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Effects of agricultural fragmentation on the bird community in sagebrush shrubsteppe

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ABSTRACT

Habitat fragmentation can change the community composition of species in remnant habitat patches. We studied the impacts of fragmentation by agriculture on the bird community in heavily fragmented areas of the sagebrush shrubsteppe in western North America. We examined whether bird communities in sagebrush habitat near orchards and vineyards were different from the community in interior sagebrush habitat, and evaluated whether observed differences could be explained by predator abundance, local vegetation, the presence of the habitat edge, or the proportion of land cover in the surrounding landscape. The bird community near agricultural edges differed from interior habitat: edge habitats had higher species diversity and were dominated by generalist bird species, while Vesper Sparrows, which are sagebrush-associated in this region, were strong indicators of interior habitat. The bird community also differed between orchard edge habitat and vineyard edge habitat, although the difference was small. Edge effects on species composition were associated with differences in the local vegetation, rather than the predator community or the proportion of urban, agricultural, and sagebrush cover on the surrounding landscape. We suggest that differences in the bird community within edge and interior habitat are the result of multiple mechanisms: avoidance of exotic grasses and attraction to high shrub cover in edge habitat, attraction to resources in adjacent habitats, and spill-over of generalist birds from the adjacent agriculture. The results of this study suggest that sagebrush bird conservation areas should be placed away from agricultural development.

1. Introduction

Fragmentation occurs as habitat conversion for agriculture continues across the globe, increasing the proportion of edge in natural habitats. Edge habitats can differ from interior habitats and are often characterized by distinct biotic communities (Harris, 1988; Sisk et al., 1997). Communities may be particularly distinct in edge habitat adjacent to anthropogenic land uses, such as agriculture, because the edges of these activities usually possess unnaturally sharp gradients of change (Sisk and Battin, 2002; Ries et al., 2004). Species diversity may be higher in edge habitat because of the addition of generalist and invasive species; however specialist species that are more likely to be of conservation concern often show reduced abundance near anthropogenic edges (Ewers and Didham, 2005).

Species may be more or less abundant in edge habitat than in interior habitat for a variety of reasons (Chalfoun et al., 2002; Ries et al., 2004; Ries and Sisk, 2004). First, species may differ in abundance due to altered interspecific interactions in edge habitat, such as competitive exclusion or predator avoidance (Piper and Catterall, 2003; Renfrew et al., 2005). Secondly, the vegetation may differ between edge and interior habitat causing individuals to prefer edge or interior habitat because of species-specific habitat preferences (Kristan et al., 2003; Davis and Brittingham, 2004). Thirdly, organisms can flow, or "spill-over" from one adjacent habitat to another (Ries and Debinski, 2001; Matthysen, 2002; Blitzer et al., 2012). Finally, organisms may be attracted to edge habitat because they require or benefit from access to both types of habitat (Leopold, 1933; Saunders et al., 1991). In addition, the extent to which a landscape is modified can also influence the strength of local scale edge effects (Donovan et al., 1997). Although more than one mechanism is usually responsible for an edge effect on community composition, few studies have assessed the relative importance of multiple potential mechanisms (Ries et al., 2004).

The sagebrush shrubsteppe of the intermountain west of North America is increasingly fragmented by agriculture

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(Noss et al., 1995; Paige and Ritter, 1999; Knick et al., 2003). Some species of birds that nest in sagebrush shrubsteppe are found at lower densities within fragmented landscapes (Knick and Rotenberry, 1995; Vander Haegen et al., 2000; Vander Haegen, 2007), which may be caused by the avoidance of habitat edges that are more common in those fragmented landscapes. Edge responses could be due to a variety of mechanisms, as bird habitat choice in sagebrush shrubsteppe can be influenced by predator distribution (Chalfoun et al., 2002; Welstead et al., 2003; Chalfoun and Martin, 2010) and vegetative characteristics (Paczek and Krannitz, 2004; Harrison and Green, 2010; Earnst and Holmes, 2012).

We examined whether and how the bird community in sagebrush shrubsteppe differs between interior habitat and edge habitat adjacent to two types of agriculture, orchard and vineyard. We then explored whether the edge effect on the bird community could be attributed to local vegetation differences, avoidance of the predator community, the presence of the habitat edge, or the proportion of land cover types in the surrounding landscape.

2. Methods

2.1. Study area

The sagebrush shrubsteppe is considered an endangered ecosystem with many sagebrush associated plants and animals identified as being of conservation concern (Noss et al., 1995; Wisdom et al., 2003). We studied sagebrush shrubsteppe in the Okanagan region of British Columbia, Canada and Washington, USA (approximately 49°N, 119°W; Fig. 1A). The Okanagan region is at the northern edge of the sagebrush shrubsteppe that covers much of the Great Basin Bird Conservation Region (BCR 9: NABCI, 2000). Sagebrush shrubsteppe in this region is a dry, largely treeless grassland characterized by bunchgrasses and big sagebrush (*Artemisia tridentata*). During our study, mean temperature and monthly precipitation in the Okanagan region during the breeding bird season (May–July) was 17.5 °C and 30.3 mm in 2011, and 18.5 °C and 49.5 mm in 2012 (Government of Canada, 2015). Land use pressure in the Okanagan is high and approximately 35% of the sagebrush habitat has been converted to other land uses (USA: 38% Dobler et al., 1996; Canada: 33% Iverson et al., 2008). Historically, fruit orchards and cattle grazing were the primary human impacts in the region. Today, the agricultural industry is increasingly dominated by wine production, and habitat conversion for agriculture continues.

2.2. Study sites

We selected study sites in patches of sagebrush shrubsteppe that were adjacent to agriculture, large enough to include interior habitat greater than 400 m from agriculture in all directions, that had similar vegetation across the study site, and where we were able to obtain permission to access the property. In total, 18 study sites were selected (Fig. 1A). At each study site, a pair of 160 m by 100 m study plots was established. Each pair consisted of one plot adjacent to agriculture (edge habitat) and one plot 400–700 m from agriculture or other anthropogenic land types (interior

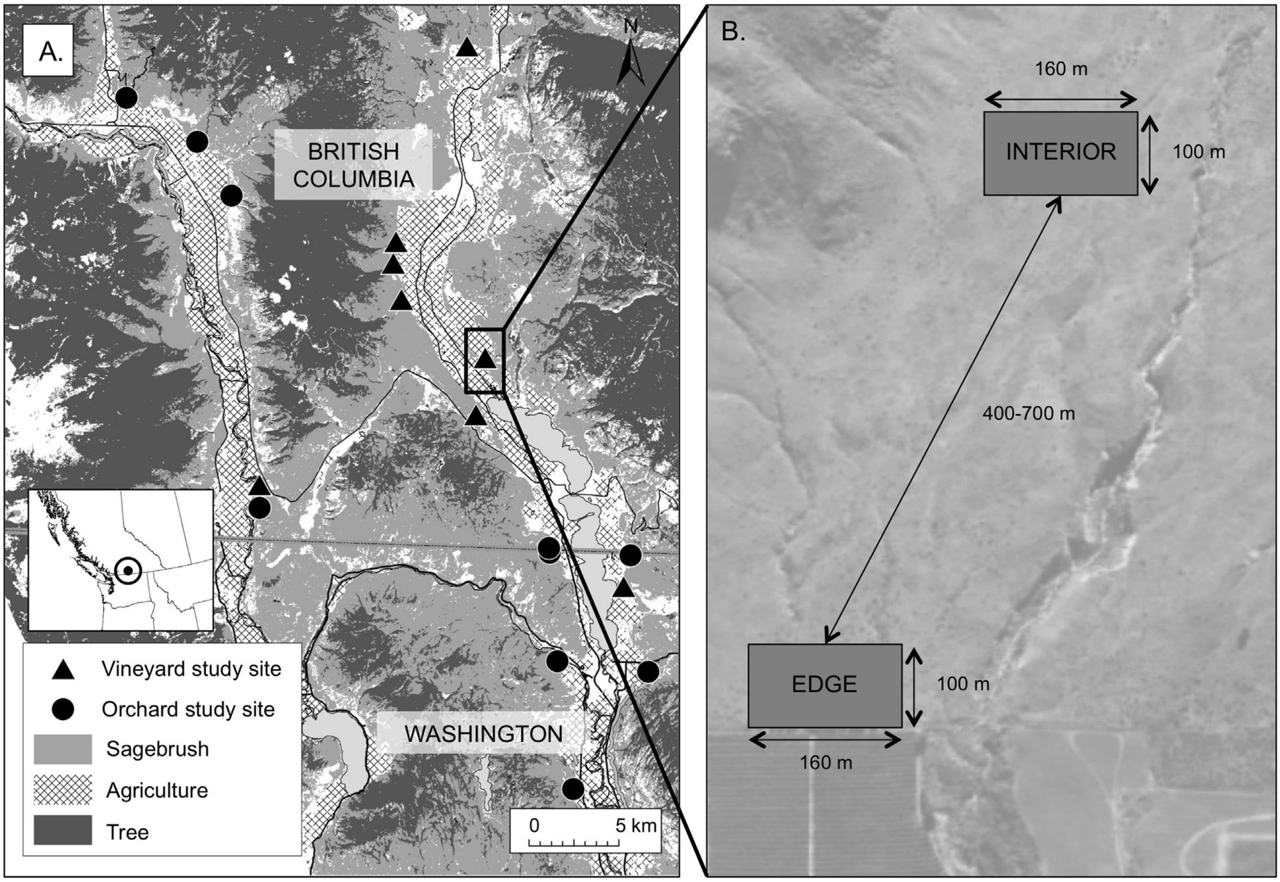

Fig. 1. (A) Sites for studying the bird community in sagebrush shrubsteppe habitat in the Okanagan region of British Columbia, Canada, and Washington, USA (approximately 49°N 119°W). Agricultural land cover is the sum of the orchard, vineyard, and pasture land cover classes. (B) Each study site consisted of a pair of study plots: one plot adjacent to agriculture (edge) and one away from agriculture (interior).

habitat; Fig. 1B), which was the maximum distance available between edge and interior plots of similar vegetation at many study sites and is well within the range of reported edge effects on grassland birds (e.g., 200 m: Renfrew et al., 2005; 1.95 km: Sliwinski and Koper 2012). Ten edge plots were situated adjacent to orchards, and eight adjacent to vineyards to test for differences between agricultural crop types. Half of the study sites were surveyed from May 1 to July 31, 2011 and the remaining half from May 1 to July 31, 2012.

2.3. Bird community

Point counts were conducted to survey the distribution and abundance of birds in sagebrush shrubsteppe habitat every eight days for a total of eight counts per plot. Each ten-minute point count was conducted by a single observer within one hour of sunrise. In order to study edge habitat within 100 m of the agricultural interface, the observer recorded all birds detected by sight or sound within 50 m of the centre of the study plot. The observer also recorded the location and activity of each bird detected on a schematic of the plot to prevent double counting and to exclude from subsequent analyses any birds that were flying over and not considered to be using the habitat. Observers were rotated regularly to reduce the impact of observer bias. Each species detected was categorized into a guild (woodland, generalist, open area, sagebrush, other) following published species descriptions and previously used guild associations (Krannitz, 2007; Rodewald, 2015). The subset of the bird community that we categorized as sagebrush-associated included Brewer's Sparrows (*Spizella breweri*), Lark Sparrows (*Chondestes grammacus*), Vesper Sparrows (*Pooecetes gramineus*), Western Meadowlarks (*Sturnella neglecta*), Grasshopper Sparrows (*Ammodramus savannarum*), and Clay-coloured Sparrows (*Spizella pallida*). Although some of these species occupy different grassland or shrubland habitat types in other areas of their range, they only breed in sagebrush shrubsteppe in our study area. As a guild, the sagebrush and grassland birds are declining faster than most other groups of birds (NABCI, 2009; NABCI, 2012). The population trends for these species in the Great Basin region from 1966 to 2013 are −0.4%, −0.4%, −0.9%, −1.1%, −1.5%, and 9.0% change per year, respectively (Sauer et al., 2014).

2.4. Predator community

We measured the density of known common nest predators in the study region at each of our study plots. Known nest predators in the study region include small mammals, Yellow-bellied Racers (*Coluber constrictor*), Gopher Snakes (*Pituophis catenifer*), Western Meadowlarks (*S. neglecta*), Brown-headed Cowbirds (*Molothrus ater*) and Black-billed Magpies (*Pica hudsonia;* Knight et al., 2014).

We measured the density of small mammals with track tubes, which collect footprints using a food bait (adapted from Mabee, 1998). Two replicate sets of track tubes were set out at each plot with 36 days between the two sets. Each replicate set consisted of twenty-four tubes spaced at 30 m intervals on a 6 × 4 grid. Track tubes were 30 cm lengths of vinyl white downspout with felt pads glued at either entrance, and a length of clear adhesive drawer liner to collect prints. Each felt pad was saturated with a mixture of mineral oil and carbon black powder. Tubes were baited with a small amount of peanut butter on the inner ceiling of the tube and set under a shrub. The tubes were then left at each study plot for four days to collect prints. We were often unable to distinguish between prints made by North American deer mouse (*Peromyscus maniculatus*), Great Basin pocket mouse (*Perognathus parvus*), and western harvest mouse (*Reithrodontomys megalotis*) because prints were faint or overlapped. We therefore identified prints from all three possible species as mouse (superfamily Muroidea). An abundance index was calculated for each replicate set at each plot by dividing the number of track tubes set out by the number of tubes that collected prints. The abundance indices from the two replicate sets of track tubes were highly correlated in a Spearman's rank correlation test ($r_s = 0.76$, $P < 0.001$), so we averaged the two replicate sets of track tubes at each plot to calculate the abundance index for each plot.

The density of Black-billed Magpies and Western Meadowlarks was determined during the ten minute point counts for bird abundance (see above for details). We used 100 m radius point counts to estimate avian predator abundance because there were very few individuals detected within 50 m. The maximum number of individuals detected during a single point count was used as the abundance metric for each species.

Snake density was measured with standardized searches and incidental observations at each plot. Standardized searches covered the entire plot during a 45–60 min search and were conducted every four days. To detect snakes present, observers walked back and forth across the plot in 10 m wide transects moving vegetation with a 1.5 m wooden rod. The first plot to be searched at each site was alternated between edge and interior after every search day to avoid any time of day bias. Incidental observations were recorded while observers were conducting other activities at each plot. Observers were rotated regularly to reduce the impact of observer bias. Approximately equal time was spent at each plot to avoid plot bias (35.8 ± 1.8 h per plot), however snake abundance per species was divided by time spent at each plot to account for any variation.

2.5. Local vegetation

Local vegetation was measured at the end of the breeding season to avoid disturbing any active bird nests. Vegetation was measured along four 100 m transects that spanned the width of each plot and were spaced 50 m apart. We measured the percent linear cover of shrubs using the line intercept method and recorded the maximum height of each shrub along each transect (Kaiser, 1983). We estimated percent cover of all forb and grass species, and percent cover of ground cover type (bare soil, rock, litter, biocrust) with a standard 20 cm by 50 cm Daubenmire plot (Daubenmire, 1959). Percent cover was estimated at every 10 m along each transect for a total of 44 Daubenmire plots per study plot. Maximum grass height was also recorded at every Daubenmire plot. We averaged the shrub, grass height, and percent cover values at each study plot. These vegetation survey methods follow methods previously used in the study area to allow for direct comparison to past and future studies (Paczek and Krannitz, 2004; Harrison and Green, 2010).

2.6. Landscape

We delineated crop type land cover (orchard, vineyard, pasture) and urban land cover in the study area by hand using 1 m ground pixel imagery available in Google Earth (2012) and data on crop type from the Washington State Department of Agriculture (2011) and British Columbia Ministry of Agriculture (2008). We classified sagebrush land cover using Landsat imagery and maximum likelihood supervised classification in ArcMap 10.0 (ESRI 2010). We quantified the proportion of the landscape that was orchard, vineyard, all agricultural types (sum of vineyard, orchard, and pasture classes), urban, and shrubsteppe at varying distances (1, 5, and 10 km radii) from the center of each study plot. We did not include the proportion of land cover types within 15 km because it was highly correlated with land cover within 10 km.

2.7. Geography

We created a data matrix of geographical attributes of each plot that would allow us to examine the effects of geography in subsequent statistical analyses. We described the mean slope and aspect of each plot from digital elevation models (DEMs). We used a 10 m DEM obtained from the USGS for plots in the United States and a 10 m DEM created from 20 m contour lines for plots in Canada. We rescaled aspect to a heat load index from zero to one because the circular scale used for aspect is not appropriate for statistical analysis ((1 − cosine(aspect-45))/2; Beers et al., 1966). We included three binomial parameters to account for variation associated with the valley (Okanagan, Similkameen), country (Canada, United States), and year (2011 and 2012) in which the study plot was monitored. We tested for correlation between the bird community and the location of each study plot using a Procrustes analysis (Jackson 1995), and there was no spatial autocorrelation (correlation = 0.18, $P = 0.32$). Calculation of all geographical variables was performed in ArcMap 10.0 (ESRI, 2010).

2.8. Statistical analysis

For the avian community data, the maximum number of individuals detected during a single point count was used as the abundance metric for each species (Nur et al., 1999). We chose to use unadjusted raw abundance in our analyses because detectability of grassland songbirds within 50 m is generally >90% (Diefenbach et al., 2003), which was confirmed by preliminary detectability analyses for species in our dataset with >80 detections.

We evaluated whether the bird community differed in edge and interior habitat in two ways: using a univariate species diversity (Simpson's index; Simpson, 1949) and a multivariate analysis of community composition. We tested for differences in Simpson's index between edge and interior habitat with three sets of paired Wilcoxon signed rank tests: the first compared all interior and edge plots, the second set compared orchard edge habitat and orchard interior habitat, and the third set similarly compared vineyard edge and interior habitat. A fourth analysis compared the Simpson's index of orchard edge and vineyard edge habitat with a Mann–Whitney U test. For comparison of community composition, we tested for differences between edge and interior habitat with blocked multi-response permutation procedures (MRBPs), which allowed us to account for any variation due to study site (McCune and Grace, 2002). We used the same three comparisons as the species diversity analysis: the first test compared all interior and edge plots, the second test compared orchard edge habitat and orchard interior habitat, and the third test similarly compared vineyard edge and interior habitat. A fourth analysis compared the community composition of orchard edge and vineyard edge habitat with an unblocked multi-response permutation procedure (MRPP) because MRPP allows for unbalanced design.

Next we examined how the communities varied at our different habitat types using indicator species analysis (Dufrêne and Legendre 1997). Indicator species analysis combines species relative abundance and frequency of occurrence to identify the species that characterize different habitat types. We conducted indicator species analysis on the bird community in edge and interior habitat types, as well as on the bird community in orchard edge and vineyard edge habitat types because the MRPP indicated that the bird community varied with agricultural type as well as edge/interior (see Section 3.1).

Finally, we used non-metric multidimensional scaling (NMDS) to explore the influence of the predator, vegetation, landscape, and geography variables on the overall structure of the bird community. NMDS is an unconstrained ordination method that uses measures of ecological distance to ordinate study sites in terms of similarity in bird composition. We used NMDS because it does not assume linear relationships among variables and is not sensitive to the presence of rare species in the dataset, allowing for the inclusion of the entire avian community in analysis (McCune and Grace, 2002). Furthermore, the unconstrained nature of NMDS allowed us to examine whether the environmental variables examined were associated in the direction of the observed edge effect; whereas, the edge effect may have been masked with a constrained ordination method due to the effect of the constraining environmental variables. First we ordinated the bird community data with NMDS, which was constrained to 3 dimensions to achieve a suitable level of minimum stress (15.70; McCune and Grace, 2002). Next, we determined which environmental variables significantly influenced the bird community by fitting a smooth surface of each environmental variable on the NMDS ordination using generalized additive models (GAMs) with thin-plate splines. The GAMs were allowed a maximum of 10 knots to ensure the models were not overfit. There was some collinearity within our environmental variables so we removed any variables with a variance inflation factor (VIF) > 10 in a step-wise fashion prior to fitting the GAMs (O'Brien 2007). We also fitted synthetic variables of the predator, vegetation, and landscape groups to the NMDS ordination to test whether the overall predator community, overall vegetation characteristics, and overall landscape land cover was related to the ordination of the bird community. We derived those synthetic variables from the first component of an unrotated principle component analysis (PCA) ordination of each group. The proportion of variance explained by the first component in the predator, vegetation, and landscape groups was 0.75, 0.63, and 0.55, respectively.

PC-ORD 6.0 was used to perform MRPPs (McCune and Mefford, 2011). All other statistical analyses were performed in R with the vegan, labdsv, usdm, and exactRankTests packages (Oksanen et al., 2012; R Core Team, 2015; Howthorn and Hornik, 2013; Naimi, 2013; Roberts, 2013). Bray–Curtis dissimilarity was used for all multivariate analyses. All permutation tests were performed with an allowed maximum of 10,000 runs.

3. Results

Thirty-nine bird species were detected during the eight point counts conducted at each of the 36 study plots (Appendix A). Thirty-six species were included in the bird community for analysis. We excluded three species from analysis that do not breed in the region but were detected early in the season when moving through the area. Chipping sparrows (*Spizella passerina*) and Vesper Sparrows were the most common bird species detected, being present at 25 and 19 study plots, respectively.

3.1. Presence of edge effects

We detected edge effects of agriculture on species diversity (Simpson's index) and community composition in sagebrush habitat. Species diversity was higher in edge habitat than interior habitat when all sites were combined ($U_{17} = 135$, $P = 0.03$). Species diversity was also higher in edge habitat at orchard sites ($U_9 = 48$, $P = 0.04$), but there was no difference in species diversity between vineyard edge and vineyard interior habitat ($U_7 = 24$, $P = 0.46$; Fig. 2). There was no difference in species diversity between orchard edge and vineyard edge habitat ($W_8 = 152$, $P = 0.81$);

The multivariate analysis indicated that bird community composition in edge habitat was also different from in sagebrush interior habitat when all sites were combined ($A = 0.04$, $T = -3.93$, $P = 0.002$), at orchard sites only ($A = 0.06$, $T = -2.94$, $P = 0.01$), and at vineyard sites only ($A = 0.07$, $T = -2.20$, $P = 0.02$). In contrast to the univariate analysis, the multivariate analysis indicated that the

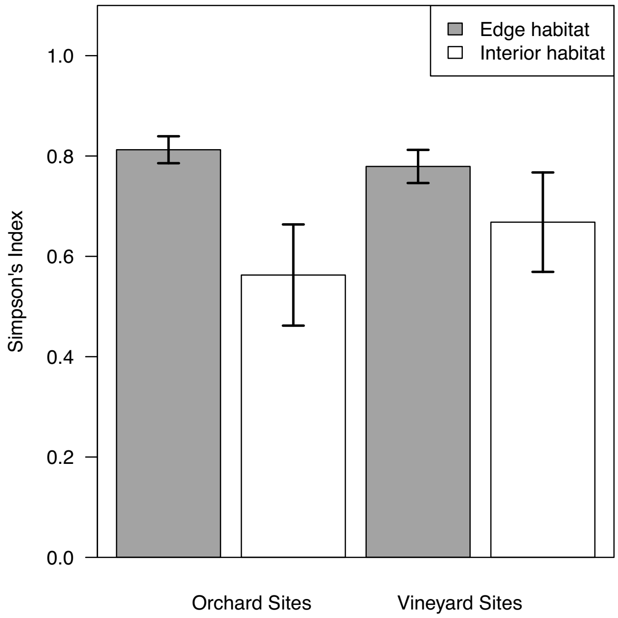

Fig. 2. Bird species diversity (Simpson's index) of sagebrush shrubsteppe in paired study plots of edge habitat and interior habitat. Paired study plots were adjacent two types of agriculture (orchard, vineyard). Errors bars represent standard error of the mean.

community composition was different between the two edge types ($A = 0.04$, $T = -4.24$, $P = 0.001$).

3.2. Community differences between habitat types

California Quail (*Callipepla californica*), a generalist species, was identified as an indicator species for edge habitat (Table 1). Within the two agricultural types of edge habitat, House Finch (*Haemorhous mexicanus*) was an indicator of orchard edge habitat, while California Quail were a weak indicator of vineyard edge habitat. Vesper Sparrow was identified as an indicator species for interior habitat. None of the other sagebrush species were strongly associated with either edge or interior habitat, although Lark Sparrows were a weak indicator of edge habitat.

3.3. Environmental drivers of the bird community

Non-metric multidimensional scaling (NMDS) of study plots suggested the bird community differed between edge and interior habitat, but that differences between orchard edge and vineyard edge habitat were slight. In the NMDS plot, edge and interior habitat were ordinated in two clusters with some overlap, with edge habitat concentrated in the upper left quadrant of the plot and interior habitat concentrated in the lower right quadrant (Fig. 3). Orchard and vineyard edge habitat were ordinated in less distinguishable groups.

Four vegetation variables and one geography variable were significantly associated with differences in the bird community between edge and interior habitat (Table 2 and Fig. 3). The bird communities in edge habitat were associated with a lower amount of bare ground cover, greater amount of exotic grass cover, and greater shrub cover. Exotic grass cover was the most strongly associated with variation in the bird community ($r^2 = 0.36$, $F = 2.16$, $P < 0.001$). The first component of the vegetation PCA, which was primarily driven by shrub cover, shrub height, and invasive grass, was also associated with differences in the bird community between edge and interior habitat ($r^2 = 0.25$, $F = 1.29$, $P = 0.003$). Elevation was also associated with variation in the bird community, with edge plots at lower elevation and interior plots at higher elevation ($r^2 = 0.29$, $F = 1.57$, $P = 0.008$). No landscape or predator variables, including synthetic variables, were strongly associated with variation in the bird community in sagebrush habitat, although the proportion of urban land cover and vineyard land cover within a 1 km radius were weakly associated with variation in the bird community ($\alpha = 0.10$; Table 2).

Table 1
Indicator values of birds in edge (*E*) and interior (*I*) sagebrush habitat types, and at orchard (*O*) and vineyard (*V*) edge habitats. Species were tested using indicator species analysis and significance was determined with permutation tests. Habitat guilds were assigned following published species descriptions and previously used guild associations. Only sagebrush bird species with > 2 detections and species with values of $P < 0.05$ are shown.

Species	Guild	Habitat indicated	Indicator value		*P*	Edge habitat indicated	Indicator value		*P*
			E	*I*			*O*	*V*	
House Finch	Generalist	Edge	0.22	0.00	0.09	Orchard	0.50	0.00	0.02
California Quail	Generalist	Edge	0.40	0.03	0.03	Vineyard	0.05	0.56	0.06
Lark Sparrow	Sagebrush	Edge	0.41	0.06	0.07	None	0.38	0.20	0.50
Vesper Sparrow	Sagebrush	Interior	0.06	0.62	0.002	None	0.16	0.11	1.00
Western Meadowlark	Sagebrush	None	0.09	0.30	0.27	None	0.05	0.28	0.45
Brewer's Sparrow	Sagebrush	None	0.08	0.17	0.64	None	0.24	0.02	0.47

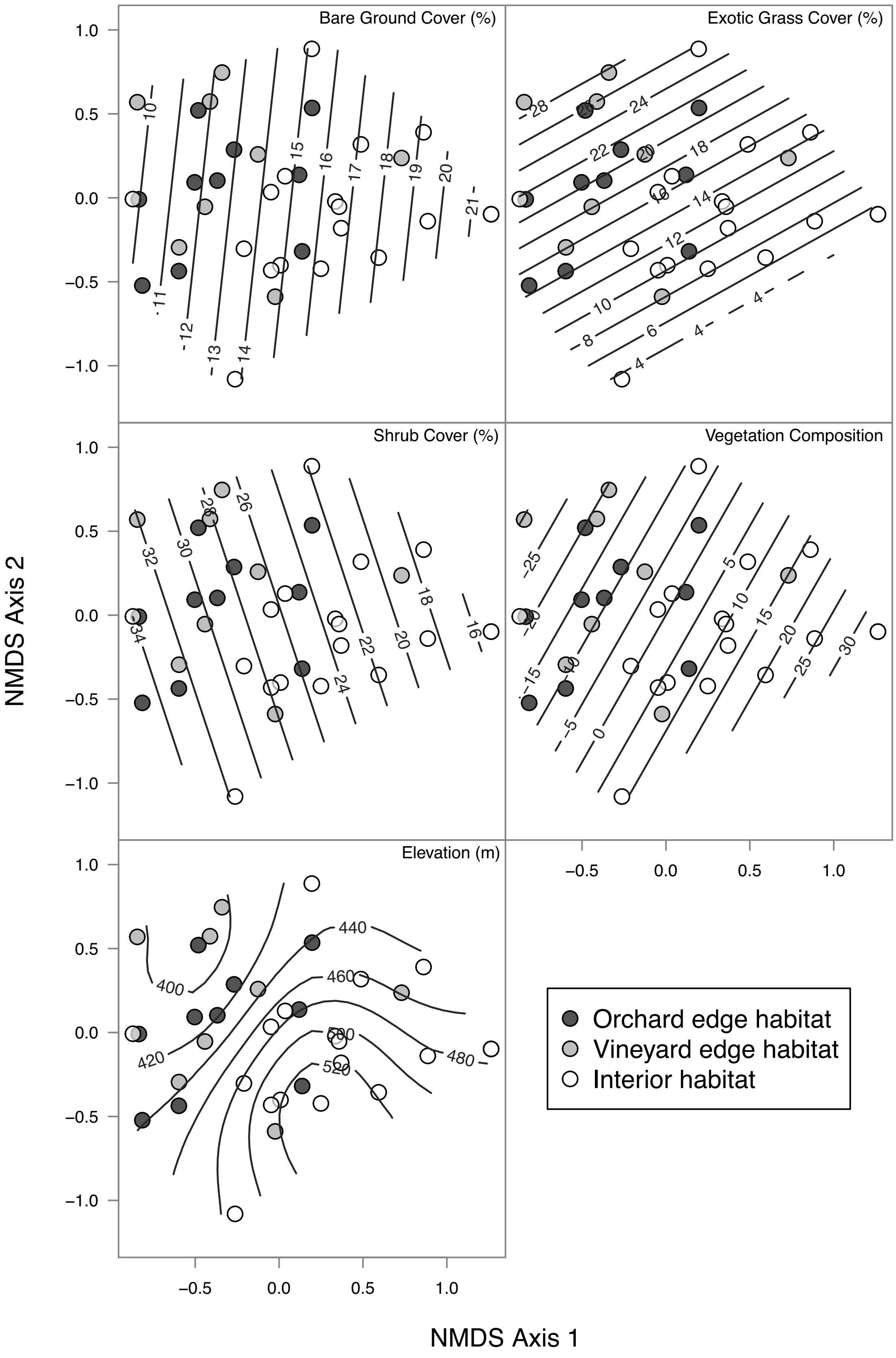

Fig. 3. Ordination of study plots from nonmetric multidimensional scaling (NMDS) of the bird community in sagebrush shrubsteppe habitat. Interior plots were located away from human disturbance and edge plots were located adjacent to orchards or vineyards. Contour lines represent environmental surfaces fitted after ordination of the bird community. Only environmental variables significantly associated with the bird community are shown.

Table 2
Relationship between a nonmetric multidimensional scaling (NMDS) of the bird community in sagebrush shrubsteppe habitat (3 axes, stress = 15.70) and four groups of environmental variables. Variables are ordered by explanatory power from highest to lowest.

Variable	Description	r^2	F	P
Predator group				
Racer	Yellow-bellied Racers (*Coluber constrictor*) per survey minute	0.07	0.27	0.20
BBMA	Max point count abundance of Black-billed Magpies (*Pica hudsonia*)	<0.01	0.00	0.72
BHCO	Max point count abundance of Brown-headed Cowbirds (*Molothrus ater*)	<0.001	0.00	0.76
Community	First component of principle components analysis of other predator group variables	<0.001	0.00	0.77
WEME	Max point count abundance of Western Meadowlarks (*Sturnella neglecta*)	<0.01	0.00	0.78
Gopher	Gopher Snakes (*Pituophis catenifer*) per survey minute	<0.01	0.00	0.93
Mice	Proportion of track tubes with Mouse (Superfamily *Muroidea*) prints	<0.01	0.00	0.94
Vegetation group				
InvGrass	Average cover of non-native grasses from 44 Daubenmire plots	0.35	2.05	<0.001
Composition	First component of principle components analysis of other vegetation group variables	0.25	1.29	0.003
Shrub	Cover of shrubs from 400 m of line intercept	0.21	1.02	0.01
Ground	Average cover of bare ground from 44 Daubenmire plots	0.16	0.76	0.02
NatGrass	Average native grass cover from 44 Daubenmire plots	0.05	0.18	0.17
Forb	Average forb cover from 44 Daubenmire plots	<0.01	0.00	0.40
Biocrust	Average cover of moss and lichens from 44 Daubenmire plots	<0.01	0.00	0.41
GrassHt	Average height of live grass at 44 points	<0.01	0.00	0.61
Rock	Average rock cover from 44 Daubenmire plots	<0.01	0.00	0.85
Landscape group				
Urban 1 km	Percent urban land cover in a 1 km radius	0.13	0.59	0.08
Shrub 1 km	Percent shrubsteppe land cover in a 1 km radius	0.08	0.35	0.09
Orchard 5 km	Percent orchard land cover in a 5 km radius	0.07	0.31	0.19
Landscape	First component of principle components analysis of other landscape group variables	0.03	0.13	0.22
Shrub 10 km	Percent shrubsteppe land cover in a 10 km radius	<0.01	0.00	0.38
Ag 5 km	Percent agricultural land cover (orchard, vineyard, pasture) in a 5 km radius	<0.01	0.00	0.51
Vine 1 km	Percent vineyard land cover in a 1 km radius	<0.01	0.00	0.90
Geography group				
Elevation	Height in meters above sea level of study plot centre	0.29	1.57	0.008
Aspect	Average plot aspect converted to a heat load scale index	<0.01	0.00	0.50
Year	Year the plot was surveyed (0 = 2011, 1 = 2012)	<0.01	0.00	0.84
Slope	Average plot slope, derived from a 10 m digital elevation model	<0.01	0.00	0.86

In agreement with the indicator species analysis, Vesper Sparrows were strongly associated with interior habitat in the NMDS plot (Fig. 4). Overall, more species were associated with edge habitat than interior habitat, as suggested by the higher diversity index calculated for edge habitat. Edge habitat was characterized by generalist and open area species, while interior habitat was characterized by sagebrush and woodland species.

4. Discussion

Fragmentation of habitat by agriculture often results in distinct biotic communities at habitat edges, and we found that fragmentation of sagebrush habitat by agriculture led to differences in the bird community at edge and interior habitats. Species diversity was higher in edge habitat than in interior habitat, but the community in edge habitat was characterized by generalist and open habitat species. Interior habitat away from the influence of agriculture had lower species diversity than edge habitat and was characterized by sagebrush and woodland species.

Bird communities in edge habitats can differ from those in interior habitats because some birds avoid predators that reduce nest survival in edge habitat (Renfrew et al., 2005). Agricultural edges have increased predator populations more often than other edge types, likely because the adjacent agriculture provides additional food sources (Chalfoun et al., 2002). In sagebrush habitat, Brewer's Sparrows have been argued to avoid habitat with high predator abundance (Welstead et al., 2003; Harrison and Green, 2010). However, we found no evidence that differences in the bird communities between interior and edge habitat was a response to known nest predators.

Unique edge communities can also occur because animals select habitat based on vegetative cues that differ between edge and interior habitat (Ries et al., 2004). In shrubsteppe and grasslands, vegetation differences in edge habitat are generally attributed to woody encroachment and invasion of weedy plants (Ribic and Sample, 2001; Krannitz, 2007; Knight et al., 2014). We found that the bird community in edge habitat was strongly associated with greater exotic grass cover. Vesper Sparrows may be an indicator species for interior habitat because *Bromus tectorum*, the dominant exotic grass species in our study area, provides less suitable nesting habitat in edge habitat than native bunchgrasses that are more abundant in interior habitat. Previous work in sagebrush shrubsteppe habitat also suggests the abundance of ground-nesting birds is negatively associated with the abundance of *B. tectorum* (Earnst and Holmes, 2012). We also found that the bird community in edge habitat was associated with greater shrub cover, which may be partially responsible for the generalist bird species associated with edge habitat, many of which are shrub-nesting species. Strong habitat preference of Brewer's Sparrows for greater shrub cover may explain why this species was not associated with interior habitat, despite previous evidence that this species avoids edge habitat (Ingelfinger and Anderson, 2004; Harrison and Green, 2010). Despite their reliance on sagebrush habitat in this study area, Lark Sparrows were found to be a weak indicator of edge habitat, which is consistent with their known preference for ecotones and disturbed areas (Martin and Parrish, 2000).

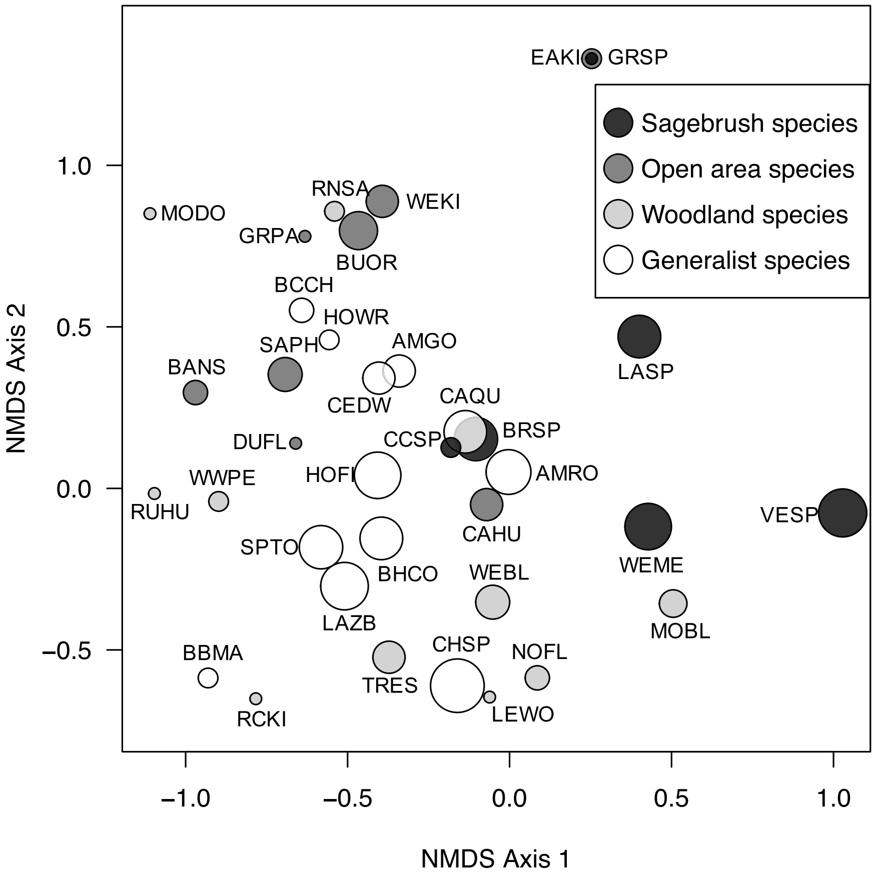

Fig. 4. Nonmetric multidimensional scaling (NMDS) of bird abundance in sagebrush shrubsteppe habitat. Point size is proportional to the number of plots each species was detected at, scaled by the natural log. Species names that correspond to the four-letter alpha codes follow convention laid out by the American Ornithologist's Union and are listed in the appendix. Habitat guilds were assigned following published species descriptions and previously used guild associations (Krannitz, 2007; Rodewald, 2015).

The presence of habitat edge itself can also explain community differences in edge and interior habitat. Access edge effects occur when individuals actively cross the edge to optimize access to resources in both adjacent habitats (Ries et al., 2004). Ecological flow edge effects occur when individuals spill-over from the adjacent habitat because the adjacent habitat is already saturated. In our study, access edge effects are supported by the presence of generalist species in edge habitat; generalist species are theorized to be more common near habitat edges because they attain resource subsidies from the adjacent matrix (Harrison and Bruna, 1999), and agricultural edges in particular are likely to provide food subsidies. Flow edge effects are also supported in our study system by the presence of generalist species in edge habitat, such as House Finches, which are associated with anthropogenic habitat (Badyaev et al., 2012).

Finally, bird communities can be influenced by the proportion of land cover types in the surrounding landscape at multiple scales, and landscape composition can influence the magnitude of edge effects (Donovan et al., 1997). For example, species that are attracted to highly human-influenced landscapes may be most abundant in edge habitat within those landscapes (Thompson et al., 2002). Conversely, the surrounding landscape can mask the presence of an edge effect if animals respond primarily to cues at landscape scales (Ewers and Didham, 2005). There is generally an overall loss of native species richness as the amount of agriculture on the landscape increases (Burel et al., 1998; Mazerolle and Villard, 1999). Previous work in the sagebrush shrubsteppe has shown sagebrush birds are found at higher densities in landscapes with a higher percentage of sagebrush cover (Knick and Rotenberry, 1995; Knick and Rotenberry, 2000), and we found evidence that the bird community is weakly influenced by the amount of sagebrush cover on the local (1 km radius) landscape. We found no evidence that the differences in the bird community between edge and interior habitat were influenced by the amount of agriculture in the surrounding landscape. The lack of strong landscape influence on bird communities in our study may be because birds are selecting habitat at smaller scales, or because the influence of the surrounding proportions of land cover may be only detectable for individual species.

Edge effects can depend on the adjacent habitat type (Ries and Sisk, 2004); however, our study is the first to test for a difference in edge effects between agricultural crop types. We found that both orchard edge and vineyard edge habitats were characterized by generalist species with high species diversity, and that there were some differences between the bird communities in orchard edge and vineyard edge habitat. We also found evidence that individual species may have different responses to the two edge types that community-scale analyses are not able to detect. We found that indicator species varied with edge crop type, and we have also previously shown that Vesper Sparrows are less abundant in orchard edge habitat than vineyard edge habitat (Knight et al., 2014). Differences in individual species responses between agricultural edge types may be due to differences in the vegetation structure and food subsidies provided by the adjacent agriculture. California Quail were found to be an indicator species for vineyard edge habitat likely because the adjacent grape vine vegetation structure is more similar to shrubland, their preferred habitat type, and the vines may provide an accessible food subsidy for this ground foraging species (Calkins et al., 2014). House Finches were found to be an indicator species for orchard edge habitat likely because the adjacent orchard trees provide abundant nest locations and food subsidies for breeding adults, which are known to cause orchard crop damage by foraging on fruit (Badyaev et al., 2012).

5. Conclusions

Our study suggests that multiple mechanisms are responsible for the observed agricultural edge effect on bird communities in sagebrush shrubsteppe habitat and supports the hypothesis that distinct communities in edge habitat are the cumulative result of varying edge sensitivities among species (Ries et al., 2004). Meta-analysis suggests that grassland habitats, such as the sagebrush shrubsteppe, may be particularly sensitive to edge effects (Fletcher et al., 2007). To date, all studies of sagebrush bird response to habitat fragmentation have found an impact on sagebrush songbirds (Knick and Rotenberry, 1995; Vander Haegen et al., 2000; Noson et al., 2006; Vander Haegen, 2007; Knight et al., 2014). In the present study, we found that edge habitats have lower abundance of Vesper Sparrows and are dominated by generalist birds, suggesting that fragmentation by agriculture reduces habitat quality for some sagebrush-associated songbirds in the Okanagan region and could lead to increased competition for resources in edge habitats. For some species, this edge effect may increase the footprint of habitat loss due to agricultural development beyond the borders of the actual agricultural field. We suggest bird conservation areas in sagebrush shrubsteppe should be placed away from agricultural areas to maintain sagebrush bird community composition and avoid potential negative impacts of generalist species such as resource competition and nest predation. Future edge effect research should differentiate between crop types in order to properly disentangle the effects of habitat fragmentation by agriculture, as our study also suggests that edge effects may vary with crop type.

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Appendix A.

Mean abundance of birds detected during ten-minute point counts in shrubsteppe habitat. Counts were conducted in study plots ($n = 36$) adjacent to agriculture (edge (E); $n = 18$) and plots away from human activity (interior (I); $n = 18$). Habitat guilds were assigned following published species descriptions and previously used guild associations (W = woodland, G = generalist, O = open area, S = sagebrush; Krannitz 2007).

Alpha code	Species	Plots	Edge	Interior	Guild
AMGO	American Goldfinch (*Spinus tristis*)	4	0.22 ± 0.55	0.11 ± 0.47	G
AMRO	American Robin (*Turdus migratorius*)	13	0.5 ± 0.71	0.5 ± 0.79	G
BANS	Bank Swallow (*Riparia riparia*)	2	0.17 + 0.51	0.00 + 0.00	O
BBMA	Black-billed Magpie (*Pica hudsonia*)	2	0.11 ± 0.32	0.00 + 0.00	G
BCCH	Black-capped Chickadee (*Poecile atricapillus*)	2	0.17 ± 0.51	0.00 + 0.00	G
BHCO	Brown-headed Cowbird (*Molothrus ater*)	9	0.67 ± 1.08	0.17 ± 0.51	G
BRSP	Brewer's Sparrow (*Spizella breweri*)	9	0.33 ± 0.77	0.56 ± 1.42	S
BUOR	Bullock's Oriole (*Icterus bullockii*)	6	0.5 ± 1.04	0.06 ± 0.24	O
CAHU	Calliope Hummingbird (*Stellula calliope*)	6	0.22 ± 0.43	0.11 ± 0.32	O
CAQU	California Quail (*Callipepla californica*)	12	0.67 ± 0.77	0.17 ± 0.38	G
CCSP	Clay-coloured Sparrow (*Spizella pallida*)	2	0.06 ± 0.24	0.06 ± 0.24	S
CEDW	Cedar Waxwing (*Bombycilia cedrorum*)	4	0.33 ± 0.69	0.00 + 0.00	G
CHSP	Chipping Sparrow (*Spizella passerina*)	25	1.22 ± 0.73	0.94 ± 1.16	G
DUFL	Dusky Flycatcher (*Epidonax oberholseri*)	1	0.06 + 0.24	0.00 + 0.00	O
EAKI	Eastern Kingbird (*Tyrannus tyrannus*)	1	0.00 + 0.00	0.11 ± 0.47	O
GRPA	Grey Partridge (*Perdix perdix*)	1	0.06 ± 0.24	0.00 + 0.00	O
GRSP	Grasshopper Sparrow (*Ammodramus savannarum*)	1	0.00 + 0.00	0.06 ± 0.24	S
HOFI	House Finch (*Carpodacus mexicanus*)	4	1.17 ± 2.98	0.00 + 0.00	G
HOWR	House Wren (*Troglodytes aedon*)	2	0.11 ± 0.32	0.00 + 0.00	G
LASP	Lark Sparrow (*Condestes grammacus*)	14	0.61 ± 0.61	0.22 ± 0.43	S
LAZB	Lazuli Bunting (*Passerina amoena*)	14	0.89 ± 0.96	0.39 ± 0.78	G
LEWO	Lewis's Woodpecker (*Melanerpes lewis*)	1	0.00 + 0.00	0.06 ± 0.24	W
MOBL	Mountain Bluebird (*Sialia currucoides*)	3	0.00 + 0.00	0.22 ± 0.55	W
MODO	Mourning Dove (*Zenaida macroura*)	1	0.06 ± 0.24	0.00 + 0.00	G
NOFL	Northern Flicker (*Colaptes auratus*)	3	0.00 + 0.00	0.17 ± 0.38	W
RNSA	Red-naped Sapsucker (*Sphyrapicus nuchalis*)	1	0.11 ± 0.47	0.00 + 0.00	W
RCKI	Ruby-crowned Kinglet (*Regulus calendula*)	1	0.06 ± 0.24	0.00 + 0.00	W
RUHU	Rufous Hummingbird (*Selasphorus rufus*)	1	0.06 ± 0.24	0.00 + 0.00	W
SAPH	Say's Phoebe (*Sayonris saya*)	7	0.28 ± 0.46	0.11 ± 0.32	O
SAVS[a]	Savannah Sparrow (*Passerculus sandwichensis*)	1	0.11 ± 0.47	0.00 + 0.00	
SPTO	Spotted Towhee (*Pipilo maculatus*)	10	0.44 ± 0.78	0.44 ± 0.86	G
TRES	Tree Swallow (*Tachycineta bicolor*)	3	0.28 ± 0.83	0.06 ± 0.24	W
VESP	Vesper Sparrow (*Pooecetes gramineus*)	19	0.28 ± 0.46	1.06 ± 0.87	S
WCSP[a]	White-crowned Sparrow (*Zonotrichia leucophrys*)	6	1.11 ± 3.6	0.83 ± 2.64	
WEBL	Western Bluebird (*Sialia mexicana*)	3	0.06 ± 0.24	0.33 ± 1.19	W
WEKI	Western Kingbird (*Tyrannus verticalis*)	6	0.28 ± 0.46	0.06 ± 0.24	O
WEME	Western Meadowlark (*Sturnella neglecta*)	13	0.39 ± 0.78	0.78 ± 1.06	S

(*Continued*)

Alpha code	Species	Plots	Edge	Interior	Guild
WEWP	Western Wood-Pewee (*Contopus sordidulus*)	2	0.11 ± 0.32	0.00+0.00	W
YRWA[a]	Yellow-rumped Warbler (*Setophaga coronata*)	5	0.17 ± 0.38	0.28 ± 0.83	

[a] Migrant species excluded from analysis

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