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## **Bird Community Response to Vegetation Cover and Composition in Riparian Habitats Dominated by Russian Olive (*Elaeagnus angustifolia*)**

### **Abstract**

Riparian systems in the western United States provide important habitat for bird communities during all times of the year. In recent decades, invasive plants, such as Russian olive (*Elaeagnus angustifolia*), have achieved broad distribution and local dominance in many western riparian areas, raising concerns over the loss of ecological function within these systems. In 2005 and 2006 we conducted avian point counts and surveyed vegetation cover at 95 points along the Snake and Columbia Rivers in southeastern Washington to investigate the effects of total woody vegetation cover and the relative proportion of Russian olive cover on breeding and wintering riparian bird communities. Our results indicated that riparian habitats dominated by Russian olive can support diverse and abundant bird communities, though cavity nesting species were noticeably sparse. Bird density and species richness were best explained by a quadratic relationship to total woody vegetation cover in both seasons, as was breeding bird community composition, with greatest density and richness in intermediate cover levels. We found no indication that the proportion of the woody vegetation comprised of Russian olive strongly influenced any of these bird community metrics. Given that Russian olive comprised 81.6% of the riparian vegetation in our study area, it is unclear from our results how Russian olive would affect bird communities in regions where native vegetation is more abundant. Regardless, complete eradication of Russian olive from riparian systems where the plant is a major component will reduce the overall habitat value for birds by eliminating significant structural complexity.

### **Introduction**

Riparian habitats occupy transitional areas between riverine and upland systems and tend to be exceptionally productive and diverse (Naiman et al. 1993, Sabo et al. 2005). The value of riparian habitats to bird communities in western North America is well established; while riparian vegetation covers less than 1% of the western landscape, it supports more breeding bird species than surrounding uplands (Knopf et al. 1988). Rich (2002) identified 78 western bird species as either riparian-obligate

or riparian-dependent during the breeding season, and Stevens et al. (1977) found riparian habitats can support migrant densities up to 10.6 times greater than those on adjacent non-riparian areas. Moreover, all riparian habitat patches can provide valuable migrant stopover habitat regardless of width or extent (Skagen et al. 1998), and some species even alter their migratory routes to maintain proximity to riparian stopover areas (Skagen et al. 2005). This makes protecting and rehabilitating riparian habitats a salient part of conservation for many western bird species.

The extensive distribution of several invasive Eurasian riparian plant species along inland rivers

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and streams has become a source of conservation concern in recent decades. Saltcedar (*Tamarix* spp.) and Russian olive (*Elaeagnus angustifolia*) are the third and fourth most frequently occurring woody riparian plants, respectively, in the western United States (Friedman et al. 2005), and the expansion of both species is being exacerbated by disruptions to natural hydrologic processes resulting from construction of dams and water withdrawals (Lesica and Miles 1999, Katz and Shafroth 2003, Stromberg et al. 2009). Avian use of saltcedar and its resulting influence on bird communities has been well documented (see review in Sogge et al. 2008), yet we have only begun to understand the ecological ramifications of Russian olive encroachment on avian habitat.

Russian olive is a small tree or large shrub that thrives in poorly-drained riparian environments. It is native to Eurasia, and was introduced into the United States in the late nineteenth or early twentieth century for multiples uses including wind breaks, soil stabilization, shade, and wildlife habitat (Christiansen 1963, U. S. Geological Survey 2000). Russian olive has a long seed germination period, numerous seed dispersal mechanisms, vegetative reproduction capability, and can thrive under conditions that are both optimal and suboptimal for native trees, making it a highly successful colonizer and competitor (Pearce and Smith 2001, Shafroth et al. 1995). Today, Russian olive has become naturalized in 37 U.S. states (Katz and Shafroth 2003), and has completely replaced native vegetation in some floodplains.

Numerous bird species have been documented using Russian olive for food or cover, including warblers (Kelly et al. 2000), owls (Roth and Powers 1979), flycatchers (Yong and Finch 1997), and hummingbirds (Smith et al. 2009). However, investigations into the impacts of Russian olive naturalization on bird communities have yielded mixed results. Knopf and Olson (1984) hypothesized that further expansion of Russian olive would create wider riparian zones, benefiting bird species that prefer tall, shrubby vegetation. Species, such as mourning dove (*Zenaida macroura*), yellow-breasted chat (*Icteria virens*), and willow flycatcher (*Empidonax traillii*), may nest at disproportionately higher rates in Russian olive with

no consequences on nest success, whereas others (e.g., black-chinned hummingbird [*Archilochus alexandri*], blue grosbeak [*Guiraca caerulea*], and many cavity-nesters) seem to avoid nesting in Russian olive altogether, perhaps indicating an actual or perceived reduction in habitat quality for these birds (Stoleson and Finch 2001). Furthermore, Russian olive stands can support high densities of nest predators, such as black-billed magpies (*Pica hudsonia*) and American crows (*Corvus brachyrhynchos*), which could lead to lower nest success rates for vulnerable species (Knight and Fitzner 1985, Gazda et al. 2002). Consequently, expansion and dominance of Russian olive may alter bird community composition with deleterious results for some species.

Recent research is challenging the widely held belief that invasive plants systematically reduce habitat quality for riparian birds, suggesting that complete eradication may be neither necessary nor beneficial (Van Riper, III et al. 2008, Stromberg et al. 2009). Bird densities tend to be positively correlated with total vegetation volume (Mills et al. 1991), and reduction or elimination of Russian olive cover could actually reduce habitat value for birds, particularly in areas where the plant dominates. Regardless, many agencies and conservation organizations have concluded that Russian olive represents a threat to native flora and fauna, and guidelines for control are commonly distributed and implemented (e.g., Parker and Williamson 2003, Parker et al. 2005, Shafroth et al. 2010), and at great cost (Shafroth et al. 2010). We investigated bird use of riparian plant communities dominated by Russian olive near the confluence of the Snake and Columbia Rivers in southeastern Washington. Our specific objectives were 1) to describe how avian communities respond to spatial variation in vegetation cover, 2) investigate how avian communities are affected by varying levels of Russian olive composition within riparian systems, and 3) to provide guidelines for habitat restoration in riparian areas where Russian olive is a dominant plant species.

## Study Area

Our study area was located near the confluence of the Snake and Columbia Rivers (46°11' N,

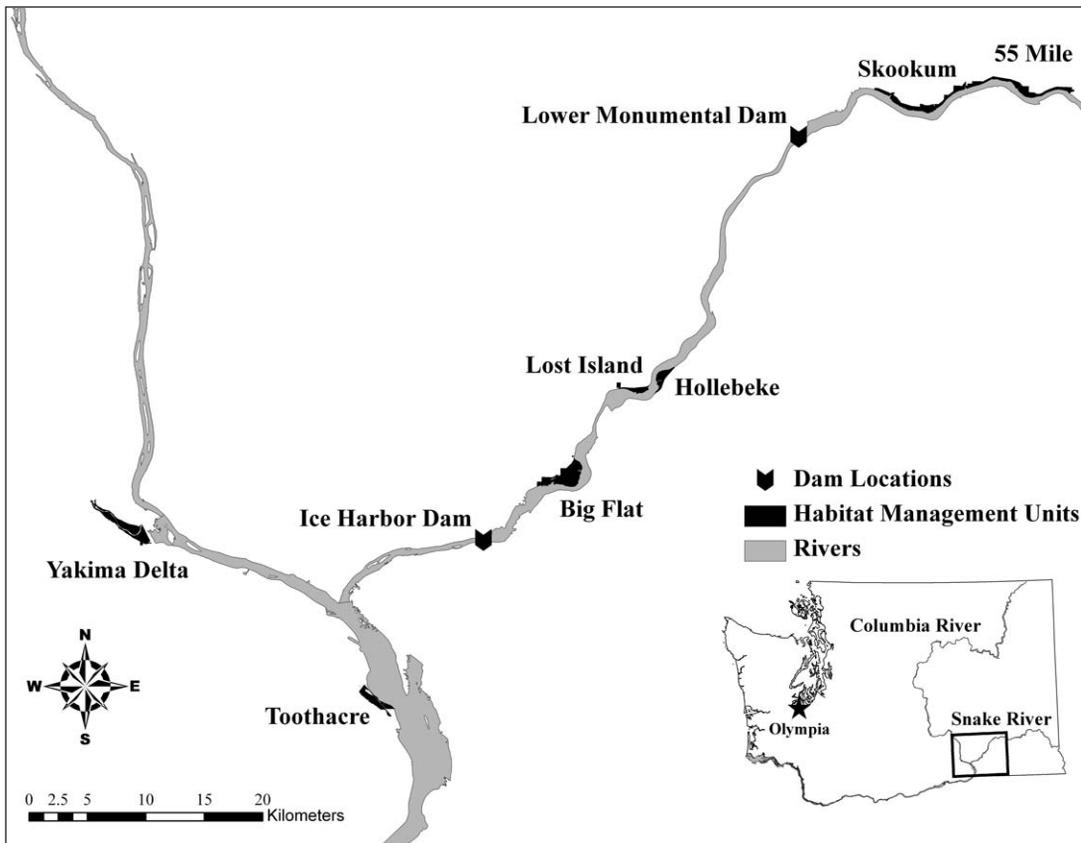


Figure 1. Locations of Habitat Management Units used to evaluate the impacts of Russian olive (*Elaeagnus angustifolia*) on avian communities during the summer and winter of 2005 and 2006.

119°2' W) in southeastern Washington (Figure 1). The climate in the area includes mild summers and cold winters, with an average annual rainfall of about 50 cm year<sup>-1</sup>. Partially as mitigation for wildlife habitat inundated by dam construction of on the lower Snake River, the U.S. Army Corps of Engineers intensively manages more than 50 parcels of land called Habitat Management Units (HMUs) along the Snake and Columbia Rivers (USFWS 2008). Seven of these HMUs were selected for our study because they contained large tracts of riparian habitat believed to be dominated by moderate to high Russian olive cover based on unpublished field surveys and observations. Five of the HMUs (Big Flat, Hollebeke, Fifty-five Mile, Lost Island and Skookum) are located along the Snake River and have irrigation systems to promote the growth of riparian plants, while the other two (Yakima Delta and Toothacre) are located on

the Columbia River and include floodplains with high water tables that allow significant Russian olive growth without irrigation. A more thorough description of riparian areas in this region can be found in Fischer et al. (2010).

## Methods

### Site Selection

In the fall of 2004, we used the most recently available (1999) geo-rectified aerial photographs to identify areas on each HMU that contained substantial riparian vegetation. We digitized woody vegetation on these aerial photographs, and superimposed them on a 100 m square grid using ArcView 3.2 (ESRI, Redlands, CA). Each grid cell was visually classified into one of four vegetation cover classes (no cover, 1-33% cover, 34-66% cover, or ≥ 67% cover) and we used a

stratified-random selection process to choose an approximately equal number of cells in each cover class on each HMU. Using the center of each grid cell as a sampling point, we selected 95 points with 10-15 points per HMU based on the amount of available riparian vegetation. Though we acknowledge that moderate habitat changes could have occurred between the time the imagery was collected (1999) and our first sampling season (2005), the information gathered from these images were merely used to ensure sampling points covered a range in vegetation cover. Vegetation measurements used for actual statistical analyses were based on contemporary, high-resolution imagery (see “Vegetation Assessment” below).

### Bird Surveys

Five different observers conducted avian point counts in the summer and winter of 2005 and 2006 following the methods outlined by Hamel et al. (1996). We visited all sampling points one time in each season, except in a few rare instances where individual points were found to be logistically inaccessible. To reduce costs and travel time, all points within a given HMU were sampled on the same day and usually by a single observer. Upon each visit to a sampling point, the observer conducted a five-minute point count, recording each individual bird seen or heard within 50 m, including those flushed due to the observer’s approach. Birds that were flying over the survey area were tallied separately, as observers could not be confident that these birds were utilizing the survey area. We did not conduct any bird surveys in heavy rain or in winds greater than 32 km hr<sup>-1</sup>, and all surveys were conducted between 0600 and 1200.

### Vegetation Assessment

We used Feature Analyst v4.0 (Visual Learning Systems, Missoula, MT, U.S.A.), an extension in ArcGIS v9.1 (ESRI), to quantify total woody vegetation cover and Russian olive cover within 50 m of each survey point. Feature Analyst is an adaptive software package that responds to the analyst’s input. Its heuristic learning algorithms utilize textural information, shape, spatial context, size, anticipated extent of coverage, and spectral information, to extract features of interest from

satellite imagery. Feature Analyst is a proven quick and accurate method of differentiating Russian olive from other plant species (Hamilton et al. 2006).

Between May and July 2005 we acquired high-resolution IKONOS satellite imagery over all HMUs. IKONOS is a commercial earth observation satellite, and was the first to collect publicly available high-resolution multispectral and panchromatic imagery at 1 m and 4 m resolution. In January of 2006, field observers verified limited areas of Russian olive and marked the locations using GPS. These locations were subsequently used to identify representative Russian olive samples on the imagery, and input into the learning routine in Feature Analyst to help distinguish Russian olive from other woody vegetation. We identified a feature type that most closely represented the typical Russian olive growth form and had the program attempt a preliminary extraction.

Using the output from this first iteration, we identified and removed polygons that were known to be incorrectly identified as Russian olive, (errors of commission), and digitized areas of missed Russian olive extent (errors of omission). This clutter removal process helps the software “learn” from any mistakes that may have occurred during the initial classification. The algorithm was implemented five times, at which point suitable results were obtained. Because of the spectral similarities of many of the vegetation types, additional manual editing had to be done to eliminate areas of confusion (i.e., other woody vegetation that have spectral reflectance properties similar to Russian olive). Finally, the residual polygons were smoothed to eliminate the jagged-edge appearance. The remaining woody vegetation cover that was not identified as Russian olive by Feature Analyst was manually digitized to quantify total woody riparian vegetation available. A more complete description of our method for quantifying riparian vegetation cover can be found in Fischer et al. (2010).

### Analyses

Prior to analyses, we removed all detections of waterbirds, raptors, swifts, swallows, nocturnal, and crepuscular birds, as well as flyovers because

our point count methods are not appropriate for these groups. Remaining species recorded in the summer were classified as riparian-dependent or not by consultation with western U.S. breeding bird data (Rich 2002). Winter birds were not assigned a riparian-dependency category because of different life history requirements and behaviors during that season. Our study was not designed in such a way that allowed us to construct species-specific detection functions, but we are confident in our detection of nearly all birds present because our sites were relatively open with scattered patches of shrubs and small trees. Moreover, previous research has indicated that detection functions for most species are constant to 50 m (Schieck 1997).

The output from the vegetation extraction revealed that there was an extremely high correlation ( $r = 0.93$ ) between total woody vegetation cover and Russian olive cover at our study points. Thus, we decided to take a two-step modeling approach for all analyses whereby we first modeled the response variables as a function of total woody vegetation cover, then modeled the residual variation as a function of the proportion of the woody vegetation comprised of Russian olive. We combined data from the two years, but we analyzed seasons separately, and all modeling was conducted with PROC GLIMMIX (SAS Institute 2002-2008) assuming a negative binomial distribution. In each step, reduced models were compared to models of interest representing competing hypotheses using Akaike's Information Criterion corrected for small sample sizes (AICc). The AICc value associated with each model is a measure of its goodness of fit and provides a means for comparison among competing models; the model with the lowest AICc value is considered the most likely and those that have values within two units ( $\Delta$  AICc) of the most likely model are considered to have substantial support (Burnham and Anderson 2002). Thus, we selected a model of interest as the most likely explanation of the data when the  $\Delta$  AICc between it and the reduced model was greater than or equal to two; if the difference was less than two (i.e., closer to 0), the reduced model was selected. For each model we also calculated an AICc weight which can be interpreted as the probability that the model is

the best explanation of the data relative to others tested (Burnham and Anderson 2002). Finally, we assessed how well each model fit the data by calculating  $\chi^2 df^{-1}$ ; this value should be very close to one if there is no evidence of overdispersion (Burnham and Anderson 2002).

For total bird density, total species richness, riparian bird density (summer only), and riparian species richness (summer only) we first compared a reduced model to models explaining the response variable as a linear and quadratic function of total woody vegetation cover. All three models included year and HMU blocking effects, and both woody cover models included a year-by-woody-cover interaction term. We output a data set of the residuals from the most parsimonious model (i.e., the model with the lowest AICc value), and deleted all points from these data sets that had no woody cover within 50 m. We then compared reduced (no Russian olive variables), linear, and quadratic Russian olive composition models of the residuals, and if there was substantial support for the reduced model, we concluded that Russian olive composition has no effect on that particular bird community metric.

To investigate how Russian olive influences bird community composition, we selected the 20 most abundant species in each season (~ 95% [summer] and 98% [winter] of detections; Table 1), and compared five bird density models. The reduced model included parameters for year, HMU, and species, and the other four models included linear or quadratic total woody vegetation cover terms with and without interactions between total woody vegetation cover and species. The interaction term between total woody vegetation cover and species served as the indicator of whether changes in woody vegetation cover cause bird community compositional changes. Again, we output the residuals from the most parsimonious model and eliminated points with no woody cover. We constructed a reduced model that included only a species term, and compared it to models explaining the residuals as a linear and quadratic function of Russian olive composition both with and without interaction terms between Russian olive composition and species. If there was not substantial support for one of the models that

TABLE 1. Total number of each land bird species recorded within 50 m of survey points in the summer and winter. Only the 20 most abundant species in each season (\*) were used for community composition analyses.

Species	Scientific Name	Riparian-Dependent		
		Breeder	Summer	Winter
Chukar	<i>Alectoris chukar</i>	No	1	0
ring-necked pheasant	<i>Phasianus colchicus</i>	No	*37	*17
California quail	<i>Callipepla californica</i>	No	*91	*91
rock pigeon	<i>Columba livia</i>	No	1	0
mourning dove	<i>Zenaida macroura</i>	No	*91	1
belted kingfisher	<i>Megasceryle alcyon</i>	Yes	1	0
downy woodpecker	<i>Picoides pubescens</i>	No	1	1
red-shafted flicker	<i>Colaptes auratus</i>	No	7	*30
western wood-pewee	<i>Contopus sordidulus</i>	No	4	0
willow flycatcher	<i>Empidonax traillii</i>	Yes	2	0
Say's phoebe	<i>Sayornis saya</i>	No	1	1
olive-sided flycatcher	<i>Contopus cooperi</i>	No	2	0
western kingbird	<i>Tyrannus verticalis</i>	No	*14	0
eastern kingbird	<i>Tyrannus tyrannus</i>	Yes	*43	0
black-billed magpie	<i>Pica hudsonia</i>	No	*93	*47
American crow	<i>Corvus brachyrhynchos</i>	No	10	1
common raven	<i>Corvus corax</i>	No	3	0
black-capped chickadee	<i>Poecile atricapillus</i>	Yes	6	*9
mountain chickadee	<i>Poecile gambeli</i>	-	0	*9
red-breasted nuthatch	<i>Sitta canadensis</i>	No	2	0
Bewick's wren	<i>Thryomanes bewickii</i>	Yes	*15	*8
house wren	<i>Troglodytes aedon</i>	Yes	4	1
marsh wren	<i>Cisothorus palustris</i>	No	2	0
ruby-crowned kinglet	<i>Regulus calendula</i>	-	0	4
hermit thrush	<i>Catharus guttatus</i>	-	0	*6
American robin	<i>Turdus migratorius</i>	No	*74	*396
varied thrush	<i>Ixoreus naevius</i>	-	0	*8
gray catbird	<i>Dumetella carolinensis</i>	Yes	4	0
European starling	<i>Sturnus vulgaris</i>	No	*18	*78
cedar waxwing	<i>Bombycilla cedrorum</i>	No	2	*47
yellow warbler	<i>Dendroica petechia</i>	Yes	8	0
yellow-rumped warbler	<i>Dendroica coronata</i>	-	0	*101
Wilson's warbler	<i>Wilsonia pusilla</i>	Yes	1	0
yellow-breasted chat	<i>Icteria virens</i>	Yes	*35	0
spotted towhee	<i>Pipilo maculatus</i>	-	0	*39
Brewer's sparrow	<i>Spizella breweri</i>	No	2	0
fox sparrow	<i>Passerella iliaca</i>	-	0	1
song sparrow	<i>Melospiza melodia</i>	Yes	*134	*300
white-crowned sparrow	<i>Zonotrichia leucophrys</i>	-	0	*472
dark-eyed junco	<i>Junco hyemalis</i>	-	0	*186
rose-breasted grosbeak	<i>Pheucticus ludovicianus</i>	No	1	0
black-headed grosbeak	<i>Pheucticus melanocephalus</i>	Yes	*86	0
lazuli bunting	<i>Passerina amoena</i>	Yes	*33	0
red-winged blackbird	<i>Agelaius phoeniceus</i>	No	*107	*17
western meadowlark	<i>Sturnella neglecta</i>	No	*13	4
Brewer's blackbird	<i>Euphagus cyanocephalus</i>	No	*15	0
brown-headed cowbird	<i>Molothrus ater</i>	No	*113	0
Bullock's oriole	<i>Icterus bullockii</i>	Yes	*84	0
house finch	<i>Carpodacus mexicanus</i>	No	*51	*22
pine siskin	<i>Spinus pinus</i>	-	0	1
American goldfinch	<i>Spinus tristis</i>	Yes	*63	*73
unknown empidonax	-	No	1	0
unknown passerine	-	-	0	2
unknown sparrow	-	-	0	26

included the interaction term, we concluded that changes in Russian olive composition do not influence bird community composition.

## Results

Over the 2 years, we conducted 181 breeding bird point counts and 172 winter bird point counts. We encountered 51 unique species that were appropriate for our analyses (Table 1). Overall species richness was far greater in the summer (41 species) than in the winter (29 species), though we encountered more individuals in the latter (1999) than in the former (1276). Fifteen of the species encountered in the summer were riparian-dependent breeders. Our point count sta-

tions ranged from 0-100% total woody vegetation cover (median = 35%) and of those sites that had woody vegetation, Russian olive composition ranged from 0-100% (median = 89%)

The quadratic total woody vegetation cover model best explained total bird density in both the summer and winter. There was almost no support for either the reduced or linear woody vegetation cover model in either season (Table 2). Smoothed lines fit to the predicted values from these models indicate that total bird density peaked at approximately 53% total woody vegetation cover in the summer (Figure 2a) and at approximately 52% cover in the winter (Figure 2b). In the summer, the residual analysis indicated the best supported

TABLE 2. A comparison of a reduced model to models explaining bird community metrics as a linear (Woody) and quadratic (Woody<sup>2</sup>) function of total woody vegetation cover in riparian habitats dominated by Russian olive. All models included the effects of year and HMU, and all models that included a woody vegetation cover term also included an interaction between year and woody vegetation cover. Calculations of all model values are described by Burnham and Anderson (2002).

Response Variable	Season	Model	AICc	ΔAICc	Likelihood	AICc Weight	χ <sup>2</sup> df <sup>-1</sup>
Total Bird Density	Summer	Woody <sup>2</sup>	1050.32	0.00	1.00	> 0.99	1.24
		Woody	1072.97	22.65	< 0.01	< 0.01	1.28
		Reduced	1081.07	30.74	< 0.01	< 0.01	1.28
	Winter	Woody <sup>2</sup>	1179.03	0.00	1.00	> 0.99	1.69
		Woody	1208.68	29.65	< 0.01	< 0.01	1.79
		Reduced	1214.30	35.27	< 0.01	< 0.01	1.44
Total Species Richness	Summer	Woody <sup>2</sup>	732.36	0.00	1.00	> 0.99	1.10
		Woody	753.20	20.84	< 0.01	< 0.01	1.13
		Reduced	768.63	36.28	< 0.01	< 0.01	1.15
	Winter	Woody <sup>2</sup>	614.98	0.00	1.00	> 0.99	1.00
		Woody	638.19	23.22	< 0.01	< 0.01	1.09
		Reduced	677.10	62.13	< 0.01	< 0.01	1.05
Riparian-Dependent Bird Density	Summer	Woody <sup>2</sup>	777.73	0.00	1.00	> 0.99	1.11
		Woody	799.95	22.21	< 0.01	< 0.01	1.04
		Reduced	809.99	32.26	< 0.01	< 0.01	1.00
Riparian-Dependent Species Richness	Summer	Woody <sup>2</sup>	531.43	0.00	1.00	> 0.99	0.83
		Woody	550.71	19.29	< 0.01	< 0.01	0.93
		Reduced	564.31	32.88	< 0.01	< 0.01	1.02

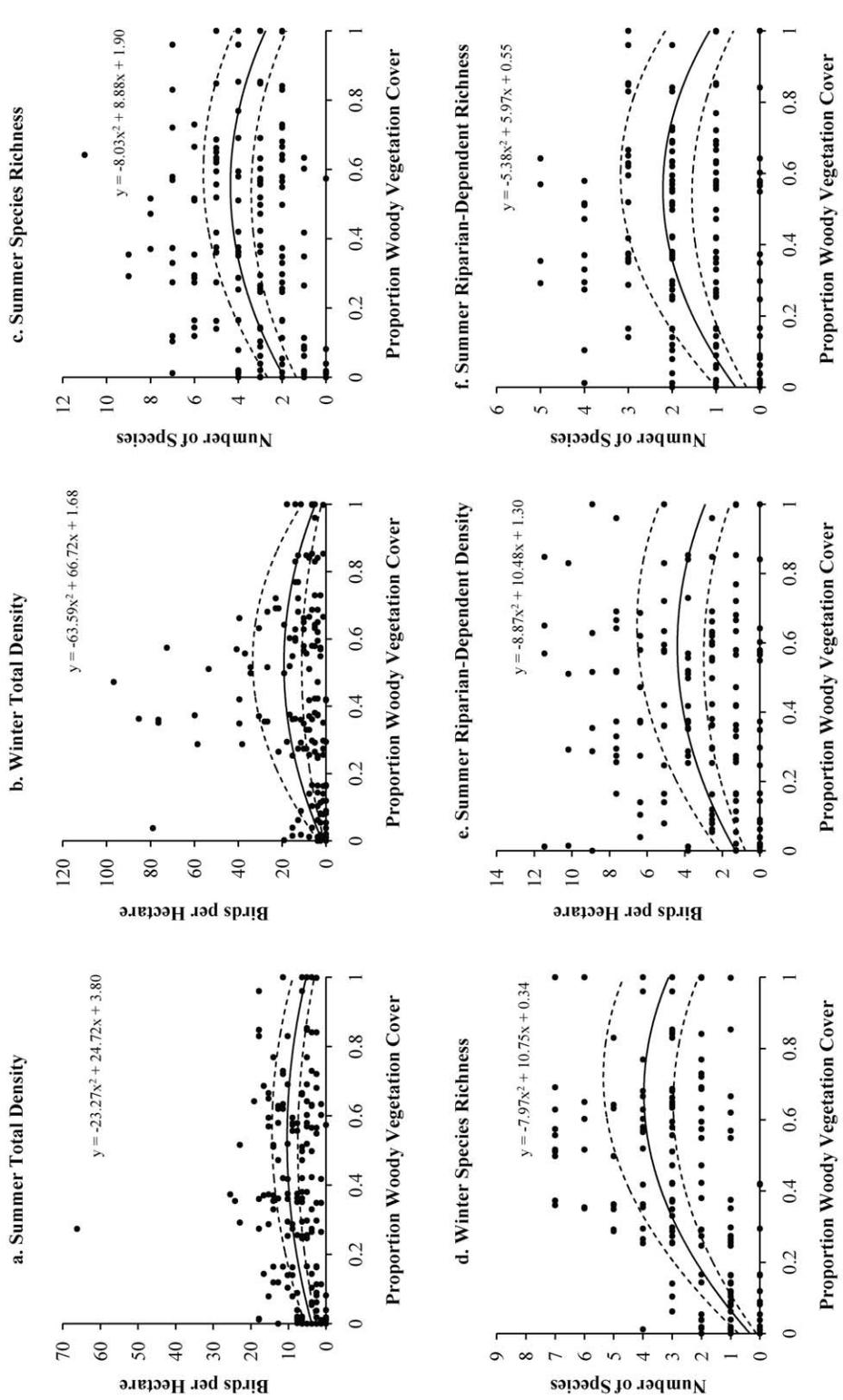


Figure 2. The relationship between bird community metrics and the proportion of a survey area covered by woody vegetation based on the best model for each response variable. Dots represent values from individual survey points, solid lines represent a smooth curve fit to the predicted values (line equation displayed) and the dashed lines represent smooth curves fit to the upper and lower 95% confidence limits for the predicted values.

TABLE 3. A comparison of a reduced model to models explaining residual variation in bird community metrics (after the effects of total woody vegetation cover had been removed) as a linear (RO) and quadratic (RO<sup>2</sup>) function of the proportion of the woody vegetation comprised of Russian olive. Winter models of total species richness beyond the quadratic could not be constructed due to an internal dependency. Calculations of all model values are described by Burnham and Anderson (2002).

Response Variable	Season	Model	AICc	ΔAICc	Likelihood	AICc Weight	χ <sup>2</sup> df <sup>-1</sup>
Total Bird Density							
	Summer	Reduced	373.80	0.00	1.00	0.57	2.01
		RO	374.98	1.19	0.55	0.31	1.98
		RO <sup>2</sup>	377.02	3.22	0.20	0.11	2.02
	Winter	RO <sup>2</sup>	391.45	0.00	1.00	0.53	1.09
		Reduced	392.30	0.85	0.65	0.35	1.28
		RO	394.49	3.04	0.22	0.12	1.29
Total Species Richness							
	Summer	Reduced	239.99	0.00	1.00	0.48	1.06
		RO	240.68	0.68	0.71	0.34	1.05
		RO <sup>2</sup>	242.03	2.04	0.36	0.17	1.03
	Winter	RO <sup>2</sup>	215.69	0.00	1.00	1.00	0.81
		Reduced	–	–	–	–	–
		RO	–	–	–	–	–
Riparian-Dependent Bird Density							
	Summer	Reduced	276.22	0.00	1.00	0.68	1.04
		RO	278.40	2.18	0.34	0.23	1.05
		RO <sup>2</sup>	280.50	4.28	0.12	0.08	1.07
Riparian-Dependent Species Richness							
	Summer	Reduced	182.43	0.00	1.00	0.59	0.65
		RO	183.71	1.28	0.53	0.31	0.64
		RO <sup>2</sup>	185.97	3.54	0.17	0.10	0.65

model did not include Russian olive composition (Table 3). In the winter, analysis of the residuals indicated the quadratic Russian olive composition model had the most support. However, there was non-trivial empirical support for the reduced model as well.

Total species richness in both the summer and winter was also best explained by a parabolic relationship with total woody vegetation cover (Table 2). Smoothed lines fit to the predicted values from these models showed that total species richness peaked at approximately 55% total woody cover in the summer (Figure 2c), whereas winter richness peaked in areas with approximately 67% cover (Figure 2d). Analysis of the residuals from

the top summer model yielded the most support for the hypothesis that Russian olive composition does not influence total species richness (Table 3). However, because PROC GLIMMIX was not able to construct the reduced or linear Russian olive composition models for total species richness residuals in the winter due to an internal dependency resulting from small sample size, we were not able to compare the competing hypotheses for this metric.

Density and richness of riparian-dependent breeding birds were similarly best explained by the quadratic total woody vegetation cover model with little support for either the reduced or linear models. Densities of these birds peaked around 59%

TABLE 4. A comparison of a reduced model to models explaining total bird density as a linear and quadratic function of total woody vegetation cover both with and without an interaction between species and woody cover variables. All models included the effects of year, HMU, and species, and all models that included a woody vegetation cover term also included an interaction between year and woody vegetation cover. Calculations of all model values are described by Burnham and Anderson (2002).

Season	Model	AICc	$\Delta$ AICc	Likelihood	AICc Weight	$\chi^2$ df <sup>-1</sup>
Summer	Woody <sup>2</sup> X Species	4715.17	0.00	1.00	> 0.99	1.19
	Woody X Species	4752.30	37.13	< 0.01	< 0.01	1.27
	Woody <sup>2</sup>	4785.62	70.46	< 0.01	< 0.01	1.51
	Woody	4806.21	91.04	< 0.01	< 0.01	1.49
	Reduced	4808.29	93.12	< 0.01	< 0.01	1.44
Winter	Woody <sup>2</sup>	4232.49	0.00	1.00	> 0.99	1.95
	Woody	4272.29	39.80	< 0.01	< 0.01	2.01
	Woody X Species	4274.19	41.70	< 0.01	< 0.01	1.89
	Reduced	4322.86	90.37	< 0.01	< 0.01	2.26
	Woody <sup>2</sup> X Species	4850.80	618.31	< 0.01	< 0.01	2.74

woody cover (Figure 2e) while riparian-dependent breeding bird richness peaked at approximately 55% cover (Figure 2f). Analysis of the residuals from the top models for both response variables indicated that it was most likely that neither was influenced by Russian olive composition (Table 3).

Our breeding bird community composition analysis indicated that density of the 20 most abundant species was best described by a model including a quadratic total woody cover explanatory variable and an interaction between species and the quadratic total woody cover variable (Table 4). This suggests that bird community composition changes along a woody cover gradient. Smoothed lines fit to the predicted values for individual species revealed that peak densities for eastern kingbirds, lazuli buntings, western kingbirds, and western meadowlarks occurred between 0 and 30% total woody vegetation cover (e.g., lazuli bunting; Figure 3a). Alternatively, we found peak densities of brown-headed cowbirds, black-billed magpies, and black-headed grosbeaks between 85 and 100% total woody vegetation cover (e.g., brown-headed cowbird; Figure 3b). Peak densities for all other species examined occurred between 40 and 70% cover (e.g., song sparrow; Figure 3c).

The results for our analysis of winter bird community composition were very different. In the

winter, there was virtually no support for either model that included an interaction between species and total woody vegetation cover, indicating that bird community composition does not change along a woody cover gradient (Table 4). Analysis of the residuals from these top woody cover models indicated that there was almost no support for the hypothesis that Russian olive composition influences bird community composition in either season (Table 5).

## Discussion

We found little evidence that the relative proportion of Russian olive in the riparian plant communities within our study area influenced density, richness, or composition of bird communities in either the summer or winter. Although apparently contradictory to results from other studies indicating that vegetation composition can be an important predictor of avian community dynamics (Rotenberry 1985, Fleishman et al. 2003), several possible explanations exist for our results. First, Russian olive dominated communities may provide structural complexity and sufficient resources such that birds do not distinguish between these habitats and those with more floristic diversity. Indeed, a wide variety of bird species with diverse life history traits have been documented utilizing

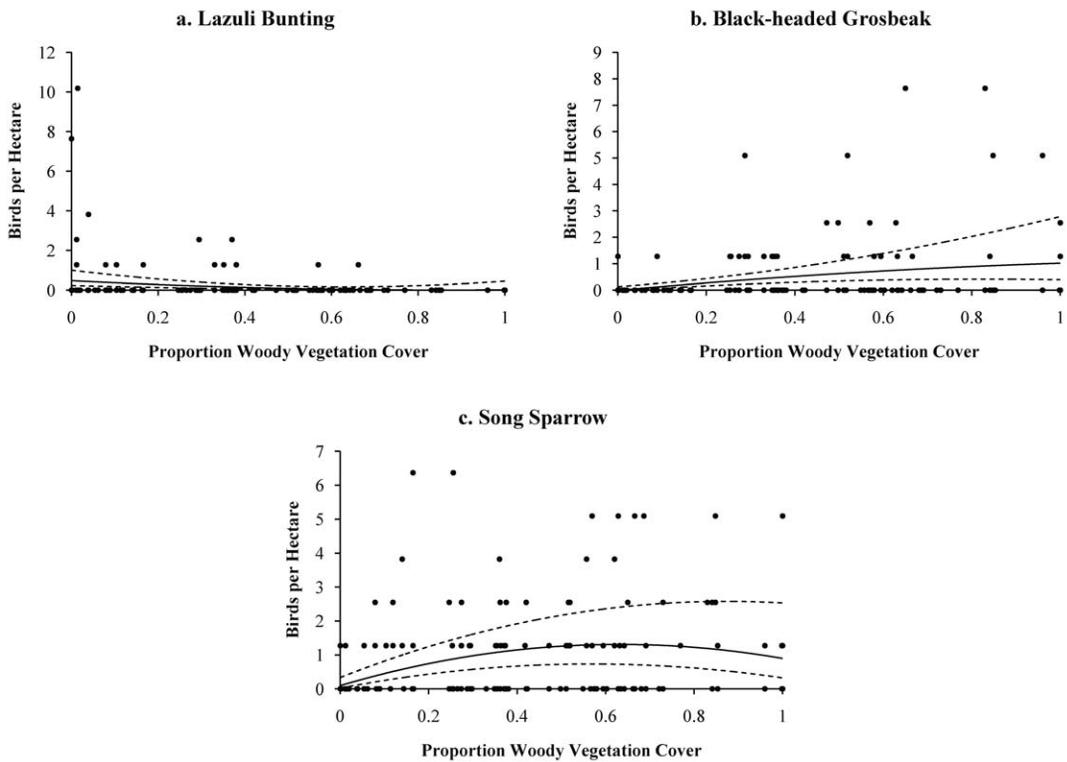


Figure 3. The relationship between breeding bird density and the proportion of a survey area dominated by woody vegetation varied for individual species in riparian areas dominated by Russian olive. Some species preferred areas with a) little woody cover, b) complete woody cover, and c) intermediate woody cover. Dots represent values from individual survey points, solid lines represent a smooth curve fit to the predicted values, and the dashed lines represent smooth curves fit to the upper and lower 95% confidence limits for the predicted values.

TABLE 5. A comparison of a reduced model to models explaining residual variation in total bird density (after the effects of total woody vegetation cover had been removed) as a linear and quadratic function of the proportion of the woody vegetation comprised of Russian olive both with and without an interaction between species and Russian olive composition. All models included a species effect. Calculations of all model values are described by Burnham and Anderson (2002).

Season	Model	AICc	$\Delta$ AICc	Likelihood	AICc Weight	$\chi^2$ df <sup>-1</sup>
Summer	Reduced	1792.23	0.00	1.00	0.57	1.44
	RO	1793.44	1.21	0.55	0.32	1.43
	RO <sup>2</sup>	1795.59	3.36	0.19	0.11	1.44
	RO X Species	1816.63	24.39	< 0.01	< 0.01	1.42
	RO <sup>2</sup> X Species	1841.66	49.43	< 0.01	< 0.01	1.39
Winter	Reduced	1545.58	0.00	1.00	0.70	1.10
	RO	1547.83	2.25	0.32	0.23	1.10
	RO <sup>2</sup>	1550.14	4.55	0.10	0.07	1.11
	RO X Species	1566.11	20.52	< 0.01	< 0.01	1.10
	RO <sup>2</sup> X Species	1601.85	56.26	< 0.01	< 0.01	1.15

Russian olive throughout their life cycles (Roth and Powers 1979, Knopf and Olson 1984, Yong and Finch 1997, Kelly et al. 2000, Smith et al. 2009). Secondly, bird species that would normally avoid Russian olive in other locations may have been forced to “settle” for less desirable habitat here given its preponderance along the rivers; except for very small tributaries and other small non-irrigated HMUs, the sites surveyed represent the only riparian habitats available along these major river drainages. Still, these explanations seem unlikely given that previous studies have shown that many bird species do avoid habitats dominated by Russian olive. For instance, Stoleson and Finch (2001) found that 18 of 29 species breeding in riparian woodlands of New Mexico, including all cavity nesters recorded, never built a nest in Russian olive. Our results were similar in that we only detected two woodpecker species during the breeding season, and the only cavity nester with greater than 10 detections was the non-native European starling.

Given that Russian olive collectively comprised approximately 81.6% of the woody vegetation on the HMUs we surveyed, and because avian habitat selection occurs at multiple spatial scales (Kristan III 2006, Meyer and Thuiller 2006), a more likely explanation is that the broad-scale dominance of Russian olive may inherently preclude regional use by some bird species. If true, we would not expect to detect any effect of Russian olive composition on avian communities at the finer scale of our investigation. Because of this possibility, we stress that our findings are only applicable to riparian habitats dominated by Russian olive, and great caution should be taken in extrapolating the results to other regions or habitat types.

We did find that total woody vegetation cover in our study area was a strong predictor of summer and winter total species density and richness, and riparian-dependent bird density and richness in the summer. Additionally, we found that summer breeding bird community composition was influenced by total woody vegetation cover, though this was not the case in the winter. One possible explanation for this dichotomy is that we encountered far fewer species in winter than during summer, and many of the migrant species with highly specialized resource requirements were not

present in that season. In addition, birds tend to change their diets in the winter, becoming more generalist in nature as overall food availability decreases. In conjunction with the vagrant nature of birds at this time of year, this likely leads to many species using many different habitat types to meet life history needs.

Interestingly, we found that overall density and richness of bird communities peaked between 50% and 70% total woody vegetation cover in both seasons. This indicates a threshold in Russian olive dominated riparian regions, above which increasing woody vegetation cover actually reduces the number of birds and the diversity of species utilizing the habitat. Points with moderate woody vegetation cover (similar to the patchiness and heterogeneity of cover classes on our study sites produced by the distribution of irrigation heads) likely provide resources for a variety of species, including those that prefer dense vegetation, edge habitat, and open areas. These results contrast with those from other studies conducted in regions with much more diverse riparian plant communities that have documented linear relationships between total vegetation volume and both bird density (Mills et al. 1991) and richness (Fleishman et al. 2003). This information suggests that bird density and richness vary as a function of an interaction between vegetation cover and composition, and that extensive coverage of riparian vegetation may actually result in low habitat value in areas severely impacted by biological invasions. However, more research into the impacts of Russian olive on bird communities in riparian systems with greater floristic diversity is necessary to fully understand this relationship.

Nonetheless, our results show that total vegetation cover exhibits a much greater influence on bird communities than vegetation composition in riparian habitats profoundly impacted by Russian olive. Consequently, complete eradication of Russian olive in such systems could actually reduce their avian habitat value (Fleishman et al. 2003). Yet we found that riparian bird communities tend to suffer as vegetation cover exceeds 60-70% as well. Thus, initial restoration efforts in such areas should focus on maintaining 50-70% woody vegetation cover to maximize avian density and richness. Van Riper III et al. (2008) recommended

restoring low levels of native vegetation (20-40%) within habitats dominated by saltcedar to positively influence avian abundance and diversity. It is unclear from our results whether such restoration efforts would similarly improve avian habitat in areas dominated by Russian olive. Indeed, restoration of native plants (e.g., willows [*Salix* spp.] and black cottonwood [*Populus trichocarpa*]) may not be possible in some places due to large scale hydrologic modifications, but this warrants further investigation.

Finally, it is important to note that habitat use is not necessarily indicative of habitat quality. While resource selection functions may be an indicator of habitat quality, the results can often be misleading, as they do not take into account survival and reproductive characteristics of a species or community (Van Horne 1983). Our study did not quantify food availability or predator concentrations and we did not measure any variables indicative of survival or breeding success. Thus, although we encountered abundant

and diverse bird communities in our study area, future research should compare such measures between riparian habitats dominated by Russian olive and other plant species to more fully understand the ecological value of these disturbed systems for birds.

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