occurrence for 16 species of passerine birds that were sufficiently abundant for analysis. We then used area-under-the-curve (AUC) values to identify models that performed well (AUC >0.75) on a temporally independent data set. Of the 16 species, 10 species had logistic-regression models with AUC values >0.75. For six of these species, AUC values were highest for the models with vegetation measurements at the 0.2–3 ha scale. For the other four species, AUC values were highest for the model with vegetation variables measured at the 50-ha scale. These results illustrate the utility of using LiDAR-derived measurements of vegetation to understand habitat associations of riparian birds and underscore the importance of using multiscale approaches to modeling wildlife habitat use.

Key words: California's Central Valley (USA); habitat model; LiDAR; remote sensing; riparian; songbirds; spatial scales; vegetation structure.

Introduction

There has been a growing awareness of the importance of understanding the spatial scale at which organisms respond to their environment (Wiens 1989). This awareness, in conjunction with 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 (Wiens et al. 1987, Saab 1999, Meyer and Thuiller 2006). 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 forest cover within a given area or forest patch configuration) measured at considerably broader spatial scales (e.g., >100 ha; Meyer and Thuiller 2006).

It is generally agreed that the spatial scale of habitat measurements should match the spatial scale at which organisms use habitat patches (Meyer and Thuiller 2006). In practice, the ability to match the scale of habitat measurements to the scale at which they are used may be limited because we lack information about space use of many organisms. In such cases, 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, Smith et al. 2008). Unfortunately, it is often unrealistic to obtain field measurements of vegetation structure at multiple spatial scales, especially for larger areas. As a result, recommendations for measuring vegetation structure for bird studies have typically suggested a scale of about 0.8 ha (e.g., a 50-m-radius plot; Ralph et al. 1993), but the rationale for this recommendation has not been clearly articulated and there are examples of studies that use measurements of

Manuscript received 12 June 2008; revised 12 December 2008; accepted 17 Deember 2008; final version received 30 January 2009. Corresponding Editor: V. C. Radeloff.
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vegetation structure collected at even finer spatial scales (Smith et al. 2008).

It is likely that some bird species and other wildlife respond to vegetation structure at a larger spatial scale than 1 ha and there is no reason to believe that all species respond to vegetation structure at the same spatial scale. In an analysis of Black-throated Blue Warblers (*Dendroica caerulescens*), Smith and co-workers (2008) found that models using vegetation-structure characteristics (e.g., basal area of conifers and sapling densities) measured at 12 ha were more strongly supported than models using the same vegetation measurements at 3 or 0.2 ha. They conclude that in some instances, studies comparing the relative importance of vegetation structure and landscape characteristics to avian-habitat associations may have underestimated the importance of vegetation structure because measurements have often been made at spatial scales much less than 12 ha.

One challenge to this line of investigation is obtaining appropriate measures of vegetation structure at multiple spatial scales. Satellite imagery, aerial photography, and other remotely sensed measures of vegetation and landscape composition have been an important source of wildlife habitat data that can be collected across large spatial extents and then summarized at varying spatial scales (Meyer and Thuiller 2006). However, until recently most remotely sensed data have provided only two-dimensional information (e.g., vegetation cover, patch size, and connectivity). Information on vegetation structure, which requires three-dimensional measures of characteristics, such as canopy height, has not been available.

Light detection and ranging (LiDAR) is one remote-sensing technique that can provide detailed information on vegetation structure. LiDAR imagery is generated by emitting laser light from a low-flying aircraft and recording the reflected light to measure the height of objects beneath the aircraft (Brock et al. 2002, Lefsky et al. 2002). LiDAR imagery has been used to generate estimates of canopy height, stem diameter, canopy cover, biomass, and other components of vegetation structure (Harding et al. 2001, Chasmer et al. 2006, Clawges et al. 2007). There has been an increasing effort to apply LiDAR imagery to understanding and predicting patterns of terrestrial wildlife distribution (Bradbury et al. 2005, Hyde et al. 2005, Goetz et al. 2007, Vierling et al. 2008). Already, the benefits of LiDAR imagery are substantial enough that some authors have suggested that these measurements may begin to replace field measurements of vegetation structure traditionally used to describe wildlife habitat (Vierling et al. 2008).

Here we investigate the ability of LiDAR measurements of canopy height and heterogeneity to describe habitat associations for passerine birds in riparian habitat in California's Central Valley (USA). Specifically, we use these measurements to conduct a multiscale analysis that compares the predictive power of models using measurements of canopy height and heterogeneity at spatial scales from 0.2 to 50 ha as predictor variables. Our objectives were to (1) evaluate the utility of LiDAR measurements to provide information about habitat associations of riparian vegetation for passerine birds, and (2) evaluate the predictive performance of vegetation measurements at the recommended 1-ha scale relative to measurements at larger and smaller spatial scales.

Methods

Study area

Our study site was the Cosumnes River Preserve, located 26 km south of Sacramento, California, USA. The lower Cosumnes River Watershed contains a mosaic of riparian, grassland, and wetland habitats within a matrix of agricultural, pastoral, and increasingly urban landscapes. The Cosumnes River, the only undammed river on the west slope of the Sierra Nevada, ranges from 2300 m to sea level, ultimately entering the Pacific Ocean via the Mokelumne River, the Sacramento–San Joaquin Delta, and ultimately San Francisco Bay. The natural and highly variable hydrologic discharge regime of the Cosumnes River is characterized by winter flooding driven largely by rainfall that usually peaks between December and March, and discontinuous summer flow during August through September (Fleckenstein et al. 2004, Booth et al. 2006).

The survey sites were located in valley-foothill riparian habitat composed of Valley oak (*Quercus lobata*), Fremont's cottonwood (*Populus fremontii*), various willows (e.g., *Salix gooddingii*, *S. lasiolepis*, *S. exigua*), Oregon ash (*Fraxinus latifolia*), boxelder (*Acer negundo*), California blackberry (*Rubus ursinus*), California rose (*Rosa californica*), and native and nonnative forbs, grasses, and sedges. Where valley-foothill riparian habitat has not been converted by agriculture or urbanization, it occurs along many watercourses throughout much of California's Central Valley (Mayer and Laudenslayer 1988). As is typical of riparian vegetation in California's Central Valley, there is substantial variability in successional stage, structure, and species composition that is associated with variation in flooding intensity and frequency, as well as past and ongoing restoration and management activities. Process-based or semi-passive restoration techniques such as levee breaches and setbacks as well as more-active techniques such as planting, burning, and grazing have been used at the Cosumnes River Preserve to achieve desired goals (Florsheim and Mount 2002, Swenson et al. 2003). Survey locations were selected to represent the full range of habitat types, management actions, and restoration schemes found on the Cosumnes River Preserve (Fig. 1).

Avian point counts

We established 70 point-count survey locations in the Cosumnes River Preserve (Fig. 1). Survey locations (hereafter "points") were located at least 200 m apart. In 2004 and 2005, point counts were conducted at all points

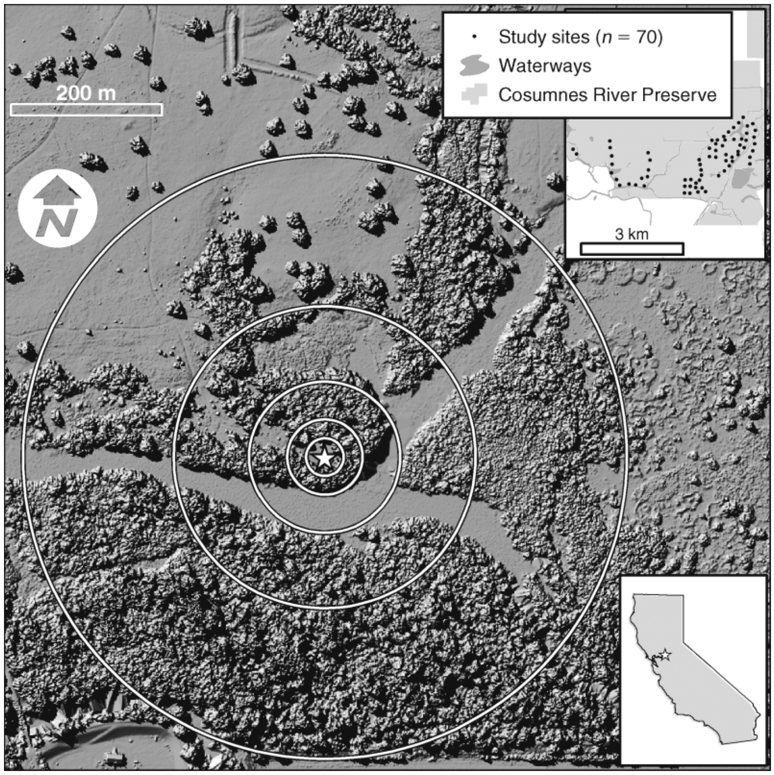

FIG. 1. Example of LiDAR data and the concentric radii (25, 50, 100, 200, and 400 m) around a point-count location in which the mean and coefficient of variation for canopy height were calculated. The upper inset shows the distribution of point-count locations within the Cosumnes River Preserve; the lower inset shows the location of the Preserve in central California, USA.

between 20 April and 21 June using standardized point-count methods (Ralph et al. 1993). Twice during each year, 5-min bird counts were conducted between sunrise and 10:00 hours PDT at each point. Counts were conducted only on days when the wind was <20 km/h and it was not raining. During these surveys, the number of birds seen or heard within a 50-m radius of the observer was recorded.

For the analysis, we excluded non-passerine birds, flyover detections, unidentified passerines, and passerines that have not been recorded breeding at the Cosumnes River Preserve. To minimize the variability in detection probability we limited our analysis to detections within 50 m of the point (Alldredge et al. 2007). We used "absence"/presence (0, 1) as the response variable, with a bird species recorded as present if it was detected in either the first or second visit to a point during a year. We recognized that this metric reflects both true presence/absence at a point, and the probability of detection given that a species is present (Royle and Nichols 2003), but assumed that detecting a species at least once during two surveys serves as a useful index of occupancy (Johnson 2008).

One of the challenges in predictive habitat modeling is determining the degree to which model predictions can be generalized to larger spatial and temporal domains (Guisan and Zimmerman 2000). This can be accomplished by evaluating model performance on temporally and/or spatially independent data sets (Bulluck et al. 2006, Vernier et al. 2008). With sufficiently large samples, model performance can be evaluated by splitting the data set into a training data set used to calibrate the model and a testing data set to evaluate the predictive performance (Guisan and Zimmerman 2000). Because the spatial extent of our sampling was only 70 points, we did not have enough data to split the data spatially. However, because many of the points were surveyed in two years, we split the data into testing and training data sets that addressed temporal uncertainty. Of the 70 points surveyed, 10 points were surveyed only in 2004, 9 points only in 2005, and the remaining 51 points were surveyed in both 2004 and 2005. To build a training data set, the 19 points that were surveyed in a single year were combined with the 51 points from which we randomly assigned a survey from one year as training data. The testing data set was the other non-assigned survey of the 51 points that were not used in the training data set. This approach maximized the generality of our model calibration and evaluation because (1) the training data set incorporated the entire spatial sample (70 points), (2) the training data included surveys conducted in both 2004 and 2005, and (3) the testing data set comprised surveys from 51 points that were conducted in different years than the surveys that were used in the training data set.

LiDAR imagery and vegetation structure metrics

Watershed Sciences LLC (Portland, Oregon, USA) collected LiDAR data for the Cosumnes River Preserve 5 July 2005 using an ALTM 3100 LiDAR system (Optec, Markham, Ontario, Canada). This aircraft-mounted system was flown over the study area at an altitude of 1100 m above the ground. Over the 7765-ha study area (Fig. 1), laser returns were collected at an average spacing of >7 returns/m^2, for a total of 3.07×10^8 data points. The three-dimensional spatial information for each point was calculated using the pulse time and scan angle of the LiDAR system, aircraft altitude, and aircraft position. This information was processed using TerraScan software (Terrasolid 2005) to remove aberrant data points. This processing also separated points into first returns, which correspond to the height of the vegetation surface, and last returns, which represent bare-ground elevation. Independent elevation measurements for 352 bare-ground reference points were collected with a real-time kinematic geographic positioning system. After the LiDAR data were processed, the elevations of the LiDAR measurements were compared to those of reference points. Ninety-five percent of the LiDAR measurements were <6.8 cm from the reference elevation. Finally, the last returns were aggregated into bare-earth digital elevation models (DEM) with 0.5-m pixel resolution, and the first returns were aggregated into a 1-m resolution DEM representing vegetation canopy height above the bare-earth elevation. Although LiDAR measurements of canopy height were made only in 2005, we applied these measurements to bird data collected in 2004 and 2005 after initial analyses demonstrated that there was no systematic difference between the two years in the ability of the 2005 LiDAR data to predict bird occurrence.

We used LiDAR measurements of canopy height to describe vegetation structure around each point at five spatial scales: 0.2, 0.8, 3.1, 12.6, and 50.2 ha. To remove the influence of bare-ground returns on our measure of mean canopy height, we excluded all grid cells with a canopy measurement <1 m from our analysis. We then used ArcGIS version 9.2 (ESRI 2006) to calculate the mean, standard deviation, and coefficient of variation (CV) of the canopy height measurements of the grid cells within a radius of 25, 50, 100, 200, and 400 m of each point. Within each radius, the mean and standard deviation were strongly and positively correlated (Spearman correlation coefficients for the five radii ranged from 0.85 to 0.94). The CV provided a measure of heterogeneity in canopy height that was not as strongly correlated with mean canopy height as the standard deviation of the measurements (Spearman correlation coefficients for the 5 radii ranged from −0.01 to −0.58). We refer to mean canopy height as "canopy height" and the CV of canopy height as "canopy heterogeneity."

Because we were interested in understanding the predictive performance of vegetation structure measured at the five different spatial scales, we evaluated correlation between the distance classes by plotting the metrics measured at each spatial scale against each other (Fig. 2). Generally, metrics from adjacent radii were strongly correlated, but this correlation was much reduced when measurements were separated by more than one radius (Fig. 2). Thus, we expected that it would be unusual that a single spatial scale would have obviously better predictive power than all others, but that a trend toward better prediction using metrics measured at fine (25–100 m) or coarse (200–400 m) spatial scales would be apparent.

Modeling habitat associations with LiDAR data

Our objectives were to investigate the utility of LiDAR measurements of canopy height and heterogeneity to describe habitat associations of riparian birds and evaluate the spatial scale of measurements with the best predictive performance. To compare the predictive performance of predictor variables measured at the five spatial scales, we first used a step-wise procedure to select the best combination of predictor variables at each spatial scale using the training data set. We then compared the predictive power of each spatial scale using receiver operating-characteristic curves and the testing data set.

For each of the five spatial scales, we used logistic regression with the canopy height and heterogeneity of canopy height to model habitat associations for each bird species. The full generalized linear model with a logit link and binomial distribution included parameters for an intercept and the effects of canopy height and the CV of canopy height:

$$\text{logit}(P_i) = \beta_0 + \beta_1 M_i + \beta_2 V_i + \beta_3 M_i V_i + \beta_4 M_i^2 + \beta_5 V_i^2 \quad (1)$$

where P is the probability of a bird occurring at the ith point, β_0 is the intercept, and $\beta_1, \ldots, \beta_5$ are coefficients describing the main, interactive, and quadratic effects of mean canopy height (M) and coefficient of variation of canopy height (V) around each point. These models were fitted for all species that occurred on >10% of the points in at least one of the two years (Appendix A). Generalized linear models were fitted using the function glm from the stats package in R (R Development Core Team 2005). To select the most parsimonious model, we used the stepAIC function from the MASS package (Venables and Ripley 2002) in R version 2.5 (R Development Core Team 2005). This function uses a stepwise model-selection procedure that begins with the full model and then removes and adds terms until the model with the lowest Akaike information criterion (AIC) is found (Venables and Ripley 2002).

To assess the performance of logistic-regression models independently of threshold values, we used receiver operating characteristic (ROC) curves (Fielding

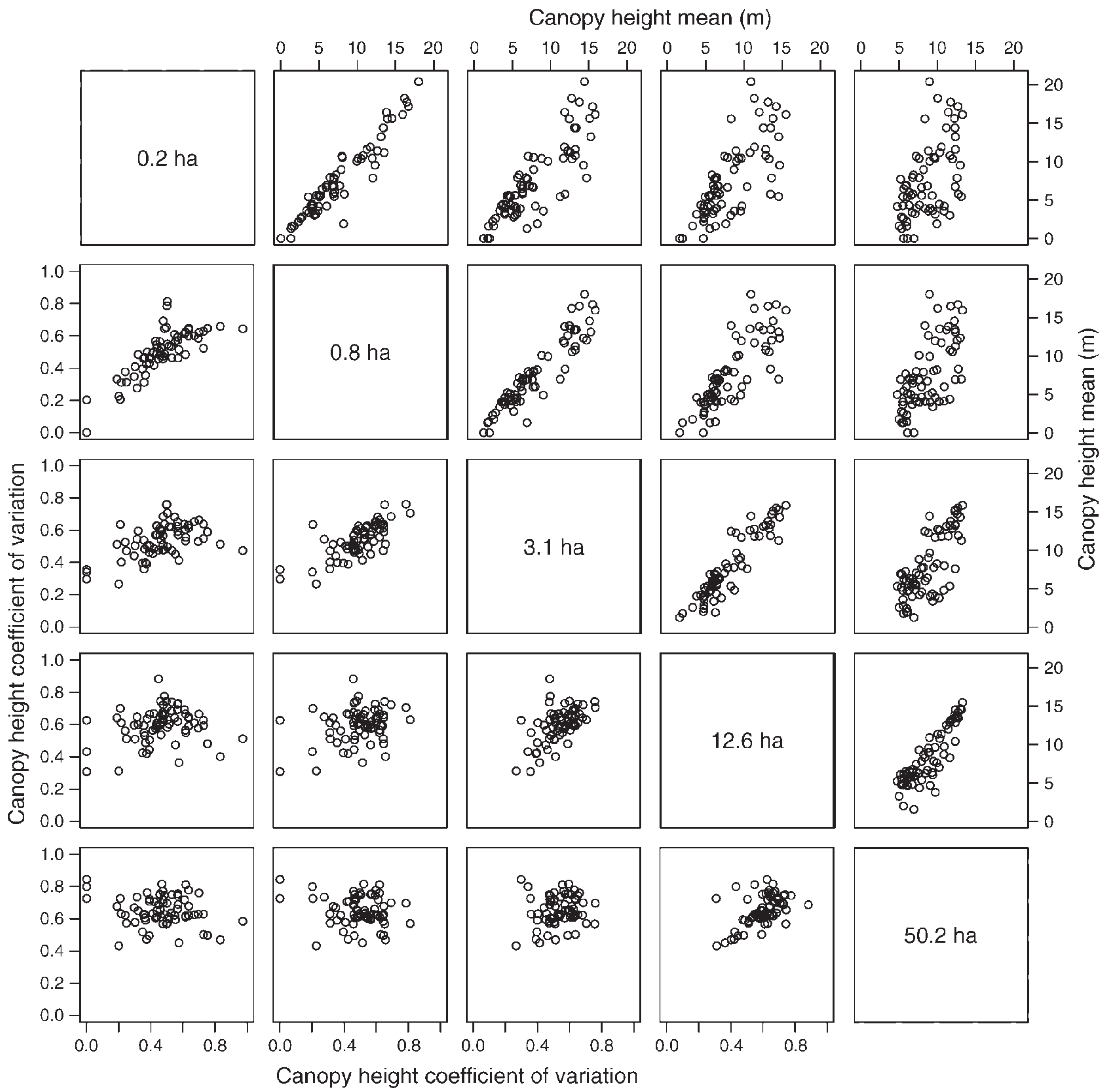

FIG. 2. Correlation between canopy height mean (above the diagonal) and coefficient of variation (below the diagonal) measured at five increasing spatial scales around each point-count station. Measurements from adjacent spatial scales are more strongly correlated than those that are at least one unit apart.

and Bell 1997). The area-under-the-curve (AUC) statistic represents model performance ranging from 1.0 (a perfect model) to 0.5 (no predictive power). Generally, the predictive ability of models can be roughly ranked as fail (AUC = 0.5 to 0.6), poor (AUC = 0.6 to 0.7), fair (AUC = 0.7 to 0.8), good (AUC = 0.8 to 0.9), and excellent (AUC = 0.9 to 1.0) (Swets 1988). To calculate the ROC curves, we used the performance function of the ROCR package (Sing et al. 2005) in R version 2.5 (R Development Core Team 2005). Because ROC curves were built with data collected at the same locations as the training data, but in different years, the AUC values should be interpreted as a measure of prediction accuracy given temporal variation, but not spatial variation.

After selecting the best model, we limited further analyses to species for which the model for at least one spatial scale had an AUC value >0.75 for the test data. This arbitrary cut-off excludes species for which models had relatively little predictive power. To evaluate the relative importance of the five spatial scales, we compared the AUC values for each spatial scale. We then selected the model for the spatial scale with the highest AUC and used contour plots to present the probability of occurrence as a function of canopy height and heterogeneity. We assumed that each point was an independent sample. If there is strong spatial autocorrelation, this assumption is violated, potentially raising the risk of type I error when interpreting the parameter estimates (Legendre et al. 2004). However, because our emphasis was on evaluating the relative predictive power of measurements at different spatial scales, rather than conducting a hypothesis test of predictor variables, we did not incorporate spatial dependence.

Results

Of the 16 passerine bird species detected with sufficient frequency for analysis, 10 species had a model for at least one spatial scale with an area-under-the-curve (AUC) value >0.75 (Fig. 3). For the other six species, all AUC values were ≤0.75. Model parameters and AUC values are presented for all species in Appendix B.

The spatial scale with the most predictive power varied among species. The habitat associations for six species (Song Sparrow [*Melospiza melodia*], Spotted Towhee [*Pipilo maculatus*], House Wren [*Troglodytes aedon*], Oak Titmouse [*Baeolophus inornatus*], Wrentit [*Chamaea fasciata*], and Ash-throated Flycatcher [*Myiarchus cinerascens*]) were best predicted by fine-scale (0.2–3.1 ha) variables, whereas the associations of four species (Red-winged Blackbird [*Agelaius phoeniceus*], Bushtit [*Psaltriparus minimus*], Bullock's Oriole [*Icterus bullockii*], and Black-headed Grosbeak [*Pheucticus melanocephalus*]) were best predicted by coarse-scale (50.2 ha) variables (Fig. 3).

Among the models with the best predictive power, the relative importance of canopy height and heterogeneity (the coefficient of variation of canopy height) varied among the 10 species. Five of the 10 species were best predicted by a model with only the linear canopy-height term: Spotted Towhee, House Wren, Oak Titmouse, Black-headed Grosbeak, and Ash-throated Flycatcher were positively associated with mean canopy height (Fig. 4). Similarly, for 3 of the 10 species, only canopy heterogeneity was important. For Wrentit and Song Sparrow, the probability of occurrence was positively associated with canopy heterogeneity, but for Bullock's Oriole the association was negative (Fig. 4). For the remaining two species (Bushtit and Red-winged Blackbird), the best model included canopy height, heterogeneity, and the interaction between these terms (Fig. 4).

Discussion

Our results suggest that LiDAR measurements of vegetation structure provided a useful tool for modeling habitat associations of riparian birds. For 10 of the 16 species we investigated, the predictive models had AUC (area-under-the-curve) values >0.70. Generally, these results were consistent with previously described habitat associations for these species. For example, the occurrence of Spotted Towhee, House Wren, Ash-throated Flycatcher, Oak Titmouse, Black-headed Grosbeak, and Bushtit increased with canopy height (Fig. 4). These patterns are consistent with increasing abundance of these species as canopy height increased after riparian-habitat restoration along the nearby Sacramento River (Gardali et al. 2006). Similarly, in region-wide habitat-association modeling of riparian birds in California's Central Valley, the abundances of Spotted Towhees, Ash-throated Flycatchers, and House Wrens were positively associated with either increasing tree height or tree diameter at breast height, and the abundance of Black-headed Grosbeaks was positively associated with the amount of cottonwood tree cover (Nur et al. 2008). Conversely, the proportion of sites occupied by Red-winged Blackbirds was greatest at sites with low canopy height, a pattern consistent with this species' association with large, open, marshy areas (Yasukawa and Searcy 1995).

For the other six species we investigated, LiDAR-derived measurements of canopy height and heterogeneity had relatively little predictive power. In some cases, these species may be responding to broadscale landscape characteristics that were not captured by our variables (Saab 1999). For example, Brown-headed Cowbirds (*Molothrus ater*) are known to respond to landscape variables such as amount of forest edge (Howell et al. 2007). In other cases, the distributional patterns of these species may be more strongly associated with components of vegetation structure or composition that were not measured in this study. For example, both the structure and composition of understory vegetation are important habitat components for some riparian birds in California's Central Valley (Nur et al. 2008). Although we focused on canopy height, LiDAR data can also be used to generate indices of foliage height diversity, total vegetation volume, and even understory structure that could be used to understand habitat associations (Clawges et al. 2008). However, because LiDAR imagery cannot provide detailed information on the species composition of vegetation, in-the-field vegetation measurements will remain an important component of understanding avian habitat suitability in systems where birds respond strongly to vegetation composition (Nur et al. 2008).

Our second objective was to compare the predictive performance of vegetation structure measurements across a range of spatial scales. For 6 of the 10 species we evaluated, vegetation measurements at a 0.8- to 3.0-ha scale performed best. For two species (Red-winged Blackbird and Bullock's Oriole) measurements at the 50.2-ha scale performed best, but measurements at other spatial scales performed nearly as well (Fig. 3). For only two species (Black-headed Grosbeak and Bushtit) was there a clear trend toward increasing predictive performance with the broader spatial scale (Fig. 3). For many species, adjacent spatial scales had similar predictive power. This result is not surprising given the relatively strong correlation among vegetation measurements at adjacent spatial scales (Fig. 2).

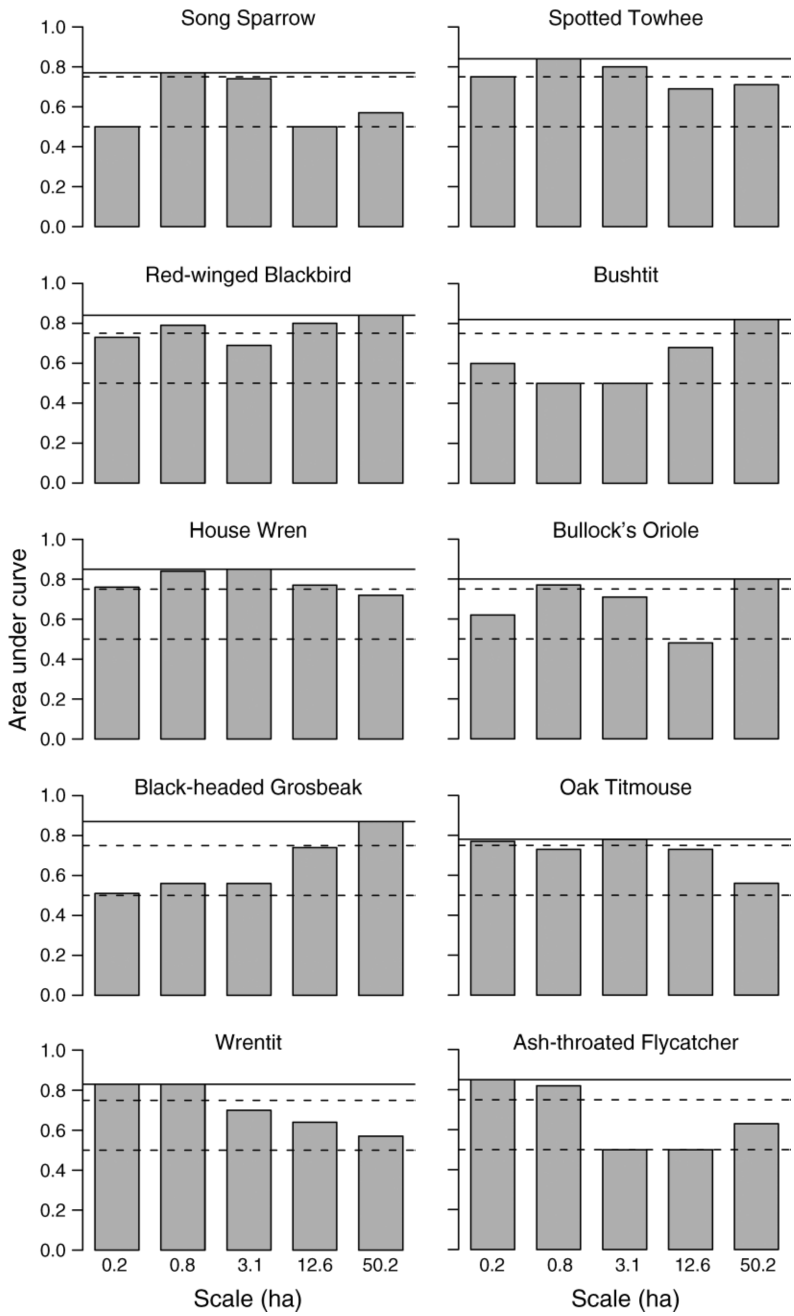

FIG. 3. Area-under-the-curve (AUC) values for 10 passerine bird species that had models for at lease one spatial scale with AUC >0.75 for the test data. The dashed horizontal lines mark AUC values of 0.5 and 0.75; the solid horizontal line marks the value of the maximum AUC.

In northern hardwood–conifer forest, Smith and co-workers (2008) demonstrated that the occurrence of Black-throated Blue Warblers was better predicted by vegetation structure measured at 3 and 12 ha than at 0.2 ha. They suggest that the response of bird species to vegetation structure may be better captured using broad-scale measurements rather than the relatively small plots used in many studies (Smith et al. 2008). We hypothesize that both the patchy nature of riparian vegetation structure and relatively small territory sizes of the birds we investigated may contribute to the greater explanatory power of relatively fine-scale (e.g., 1 ha) vegetation measurements.

Smith and co-workers (2008) suggested that comparisons of the contribution of landscape composition and vegetation structure to avian-habitat associations may fail to capture the importance of vegetation structure if the spatial scale of measurement is too small. Our results

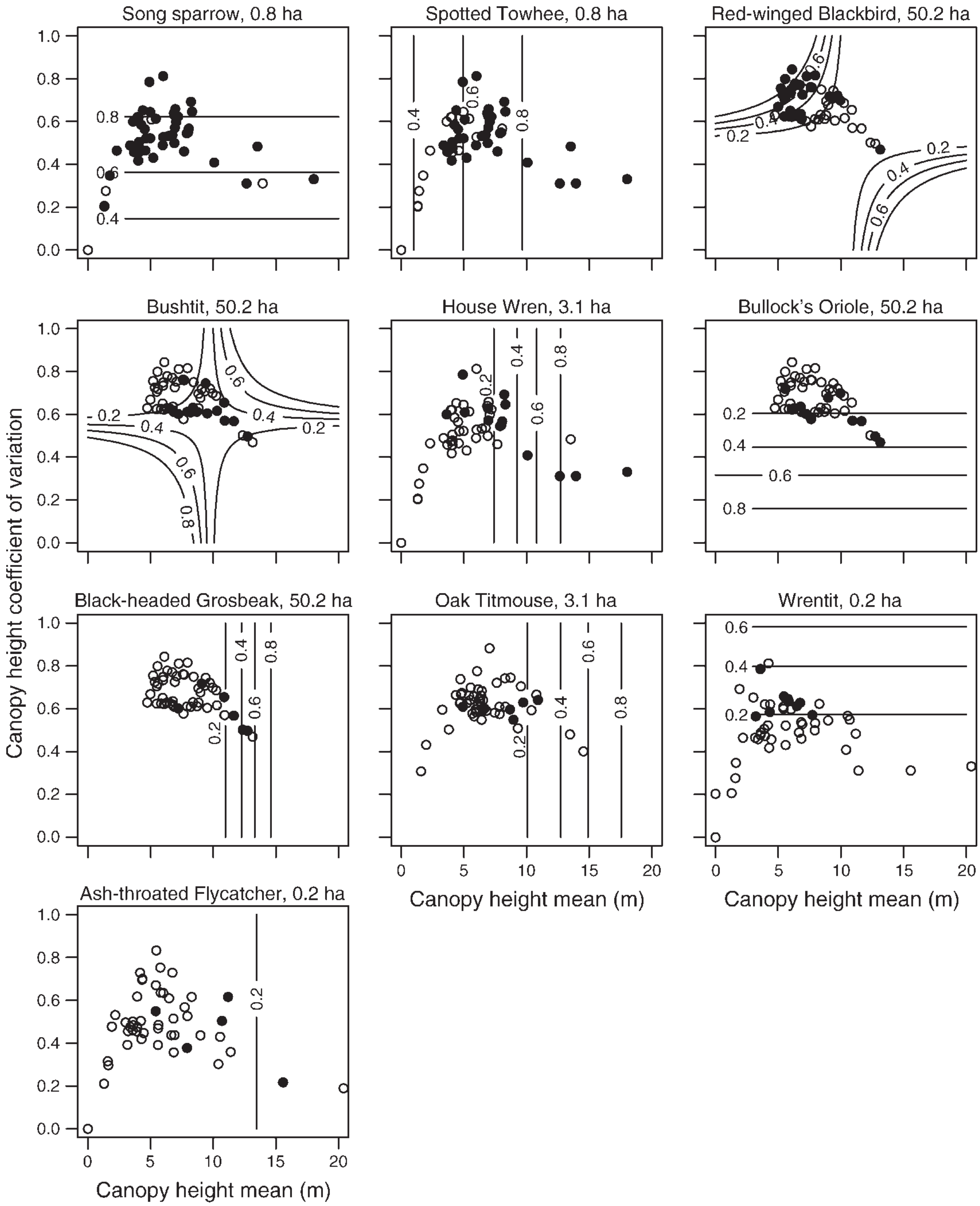

Fig. 4. Contour plots of logistic-model predictions of the probability of occurrence of a bird species as a function of canopy height mean and canopy height coefficient of variation (canopy heterogeneity) derived from LiDAR imagery at one of the five spatial scales (0.2, 0.8, 3.1, 12.6, and 50.2 ha). Models were built from a training data set of 70 point-count surveys conducted in either 2004 or 2005. Plotted points are the testing data (51 points that were collected at the same locations as the training data, but in a different year). Solid circles are points where a species was detected; open circles are points where a species was not detected.

suggest that in the riparian systems that we studied, vegetation measurements at ~1 ha are appropriate for most, but not all, species. Habitat associations developed using vegetation measurements at a spatial scale <1 ha should be interpreted with caution. For some species, however, vegetation measurements at relatively broad spatial scales were important, and this possibility should also be held in mind when interpreting habitat associations based on measurements made at a single spatial scale. These results underline the need for more information about the spatial scale at which birds respond to vegetation structure.

There was a tendency for species to have either relatively simple habitat associations with vegetation structure measured at a relatively fine spatial scale, or complex habitat associations with characteristics measured at a broad spatial scale. At one end of this spectrum, the habitat associations for Spotted Towhee, House Wren, Oak Titmouse, and Ash-throated Flycatcher were best described by models using only mean canopy height measured at fine spatial scales (0.2–3.0 ha). At the other end of this spectrum, the habitat associations of Bushtit, Bullock's Oriole, and Red-winged Blackbird were described by vegetation height and/or heterogeneity measured at a broad spatial scale (50.2 ha).

Our results should be interpreted in light of the fact that the data were collected over a relatively small area in just two years. The habitat associations of riparian birds may vary substantially across even modest distances. Nur et al. (2008) reported that the habitat associations of riparian birds differed among three regions of California's Central Valley. Temporal variation in bird population sizes may also influence the predictive accuracy of habitat models, especially when bird distributions change dramatically from one year to the next (Bulluck et al. 2006). Although the proportion of points at which a species was detected was generally consistent from one year to the next (Appendix A), we accommodated this source of variability by using both years of data for both the training and testing data sets.

Management implications

Our work illustrates the utility of LiDAR measurements of canopy height and heterogeneity over large spatial extents for describing the spatial scale of bird-habitat associations. With traditional field measurements of vegetation structure, information is available only where survey crews can collect information, which is often limited to the locations where point counts are conducted. In contrast, with LiDAR imagery, information on vegetation structure is available for the entire LiDAR footprint. As we have demonstrated, this information can be used to evaluate the spatial scale at which birds may be responding to canopy height and heterogeneity, and subsequently to build predicted-distribution maps for the entire spatial extent. Our results confirm earlier conclusions that measuring vegetation structure at inappropriate spatial scales may underestimate the importance of vegetation structure in developing habitat-association models (Smith et al. 2008).

There is increasing interest in the role that habitat restoration can play in the recovery of bird communities that have been negatively impacted by changes in riparian vegetation over the last century (Gardali et al. 2006). Our results suggest that the degree to which birds respond to riparian restoration will vary among species depending on the spatial extent of restoration and the specific vegetation structure that is created. For species that respond to fine-scale variation in vegetation structure, even very small restoration projects may be beneficial. For species that respond to more complex habitat characteristics across large spatial extents, successful habitat restoration will need to include other objectives. First, they will need to occur across relatively large areas. Alternatively, small restoration projects may be more effective for these species if they are located adjacent to existing areas of riparian habitat. Second, because many of these species respond not just to canopy height, but also to canopy height heterogeneity, restoration strategies that use planting patterns or disturbance (e.g., floods) that create heterogeneity in vegetation structure will be important. This result echoes the recommendation that a mosaic of habitat types, rather than large areas of mature riparian forest, should be the desired endpoint for riparian habitat restoration of California's Central Valley region (Golet et al. 2003).

Acknowledgments

Financial support for this project was provided by the California Bay–Delta Authority (Contract ERP 01-N01, ERP 02D-P66, and CALFED Science Fellowship U-04-SC-005 to N. E. Seavy). PRBO Conservation Science contributions to the manuscript were written at the Palomarin Field Station, which received support from the National Science Foundation (DBI-0533918). Logistical support was provided by the Cosumnes River Preserve Staff and partners including the U.S. Bureau of Land Management, The Nature Conservancy, and Ducks Unlimited. We thank numerous PRBO project leaders, field biologists, and intern biologists who managed the field work and collected data for this study. Comments from D. Stralberg, J. A. Wiens, and two anonymous reviewers improved the manuscript. This is PRBO Conservation Science contribution number 1665.

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APPENDIX A

A table showing the frequency of occurrence for passerine birds detected during point-count surveys on the Cosumnes Reserve, California, USA, in 2004 and 2005 (*Ecological Archives* A019-076-A1).

APPENDIX B

A table showing the parameter estimates and area-under-the-curve values for the best logistic-regression model identified using stepwise model selection for 16 species of riparian bird species (*Ecological Archives* A019-076-A2).