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Use of Data on Avian Demographics and Site Persistence during Overwintering to Assess Quality of Restored Riparian Habitat

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Abstract: *Monitoring responses by birds to restoration of riparian vegetation is relatively cost-effective, but in most assessments species-specific abundances, not demography, are monitored. Data on birds collected during the nonbreeding season are particularly lacking. We captured birds in mist nets and resighted banded birds to estimate species richness and diversity, abundance, demographic indexes, and site-level persistence of permanent-resident and overwintering migrants in remnant and restored riparian sites in California. Species richness in riparian remnants was significantly higher than in restored sites because abundances of uncommon permanent residents were greater in remnants. Species richness of overwintering migrants did not differ between remnants and restored sites. Responses among overwintering migrants (but not permanent residents) to remnant and restored riparian sites differed. Capture rates were higher in remnant or restored riparian sites for 7 of 10 overwintering migratory species. For Lincoln's Sparrows (*Melospiza lincolnii*) and White-crowned Sparrows (*Zonotrichia leucophrys*) proportions of older birds were significantly higher in remnants, even though capture rates of these species were higher in restored sites. Overwinter persistence of 4 migrant species was significantly higher in remnant than in restored sites. A higher proportion of Hermit Thrushes (*Catharus guttatus*, 56.3%), older Fox Sparrows (*Passerella iliaca*, 57.1%), Lincoln's Sparrows (59.7%), and White-crowned Sparrows (67.8%) persisted in remnants than restored sites. Our results suggest restored riparian sites provide habitat for a wide variety of species in comparable abundances and diversity as occurs in remnant riparian sites. Our demographic and persistence data showed that remnants supported some species and age classes to a greater extent than restored sites.*

Keywords: Fox Sparrow, habitat restoration, Lincoln's Sparrow, *Melospiza lincolnii*, *Passerella iliaca*, White-crowned Sparrow, winter ecology, *Zonotrichia leucophrys*

Utilización de Datos Demográficos de Aves y de Persistencia de Sitio Durante el Invierno para Evaluar la Calidad de Hábitat Ribereño Restaurado

Resumen: *El monitoreo de la respuesta de aves a la restauración de vegetación ribereña es relativamente rentable, pero en la mayoría de las evaluaciones se monitorean las abundancias de especies, no la demografía. Se carece particularmente de datos sobre aves recolectados durante la época no reproductiva. Capturamos aves con redes de niebla y reavistamos aves anilladas para estimar la riqueza y diversidad de especies, abundancia, índices demográficos y persistencia a nivel de sitio de especies residentes permanentes y migratorias invernantes en sitios remanentes y restaurados en California. La riqueza de especies en remanente ribereños fue significativamente mayor en sitios restaurados porque la abundancia de residentes permanentes no comunes fue mayor en los remanentes. La riqueza de especies migratorias invernantes no difirió entre sitios remanentes y restaurados. La respuesta de las migratorias invernantes (pero no residentes permanentes) a los sitios remanentes y restaurados fue diferente. Las tasas de captura fueron mayores en sitios remanentes o*

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restaurados para 7 de 10 especies migratorias invernantes. La proporción de aves viejas de Melospiza lincolnii *y* Zonotrichia leucophrys *fue significativamente mayor en remanentes, aun cuando las tasas de captura de estas especies fueron mayores en sitios restaurados. La persistencia durante el invierno de 4 especies migratorias fue significativamente mayor en sitios remanente que en restaurados. Una mayor proporción de* Catharus guttatus *(56.3%),* Passerella iliaca *viejos (57.1%),* Melospiza lincolnii *(59.7%) y* Zonotrichia leucophrys *(67.8%) persistió en sitios remanentes que en restaurados. Nuestros resultados sugieren que los sitios ribereños restaurados proporcionan hábitat para una amplia variedad de especies en abundancias y diversidad comparables a las que ocurren en sitios ribereños remanentes. Nuestros datos demográficos y de persistencia muestran que los remanentes presentaron algunas especies y clases de edad en mayor extensión que los sitios restaurados.*

Palabras Clave: ecología invernal, *Melospiza lincolnii*, *Passerella iliaca*, restauración de hábitat, *Zonotrichia leucophrys*

Introduction

Due to heavy use and pollution of riparian areas and their disproportionately large contribution to ecosystem function, conservation of riparian zones is a high priority (Rich et al. 2004; RHJV 2004). Riparian ecosystems often have a higher diversity of species and are more productive than surrounding uplands, and they support higher densities of riparian obligates and other bird species than adjoining areas during breeding and migration (Knopf et al. 1988; Golet et al. 2008). The extent of anthropogenic changes to riparian ecosystems is increasing (Knopf et al. 1988; Poff et al. 1997), and the effects of the changes are exacerbated because riparian ecosystems are catchments for the effects of land uses in the watershed (Dudgeon et al. 2006).

Public agencies and private organizations have invested millions of dollars in restoring riparian systems (Faber 2003; Golet et al. 2008). Key elements of most successful restoration programs are evaluation and adaptive management (Block et al. 2001; Golet et al. 2008). Monitoring the response of birds is a relatively easy, cost-effective way to assess biological effects of changes in natural systems, but the response variables monitored most often are species richness or abundance (Block et al. 2001; Ruiz-Jaen & Aide 2005). For example, Gardali et al. (2006) evaluated a riparian-vegetation restoration by comparing abundance of breeding songbirds in restored and remnant riparian forests. Abundance of songbirds occupying riparian areas has also been studied during autumn migration. Humple and Geupel (2002) found that numerous species use riparian remnants for feeding and resting during migration, but they did not investigate use of restored sites. Few researchers have evaluated riparian restoration by monitoring reproductive success, survival, or other demographic variables (but see Gardali & Nur 2006; Golet et al. 2008), and we know of no studies in which a restoration was evaluated on the basis of winter populations of birds.

Site-specific studies that evaluate responses of birds to restoration of vegetation are incomplete if they do not include data from the nonbreeding season because a variety of species are present only in winter. In addition, reproductive success may be affected if habitat quality during the nonbreeding season affects a bird's body condition or timing of migration (Marra et al. 1998; Faaborg et al. 2010). Abundance data from the nonbreeding season alone may be a misleading indicator of population size and habitat quality because many, primarily tropical, wintering migrants segregate by sex, age class, and latitude (e.g., Ketterson & Nolan 1976; Holmes et al. 1989; Latta & Faaborg 2002). Moreover, abundance cannot generally be equated with survival, so data on persistence of overwintering migrants at given sites may be needed to assess habitat quality (Faaborg et al. 2010).

We estimated species richness and diversity in the nonbreeding season and abundance of permanent resident and overwintering migratory birds in remnant and restored riparian areas in California. We compared the species richness and diversity of birds in these 2 areas in winter and then contrasted these results with comparisons of demographic and site-persistence data to more fully assess associations of remnant and restored riparian sites with overwintering birds.

Methods

Study Sites

Our 8 study sites were in the Sacramento and San Joaquin river valleys of California. We selected sites on the basis of availability and similarity of vegetation. In Sacramento Valley, we established 4 plots in October 2004: 2 in remnant riparian areas (Kaiser, 45.2 ha; Sul Norte, 25.0 ha) and 2 in restored riparian areas (Stony Creek, 65.6 ha; Kopta Slough, 86.0 ha). Mean distance between centers of sites was 27.3 km (range 3.0–51.8 km). Sacramento Valley forest remnants were primarily a mix of Fremont's cottonwood (*Populus fremontii*) and willow (*Salix* spp.). There were a few valley oak (*Quercus lobata*), and the understory was mugwort (*Artemesia douglasiana*) and grasses. At restored sites, periodic flooding was reestablished and the native shrubs and trees mentioned earlier were planted in 1989–1992 (Kopta Slough) and 1991–1992 (Stony Creek).

In San Joaquin Valley, we established 4 plots in October 2003: 3 in remnant riparian areas (Willow unit, 6.0 ha; Lost Lake Island, 6.7 ha; Lara Field, 6.6 ha), and 1 in a restored riparian area (Hagemann's Field, 8.1 ha). Mean distance between centers of sites was 99.4 km (range 1.2–148.0 km). Remnants had Fremont's cottonwood, valley oak, and California sycamore (*Platanus racemosa*). The shrub vegetation layer was of willows, white alder (*Alnus rhombifolia*), California blackberry (*Rubus ursinus*), and mugwort. Remnants also had dense areas of sandbar willow (*Salix exigua*), Himalayan blackberry (*Rubus armeniacus*), and non-native grasses. Hagemann's Field was restored in 2002–2003. Cuttings of Fremont cottonwood, valley oak, and arroyo willow (*Salix lasiolepsis*) were planted in a mosaic on the basis of edaphic and hydrologic conditions required by each species. Shrubs included California rose (*Rosa californica*), California blackberry, and coyote brush (*Baccharis pilularis*), and the understory contained mugwort, gumplant (*Grindelia squarrosa*), and creeping wild rye (*Leymus triticoides*).

Sampling of Birds

We followed established protocols to determine mist net locations (DeSante et al. 2008). We attempted to place nets as uniformly and systematically as possible within each plot, but because plots were linear or irregularly shaped, sometimes nets were located opportunistically. We captured birds in mist nets in early winter (November), midwinter (December–January), and late winter (January–February) 2003–2008 (Supporting Information). Due to financial constraints we did not sample all sites in all years, but we sampled all sites a minimum of 3 years. Within each river valley, we generally sampled sites on consecutive days. We based order of visits on logistical considerations (Supporting Information). We deployed 16 mist nets (12 × 2.5 m, 30-mm mesh) at each site for 3 consecutive days: 3 h the first afternoon, all day the next day, and 3 h in the morning of the last day. The exception to this procedure was in winter 2003–2004, when we deployed nets for 2 full days. We began sampling approximately 15 min after sunrise and stopped sampling at 1600. We did not sample when excessive cold, high winds, or rain might have harmed birds. Bird abundance was expressed as birds captured/100 mist net hours (mnh), where one mist net opened for 1 h equaled 1 mnh.

We identified to species, sexed, and aged all captured birds. We based age on skull pneumatization, plumage characteristics, or patterns of molt whenever possible (Pyle 1997). We aged birds as either juvenile (hatch-year or second-year birds in their first winter) or adult (after hatch-year or after second-year birds in their second or any subsequent winter). We banded all birds with a numbered U.S. Geological Survey band. We banded individuals of selected species with a combination of 3 color bands such that each individual was uniquely identified. We fitted the 3 bands only on the most abundant species and those that were large enough to carry the bands without being affected. We fitted with color-coded bands Bewick's Wren (*Thryomanes bewickii*), Spotted Towhee (*Pipilo maculatus*), and Song Sparrow (*Melospiza melodia*) (all permanent residents) and Hermit Thrush (*Catharus guttatus*), Fox Sparrow (*Passerella iliaca*), Lincoln's Sparrow (*Melospiza lincolnii*), White-crowned Sparrow (*Zonotrichia leucophrys*), and Golden-crowned Sparrow (*Zonotrichia atricapilla*) (all overwintering birds).

Use of mist nets bias data in several ways: in some habitats nets do not sample birds that occur in all vegetation strata; very small or large birds may be ineffectively sampled; and abundance of species traveling widely may be overestimated (Remsen & Good 1996). We minimized these biases by deploying nets in sites with similar vegetation structure, limiting analyses of capture frequencies to within-species comparisons, and assuming capture probabilities for a species were equal among sites.

Resighting

We resighted birds November through February 2004–2005 and 2006–2007 in the Sacramento River valley and November–February 2004–2005 in the San Joaquin River valley (Supporting Information). We based estimates of site-level persistence on these years only. Following banding, we searched each plot (mean [SE] = 55.3 h [3.0]) for color-banded individuals. Search areas extended approximately 100 m beyond plot boundaries. Although a few color-banded individuals may have remained unidentified, consistent resighting effort among sites and years ensured comparability of results between similar sites. Overwinter site persistence was the proportion of birds detected (by resighting or recapture) at any time >24 h after initial capture (Holmes et al. 1989; Latta & Faaborg 2001, 2002). We treated birds banded in a previous year as birds banded during the first round of the current year.

Vegetation Structure

At each site we used the relevé method (Ralph et al. 1993) to characterize vegetation structure in a 50-m radius surrounding 3–16 (mean [SE] = 5.00 [1.76]) randomly located points. We based the number of samples on site size. We estimated the percent cover of each vegetation layer (herb <0.5 m tall; shrub 0.5–5.0 m tall; tree >5.0 m tall). Within each layer we recorded plant species composition and each species' relative cover as a percentage of total cover. We measured the maximum height for tree and shrub layers, diameter at breast height (dbh) of trees, and the height of the lowest branches of the tree layer (i.e., minimum tree height) and calculated canopy height by subtracting mean minimum tree height from mean maximum tree height. We used the means (SE) from multiple points within a site in analyses. We examined vegetation structure once at each site in April–July 2001 (Kaiser, Sul Norte), 2003 (Kopta Slough), 2004 (Stony Creek), or 2005 (all other sites). We assumed the values of vegetation measurements did not change substantially over the project period.

Statistical Analyses

We used SAS (SAS 2008) and online worksheets (McDonald 2009) for statistical analyses. We considered a probability of type I error ≤ 0.05 significant. We pooled data within a site across years to increase sample sizes. We did not analyze variation within the 5 remnant or 3 restored sites; rather, we pooled data within remnant sites and within restored sites. We tested site-specific data on capture rates for normality. When we could not transform data to achieve normality, we used a nonparametric Mann–Whitney U test to compare species richness, capture rates, and diversity among all Sacramento River valley sites, among all San Joaquin River valley sites, and among all bird species, all permanent residents, and all overwintering migrants in remnant and restored areas.

We used rarefaction to create species accumulation curves and to compare species richness among all Sacramento River valley sites, among all San Joaquin River valley sites, and among all bird species, all permanent residents, and all overwintering migrants in remnant and restored areas. We calculated the slope of each species accumulation curve for the last 100 individuals captured (slope close to zero indicates curve is approaching its asymptote and that few additional species would be added with continued sampling). Rarefaction allows assemblages with unequal sampling effort in terms of area or number of individuals sampled to be compared. The rarefaction calculates the expected species richness if sampling effort was constant among sites, but does not provide an estimate of asymptotic richness. Instead, for each accumulation curve, we calculated a Chao 1 nonparametric estimator of total species richness and its variance (Chao 1984). Chao 1 estimates do not require equal sample sizes, but with larger samples a smaller CI is achieved (Chao 2010). We evaluated the statistical significance of differences in species richness by comparing Chao 1 estimates of species richness and their 95% CIs.

We compared species diversity between Sacramento River valley sites and San Joaquin River valley sites and between remnant and restored sites, by calculating the Shannon index for each of the 8 sites. Because the theoretical basis for the diversity index is entropy and comparisons of the index among sites are misleading, we followed Jost (2006) and converted diversity to the effective number of species. Effective number of species represents the number of equally abundant species and its mathematical properties allow comparisons among groups. We used the effective number of species to determine the magnitude of the difference between remnants and restored areas in effective numbers of all birds, permanent residents, and overwintering migrants.

We calculated evenness indexes for all remnant and restored areas for all birds, permanent residents, and overwintering migrants (Magurran 1988). Evenness is a measure of the distribution of individuals among taxa. Evenness is 1.0 when the number of individuals of each species is the same. We used similarity measures to determine whether bird communities differed through species replacement (Magurran 1988), and we used Jaccard's index to compare the similarity of communities on the basis of presence or absence of species.

We used chi-square tests of independence to examine differences in captures between remnant and restored areas for all species with >20 captures. We based comparisons on actual numbers (not rates) of captures and expected values on the number of hours nets were deployed (Blake & Rougès 1997). Because the number of planned comparisons was large, we used the Dunn–Šidák method to decrease α and reduce the probability of a type I error. Following Holmes et al. (1989) and Latta and Faaborg (2001, 2002), we used a chi-square test to examine differences in the proportion of adults and proportion of site-persistent birds with >20 captures between remnant and restored areas. We only conducted tests involving age classes when we aged $>55\%$ of captured birds and we concluded a priori that methods of determining age were unlikely to leave ages of a given age class undetermined.

For vegetation data we determined a mean and SE for each structural variable at each site. We then calculated a mean and SE for the 5 remnant and 3 restored plots. We determined significance of differences in structural characteristics by comparing 95% CIs.

Results

Abundance

During the nonbreeding season, we captured 4071 individuals of 54 species in 10,341 mnh at remnant and restored riparian sites (Supporting Information). More species (32) were permanent residents, but more individuals (2922) were winter residents. Species accumulation curves for each site appeared to reach or approach their asymptote (slopes ≤ 0.01) (Figs. 1a & 1b). Within each valley observed species richness ($U = 0.19$, df $= 1$, $p = 0.66$), capture rates ($U = 0.33$, df $= 1$, $p = 0.56$), and diversity ($U = 0.33$, df $= 1$, $p = 0.56$) did not differ among

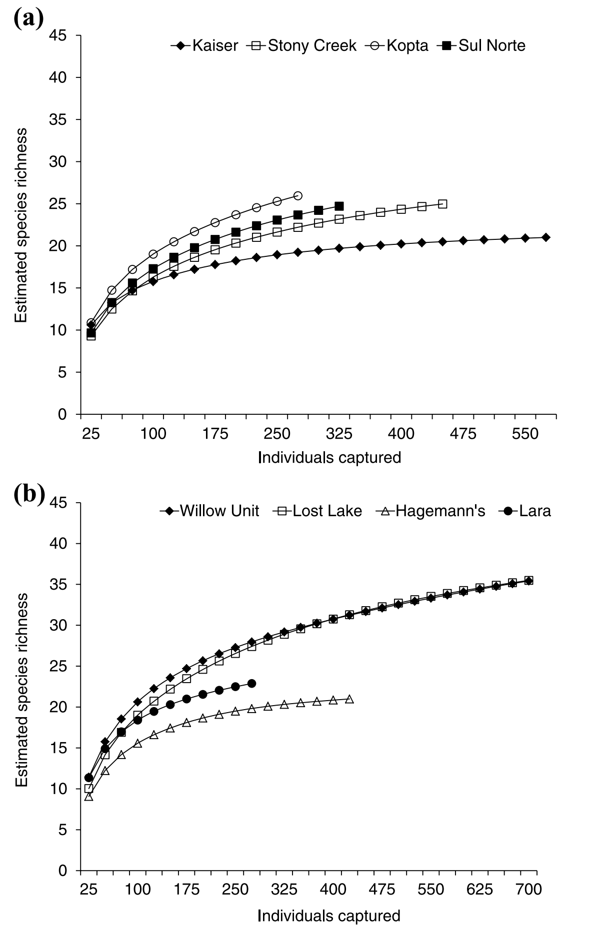

Figure 1. Species accumulation curves of birds captured at (a) 4 sites in the Sacramento River valley, California (U.S.A.), (Kaiser and Sul Norte, riparian remnant; Stony Creek and Kopta Slough, restored riparian), and (b) 4 sites in the San Joaquin River valley, California (Willow Unit, Lost Lake, and Lara Field, riparian remnants; Hagemann's Field, restored riparian).

sites. Thus, in further analyses, we pooled sites from the 2 valleys.

When all species from the Sacramento and San Joaquin valleys were included in the analysis, accumulation curves appeared to approach their asymptotes at remnant and restored sites (Fig. 2a). The slope of the species accumulation curves for the last 100 captures was <0.01 for both remnant and restored sites (Table 1). With all species combined, observed species richness ($U = 0.20$, df = 1, $p = 0.65$), capture rates ($U = 0.02$, df = 1, $p = 0.88$), and diversity ($U = 1.80$, df = 1, $p = 0.18$) (Table 1) did not differ significantly between remnant and restored sites. Evenness was similar between remnant (0.67) and restored sites (0.71). The 5 most abundant species in remnants were Ruby-crowned Kinglet (*Regulus calendula*), White-crowned Sparrow, Lincoln's Sparrow, Golden-crowned Sparrow, and Bushtit (*Psaltriparus minimus*), and these species accounted for 64% of captures (Table 2). In restored sites, the same species accounted for 71% of captures. All of these species except Bushtit were overwintering migrants.

Results from the Chao 1 estimator of species richness (±95% CI) indicated a significant difference in species richness between remnant and restored sites (Table 1). Estimated species richness of birds in the remnant sites (75.5 ± 23.8) was significantly greater than in restored sites (33.1 ± 0.5). The effective number of species showed there was a 16.5% change in the number of species (Table 1) between remnant and restored sites. Values of similarity indexes were moderately low; 61.5% of species occurred in both the remnants and restored sites.

These differences in bird communities between remnant and restored sites were associated with differences among permanent residents. As with all species combined, accumulation curves for permanent residents approached their asymptotes at remnant and restored sites (Fig. 2b) (slopes for last 100 captures were ≤0.01). Observed species richness ($U = 1.10$, df = 1, $p = 0.29$), capture rates ($U = 1.81$, df = 1, $p = 0.30$), and diversity ($U = 1.09$, df = 1, $p = 0.30$) (Table 1) of permanent residents did not differ significantly between remnant and restored sites. Evenness of permanent resident species was similar between remnant (0.69) and restored sites (0.73). The 5 most abundant permanent resident species in remnants were Bushtit, Song Sparrow, Spotted Towhee, Bewick's Wren, and Lesser Goldfinch (*Carduelis psaltria*), and they accounted for 76% of all captures (Table 2). The same 5 species accounted for 81% of captures in restored sites. However, rarefaction curves showed species richness of permanent residents in restored sites was lower than in remnants (Fig. 2b), and results from the Chao 1 estimator of species richness indicated a significant difference in species richness between remnant and restored sites (Table 1). Estimated species richness of birds in remnants (45.5 ± 18.5) was significantly greater than in restored sites (18.0 ± 0.0). The percent change in number of species was 23.0% (Table 1), and 56% of species occurred in both remnant and restored sites.

In contrast, abundances of overwintering migrants in remnant and restored sites did not differ significantly. Species accumulation curves for both remnant and restored sites approached an asymptote (Fig. 2c) (slopes for the last 100 captures were <0.01). Observed species richness ($U = 0.02$, df = 1, $p = 0.88$), capture rates ($U = 0.02$, df = 1, $p = 0.88$), and diversity ($U = 1.80$, df = 1, $p = 0.18$; Table 1) of overwintering migrants did not differ significantly between remnant and restored sites. Evenness of overwintering migrants was similar between remnant (0.65) and restored sites (0.68). The 5 most abundant overwintering migrant species in remnants (Ruby-crowned Kinglet, White-crowned Sparrow, Lincoln's

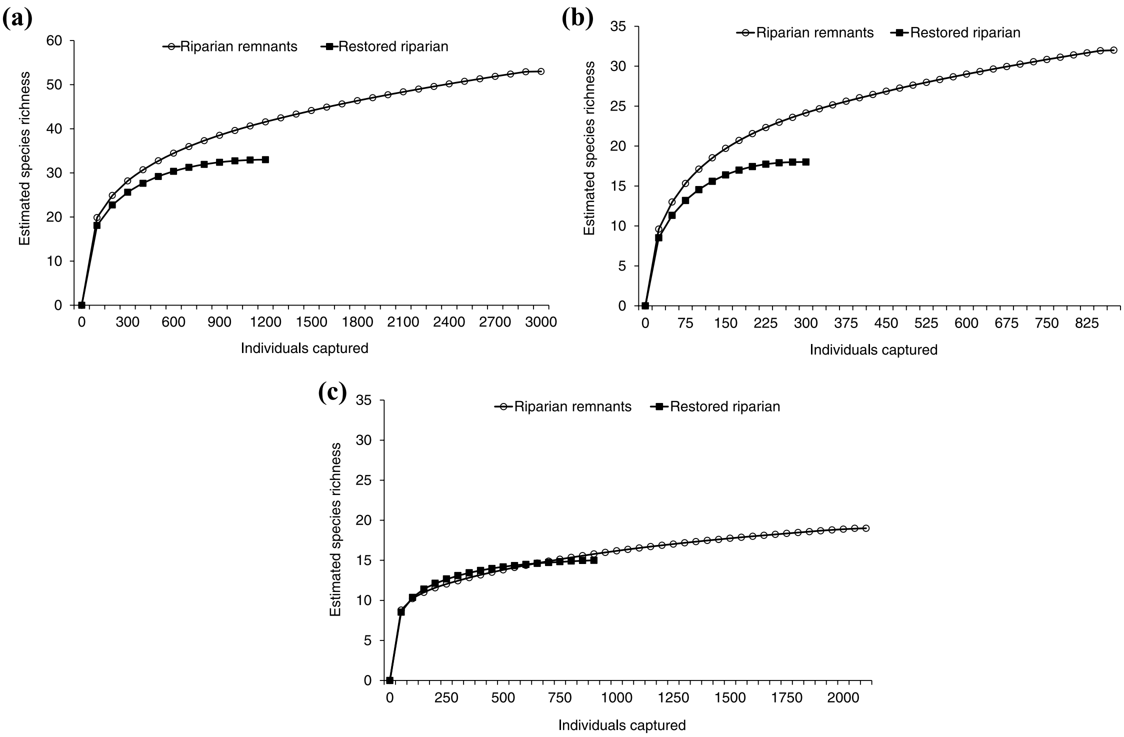

Figure 2. Species accumulation curves for (a) all bird species, (b) all permanent-resident species, and (c) all overwintering migrant species in riparian remnant areas and restored riparian areas in the Sacramento River and San Joaquin River valleys of California (U.S.A.).

Sparrow, Golden-crowned Sparrow, Hermit Thrush) accounted for 86% of captures, whereas in restored sites the 5 most abundant species (Ruby-crowned Kinglet, White-crowned Sparrow, Lincoln's Sparrow, Golden-crowned Sparrow, Dark-eyed Junco [*Junco hyemalis*]) accounted for 89% of captures (Table 2). Rarefaction curves and the Chao 1 estimator of species richness (Table 1) showed little difference in species richness between remnant and restored sites (Fig. 2c). Estimated species richness of birds in remnants (23.0 ± 8.3) was not significantly different than species richness in restored sites (15.2 ± 1.2). The percent change in the number of species was 6% (Table 1), and 70% of species occurred in both the riparian remnants and the restored habitat.

Species-Specific Patterns of Abundance and Site Persistence

Among permanent-resident species, only House Finches (*Carpodacus mexicanus*) had significantly higher capture rates in one treatment (remnant) than the other ($\chi^2 = 10.48$, $p < 0.01$) (Table 3). Among the 10 most abundant overwintering migrants, 7 were significantly more common in remnant or restored sites (Table 3). The Ruby-crowned Kinglet ($\chi^2 = 14.93$, $p < 0.01$), Hermit

Table 1. Measures of bird species richness and diversity in riparian remnants and restored riparian areas in the Sacramento River and San Joaquin River valleys (California, U.S.A.).

	All birds		*Permanent residents*		*Overwintering migrants*	
Abundance or diversity measure	*remnant*	*restored*	*remnant*	*restored*	*remnant*	*restored*
Sample size	2913	1158	856	291	2055	867
Slope of species accumulation curve for last 100 bird captures	<0.01	<0.01	<0.01	0.01	<0.01	<0.01
Species richness	53	33	32	18	19	15
Capture rate (birds/100 mnh[a])	39.5	38.9	11.6	9.8	27.9	29.2
Shannon index	2.66	2.48	2.38	2.12	1.91	1.85
Evenness	0.67	0.71	0.69	0.73	0.65	0.68
Chao 1 (95% CI)	75.5 (±23.8)	33.1 (±0.5)	45.5 (±18.5)	18.0 (±0.0)	23.0 (±8.3)	15.2 (±1.2)
Effective number of species[b]	14.3	11.9	10.8	8.3	6.8	6.4

[a]*Mist net hours, where 1 mnh = 1 12-m mist net opened for 1 h.*
[b]*Effective number of species represents the number of equally abundant species (Jost 2006).*

Table 2. Percentage of total captures of the most abundant species in remnant riparian and restored riparian sites in the Sacramento River and San Joaquin River valleys (California, U.S.A.).

		Among all OM or all PR		*Among all birds captured*	
	Status*	*remnant*	*restored*	*remnant*	*restored*
Ruby-crowned Kinglet	OM	32.9	22.8	23.2	17.1
White-crowned Sparrow	OM	19.9	30.0	14.0	22.5
Lincoln's Sparrow	OM	13.1	21.6	9.3	16.1
Golden-crowned Sparrow	OM	14.6	10.3	10.3	7.7
Bushtit	PR	23.1	31.3	6.8	7.9
Song Sparrow	PR	17.5	17.2	5.1	4.3
Spotted Towhee	PR	16.0	11.0	4.7	2.8
Bewick's Wren	PR	12.4	16.5	3.6	4.1
Hermit Thrush	OM	5.8	2.8	4.1	2.1
Dark-eyed (Oregon) Junco	OM	1.7	4.5	1.2	3.4
Lesser Goldfinch	PR	6.7	5.2	2.0	1.3

**Abbreviations: OM, overwintering migrant; PR, permanent resident.*

Thrush ($\chi^2 = 9.90, p < 0.01$), Fox Sparrow ($\chi^2 = 13.32, p < 0.01$), and Yellow-rumped Warbler (*Setophaga coronata*) ($\chi^2 = 13.50, p < 0.01$) had significantly higher capture rates in remnants, whereas White-crowned Sparrow ($\chi^2 = 31.27, p < 0.01$), Lincoln's Sparrow ($\chi^2 = 31.28, p < 0.01$), and Dark-eyed Junco ($\chi^2 = 21.46, p < 0.01$) had significantly higher capture rates in restored sites.

Among permanent residents, the proportion of adult Bewick's Wren and Spotted Towhee were not significantly different in remnants and restored sites (Table 4). Among overwintering migrants the proportion of adult Lincoln's Sparrow ($\chi^2 = 5.71, p = 0.02$) and White-crowned Sparrow ($\chi^2 = 40.95, p < 0.01$) did not differ significantly between remnant and restored sites (Table 4). For both species the proportion of older birds was significantly higher in remnants than restored sites.

Among permanent residents, there were no significant differences in site-level persistence of any species between sites, and there were no significant differences in persistence of age classes of these species (Table 4). Among overwintering migrants, 3 species showed significant differences in site-level persistence between remnant and restored sites (Table 4). Hermit Thrush ($\chi^2 = 5.89, p = 0.01$), Lincoln's Sparrow ($\chi^2 = 15.59, p < 0.01$), and White-crowned Sparrow ($\chi^2 = 7.97, p < 0.01$) were

Table 3. Number of captures and capture rates of permanent residents and winter residents for all species with a total of >20 captures in riparian remnant and restored riparian sites of the Sacramento River and San Joaquin River valleys (California, U.S.A.).

	Remnant		*Restored*		
	captures	*capture rate*[a]	*captures*	*capture rate*[a]	χ^2
Permanent residents					
Oak Titmouse	19	0.26	9	0.30	0.16
Bushtit	198	2.69	91	3.06	1.02
Bewick's Wren	106	1.44	48	1.61	0.43
House Wren	44	0.60	10	0.34	2.75
Spotted Towhee	137	1.86	32	1.08	7.85
Song Sparrow	150	2.04	50	1.68	1.35
House Finch	26	0.35	0	0.00	10.48[b]
Lesser Goldfinch	57	0.77	15	0.50	2.19
American Goldfinch	12	0.16	10	0.34	2.99
Overwintering migrants					
Ruby-crowned Kinglet	677	9.19	198	6.66	14.93[b]
Hermit Thrush	119	1.62	24	0.81	9.90[b]
Orange-crowned Warbler	55	0.75	26	0.87	0.44
Yellow-rumped Warbler	63	0.86	6	0.20	13.50[b]
Savannah Sparrow	18	0.24	11	0.37	1.19
Fox Sparrow	91	1.24	13	0.44	13.32[b]
Lincoln's Sparrow	270	3.66	187	6.29	31.28[b]
White-crowned Sparrow	408	5.54	260	8.74	31.27[b]
Golden-crowned Sparrow	300	4.07	89	2.99	6.35
Dark-eyed (Oregon) Junco	34	0.46	39	1.31	21.46[b]

[a] *Rate expressed as captures/100 mnh (mnh defined in Table 1 footnote).*
[b] *Statistically significant difference (alpha ≤0.05) in capture rates.*

Table 4. Number and percentage of individuals of 2 permanent-resident species and 5 overwintering-migrant species that exhibited within-winter site persistence in riparian remnants or restored riparian areas in the Sacramento River and San Joaquin River valleys of California (U.S.A.).

		Riparian remnants			*Restored riparian*			p[c]		
Species	*Age class[a]*	*banded*	*site persistent[b]*	*percent persistent*	*banded*	*site persistent[b]*	*percent persistent*	*proportion adult*	*site persistence[b]*	*persistence of age classes*
Permanent residents										
Bewick's Wren	juvenile	23	18	78.3	15	9	60.0	0.56	0.19	0.29
	adult	13	11	84.6	6	3	50.0			
	undetermined	29	21	72.4	16	12	75.0			
	all	65	50	76.9	37	24	64.9			
Spotted Towhee	juvenile	40	27	67.5	17	9	52.9	0.14	0.47	0.15
	adult	36	22	61.1	13	9	69.2			
	undetermined	12	8	66.7	3	1	33.3			
	all	88	57	64.8	33	19	57.6			
Overwintering migrants										
Hermit Thrush	juvenile	45	20	44.4	11	2	18.2	0.64	0.02	0.91
	adult	22	14	63.6	4	1	25.0			
	undetermined	16	9	56.3	1	0	0.0			
	all	83	43	51.8	16	3	18.8			
Fox Sparrow	juvenile	22	12	54.5	4	2	50.0	0.12	0.75	3.18E-10
	adult	14	8	57.1	0	0	0.0			
	undetermined	24	12	50.0	8	5	62.5			
	all	60	32	53.3	12	7	58.3			
Lincoln's Sparrow	juvenile	79	51	64.6	58	26	44.8	0.02	<0.01	0.49
	adult	46	27	58.7	15	5	33.3			
	undetermined	81	45	55.6	73	25	34.2			
	all	206	123	59.7	146	56	38.4			
White-crowned Sparrow	juvenile	157	95	60.5	159	88	55.3	1.56E-10	<0.01	0.45
	adult	160	120	75.0	46	26	56.5			
	undetermined	0	0		0	0				
	all	317	215	67.8	205	114	55.6			
Golden-crowned Sparrow	juvenile	79	62	78.5	33	23	69.7	0.54	0.30	0.70
	adult	64	54	84.4	22	18	81.8			
	undetermined	70	54	77.1	18	13	72.2			
	all	213	170	79.8	73	54	74.0			

[a]*Juveniles, birds in their first winter; adults, birds in their second or any subsequent winter; all, birds of all age classes combined.*
[b]*Site-level persistence was defined as birds detected at any time >24 h after initial capture.*
[c]*Chi-square tests of independence comparing the proportion of adult birds, site-level persistence of all birds with >20 captures, and site-level persistence of birds of different age classes between riparian remnants and restored riparian areas.*

more persistent in remnants. In addition, adult Fox Sparrows were more persistent in remnants ($\chi^2 = 39.56$, $p < 0.01$). In all other cases, there were no significant site-level persistence differences.

Vegetation Structure

We found no significant differences in vegetation structure between riparian remnants and restored sites (Supporting Information). Although there was considerable variation in structural vegetation values among remnant sites and among restored sites, remnant plots appeared to be more complex structurally. For example, remnants had a higher mean maximum tree dbh and lower mean values for tree, shrub, and herb cover. Restored sites had generally higher mean cover values in tree, shrub, and herb vegetative layers.

Discussion

Four of 5 of the most abundant species across the 8 sites were overwintering migrants, which is consistent with Gaines' (1977) observation of a high proportion of migrants among wintering birds in riparian areas. When we pooled data on permanent residents and overwintering migrants from all sites, the same species were most abundant in both restored and remnant sites, and capture rates, observed species richness, and diversity did not differ significantly between remnant and restored sites. But on the basis of rarefaction curves, values of demographic variables, and site-level persistence, there were species-specific differences among restored and remnant sites.

Chao's estimate of species richness was significantly greater in remnants than restored sites. Because the most abundant species occurred in both remnant and restored sites, this result may be associated with the greater number of uncommon permanent resident species in the remnants; 61.5% of species occurred in both the remnants and the restored sites. Estimators of species richness from remnant and restored sites were significantly different for permanent residents, but not for winter residents. The percent change in the number of species between remnant and restored sites was greater (23%) for permanent residents than for winter residents (6%), and similarity indexes were 56% for permanent residents and 70% for winter residents.

These patterns may reflect the older, generally more complex structure of riparian remnants. The stratified cottonwood-willow forest typical of riparian remnants in California may facilitate high bird densities because trunk-, branch-, and foliage-foraging space are relatively high (Gaines 1977). Denser vegetation as seen in our restored sites, with higher cover values in all layers, may contain more food for ground-foraging granivores (Ammon 1995; Chilton et al. 1995; Weckstein et al. 2002). Our species-specific results are consistent with this interpretation; arboreal forage insectivores, such as Ruby-crowned Kinglet, Hermit Thrush, and Yellow-rumped Warbler, were significantly more abundant in remnants, and ground-foraging granivores, such as White-crowned Sparrow, Lincoln's Sparrow, and Dark-eyed Junco, were significantly more abundant in restored sites. These differences could also be associated with bird responses to structural vegetation layers within sites or at finer resolution than we measured (Latta & Faaborg 2001; Johnson et al. 2006).

The distribution of sex and age classes of overwintering migrants is associated with habitat quality for some Parulid warblers; younger birds and females often occupy areas of low habitat quality (Holmes et al. 1989; Latta & Faaborg 2001, 2002). Similar data on non-Parulids are rare (Ketterson & Nolan 1976, 1982). For Lincoln's and White-crowned sparrows the proportion of older birds was significantly higher in remnants than in restored sites, even though capture rates were higher for these species in restored sites. Adult White-crowned Sparrows dominate immature individuals (Keys & Rothstein 1991), so our observation of a greater proportion of adult birds in remnants suggests this habitat may be of higher quality. We do not know, however, whether social dominance hierarchies exist in these habitats.

Survival is the key demographic variable reflecting fitness during the nonbreeding period. In winter birds seek foraging habitats where they can maintain inter- and intraspecific competitive advantage, avoid predators, and maintain body condition (Faaborg et al. 2010). Overwintering site persistence may be a proxy for winter survival (Holmes et al. 1989, Faaborg et al. 2010). Site-level persistence for 4 species differed between riparian remnants and restored sites (Hermit Thrush, 56.3%; older Fox Sparrow, 57.1%; Lincoln's Sparrow, 59.7%; White-crowned Sparrow, 67.8%), and persistence consistently was greater in riparian remnants. For species with significantly different site persistence between remnant and restored sites, our results were similar to those for winter-season studies in the tropics in which site-level persistence ranges from 42% to 80% (Holmes et al. 1989; Wunderle & Latta 2000; Latta & Faaborg 2001). It is difficult to compare our results with results of studies in temperate regions because extensive recapture and resighting efforts are not often conducted in the nonbreeding season. Ketterson and Nolan (1982) and Rabenold and Rabenold (1985) recaptured 8–53% of Dark-eyed Juncos, Brown et al. (2000) found 35% of Hermit Thrushes consistently occupied sites in Louisiana, and Somershoe et al. (2009) demonstrated site-level persistence of birds in winter of 2–35% for several passerines in Florida. But these results likely underestimate site-level persistence because they were all derived from mist net recaptures rather than resighting. Sandercock and Jaramillo (2002) estimated site-level persistence of juvenile (6–18%) and adult (8–28%) emberizids, including Fox, Lincoln's, White-crowned, and Golden-crowned sparrows, but their results are also not directly comparable to ours because they used mark-recapture models to estimate site-level persistence.

For permanent-resident species, neither the proportion of adult birds, nor site-level persistence, differed significantly between remnant and riparian sites. This does not suggest permanent residents perceived remnants and restored sites as comparable. Estimates of species richness of permanent residents in remnant and restored sites were significantly different, and this pattern was associated with the occurrence of uncommon species. But the distribution of permanent residents is likely a function of breeding-season requirements. Birds generally maintain territories throughout the year; the probability of survival and reproduction is higher for birds that are familiar with food and resources in their territories (Shields 1984). Thus, differences in sex ratios or site-level persistence of overwintering birds should not be expected, although there could be an undetected difference in winter survival of permanent residents between remnant and restored sites.

Our study provides new data that add to understanding of the winter ecology of several seldom-studied species, including Fox, Lincoln's, and White-crowned sparrows. Age-class segregation and site persistence have not been reported previously for Fox (Weckstein et al. 2002) or Lincoln's sparrows (Ammon 1995). Slightly more is known of the winter ecology of White-crowned Sparrow (Chilton et al. 1995). Our results highlight the increase in site-level persistence of some species and age classes of overwintering migrants in remnants, which may mean remnants are associated with higher survival rates than restored sites, especially for the species we studied. Questions remain as to whether observed differences in the proportion of adults and site persistence between remnant and riparian sites reflects individual choice, age-based differences in habitat requirements, or dominance interactions (Holmes et al. 1989; Wunderle & Latta 2000; Latta & Faaborg 2002).

Our results also point to the information gained by using a variety of measures in evaluating bird responses to restoration of riparian areas. Although avian species richness or abundance in the breeding season are most often used to quantify bird responses to riparian restoration (Block et al. 2001; Johnson et al. 2006; Golet et al. 2008), our results suggest that such measures may be misleading. Introducing seasonality as a variable and measuring overwinter site persistence of both sexes and of different age classes across a suite of species may provide a more accurate evaluation of responses of birds to riparian restoration, but species-specific responses should be expected.

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Supporting Information

Tables of capture and resighting effort for birds (Appendix S1), capture rate of birds in the nonbreeding season (Appendix S2), and values of vegetation variables at riparian remnant and restored sites (Appendix S3) are available as part of the online article. The authors are responsible for content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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