Biological Conservation xxx (2010) xxx–xxx

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Multi-scale factors affecting bird use of isolated remnant oak trees in agro-ecosystems

Craig A. DeMars [a,*], Daniel K. Rosenberg [a,b], Joseph B. Fontaine [a,c]

[a] Department of Fisheries & Wildlife, 104 Nash Hall, Oregon State University, Corvallis, OR 97331-3803, United States
[b] Oregon Wildlife Institute, P.O. Box 1061, Corvallis, OR 97339, United States
[c] School of Environmental Science, Murdoch University, 90 South Street, Murdoch, Western Australia 6150, Australia

ARTICLE INFO

Article history:
Received 9 November 2009
Received in revised form 28 January 2010
Accepted 21 March 2010
Available online xxxx

Keywords:
Bird conservation
Habitat remnants
Isolated trees
Oak savanna
Scattered trees
Sustainable agriculture

ABSTRACT

With recent emphasis on sustainable agriculture, conservation of native biota within agricultural systems has become a priority. Remnant trees have been hypothesized to increase biological diversity in agro-ecosystems. We investigated how remnant Oregon white oak (*Quercus garryana*) trees contribute to conserving bird diversity in the agro-ecosystem of the Willamette Valley, Oregon, USA. We compared bird use of isolated oak trees in three landscape contexts – croplands, pastures, and oak savanna reserves – and ranked the relative importance of four factors thought to influence bird use of individual trees: (i) tree architecture; (ii) tree isolation; (iii) tree cover in the surrounding landscape; and (iv) landscape context, defined as the surrounding land use. We evaluated species-specific responses and four community-level responses: (i) total species richness; (ii) richness of oak savanna-associates; (iii) tree forager richness; and (iv) aerial and ground forager richness. We documented 47 species using remnant oaks, including 16 species typically occurring in oak savanna. Surprisingly, landscape context was unimportant in predicting frequency of use of individual trees. Tree architecture, in particular tree size, and tree cover in the surrounding landscape were the best predictors of bird use of remnant trees. Our findings demonstrate that individual remnant trees contribute to landscape-level conservation of bird diversity, acting as keystone habitat structures by providing critical resources for species that could not persist in otherwise treeless agricultural fields. Because remnant trees are rarely retained in contemporary agricultural landscapes in the United States, retention of existing trees and recruitment of replacement trees will contribute to regional conservation goals.

1. Introduction

Agricultural conversion of natural environments is a major factor in the current global decline of biodiversity (Tilman et al., 2001; Foley et al., 2005). Approximately half of the earth's habitable land has been modified to some degree for agricultural purposes (Clay, 2004) and current trends indicate that the global agricultural footprint could increase a further 18% by 2050 (Tilman et al., 2001). This high degree of agricultural impact on global terrestrial ecosystems suggests that conservation of biodiversity can no longer be solely focused on protected areas (Fischer et al., 2006; Vandermeer and Perfecto, 2007). Moreover, in many highly modified landscapes, existing reserve networks may be insufficient for conservation of biodiversity (Brooks et al., 2004; Rodrigues et al., 2004). Consequently, an emerging research theme in conservation biology has been the assessment of structural elements thought to be important for conserving biodiversity in agricultural systems (Harvey et al., 2006; Sekercioglu et al., 2007; Haslem and Bennett, 2008).

In North America, agricultural conversion has particularly impacted oak savanna, one of the continent's most imperiled ecosystems (Noss et al., 1995). In many agricultural areas, biological legacies (sensu Franklin et al., 2000) from historic landscapes exist as scattered large trees which have often been retained by landowners for cultural reasons (Harvey and Haber, 1999; Fischer and Bliss, 2008). Previous studies in tropical and Australian agricultural systems demonstrate that isolated remnant trees provide numerous ecological functions important to birds including landscape connectivity for woodland species (Fischer and Lindenmayer, 2002b; Robertson and Radford, 2009), foraging sites (Luck and Daily, 2003), and nesting sites (Manning et al., 2004). Manning et al. (2006) further suggest that isolated trees are keystone structures in human-modified landscapes because an individual tree's ecological influence is disproportionate to its actual physical footprint. Within scattered tree landscapes critical management priorities

---

* Corresponding author. Address: 1017 Hoover Street, Nelson, BC, Canada V1L 4X9. Tel.: +1 250 352 6313.
E-mail addresses: Craig.DeMars@oregonstate.edu (C.A. DeMars), Dan.Rosenberg@oregonstate.edu (D.K. Rosenberg), J.Fontaine@murdoch.edu.au (J.B. Fontaine).

0006-3207/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2010.03.029

are to determine: (i) an appropriate spatial pattern of trees that best maintains landscape-level biodiversity (Manning et al., 2006); (ii) the characteristics of individual trees that best provide wildlife habitat (Tews et al., 2004); (iii) the influence of the surrounding matrix on wildlife use of individual isolated trees (Ricketts, 2001; Kupfer et al., 2006).

Here, we investigated the potential role that isolated remnant oak trees play in conserving oak savanna-associated bird diversity in a North American agro-ecosystem. We compared bird use of isolated Oregon white oak (*Quercus garryana*) remnant trees in three different landscape contexts within the agricultural matrix of the Willamette Valley, Oregon, USA. We evaluated the relative importance of site-specific and landscape-level factors thought to influence bird use of individual remnant trees. We ranked the following four factors on how well each could explain bird use of individual remnant trees: (i) tree architecture, (ii) tree isolation, defined as the distance to the nearest tree or patch, (iii) tree cover in the surrounding landscape, and (iv) landscape context, defined as the dominant land use in the surrounding landscape. We investigated species-specific responses and four community-level responses: (i) total bird species richness; (ii) species richness of native birds associated with oak savanna; (iii) species richness of tree-foraging birds; and (iv) species richness of aerial- and ground-foraging birds, grouped collectively as species that do not typically forage on trees or within tree canopies.

2. Methods

2.1. Study area

We conducted our study in the southern half of the Willamette Valley (43°56′–44°54′W, 122°53′–123°22′N), which lies between the Cascade and Coast Ranges in western Oregon. The Willamette Valley (elevation 70–120 m) has a Mediterranean temperate climate characterized by long wet winters (mean annual precipitation = 110.9 cm) and short dry summers (OCS, 2006). Outside of urban development, predominant land uses in our study area are grass seed production and, to a lesser extent, livestock grazing.

Prior to Euro-American settlement in the 1850s, white oak savannas and woodlands were prominent vegetation types in the landscape mosaic of the Willamette Valley, occupying xeric sites above riparian bottomland forests but below higher elevation conifer stands (Thilenius, 1968). In the last century, white oak savanna has declined to <1% of its historic range while white oak woodlands have been reduced from an estimated 162,000 ha to <11,000 ha (Vesely and Tucker, 2004; ODFW, 2006). Agricultural conversion, urban expansion, and conifer invasion from cessation of historic fire regimes have been primary factors in these declines (Towle, 1983; Vesely and Tucker, 2004). Much of the remaining white oak habitats are now found on private lands, occurring in small, fragmented patches or as scattered remnant trees in agricultural fields (ODFW, 2006).

We sampled individual white oak remnant trees in three different landscape contexts that represent the current rural landscape mosaic of the Willamette Valley: croplands, pastures, and oak savanna reserves. We sampled all sites encountered within the study area that contained isolated remnant trees except for two instances where we were unable to obtain access to private land. Because of the rarity of remnant, savanna-form oak trees in the Willamette Valley (ODFW, 2006), we believe our final sample size represented a large proportion of the fields containing these trees in the southern Willamette Valley. Cropland sites were either grass seed production fields (nine sites) or nursery operations (four sites) where small saplings (<1.5 m high) of maple (*Acer* spp.), Douglas-fir (*Pseudotsuga menziesii*), and noble fir (*Abies procera*) were grown. Pasture sites were either sheep or cattle grazed. Savanna reserves, characterized by a diverse understory of grasses, forbs and shrubs, were those sites actively managed to replicate historic oak savanna conditions.

Within each site, we identified white oak remnant trees as those trees with a diameter-at-breast height of ⩾50 cm and having an open-grown “mushroom”-shaped canopy with thickened lateral limbs (Peter and Harrington, 2002). We evaluated all potential trees within a site for their structural characteristics and relative isolation in an effort to select trees that represented the variation in these attributes within our study area. For cropland and pasture sites, only one tree was selected per site. We selected multiple trees at each reserve site because of the limited number of reserve sites and their relatively large size. To prevent double counting of birds, we selected individual trees that were separated by >250 m to minimize the potential for shared characteristics among sampled trees in this rare habitat type. The mean inter-tree distance was 31.7 km (range 1.2–94.1) for cropland sites, 32.0 km (0.4–72.1) for pasture sites, and 43.5 km (0.4–88.3) for reserves, demonstrating the similarity of inter-tree distances among sites despite the sampling of multiple trees within reserves. In total, we selected 35 trees with 13 trees situated in croplands, 13 in pastures and nine in reserves.

2.2. Bird surveys

We conducted bird surveys between 15 May and 1 July 2007. We surveyed each tree five times and randomized the order in which trees were surveyed on subsequent surveys. Surveys took place between 600 and 1000 on days with no rain and wind speed <15 kph. Each 20 min survey consisted of observing the focal tree for 5 min from a distance of 30 m in four cardinal directions. We recorded all birds that landed on the tree. We further documented the primary behavior – singing, foraging, perching or nesting – for each bird detected. At the end of the observation period, we visually inspected the tree canopy for an additional 2 min from the tree base and recorded any previously undetected birds.

2.3. Tree architecture

To capture variation in tree architecture, we developed two structural indices: a tree size index and a tree complexity index. For tree size, we used an index similar to Fischer and Lindenmayer (2002a) by multiplying tree height by basal area and canopy volume. We used a laser range finder to estimate height and measured diameter-at-breast height to calculate basal area. To estimate canopy volume, we used program Tree Analyser (Phattaralerphong and Sinoquet, 2006) which computes canopy volume by creating a virtual 3-D reconstruction of the canopy from binary digital photographs. We used four photographs per tree taken in each of the four cardinal directions where possible, which we analyzed with Tree Analyser using program GIMP version 2.2.17 (GNU Image Manipulation Program, http://www.gimp.org).

We developed a tree complexity index to capture variation in structure beyond tree size. This index is the summation of three variables each scored on a scale of 1–4: number of dead limbs, number of mistletoe patches, and lichen cover. In general, this index yields higher scores for older trees that have high structural diversity and presumably a larger number of foraging niches (Mazurek and Zielinski, 2004).

Because Oregon white oak trees are an important source of cavities for cavity-nesting birds (Gumtow-Farrior, 1991; Viste-Sparkman, 2005), we also recorded the number of cavities visible on each tree.

Please cite this article in press as: DeMars, C.A., et al. Multi-scale factors affecting bird use of isolated remnant oak trees in agro-ecosystems. Biol. Conserv. (2010), doi:10.1016/j.biocon.2010.03.029

2.4. Landscape variables

To determine the spatial context of an individual tree, we estimated tree isolation and tree cover in the surrounding landscape. We used a laser range finder to estimate the distance to the nearest tree and patch for distances ⩽150 m. For distances >150 m, we used the ruler function in ArcGIS to estimate distances from digital orthophoto maps (year 2000; 1-m resolution; OGEO, 2007). We defined patch as >5 contiguous trees.

We used ArcGIS to estimate forest cover and oak woodland cover surrounding each study tree at multiple spatial extents using recent vegetation maps (1:24,000 scale; NHI, 2007). To calculate forest cover, we included all polygons classified as forest regardless of tree species composition. Because the bird community composition of conifer-dominated forests can differ markedly from the bird community associated with oak woodlands (Hagar and Stern, 2001), we also calculated oak woodland cover by excluding polygons that had an oak component of <25%. In both forest and oak woodland cover estimation, we used 50 m buffer increments for the first 1000 m, 100 m increments for the next 1000 m, and then 500 m increments to a maximum buffer of 5000 m. For community-level responses, we used program Focus (Holland et al., 2004) to determine the spatial scale at which each community most strongly responded to each cover variable. Program Focus iteratively samples subsets of non-overlapping points and fits a regression line to each subset to create a distribution of model fit statistics. We considered the spatial scale with the highest mean R^2 value to be the characteristic scale of response for each community. We used a similar approach for species-specific responses by selecting the spatial scale with the lowest deviance from repeated logistic regression analyses.

2.5. Statistical analyses

To ensure variation in bird detectability among sites did not confound parameter estimates, we evaluated whether the probability of detecting a bird on an individual tree varied depending on tree canopy size, the main variable thought to affect detection probability. Given the uniqueness of surveying a single tree for bird use compared to standard avian point counts, we used a novel approach to test for heterogeneity in detection probabilities. We used EstimateS (Colwell, 2006) to generate sample-based rarefaction curves of species accumulation for small- and large-canopied trees. We pooled data of the five smallest-canopied trees and the five largest-canopied trees and compared slopes of rarefaction curves for each of these two canopy types. We interpreted a difference in the slopes of rarefaction curves to be indicative of a difference in detection probabilities between canopy types.

For species-level analyses, we assessed those species detected at ⩾5 sites. For each species, we used Fisher's exact test to compare proportional use of trees in agricultural sites versus trees in oak savanna reserves. For community-level analyses, we considered all species detected with no minimum site detection threshold. We assigned species to each community group *a priori* from a list of potential birds associated with Willamette Valley oak habitats (Altman et al., 2001; Marshall et al., 2003). We assessed four community responses: (i) total species richness; (ii) richness of oak savanna associates; (iii) tree forager richness; and (iv) aerial and ground forager richness.

We used EstimateS to calculate expected species richness functions (Mao Tau estimator; Colwell, 2006) for each landscape context. We pooled data from the five visits for each site and considered each site as a sample, thereby creating nine reserve samples, 13 pasture samples and 13 crop samples. The resulting rarefaction curves allow comparison of species richness estimates at a similar sampling effort when sample sizes or the number of individuals encountered is uneven (Gotelli and Colwell, 2001).

To evaluate how explanatory variables influenced bird use of individual trees, we used a two-stage information-theoretic model selection approach. Prior to model development, we evaluated Pearson's correlation coefficients among all explanatory variables. High correlation ($r = 0.89$) occurred between forest cover and oak woodland cover and thus these two variables were not included in the same model. None of the other variables were strongly correlated ($r < 0.70$). We therefore developed the following *a priori* models using Poisson regression for community-level species richness responses and logistic regression for species-level responses:

i. Tree architecture
   Bird use = tree size index + tree complexity index + cavities
ii. Tree isolation
   Bird use = distance to nearest tree and
   Bird use = distance to nearest patch
iii. Tree cover
   Bird use = forest cover at characteristic scale of response and
   Bird use = oak woodland cover at characteristic scale of response

We evaluated each model using Akaike's Information Criterion corrected for small sample sizes (AIC_c, Burnham and Anderson, 2002). In the first stage of model selection, we selected the model with the lowest AIC_c value as the most parsimonious model for each factor. For tree architecture, we evaluated all subsets of the full three-variable model. For tree isolation and tree cover factors, we assessed the two competing models within each factor.

In the second stage of model selection, we combined the top model for each factor along with an indicator variable for landscape context and fit this model to the data:

Bird use = top tree architecture model + top tree isolation model + top tree cover model + landscape context indicator variable

For each community-level response, we evaluated all subsets of this four-variable model as well as a five-variable model that included a term for potential statistical interaction between tree cover and landscape context (Kupfer et al., 2006). For species-specific responses, we evaluated all subsets of the four-variable model but we did not consider interaction models as the relative rarity of many species precluded testing of models with a high number of variables.

For each response, we considered for inference all models that were ⩽2 AIC units of the top model and we evaluated the relative support for the top model with model weights (Burnham and Anderson, 2002). To assess each top model's strength of association, we calculated Mc Fadden's adjusted-R^2 statistics for logistic regression models (R^2_{adj}; Long, 1997) and a deviance-based R^2 measure for Poisson regression models ($R^2_{D\gamma}$; Mittlbock and Waldhor, 2000). We assessed the relative importance of the four factors (tree architecture, tree isolation, tree cover and landscape context) by summing Akaike weights of all models that contained a particular factor to arrive at a relative importance value ($\omega_+(i)$) for each factor (Burnham and Anderson, 2002). For parameter estimates, we report mean, standard error (SE) and, given our small sample size, 90% confidence intervals.

3. Results

We recorded 47 species of birds using remnant trees from 528 detections (see Appendix). European Starling ($n = 20$ sites; see Appendix for scientific names) was most frequently encountered

Please cite this article in press as: DeMars, C.A., et al. Multi-scale factors affecting bird use of isolated remnant oak trees in agro-ecosystems. Biol. Conserv. (2010), doi:10.1016/j.biocon.2010.03.029

followed by American Robin ($n = 18$) and American Goldfinch ($n = 17$). Among oak savanna associates, American Goldfinch and Lazuli Bunting ($n = 11$) were most frequently observed. Bullock's Oriole ($n = 10$) was the most frequently observed tree foraging species. The majority of species were detected at <10 sites. Of the 23 species detected at $\geqslant 5$ sites, eight species occupied a higher proportion of reserve sites than agricultural sites with Lazuli Bunting, Spotted Towhee and House Wren most strongly associated with reserves ($p \leqslant 0.10$, Fisher's exact test). Sample-based rarefaction curves for assessing variation in avian detection probabilities suggested rates of species accumulation were similar among the sampled trees (DeMars, 2008) and we therefore made no adjustments in our analyses.

Surprisingly, estimated species richness was similar in agricultural and reserve sites with confidence intervals overlapping among the three landscape contexts (Fig. 1). Observed site-specific values of total species richness varied from 3 to 14 ($\bar{x} = 6.9$, SE 2.9). Pasture sites had the highest total species richness (species observed [S_{obs}] = 42) followed by crop sites ($S_{\text{obs}} = 34$) and reserve sites ($S_{\text{obs}} = 20$). For oak savanna associates, species richness was highest on crop ($S_{\text{obs}} = 15$) and pasture sites ($S_{\text{obs}} = 15$) and lowest on reserves ($S_{\text{obs}} = 6$). Foraging guilds followed a similar pattern. Tree forager richness was highest on pasture sites ($S_{\text{obs}} = 16$) followed by crop sites ($S_{\text{obs}} = 9$) and reserves ($S_{\text{obs}} = 8$). Aerial and ground forager richness was highest on pasture ($S_{\text{obs}} = 25$) and crop sites ($S_{\text{obs}} = 25$) and lowest on reserves ($S_{\text{obs}} = 12$).

3.1. Model selection

3.1.1. Species level

We evaluated the relative influence of the four explanatory factors on species-specific use of individual trees for 23 species (Table 1). Tree cover (14 species) and tree architecture (11 species) were the most frequent factors in the top models. A tree isolation variable was in the top model of seven species. Only one species, Lazuli Bunting, had a landscape context variable in the top model. Tree cover was the most important factor for 11 species, tree architecture for seven species, tree isolation for four species and landscape context for one species. McFadden's (R^2_{adj} for top models varied from 0 to 0.62 with the majority of models having values <0.20, consistent with lack of clear selection for any variable type.

3.1.2. Community level

Tree cover and tree architecture were also the most important factors for predicting community-level responses. Values of $R^2_{\text{D}\gamma}$ for top community-level models varied from 0.29 to 0.77 (Table 2). The top model for predicting total species richness was a single variable model describing a negative correlation with forest cover in an 800 m buffer ($\beta = -0.83$, SE = 0.41, CI: -0.16, -1.50). The second ranked model also contained this forest cover variable along with tree size and cavity variables. Evidence for tree size (CI: -0.002, 0.022) and cavity (CI: -0.084, 0.002) effects, however, was relatively weak as confidence intervals overlapped zero for both variables. The single-variable forest cover model was over twice as likely as the remaining two models in the model set.

For oak savanna associates, the top model for species richness was a two-variable model describing a positive correlation with tree size ($\beta = 0.018$, SE = 0.010, CI: 0.002, 0.034) and a negative correlation with oak cover in a 1400 m buffer ($\beta = -2.49$, SE = 1.61, CI: -5.14, 0.16). The second and third ranked models were single variable models describing tree size and oak cover respectively. All three models had model weights within 0.03 of each other, indicating similar strengths of evidence for these two variables in explaining richness of oak savanna associates.

Richness of tree foragers was best predicted by a single variable model describing a positive correlation with tree size ($\beta = 0.024$, SE = 0.010, CI: 0.008, 0.040). This model was almost twice as likely as the only other model within 2 AIC units. The top model for aerial and ground forager richness was a single variable model describing a negative correlation with forest cover in a 150 m buffer ($\beta = -0.97$, SE = 0.40, CI: -1.63, -0.31). No other models were within 2 AIC units of this model.

Assessing the relative importance of the four explanatory factors, tree architecture, in particular tree size, was the most important factor for explaining the richness of oak savanna associates and tree foragers (Table 3). For total species richness and the richness of aerial and ground foragers, tree cover was most important. Landscape context had little impact in explaining community-level responses, ranking far behind the other three factors, consistent with the results from the species-level analysis. Because we found no meaningful relationships between landscape context and bird use, we considered the potential lack of independence of data within a single management unit irrelevant.

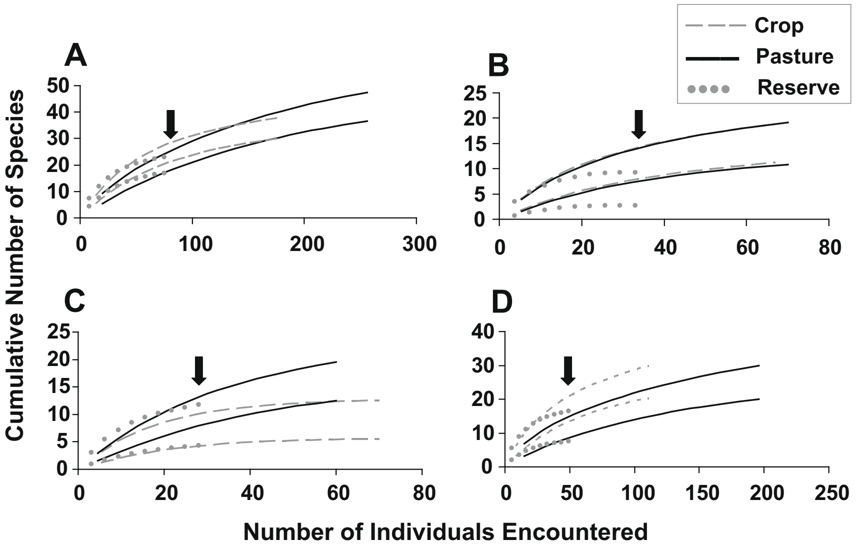

Fig. 1. Ninety percent confidence intervals for sample-based rarefaction curves for: (a) total species richness; (b) oak savanna associate richness; (c) tree forager species richness; and (d) aerial and ground forager richness. Solid arrow indicates where sampling effort is equal among the three landscape types.

Please cite this article in press as: DeMars, C.A., et al. Multi-scale factors affecting bird use of isolated remnant oak trees in agro-ecosystems. Biol. Conserv. (2010), doi:10.1016/j.biocon.2010.03.029

Table 1
Top models for 23 species detected at ⩾5 sites. Logistic regression coefficients (SE) for each model are presented sequentially beginning with the intercept (β_0).

Species	Model[a]	ω_i [b]	R^2_{adj} [c]	β_0	β_1	β_2	β_3
Red-tailed Hawk (*Buteo jamaicensis*)	SIZE	0.23	0.16	−3.31 (0.97)	0.13 (0.06)		
Western Wood-Pewee (*Contopus sordidulus*)	CAVI + OAK(5000)	0.24	0.08	−0.05 (1.12)	0.27 (0.20)	−20.72 (14.38)	
Western Scrub Jay (*Aphelocoma californica*)	CAVI + FOR(800)	0.57	0.39	−2.31 (1.09)	−10.17 (37.72)	8.87 (4.67)	
Black-capped Chickadee (*Poecile atricapilla*)	DIST.T	0.29	0.19	1.43 (1.16)	−0.040 (0.018)		
White-Breasted Nuthatch (*Sitta carolinensis*)	SIZE + COMP	0.17	0.06	0.55 (1.70)	0.11 (0.06)	−0.59 (0.37)	
House Wren (*Troglodytes aedon*)	FOR(100)	0.52	0.45	−3.45 (1.02)	5.60 (1.93)		
American Robin (*Turdus migratorius*)	DIST.P	0.67	0.08	−0.14 (0.53)	0.0013 (0.0027)		
European Starling (*Sturnus vulgaris*)	OAK(1600)	0.26	0.06	1.32 (0.63)	−11.65 (5.95)		
Cedar Waxwing (*Bombycilla cedrorum*)	FOR(750)	0.66	0.55	1.13 (0.99)	−140.78 (85.00)		
Common Yellowthroat (*Geothlypis trichas*)	COMP + OAK(500)	0.50	0.24	2.65 (2.13)	−1.17 (0.55)	7.68 (3.27)	
Western Tanager (*Piranga ludoviciana*)	SIZE	0.34	0.12	−3.10 (0.90)	0.011 (0.06)		
Black-headed Grosbeak (*Pheucticus melanocephalus*)	SIZE + FOR(100)	0.65	0.39	−4.24 (1.77)	0.033 (0.016)	−7586.03 (3184.71)	
Lazuli Bunting (*Passerina amoena*)	TYPE	0.23	0.10	1.25 (0.80)	−2.96 (1.11)	−2.96 (1.11)	
Spotted Towhee (*Pipilo maculatus*)	DIST.P	0.23	0.09	0.04 (0.93)	−0.015 (0.009)		
Chipping Sparrow (*Spizella passerina*)	SIZE + DIST.P + OAK(1600)	0.52	0.18	1.12 (1.51)	0.17 (0.08)	−0.012 (0.007)	−29.98 (17.07)
Savannah Sparrow (*Passerculus sandwichensis*)	SIZE + DIST.P + FOR(150)	0.56	0.62	1.57 (2.12)	−0.81 (0.38)	0.019 (0.014)	−812.99 (1235.27)
White-crowned Sparrow (*Zonotrichia leucophrys*)	FOR(150)	0.34	0.17	−0.54 (0.46)	−103.66 (123.85)		
Song Sparrow (*Melospiza melodia*)	COMP + FOR(100)	0.25	0.14	1.82 (2.07)	−0.61 (0.43)	−6309.29 (30200.55)	
Brewer's Blackbird (*Euphagus cyanocephalus*)	DIST.P	0.32	0.17	−3.06 (0.88)	0.0092 (0.0038)		
Bullock's Oriole (*Icterus bullockii*)	Intercept	0.21	0	−0.92 (0.37)			
House Finch (*Carpodacus mexicanus*)	SIZE + OAK(400)	0.27	0.17	1.39 (0.85)	0.083 (0.054)	−15.81 (10.83)	
Lesser Goldfinch (*Carduelis psaltria*)	DIST.P + FOR(50)	0.30	0.10	0.29 (0.95)	−0.0092 (0.0068)	−98.33 (499.26)	
American Goldfinch (*Carduelis tristis*)	FOR(1400)	0.41	0.08	0.93 (0.55)	−7.38 (3.42)		

[a] Variable codes: CAVI = number of tree cavities; COMP = tree complexity; DIST.T = distance to nearest tree; DIST.P = distance to nearest patch; SIZE = tree size; OAK (x) = oak woodland cover in buffer size x; FOR (x) = forest cover in buffer size (x).

[b] Model weight representing the relative probability that the model under consideration is the best approximating model.

[c] McFadden's adjusted R^2.

4. Discussion

The ability of agricultural fields to contribute to regional conservation is a key goal of many sustainable agriculture programs. We documented 47 bird species using remnant trees in agro-ecosystems, suggesting that these trees are serving some function in supporting species that would not persist in otherwise treeless agricultural landscapes. Importantly, 16 oak savanna-associated species used these trees, including species of regional conservation concern such as White-Breasted Nuthatch and Chipping Sparrow (ODFW, 2006). Contrary to our expectations, for the majority of species, frequency of use of individual trees was similar among crop, pasture and reserve sites. Moreover, none of the species detected were confined only to reserve sites, further indicating the potential for agriculturally-situated trees to positively contribute to landscape-level conservation of a wide range of bird species.

Behavioral observations of bird use suggest that individual isolated trees are focal habitat structures for roosting, foraging, singing and nesting (DeMars, 2008). For many oak savanna-associated birds, an agriculturally-situated remnant oak tree may provide critical resources necessary for persistence in what otherwise might be an inhospitable matrix. For tree foragers in particular, isolated trees provide foraging opportunities that would not exist in treeless agro-ecosystems. Further, isolated trees may act as important stopover points for tree foraging species moving among woodland patches (Fischer and Lindenmayer, 2002b; Robertson and Radford, 2009). For aerial and ground foraging species, individual isolated trees likely provide safe refuges for roosting (Dean et al., 1999) and prominent perches for singing (Slabbekoorn, 2004).

In our study, two factors had the greatest influence on avian use of oak remnant trees: tree size and tree cover in the surrounding landscape. Increasing tree size was associated with higher bird use, particularly among tree foragers and oak savanna associates. Larger legacy-type trees likely provide more and higher quality resources for birds than smaller, younger trees (Dean et al., 1999; Mazurek and Zielinski, 2004). Previous studies have illustrated

Please cite this article in press as: DeMars, C.A., et al. Multi-scale factors affecting bird use of isolated remnant oak trees in agro-ecosystems. Biol. Conserv. (2010), doi:10.1016/j.biocon.2010.03.029

Table 2
Poisson regression coefficients (SE) of top models (<2 ΔAIC_c) predicting community-level responses of avian use of isolated white oak legacy trees. See Table 1 for variable codes.

Response Model	ω[a]	$R^2_{D\gamma}$[b]	Parameter estimates Intercept	SIZE	CAVI	Tree cover[c]
Total species richness						
FOR(800)	0.25	0.29	2.02			−0.83
			(0.09)			(0.41)
SIZE + CAVI + FOR(800)	0.18	0.52	2.01	0.010	−0.041	−0.76
			(0.13)	(0.007)	(0.026)	(0.41)
SIZE + CAVI	0.12	0.30	1.88	0.012	−0.042	
			(0.10)	(0.007)	(0.026)	
Intercept	0.09	0	1.91			
			(0.06)			
Oak associate richness						
SIZE + OAK(1400)	0.21	0.64	1.00	0.018		−2.49
			(0.21)	(0.010)		(1.61)
SIZE	0.21	0.41	0.76	0.021		
			(0.15)	(0.010)		
OAK(1400)	0.18	0.37	1.22			−2.83
			(0.16)			(1.56)
Intercept	0.10	0	1.00			
			(0.10)			
Tree forager richness						
SIZE	0.33	0.44	0.50	0.024		
			(0.17)	(0.010)		
SIZE + OAK(150)	0.18	0.48	0.47	0.027		0.49
			(0.19)	(0.011)		(0.41)
Aerial/ground forager richness						
FOR(150)	0.49	0.77	1.64			(−0.97)
			(0.08)			(0.40)

[a] Model weight representing the relative probability that the model under consideration is the best approximating model.

[b] Deviance-based R^2 measure for Poisson regression.

[c] Forest (FOR) or oak woodland (OAK) cover in buffer size (x).

Table 3
Relative importance values ($\omega_+(i)$) of the four explanatory factors for each of the community-level responses. Relative importance values are the sum of Akaike weights of all models containing a particular factor.

	Species richness	Oak savanna associates	Tree foragers	Aerial/ground foragers
Tree architecture	0.44	0.59	0.74	0.23
Tree isolation	0.25	0.23	0.23	0.23
Tree cover	0.62	0.54	0.35	0.87
Landscape context	0.13	0.09	0.11	0.09

the importance of large oak trees to cavity-nesting species (Gumtow-Farrior, 1991; Viste-Sparkman, 2005) but our findings provide evidence that large oak trees in agro-ecosystems are potentially important to a wide range of oak savanna-associated species.

Tree cover in the surrounding landscape was a primary factor in predicting total species richness on individual trees. Total species richness generally decreased with increasing tree cover, contrasting with previous studies in agricultural systems where bird species richness was positively correlated to increasing tree cover (Luck and Daily, 2003; Harvey et al., 2006; Posa and Sodhi, 2006; Sekercioglu et al., 2007). Our finding of decreased bird use with increasing tree cover was likely influenced by the landscape matrix. In the Willamette Valley where open habitats created by agricultural conversion dominate the landscape, we recorded few forest obligate birds using isolated trees, birds that would likely respond positively to increasing tree cover. In open habitats, increasing bird use of isolated trees with decreasing tree cover suggests that the role of isolated trees as focal habitat structures increases as trees become rarer in the landscape. Thus, an isolated tree becomes a "habitat magnet", concentrating tree-dependent species around this focal habitat structure on the landscape and resulting in higher bird use. Conversely, as tree cover increases, tree-associated resources are more abundant and dispersed on the landscape, likely resulting in lower per capita avian use of individual trees.

Tree isolation ranked behind tree size and tree cover for predicting bird use of individual trees. In general, the number of species using individual trees increased with increasing tree isolation, consistent with results from Africa where increasing isolation of individual savanna trees was associated with greater intensity of use by birds and mammals (Dean et al., 1999). The positive correlation of bird use to increasing tree isolation is consistent with the positive correlation of bird use to decreasing tree cover in the landscape. Specifically, the inverse relationship between intensity of bird use and tree availability emphasizes the importance of the resources that isolated trees provide to many birds in agro-ecosystems. Moreover, the intensification of bird use with decreasing tree availability supports the hypothesis that the importance of isolated trees as keystone habitat features increases as trees become rarer on the landscape (Manning et al., 2006).

Our most surprising and potentially important finding was the small influence that landscape context had on bird use of isolated oak trees. Overall species richness was similar between trees located in agricultural fields and trees situated in savanna reserves. Importantly, this relationship also held true for species richness of oak savanna associates. The high use of agriculturally-situated trees suggests that individual trees are important habitat components to many savanna species occupying agricultural fields during the breeding season. Moreover, high use of agriculturally-situated trees highlights the importance of off-reserve conservation of habitat remnants, even at the scale of a single tree, for conserving native biodiversity within anthropogenically-modified landscapes (Franklin, 1993; Schwartz and van Mantgem, 1997; Manning et al., 2009).

Please cite this article in press as: DeMars, C.A., et al. Multi-scale factors affecting bird use of isolated remnant oak trees in agro-ecosystems. Biol. Conserv. (2010), doi:10.1016/j.biocon.2010.03.029

4.1. Conservation implications

The most immediate management issue regarding isolated remnant trees in agro-ecosystems is their declining abundance due to current land use practices and senescence of existing trees (Thysell and Carey, 2001; Gibbons et al., 2008). Although the role that isolated trees play in the demography of bird populations is yet to be assessed, continued decline in abundance of these trees has the potential to negatively impact a wide array of oak savanna-associated birds, particularly those species that could not persist in treeless agricultural fields. Reversing the decline of isolated oak trees in agro-ecosystems will require land managers to work with willing landowners to conserve existing trees and foster the recruitment of younger replacement trees. Potential strategies for facilitating conservation and recruitment include active planting of trees, exclusion fencing and fast-rotational grazing schemes (Fischer et al., 2009). Further, modification of existing landowner incentive programs and habitat conservation policies will be necessary to recognize the potential ecological benefits of restoration at the single-tree scale.

Our findings have further implications with respect to current oak savanna restoration efforts (Campbell, 2004; Vesely and Tucker, 2004). Clearly, the ultimate goal of many oak savanna restoration projects is to restore habitat for a broad complement of oak-associated wildlife species. Achieving this goal generally requires conservation or restoration of large savanna-form trees along with the native herbaceous understory. The rarity of oak savanna in North America necessitates that this type of restoration should be a high priority wherever possible (Noss et al., 1995). However, in agriculturally-dominated systems such as the Willamette Valley, this type of restoration is likely not feasible over the entire region. Our results suggest that oak savanna restoration in agricultural systems does not necessarily need to be an all-or-nothing proposition. Large savanna-form oak trees scattered in agricultural fields have wildlife value, particularly for many oak-associated birds. Moreover, individual trees have a relatively small physical footprint thus allowing minimal impact on agricultural production and contributing to biological diversity at a small cost to production.

Our results have broader implications when considering habitat management strategies for conserving wildlife in agricultural systems. Paradigms developed in the late twentieth century for conserving wildlife in agro-ecosystems focused on the use of hedgerows, fencerows, shelterbelts and other strip-cover habitats (Pimentel et al., 1992; Best et al., 1995). Recently developed paradigms suggest that agricultural systems that attempt to incorporate ecological patterns and processes of underlying historical natural systems may be more successful at conserving biodiversity (Fischer et al., 2006; Vandermeer and Perfecto, 2007). In the context of the Willamette Valley's agricultural matrix, scattered large white oak trees should therefore be considered part of a landscape-level management strategy for improving conservation of oak savanna-associated bird populations.

Acknowledgements

This project would have been impossible without the assistance of many private landowners and public agencies that facilitated access to their properties. We thank G. Fitzpatrick for initiating discussions on research of isolated oak trees and J. Miller and S. Zack for their review of field methods and earlier drafts of the manuscript. We also thank M. Betts, J. Hagar, D. Robinson, and two anonymous referees for further reviews of the manuscript. This research was supported in part by scholarships to C. DeMars from the Northwest Scientific Association and the Oregon Chapter of The Wildlife Society.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.03.029.

References

Altman, B., Hayes, M., Janes, S., Forbes, R., 2001. Wildlife of westside grasslands and chaparral habitats. In: Johnson, D.H., O'Neil, T.A. (Eds.), Wildlife–habitat Relationships in Oregon and Washington. Oregon State University Press, Corvallis, OR, pp. 736–738.

Best, L.B., Freemark, K.E., Dinsmore, J.J., Camp, M., 1995. A review and synthesis of habitat use by breeding birds in agricultural landscapes of Iowa. American Midland Naturalist 134, 1–29.

Brooks, T.M. et al., 2004. Coverage provided by the global protected-area system: is it enough? Bioscience 54, 1081–1091.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach, second ed. Springer, New York, NY. 488 p.

Campbell, B.H., 2004. Restoring Rare Native Habitats in the Willamette Valley: A Landowner's Guide for Restoring Oak Woodlands, Wetlands, Prairies, and Bottomland Hardwood and Riparian Forests. Defenders of Wildlife, West Linn, OR. 123 p.

Clay, J., 2004. World Agriculture and the Environment: A Commodity-by-commodity Guide to Impacts and Practices. Island Press, Washington, DC.

Colwell, R.K., 2006. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples, Version 8. <purl.oclc.org/estimates>.

Dean, W.R.J., Milton, S.J., Jeltsch, F., 1999. Large trees, fertile islands, and birds in arid savanna. Journal of Arid Environments 41, 61–78.

DeMars, C.A., 2008. Conserving Avian Diversity in Agricultural Systems: The Role of Isolated Oregon White Oak Legacy Trees. Oregon State University, M.S. Thesis, Corvallis, OR, 138 p.

Fischer, A.P., Bliss, J.C., 2008. Behavioral assumptions of conservation policy: conserving oak habitat on family-forest land in the Willamette Valley, Oregon. Conservation Biology 22, 275–283.

Fischer, J., Lindenmayer, D.B., 2002a. The conservation value of paddock trees for birds in a variegated landscape in southern New South Wales. 1. Species composition and site occupancy patterns. Biodiversity and Conservation 11, 807–832.

Fischer, J., Lindenmayer, D.B., 2002b. The conservation value of paddock trees for birds in a variegated landscape in southern New South Wales. 2. Paddock trees as stepping stones. Biodiversity and Conservation 11, 833–849.

Fischer, J., Lindenmayer, D.B., Manning, A.D., 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment 4 (2), 80–86.

Fischer, J., Stott, J., Zerger, A., Warren, G., Sherren, K., Forrester, R.I., 2009. Reversing a tree regeneration crisis in an endangered ecoregion. Proceedings of the National Academy of Sciences of the United States of America 106, 10386–10391.

Foley, J.A. et al., 2005. Global consequences of land use. Science 309, 570–574.

Franklin, J.F., 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecological Applications 3, 202–205.

Franklin, J.F., Lindenmayer, D.B., Macmahon, J.A., Mckee, A., Magnusson, D.A., Perry, D.A., Waide, R., Foster, D.R., 2000. Threads of continuity: ecosystem disturbances, biological legacies and ecosystem recovery. Conservation Biology in Practice 1, 8–16.

Gibbons, P., Lindenmayer, D.B., Fischer, J., Manning, A.D., Weinberg, A., Seddon, J., Ryan, P., Barrett, G., 2008. The future of scattered trees in agricultural landscapes. Conservation Biology 22, 1309–1319.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4, 379–391.

Gumtow-Farrior, D.L., 1991. Cavity Resources in Oregon White Oak and Douglas-fir Stands in the Mid-Willamette Valley, Oregon. Oregon State University, M.S. Thesis, Corvallis, OR, 89 p.

Hagar, J.C., Stern, M.A., 2001. Avifauna in oak woodlands in the Willamette Valley, Oregon. Northwestern Naturalist 82, 12–25.

Harvey, C.A., Haber, W.A., 1999. Remnant trees and the conservation of biodiversity in Costa Rican pastures. Agroforestry Systems 44, 37–68.

Harvey, C.A., Medina, A., Sanchez, D.M., Vilches, S., Hernandez, B., Saenz, J.C., Maes, J.M., Casanoves, F., Sinclair, F.L., 2006. Patterns of animal diversity in different forms of tree cover in agricultural landscapes. Ecological Applications 16, 1986–1999.

Haslem, A., Bennett, A.F., 2008. Birds in agricultural mosaics: the influence of landscape pattern and countryside heterogeneity. Ecological Applications 18, 185–196.

Holland, J.D., Bert, D.G., Fahrig, L., 2004. Determining the spatial scale of species' response to habitat. Bioscience 54, 227–233.

Kupfer, J.A., Malanson, G.P., Franklin, S.B., 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Global Ecology and Biogeography 15, 8–20.

Long, J.S., 1997. Regression Models for Categorical and Limited Dependent Variables. Sage Publications, Thousand Oaks. 328 p.

Please cite this article in press as: DeMars, C.A., et al. Multi-scale factors affecting bird use of isolated remnant oak trees in agro-ecosystems. Biol. Conserv. (2010), doi:10.1016/j.biocon.2010.03.029

Luck, G.W., Daily, G.C., 2003. Tropical countryside bird assemblages: richness, composition, and foraging differ by landscape context. Ecological Applications 13, 235–247.

Manning, A.D., Lindenmayer, D.B., Barry, S.C., 2004. The conservation implications of bird reproduction in the agricultural "matrix": a case study of the vulnerable superb parrot of south-eastern Australia. Biological Conservation 120, 363–374.

Manning, A.D., Fischer, J., Lindenmayer, D.B., 2006. Scattered trees are keystone structures – implications for conservation. Biological Conservation 132, 311–321.

Manning, A.D., Gibbons, P., Lindenmayer, D.B., 2009. Scattered trees: a complementary strategy for facilitating adaptive responses to climate change in modified landscapes? Journal of Applied Ecology 46, 915–919.

Marshall, D.B., Hunter, M.G., Contreras, A.L., 2003. Birds of Oregon: A General Reference. Oregon State University Press, Corvallis, OR. 768 p.

Mazurek, M.J., Zielinski, W.J., 2004. Individual legacy trees influence vertebrate wildlife diversity in commercial forests. Forest Ecology and Management 193, 321–334.

Mittlbock, M., Waldhor, T., 2000. Adjustments for R^2-measures for Poisson regression models. Computational Statistics and Data Analysis 34, 461–472.

NHI (Northwest Habitat Institute), 2007. Willamette Valley Oak Map. <www.nwhi.org//index/gisdata#Willamette%20Valley%20Specific%20GIS%20Data>.

Noss, R.F., LaRoe III, E.T., Scott, J.M., 1995. Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. Biological Report 28, US Department of Agriculture, Washington.

OCS (Oregon Climate Service), 2006. Zone 2 – Climate Data Archives. Oregon State University, College of Oceanic and Atmospheric Sciences. <www.ocs.oregonstate.edu/index.html>.

ODFW (Oregon Department of Fish and Wildlife), 2006. The Oregon Conservation Strategy. Oregon Department of Fish and Wildlife, Salem, Oregon.

OGEO (Oregon Geospatial Enterprise Office), 2007. Oregon Digital Orthophoto Quads. <online.wr.usgs.gov/hgpo/doq>.

Peter, D., Harrington, C., 2002. Site and tree factors in Oregon white oak acorn production in western Washington and Oregon. Northwest Science 76, 189–201.

Phattaralerphong, J., Sinoquet, H., 2006. A photographic gap fraction method for estimating leaf area of isolated trees: assessment with 3D digitized plants. Tree Physiology 26, 1123–1136.

Pimentel, D., Stachow, U., Takacs, D.A., Brubaker, H.W., Dumas, A.R., Meaney, J.J., O'Neil, J.A.S., Onis, D.E., Corzilius, D.B., 1992. Conserving biological diversity in agricultural/forestry systems. BioScience 42, 354–362.

Posa, M.R.C., Sodhi, N.S., 2006. Effects of anthropogenic land use on forest birds and butterflies in Subic Bay, Philippines. Biological Conservation 129, 256–270.

Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. The American Naturalist 158, 87–99.

Robertson, O.J., Radford, J.Q., 2009. Gap crossing decisions of forest birds in a fragmented landscape. Austral Ecology 34, 435–446.

Rodrigues, A.S.L. et al., 2004. Effectiveness of the global protected area network in representing species diversity. Nature 428, 640–643.

Schwartz, M.W., van Mantgem, P.J., 1997. The value of small preserves in chronically fragmented landscapes. In: Schwartz, M.W. (Ed.), Conservation in Highly Fragmented Landscapes. Chapman and Hall, New York, NY.

Sekercioglu, C.H., Loarie, S.R., Brenes, F.O., Ehrlich, P.R., Daily, G.C., 2007. Persistence of forest birds in the Costa Rican agricultural countryside. Conservation Biology 21, 482–494.

Slabbekoorn, H., 2004. Singing in the wild: the ecology of birdsong. In: Marler, P., Slabbekoorn, H. (Eds.), Nature's Music: The Science of Birdsong. Elsevier Academic Press, San Diego, CA, pp. 179–205. 513 p.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31, 79–92.

Thilenius, J.F., 1968. The *Quercus garryana* forests of the Willamette Valley, Oregon. Ecology 49, 1124–1133.

Thysell, D.R., Carey, A.B., 2001. *Quercus garryana* communities in the Puget Trough, Washington. Northwest Science 75, 219–235.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. Science 292, 281–284.

Towle, J.C., 1983. Changing geography of Willamette Valley woodlands. Oregon Historical Quarterly 1, 66–87.

Vandermeer, J., Perfecto, I., 2007. The agricultural matrix and a future paradigm for conservation. Conservation Biology 21, 274–277.

Vesely, D., Tucker, G., 2004. A Landowner's Guide for Restoring and Managing Oregon White Oak Habitats. USDI Bureau of Land Management, Salem, OR. 65 p.

Viste-Sparkman, K., 2005. White-breasted Nuthatch Density and Nesting Ecology in Oak Woodlands of the Willamette Valley, Oregon. Oregon State University, M.S. Thesis, Corvallis, OR, 106 p.

Please cite this article in press as: DeMars, C.A., et al. Multi-scale factors affecting bird use of isolated remnant oak trees in agro-ecosystems. Biol. Conserv. (2010), doi:10.1016/j.biocon.2010.03.029