

FEATURE ARTICLES

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FACTORS INFLUENCING SPECIES RICHNESS AND COMMUNITY COMPOSITION OF BREEDING BIRDS IN A DESERT RIPARIAN CORRIDOR

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Abstract. The San Pedro River in southeastern Arizona is one of the last free-flowing rivers in the southwestern United States that maintains significant stretches of perennial water. While critical for birds, this river is vulnerable to salt cedar (tamarisk, *Tamarix* spp.) invasion, woody encroachment into grassland, and alteration of hydrologic regime resulting from groundwater pumping. Bird species richness and community composition metrics provide a means to assess effects of management or conservation efforts. To estimate these metrics, we used methods that incorporated species detection probabilities from data collected at 160 points at 23 sites on the San Pedro River during 1998–2001. Species richness, co-occurrence, and uniqueness were estimated as a function of four riparian vegetation types (cottonwood-willow [*Populus-Salix*], salt cedar, mesquite [*Prosopis* spp.], and grassland), three hydrologic regimes (perennial, intermittent, and ephemeral), and riparian location (floodplain and terrace). We found significantly higher species richness in cottonwood and mesquite compared with salt cedar and grassland. Intermittent and perennial flow sites had higher species richness compared with ephemeral. Cottonwood and mesquite supported more unique species compared with grassland and salt cedar, and cottonwood or perennial sites supported canopy or water-dependent species, for which habitat is rare on the landscape. Within the intermittent class, salt cedar maintained an estimated 0–2 unique species compared with native woody vegetation types, while cottonwood and mesquite contributed an estimated 20–21 unique species compared with salt cedar. Thus, while maintaining relatively high species richness, salt cedar contributed little to regional avian diversity compared with native woody riparian vegetation. This research has important implications for regional conservation planning and riparian restoration efforts.

Key words: *detection, mark-recapture, riparian, San Pedro River, species richness, species uniqueness.*

Factores que Influencian la Riqueza de Especies y la Composición de la Comunidad de Aves Reproductivas en un Corredor Ribereño del Desierto

Resumen. El Río San Pedro, en el sudeste de Arizona, es uno de los últimos ríos que corren libremente en el suroeste de Estados Unidos y que mantiene porciones significativas de agua perenne. Aunque este río es crítico para las aves, es vulnerable a la invasión de *Tamarix chinensis*, a la intrusión del bosque en el pastizal y a la alteración del régimen hidrológico resultante del bombeo de agua subterránea. Las mediciones de riqueza de especies y de composición de la comunidad de aves permiten evaluar los efectos de los esfuerzos de manejo y conservación. Para realizar estas mediciones, usamos métodos que incorporaron las probabilidades de detección de las especies a partir de datos recolectados en 160 puntos en 23 sitios en el Río San Pedro entre 1998 y 2001. La riqueza de especies, la co-presencia y la singularidad fueron estimadas como una función de cuatro tipos de vegetación ribereña (ambiente de alamo y sauce [*Populus* y *Salix* spp.], de cedro salado [*Tamarix* spp.], de mesquite [*Prosopis* spp.] y pastizal), tres regímenes hidrológicos (perenne, intermitente y efímero) y dos ubicaciones ribereñas (planicie aluvial y terraza). Encontramos una riqueza de especies significativamente mayor en la alameda y el mesquite comparados con el ambiente dominado por cedro salado y el pastizal. Los sitios de flujo intermitente y perenne tuvieron mayor riqueza de especies que los efímeros. La alameda y el mesquite albergaron más especies únicas que el pastizal y el ambiente de cedro salado, y la alameda y los sitios perennes albergaron especies del dosel y que dependen del agua, para los cuales el hábitat es raro en el paisaje. Dentro de la clase intermitente, el ambiente de cedro salado mantuvo aproximadamente 0–2 especies

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únicas comparado con los tipos de vegetación de bosque nativo, mientras que la alameda y el mesquite albergaron unas 20–21 especies únicas comparados con el ambiente de cedro salado. De este modo, aunque mantiene una riqueza de especies relativamente alta, el ambiente de cedro salado contribuyó poco a la diversidad regional de aves comparado con la vegetación ribereña de bosque nativo. Esta investigación tiene implicancias importantes para los planes de conservación regional y para los esfuerzos de restauración ribereños.

INTRODUCTION

Riparian systems in the arid and semiarid southwestern United States maintain some of the highest avian density and species richness totals in temperate North America (Szaro 1980, Rice et al. 1983, Knopf et al. 1988, Krueper et al. 2003). Avian use of riparian woodlands and forests has consistently been found to exceed that of adjacent uplands in the region (Wauer 1977, Johnson and Haight 1985, Szaro and Jakle 1985). Beyond a focus on riparian-upland gradients in avian diversity, however, little is known about environmental factors related to variation in species richness and community composition within southwestern riparian corridors.

Potential changes in riparian vegetation, such as declines in native riparian forests, increases in salt cedar (*Tamarix* spp.), and woody encroachment into grasslands (Stromberg et al. 1996, Goode and Maddock 2000, Turner et al. 2003, Lytle and Merritt 2004, Morissette et al. 2006) may alter vegetation structure, which in turn could affect species richness and community composition. Previous studies have documented higher avian species richness in cottonwood-willow (*Populus* and *Salix* spp.) than mesquite (*Prosopis* spp.) or salt cedar on the lower Colorado and middle Rio Grande Rivers (Anderson et al. 1977, Ellis 1995), though no difference in avian species richness was observed on the lower Rio Grande (Engel-Wilson and Ohmart 1978). Additional research is needed to investigate the generality of these species richness patterns across the Desert Southwest.

Alteration of hydrologic regime due to pumping of alluvial aquifers is an important driver of changes in vegetation composition and structure. Native, phreatophytic vegetation such as cottonwood and willow occurs in areas with shallow groundwater and more perennial surface water conditions, and more deeply rooted, nonnative salt cedar occurs in more intermittent to ephemeral hydrologic conditions (Stromberg et al. 1996, Lite and Stromberg 2005). Spatial variation on the San Pedro River provides a unique opportunity to study the importance of vegetation type and hydrologic regime since different vegetation types occur along the hydrologic gradient. Given the dependence of birds on surface water as well as certain types of vegetation, it is important to disentangle the related effects of habitat and hydrology on species richness or community composition.

Environmental factors hypothesized to increase species richness in riparian habitats include increased vertical structural complexity, moisture, and disturbance levels (Naiman et al. 1993, Pollock et al. 1998, Mittlebach et al. 2001). We hypothesized that species richness would be highest in cottonwood because of its greater structural heterogeneity, followed by mesquite

and salt cedar, and lowest in grassland with low structural heterogeneity. We also expected that increased primary productivity related with mesic environments would increase species richness, and hypothesized that species richness would be highest in wet sites and lowest in dry sites when controlling for variation in vegetation type and floodplain location. Because areas close to the river channel undergo more flooding disturbance, we also hypothesized increased species richness in the floodplain relative to the topographically higher terrace within a given hydrologic class.

In addition to comparing species richness between locations, comparing species community composition (e.g., degree of similarity and uniqueness) is a way to investigate the relative importance of a given area or habitat type with respect to another (Nichols et al. 1998, Sabo et al. 2005). Based on previous studies of species richness and turnover (Boulinier et al. 2001), we hypothesized that focal habitats with higher richness would have lower species co-occurrence (higher uniqueness) compared with adjacent habitats with lower species richness. For example, we hypothesized that cottonwood would have higher uniqueness compared with grassland.

Beyond statistical measures of species richness and community composition, we were interested in the occurrence and overall spatial distribution of species within the riparian corridor. Hunter et al. (1987) identified 17 riparian-obligate species that have declined or been extirpated in southwestern riparian systems since 1900. On the San Pedro, species of particular concern include canopy and water-obligate species for which habitat is rare on the landscape.

Our overall goal was to investigate environmental factors related to variation in species richness or community composition on the San Pedro River. Specifically, we compared species richness, co-occurrence, and uniqueness as a function of vegetation type, hydrologic regime, and floodplain location.

METHODS

STUDY AREA

Data to estimate avian community metrics were collected on the upper and lower San Pedro River in Cochise County, Arizona. Study sites extended from 2 km north of the United States–Mexico border to 145 km north of the international border near Cascabel. Elevation of study sites varied from 1300 m at the international boundary to 900 m in the northernmost site. Study sites included 16 areas within the San Pedro Riparian National Conservation Area (NCA) managed by the Bureau of Land Management (BLM), as well as seven sites on privately owned land north of the NCA.

The San Pedro River watershed has two major zones of riparian vegetation extending perpendicularly from the river channel upslope to the surrounding desert scrub communities. Immediately adjacent to the river is a primary floodplain zone that consists of gallery woodlands and forests dominated by Fremont cottonwood (*Populus fremontii*) and Gooding willow (*Salix gooddingii*). Floodplain reaches characterized by ephemeral surface flow support nonnative, more deeply rooted salt cedar (*Tamarix chinensis* or *T. ramosissima*). Plants characteristic of the primary floodplain are early-successional species that require flooding events to maintain recruitment. Farther upslope, a secondary terrace riparian zone is dominated by mesquite interspersed with patches of sacaton grass (*Sporobolus wrightii*). The boundary between the floodplain and terrace occurs at a relatively abrupt transition in topography (or “cutbank”); the terrace generally supports later-successional plants that are less dependent on shallow groundwater or frequent flood events.

BIRD SAMPLING

Bird data were collected at 160 point-count sampling locations on 23 sites in the upper and lower reaches of the San Pedro River. Each site consisted of 5–14 point count locations on 2–4 transects located perpendicular from the river, extending through floodplain and terrace riparian zones. Points were located ≥ 100 m apart from one another and >60 m from a given edge type within the riparian corridor so that species richness estimates would reflect community attributes pertaining to a given vegetation type.

Each point represented the center of a variable circular plot truncated at 50 m radius to minimize the influence of adjacent habitats. Observers recorded all birds seen or heard during 6–15 visits at each point during 15 May to 31 July 1998–2001. Of the total point-count locations, 13, 28, 87, and 32 points from 2, 4, 13, and 4 sites were visited in one, two, three, and four years, respectively. The 13 points from two sites visited in only one year were discontinued due to fire and loss of access. A total of 10 experienced observers conducted surveys during the four-year study. At the beginning of each field season, a minimum of 2.5 weeks of training on survey techniques, including identification of birds by sight and sound, was completed prior to data collection. Within a given year, observers were rotated between sites so that each point count location was surveyed approximately the same number of times by each observer.

CLASSIFICATION OF VEGETATION TYPE AND HYDROLOGIC REGIME

Each site was classified by hydrologic regime, and each point-count sampling location within site was classified by riparian location and dominant vegetation type. Riparian location was defined as floodplain or terrace depending on whether a point was located toward the river channel or upslope from the cutbank. We used differentially corrected Universal Transverse Mercator coordinates of points within a classified image of the upper San Pedro (Watts et al. 1996) to classify vegetation

associations dominated by cottonwood-willow (henceforth called cottonwood), salt cedar, mesquite, or grassland based on canopy cover $>75\%$. We also estimated canopy cover to the nearest 5% at each point count location, where canopy cover was defined as the area of ground covered by a vertical projection of the highest-level canopy, ignoring gaps <5 m. Using the later approach, the interior of cottonwood stands ranged from woodlands (canopy cover 50%–75%) to forest (canopy cover 75%–100%). Mean maximum height of the canopy, which provides an index to vertical structural heterogeneity, was similar for salt cedar and mesquite but otherwise varied considerably among the dominant vegetation types, averaging (\pm SD) 21 ± 6 , 5 ± 2 , 6 ± 1 , and 1 ± 1 m for cottonwood, mesquite, salt cedar, and grassland, respectively.

We used surface water flow duration to classify hydrologic regime at each site according to three classes (perennial, intermittent, and ephemeral). We collected surface water data at two sampling points located 100 m apart along the river channel during repeated visits (average 24 visits per site) between 15 May and 30 July 1999–2001. We calculated flow duration as percent of visits that water was present out of the total number of visits to a site following Lite (2003). We classified sites with flow durations of $>92\%$ as perennial, $<92\%$ but $>40\%$ as intermittent, and $<40\%$ as ephemeral. One site (STE) had flow duration of 91% due to drought conditions in May–June 2000 but was classified as perennial based on extensive surface and ground water sampling conducted at that site (Lite 2003). Hydrologic regime, measured in the river channel, was assumed to extend through the floodplain and terrace riparian zones. Mean hydrologic conditions across years was used to represent the average over the study period. We used surface water duration to classify sites according to hydrologic regime since surface water duration on the San Pedro River has been found to covary closely with other key hydrologic factors such as groundwater depth and fluctuation (Lite and Stromberg 2005, Stromberg et al. 2006), which are much more difficult to measure.

We used three predictor variables to investigate environmental factors related with variation in species richness and community composition on the San Pedro River. First, we estimated species richness, co-occurrence, and uniqueness for each of the four dominant vegetation types: cottonwood, grassland, mesquite, and salt cedar. Next, we estimated species richness and community composition by both hydrologic regime (perennial, intermittent, and ephemeral) and riparian location (floodplain and terrace), yielding six classes. This analysis enabled us to assess avian community metrics by hydrologic regime within riparian location and riparian location within hydrologic regime. Finally, we estimated species richness and community composition by both vegetation type and hydrologic regime. This classification yielded 12 combinations, but only 9 of those occurred on the San Pedro. Salt cedar occurred in the ephemeral and intermittent sites, and cottonwood and grassland occurred in the intermittent and perennial sites; only mesquite occurred in all three hydrologic classes.

STATISTICAL ANALYSES

Our first goal was to tabulate the percentage of points at which individual species were detected by vegetation and hydrologic classes to provide a context for the species richness and composition metrics. This provided an overall indication of the spatial distribution of breeding bird species by vegetation type, flow regime, and across the riparian corridor.

We then estimated species richness and community composition with methods that incorporated heterogeneous species detection probabilities (Nichols and Conroy 1996, Boulinier et al. 1998, Nichols et al. 1998, Hines et al. 1999). Our approach provides estimates of species richness that include both observed and presumably present but unobserved species, and may improve comparison of species richness and community composition across habitats with different species detection probabilities (Nichols and Conroy 1996, Boulinier et al. 1998, Nichols et al. 1998, Hines et al. 1999).

We used a spatial version of Pollock's robust design to estimate species richness and community composition metrics (Pollock 1982, Nichols et al. 1998). Within three separate robust design analyses, we defined primary strata according to the three spatially defined predictor variables: vegetation type, hydrologic regime-riparian location, and vegetation type-hydrologic regime. We were interested in estimating average species richness and composition over the four-year sampling period.

The first step in our modeling was to address the assumption of closure. Normally, closure pertains to populations (i.e., birth, death, immigration, and emigration), but in the species richness context closure pertains to the community (i.e., local colonization or extinction of species). We addressed this assumption in two ways. First, we selected a modeling framework (the robust design) in which this assumption is relaxed between primary strata. Thus, we allowed for temporary emigration, extinction, and recolonization across vegetation types and hydrologic regimes within the study area. Second, we removed vagrants, accidentals, and migrants, and included breeding birds that occur annually even if relatively rare. Specifically, we included birds categorized as abundant, common, fairly common, uncommon, or rare, but occurring annually, from 15 years of careful recordings in the area (Krueper 1999) and an additional four years of intensive data collection (Brand 2004). We felt that the bird species included in the analyses were relatively stable and supported our closure assumption within primary strata for San Pedro breeding birds.

All analyses were implemented in program MARK (White and Burnham 1999). The data were input into MARK as a presence-absence x -matrix with species as the rows and the point count location as the secondary strata, nested within primary strata. Temporal replication was pooled into species presence-absence for each point-count location, and the number of visits to each point count location was included as a covariate to model species detection probabilities (see below).

We used two metrics to assess community composition. First, to estimate species co-occurrence between focal and adjacent habitat pairs, we estimated $\hat{\Phi}^{xy}$, defined as the probability that a species present in focal habitat x would also be present at the adjacent habitat y during the sampling period (Nichols et al. 1998). The metric $\hat{\Phi}^{xy}$ and the variance for $\hat{\Phi}^{xy}$ were obtained directly from Pollock's robust design (Pollock 1982, Nichols et al. 1998) using pairs of focal and adjacent habitats defined by: (1) vegetation type, (2) hydrologic regime-riparian location, or (3) vegetation type-hydrologic regime. We compared all 12 combinations of the four vegetation types to investigate species co-occurrence along the gradient in vegetation structural heterogeneity. For the six hydrology-riparian location classes and nine vegetation-hydrology classes, we used focal and adjacent habitat pairs with at least one vegetation type, riparian location, or hydrologic class in common to investigate species co-occurrence along the gradients in productivity and riparian location, while holding the other variables constant (18 and 32 separate analyses, respectively). Second, to assess the number of species that occur at only one of two vegetation-hydrologic classes, we estimated \hat{B}^{xy} , defined as the number of species present at adjacent habitat y but not at a focal habitat x during the sampling period (Nichols et al. 1998). The metric \hat{B}^{xy} was calculated as $\hat{B}^{xy} = \hat{N}^y - \hat{\Phi}^{xy} \hat{N}^x$, and the variance of \hat{B}^{xy} was calculated using the delta method (Seber 1982, Powell 2007), where \hat{N}^y , \hat{N}^x , $\hat{\Phi}^{xy}$, and associated variance estimates were obtained from Pollock's robust design (Pollock 1982, Nichols et al. 1998).

We used Akaike's information criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002) to select the best model for species detection probabilities within the robust design analyses. We made a number of decisions a priori to select the candidate model set. First, we included heterogeneity in species detection probabilities (model M_h) for all models, since heterogeneity of detection probability has been found to be particularly important for species richness estimates (Boulinier et al. 1998). We used the Pledger (2000) approach to model M_h using a mixture effect (π) along with two mixtures of detection probabilities with an additive effect between them. Thus, for model M_h , a proportion (π) of the species is assumed to have detection probability p_A , and the remainder $(1 - \pi)$, to have detection probability p_B . Second, we chose not to model behavioral heterogeneity in detection probability (model M_b) because the secondary strata that consist of spatial points have no logical ordering to distinguish initial capture probabilities (p) from recapture probabilities (c), and so model M_b was not appropriate in our situation. Third, we allowed detection probability to vary by secondary strata to account for site-to-site variability (analogous to model M_l). Further, to accommodate heterogeneity in species detection probabilities across the spatial points (i.e., model M_{th}), we fit a model linear on the logit scale, where $\text{logit}(p_{Ai}) = \text{logit}(p_{Bi}) + \text{constant}$ for the $i = 1, \dots, k$ secondary strata (spatial points) within a primary stratum. To improve model parsimony, we also modeled secondary strata by site,

where detection probabilities for point count locations within sites were assumed to be the same. Fourth, the number of visits to each point over the course of four years was included as a survey effort adjustment by using an individual covariate specific to the secondary strata. Finally, we allowed variation by vegetation type, riparian location, or hydrologic classes for all analyses, including detection probabilities, the mixture effect, as well as the individual covariates. Thus, sources of variation in species detectability were modeled in terms of species detection heterogeneity, spatial variation (at both the level of the point count location as well as the level of the site), and groups (different vegetation and hydrologic classes) yielding six candidate models each to estimate species richness using the Pledger (2000) mixture model approach within Pollock's robust design (Pollock 1982, Nichols et al. 1998). Estimates were obtained by model averaging when the best model carried less than 90% AIC_c weight. All results are presented as means \pm SE.

RESULTS

SPECIES COMPOSITION

During the avian breeding season, we detected 114 species in four years of sampling. After removing vagrants, accidentals, and species in migration during the late spring or early fall from our dataset to meet the assumption of closure, we detected 76 species considered part of the San Pedro breeding bird community (Appendix). Of the \sim 100 breeding species known to occur on the San Pedro (Krueper 1999), we tended to miss certain types of species due to our sampling methods. These included nocturnal species, waterbirds (we did not sample near cienegas or ponds), and birds associated with human dwellings.

Yellow-breasted Chat, Abert's Towhee, and Brown-headed Cowbird were the most widely distributed species in the riparian corridor, detected in $>75\%$ of all sampled points (Latin names in Appendix; Appendix). Species distributed widely across the wooded riparian corridor (cottonwood, salt cedar, and mesquite) with lower or no occurrences in grassland included the above species as well as Bewick's Wren, Ash-throated Flycatcher, Summer Tanager, Bell's Vireo, Gila Woodpecker, and House Finch. Verdin, Northern Cardinal, and Crissal Thrasher were most prevalent in mesquite, while Botteri's Sparrow, Eastern Meadowlark, and Cassin's Sparrow were most prevalent in grassland. Some species were fairly equally distributed across cottonwood and salt cedar (e.g., White-winged Dove and Bullock's Oriole); other species that occurred primarily in cottonwood also occurred in salt cedar in intermittent but not ephemeral reaches (White-breasted Nuthatch, Yellow-billed Cuckoo, Black Phoebe, and Gray Hawk). Species most prevalent in cottonwood included Yellow Warbler, Lesser Goldfinch, Western Wood-Pewee, White-breasted Nuthatch, Great Blue Heron, Bridled Titmouse, Great-horned Owl, and Mallard, some of which occurred exclusively in cottonwood. Water-obligate species such as Great-blue Heron and Mallard showed increasing prevalence in perennial flow sites.

SPECIES RICHNESS

Our estimates ranged from 0%–27% higher than standard methods that estimate species richness based on number of species enumerated in the sample (Fig. 1, Appendix). Traditional methods provided similar results to ours in cottonwood and mesquite but would have overestimated differences among vegetation types, with lower estimates of species richness in salt cedar and grassland (Fig. 1, Appendix). Still, we found significantly higher species richness in cottonwood and mesquite compared with salt cedar and grassland (Fig. 1), with higher richness in mesquite and lower richness in salt cedar than predicted. For both the floodplain and terrace, intermittent flow sites had highest species richness, followed by perennial flow, with significantly lower species richness in the ephemeral hydrologic class. Contrary to our predictions, species richness was similar in floodplain and terrace in the ephemeral and perennial hydrologic regimes, and higher in the terrace than floodplain in intermittent sites (Fig. 1).

Of all vegetation-hydrology combinations on the San Pedro, species richness was highest in cottonwood intermittent, cottonwood perennial, and mesquite intermittent flow sites (Fig. 1). Richness was higher in intermittent than perennial flow classes for all three native vegetation types (cottonwood, mesquite, and grassland). In contrast, salt cedar had higher species richness in the ephemeral compared with intermittent hydrologic class.

There was no difference in species richness between vegetation types (salt cedar and mesquite) in ephemeral sites. However, within intermittent sites, there were an average of 19–20 fewer species in salt cedar and 12–13 fewer species in grassland compared with cottonwood and mesquite. Within perennial flow sites, cottonwood had the highest estimated species richness, followed closely by mesquite and more distantly by grassland (Fig. 1).

SPECIES CO-OCCURRENCE AND UNIQUENESS

We found that when considering vegetation type alone, focal habitats with higher species richness were less likely to share species (had lower probability of co-occurrence) with adjacent habitats, as predicted. For example, in addition to having high species richness, cottonwood and mesquite were less likely to share species with salt cedar and grassland. Conversely, it was more likely that species present in grassland or salt cedar would also occur in cottonwood or mesquite (Table 1). Mesquite had greater estimated uniqueness and salt cedar had lower estimated uniqueness than predicted, which mimicked observed species richness patterns.

Species co-occurrence and uniqueness metrics provide a means to assess the importance of a focal habitat in relation to an adjacent habitat. Of all vegetation-hydrologic class pairs, cottonwood was the most distinct, with an estimated 27 unique species compared with grassland in perennial flow

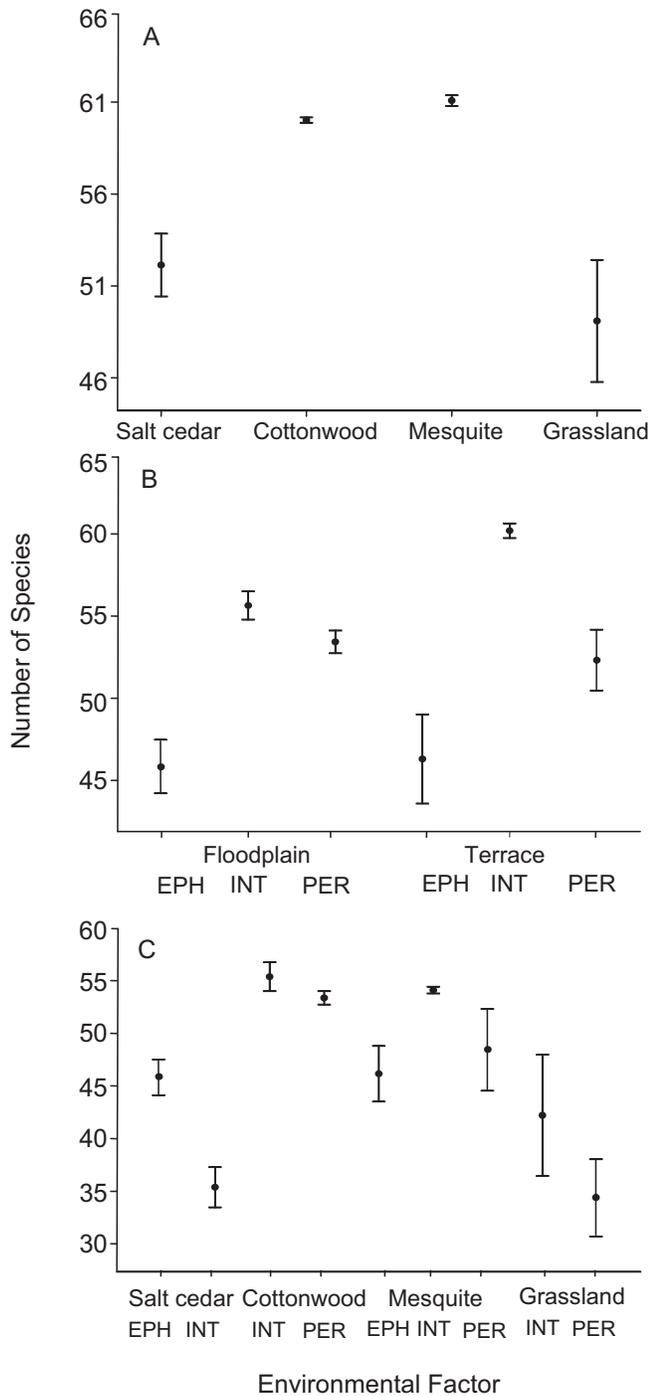


FIGURE 1. Avian species richness (mean ± SE) as a function of (A) four vegetation types, (B) three hydrologic regimes within riparian location (floodplain and terrace), and (C) nine combined vegetation-hydrologic regime classes on the San Pedro River, Arizona, 1998–2001. EPH = ephemeral surface water flow, INT = intermittent surface water flow, and PER = perennial water flow. Species richness estimates incorporate heterogeneous species detection probabilities. Survey effort is shown in the Appendix.

TABLE 1. Estimated avian species co-occurrence ($\hat{\Phi}^{xy}$, the probability that a species present in the focal habitat will also be present in the adjacent habitat) and number of unique species (\hat{B}^{xy} , the number of species present in the adjacent habitat that are not present in the focal habitat) in pairs of vegetation types on the San Pedro riparian corridor, Arizona 1998–2001. Survey effort is shown in the Appendix.

Focal habitat	Adjacent habitat	$\hat{\Phi}^{xy} \pm SE$	$\hat{B}^{xy} \pm SE$
Cottonwood	Mesquite	0.82 ± 0.05	12.0 ± 3.0
Mesquite	Cottonwood	0.80 ± 0.05	10.9 ± 3.1
Cottonwood	Salt cedar	0.77 ± 0.06	6.2 ± 4.1
Salt cedar	Cottonwood	0.88 ± 0.05	14.1 ± 2.9
Cottonwood	Grassland	0.65 ± 0.08	10.3 ± 5.8
Grassland	Cottonwood	0.79 ± 0.06	21.1 ± 4.1
Mesquite	Salt cedar	0.77 ± 0.06	5.2 ± 4.1
Salt cedar	Mesquite	0.90 ± 0.04	14.0 ± 2.7
Mesquite	Grassland	0.71 ± 0.08	5.7 ± 5.8
Grassland	Mesquite	0.88 ± 0.05	17.5 ± 3.9
Salt cedar	Grassland	0.69 ± 0.08	13.4 ± 5.7
Grassland	Salt cedar	0.73 ± 0.07	16.3 ± 4.7

sites (Table 2). In the intermittent hydrologic class, salt cedar contained no unique species compared with cottonwood and an estimated two unique species compared with mesquite, while cottonwood and mesquite contained an estimated 20 and 21 unique species compared with salt cedar, respectively. Salt cedar contained an estimated 6 unique species compared with grassland, while grassland contained an estimated 13 unique species with salt cedar within the intermittent hydrologic class.

On the floodplain, the perennial and intermittent hydrologic classes shared more species with each other but shared fewer species with the ephemeral class (Table 3). On the terrace, intermittent sites had highest estimated numbers of unique species, mimicking observed patterns of high species richness in the intermittent compared with perennial and ephemeral flow classes. When comparing species composition across the floodplain and terrace, we found the most similar species co-occurrences in the driest sites, with decreasing similarity and increasing uniqueness as conditions became wetter (Table 3).

DISCUSSION

Species richness and composition metrics are useful for testing predictions related to environmental gradients (Wiens 1989) and assessing potential effects of management or conservation actions on wildlife species (Conroy and Noon 1996, Flather 1996, Wiens et al. 1996). Potential changes in riparian vegetation composition and structure on the San Pedro, such as declines in native riparian forests, increases in salt cedar, and woody encroachment into grasslands (Stromberg et al. 1996, Goode and Maddock 2000, Turner et al. 2003,

TABLE 2. Estimated avian species co-occurrence ($\hat{\Phi}^{xy}$, the probability that a species present in the focal habitat will also be present in the adjacent habitat) and number of unique species (\hat{B}^{xy} , the number of species present in the adjacent habitat that are not present in the focal habitat) in pairs of habitats comparing vegetation type within hydrologic regime and hydrologic regime within vegetation type on the San Pedro riparian corridor, Arizona 1998–2001. Survey effort is shown in the Appendix.

Blocking variable	Focal habitat	Adjacent habitat	$\hat{\Phi}^{xy} \pm SE$	$\hat{B}^{xy} \pm SE$
<i>Vegetation type within hydrologic regime</i>				
Perennial	Cottonwood	Mesquite	0.74 ± 0.09	9.0 ± 6.2
	Mesquite	Cottonwood	0.82 ± 0.06	13.9 ± 4.5
	Cottonwood	Grassland	0.49 ± 0.09	8.5 ± 6.4
	Grassland	Cottonwood	0.76 ± 0.08	27.4 ± 4.2
	Mesquite	Grassland	0.59 ± 0.11	6.1 ± 7.0
	Grassland	Mesquite	0.82 ± 0.11	20.0 ± 6.5
Intermittent	Cottonwood	Mesquite	0.78 ± 0.06	10.9 ± 3.3
	Mesquite	Cottonwood	0.80 ± 0.06	12.2 ± 3.5
	Cottonwood	Salt cedar	0.63 ± 0.07	0.3 ± 4.6
	Salt cedar	Cottonwood	1.00 ± 0.03	20.1 ± 2.6
	Cottonwood	Grassland	0.59 ± 0.11	9.7 ± 8.4
	Grassland	Cottonwood	0.79 ± 0.08	21.9 ± 5.8
	Mesquite	Salt cedar	0.61 ± 0.07	2.2 ± 4.5
	Salt cedar	Mesquite	0.94 ± 0.04	20.8 ± 2.4
	Mesquite	Grassland	0.63 ± 0.11	8.0 ± 8.4
	Grassland	Mesquite	0.81 ± 0.07	20.0 ± 5.5
	Salt cedar	Grassland	0.82 ± 0.14	13.2 ± 7.8
	Grassland	Salt cedar	0.69 ± 0.09	6.3 ± 5.9
Ephemeral	Mesquite	Salt cedar	0.87 ± 0.06	5.6 ± 4.1
	Salt cedar	Mesquite	0.88 ± 0.07	6.0 ± 4.7
<i>Hydrologic regime within vegetation type</i>				
Cottonwood	Perennial	Intermittent	0.91 ± 0.05	6.8 ± 2.9
	Intermittent	Perennial	0.88 ± 0.05	4.8 ± 2.9
Grassland	Perennial	Intermittent	0.78 ± 0.15	15.3 ± 8.4
	Intermittent	Perennial	0.63 ± 0.12	7.6 ± 7.5
Mesquite	Perennial	Intermittent	0.88 ± 0.05	11.4 ± 4.3
	Intermittent	Perennial	0.79 ± 0.09	5.7 ± 6.2
	Perennial	Ephemeral	0.84 ± 0.08	5.7 ± 5.8
	Ephemeral	Perennial	0.88 ± 0.09	7.7 ± 6.4
	Intermittent	Ephemeral	0.80 ± 0.07	3.2 ± 4.9
	Ephemeral	Intermittent	0.93 ± 0.04	11.0 ± 3.2
Salt cedar	Intermittent	Ephemeral	0.85 ± 0.07	15.7 ± 3.5
	Ephemeral	Intermittent	0.66 ± 0.08	5.2 ± 4.3

Lytle and Merritt 2004, Morisette et al. 2006) have the potential to greatly affect bird species richness and community composition.

Our results corroborate the prediction that species richness and uniqueness increases with higher structural heterogeneity. High species richness and uniqueness in cottonwood relative to grassland and salt cedar were likely related with the greater stature of cottonwoods. Presence of upper canopy is necessary for a variety of species that nest at heights >5m (e.g., Western Wood-Pewee, Great-horned Owl,

TABLE 3. Estimated avian species co-occurrence ($\hat{\Phi}^{xy}$, the probability that a species present in the focal habitat will also be present in the adjacent habitat) and number of unique species (\hat{B}^{xy} , the number of species present in the adjacent habitat that are not present in the focal habitat) in pairs of habitats comparing hydrologic regime within riparian location (floodplain and terrace) and riparian location within hydrologic regime on the San Pedro riparian corridor, Arizona 1998–2001. Survey effort is shown in the Appendix.

Blocking variable	Focal habitat	Adjacent habitat	$\hat{\Phi}^{xy} \pm SE$	$\hat{B}^{xy} \pm SE$
<i>Hydrologic regime within riparian location</i>				
Floodplain	Perennial	Intermittent	0.92 ± 0.04	6.7 ± 2.4
	Intermittent	Perennial	0.88 ± 0.05	4.5 ± 2.7
	Perennial	Ephemeral	0.69 ± 0.07	9.1 ± 4.1
	Ephemeral	Perennial	0.80 ± 0.06	16.6 ± 3.2
	Intermittent	Ephemeral	0.72 ± 0.07	5.8 ± 4.1
	Ephemeral	Intermittent	0.87 ± 0.05	15.5 ± 3.0
Terrace	Perennial	Intermittent	0.90 ± 0.04	13.1 ± 2.8
	Intermittent	Perennial	0.78 ± 0.06	5.1 ± 4.0
	Perennial	Ephemeral	0.77 ± 0.08	6.1 ± 5.1
	Ephemeral	Perennial	0.87 ± 0.06	11.8 ± 4.2
	Intermittent	Ephemeral	0.74 ± 0.07	2.1 ± 5.2
	Ephemeral	Intermittent	0.96 ± 0.03	15.9 ± 3.1
<i>Riparian location within hydrologic regime</i>				
Perennial	Floodplain	Terrace	0.73 ± 0.07	13.3 ± 4.0
	Terrace	Floodplain	0.75 ± 0.06	14.5 ± 3.6
Intermittent	Floodplain	Terrace	0.82 ± 0.05	14.5 ± 3.0
	Terrace	Floodplain	0.76 ± 0.06	10.0 ± 3.5
Ephemeral	Floodplain	Terrace	0.88 ± 0.07	6.0 ± 4.7
	Terrace	Floodplain	0.87 ± 0.06	5.6 ± 4.1

and Cassin’s Kingbird). Similarly, canopy-nesting species showed marked decreases in abundance or local extirpation with loss of broadleaf habitats across southwestern systems (Hunter et al. 1987), though salt cedar may attain sufficient stature for low-canopy nesting species such as Summer Tanager and Bullock’s Oriole (Anderson et al. 1977, Hunter et al. 1988). Cottonwood woodlands also generally have a multi-layered structure with high vegetation height diversity (Lytle and Merritt 2004, Lite and Stromberg 2005), which has been found to contribute to species richness in other desert riparian systems (Szaro 1980, Anderson and Ohmart 1977, Farley et al. 1994).

Our results also corroborate the prediction that species richness and uniqueness decrease with lower structural diversity. Riparian grassland had low richness and uniqueness in relation to adjacent habitats, which is generally found in grasslands that support only a few, dominant bird species that typically nest on the ground (Wiens 1989). Despite relatively low richness, however, grasslands consistently maintained an estimated 6–13 species compared with cottonwood, mesquite, and salt cedar, when considering vegetation type alone and within hydrologic class. Grassland specialists on the San Pedro include Botteri’s Sparrow, Cassin’s Sparrow, Eastern

Meadowlark, and Scaled Quail, many of which have undergone rangewide declines or are species of some conservation concern (Webb and Bock 1996, Rich et al. 2004). Thus, riparian grasslands remain important for maintenance of regional diversity.

At intermediate levels of vertical structure, species richness and uniqueness in mesquite was higher than expected and similar to that in cottonwood. High species richness in mesquite on the San Pedro contrasts with lower species richness in relation to cottonwood on the Lower Colorado River (Anderson et al. 1977). In addition to woody structure, the herbaceous layer has a strong influence on avian communities in both mesquite and cottonwood stands on the San Pedro (Krueper et al. 2003) and may contribute to comparable levels of species richness in these vegetation types. Mesquite stands have a more variable height profile than salt cedar, which may influence species richness. Additionally, mesquite provides an intermediate zone between the floodplain and uplands, and may contain additional species due to spillover or “mass effects” that result from individual movements from adjacent habitats (Kunin 1998). Further work is needed to isolate aspects of landscape position or vegetation structure that contribute to high species richness and uniqueness in mesquite.

Contrary to predictions based on structural heterogeneity, species richness was lower in salt cedar than in mesquite and similar to that in grassland. One reason for the difference in species richness may be low associated woody diversity in salt cedar stands (Bagstad et al. 2006). Insects were also less diverse in salt cedar habitats on the Lower Colorado River, which may in turn depress avian richness (Yard et al. 2004).

As expected based on structural differences, bird species richness was also substantially lower in salt cedar than cottonwood. Ellis (1995) and Anderson et al. (1977) likewise found lower species richness in salt cedar than cottonwood on the middle Rio Grande and Lower Colorado, though species richness was similar among these floodplain vegetation types on the lower Rio Grande (Engel-Wilson and Ohmart 1978). Ellis (1995) also found that salt cedar had lower uniqueness than cottonwood, with 6 species unique to salt cedar and 14 species unique to cottonwood, very similar to what we found in this study. However, we also found that these differences were most pronounced when holding hydrologic regime constant. Salt cedar in the intermittent flow regime contained no unique species compared with cottonwood, in contrast to 20 unique species in cottonwood compared with salt cedar. Thus, while salt cedar stands maintained intermediate to high levels of species richness on the San Pedro as on other river systems in the region (Fleishman et al. 2003, Sogge et al. 2008), salt cedar contributed little to regional avian diversity compared with the relatively large stands of high-quality native vegetation on the San Pedro. Our results further highlight the importance of comparing avian use of salt cedar with native vegetation types along

a gradient in habitat quality characterized by hydrology, elevation, stand size, and other potentially confounding factors (Hunter et al. 1987, Hunter et al. 1988, Hinojosa-Huerta 2006, Van Riper et al. 2008).

In contrast with our prediction of higher richness and uniqueness in the wettest sites, we found that the intermittent flow regime generally had higher species richness than the perennial flow regime in the floodplain and terrace, and within cottonwood, mesquite, and grassland. While many studies have found a positive relationship between species richness and productivity as predicted in this study (Mittelbach et al. 2001), a hump-shaped relationship has also been observed with highest species richness in sites with intermediate levels of productivity or flooding (Naiman et al. 1993, Pollock et al. 1998, Mittelbach et al. 2001). Increased variability in hydrologic conditions may increase temporal variation in plant and insect resources (Stromberg 2007), which in turn may increase avian species richness. These results suggest that the breeding bird community may be somewhat resilient to alteration of hydrologic regime from perennial to intermittent conditions.

Despite slightly lower species richness estimates, however, perennial flow sites did maintain unique species in the floodplain. Swimming and wading birds such as Great Blue Heron, Green Heron, and Mallard were most prevalent in cottonwood in perennial flow reaches. Other species not detected during formal surveys but observed on the San Pedro included Pied-billed Grebe (*Podilymbus podiceps*), Common Moorhen (*Gallinula chloropus*), American Coot (*Fulica americana*), Black-crowned Night Heron (*Nycticorax nycticorax*), and Black-bellied Whistling Duck (*Dendrocygna autumnalis*; LAB, pers. obs.), all of which require reaches with perennial surface water on the San Pedro (Krueper 1999). Thus, a significant guild of water-obligate birds appears to depend on presence of perennial flow conditions on the San Pedro. There was also a threshold below the intermittent and perennial hydrologic classes where species richness and uniqueness declined substantially in the ephemeral flow sites. Lower species richness in ephemeral sites likely results from surface water loss, decreased uniqueness between the floodplain and terrace vegetation, and replacement of floodplain vegetation by salt cedar in locations where the depth-to-groundwater requirements for cottonwood and willow trees have been exceeded (Lite and Stromberg 2005).

The relationship between avian species richness and uniqueness estimates provides useful insights into the relative importance of vegetation types or hydrologic regime for breeding birds along the San Pedro riparian corridor. When considering species richness alone, cottonwood and mesquite vegetation types, and the intermittent flow regime stand out as most important for maintaining high avian diversity. In addition, species co-occurrence and uniqueness patterns provide insights as to the relative contribution of grassland and perennial flow regime to the maintenance of regional bird diversity.

Furthermore, when considering species uniqueness across all habitats, salt cedar contributed little to regional diversity, with only 0–6 unique species. In contrast, cottonwood, mesquite, and grassland, contributed an estimated 20, 21, and 13 unique species, respectively, compared with salt cedar when holding hydrology constant.

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APPENDIX. Percent of points at which species were detected by vegetation-hydrologic class and across all classes, listed in order of the total number of detections (n) during surveys from 160 point-count locations on the San Pedro riparian corridor, Arizona 1998–2001. The percent of points detected was calculated as the number of points that a species was detected divided by the number of points sampled, multiplied by 100. Survey effort includes the number of sites, points, and average number of visits per point by vegetation-hydrologic class and across all classes.

Species	Salt cedar		Cottonwood		Mesquite			Grassland		All	n
	EPH	INT	INT	PER	EPH	INT	PER	INT	PER		
Yellow-breasted Chat (<i>Icteria virens</i>)	95	100	82	100	82	82	86	17	25	79	934
Lucy's Warbler (<i>Vermivora luciae</i>)	80	60	61	41	100	95	86	17	0	66	715
Abert's Towhee (<i>Pipilo aberti</i>)	100	100	93	95	53	79	86	33	13	76	497
Yellow Warbler (<i>Dendroica petechia</i>)	50	40	93	100	24	31	29	17	0	49	450
Brown-headed Cowbird (<i>Molothrus ater</i>)	90	100	82	73	71	92	100	33	44	79	446
Bewick's Wren (<i>Thryomanes bewickii</i>)	90	80	96	86	76	77	100	0	0	74	429
Ash-throated Flycatcher (<i>Myiarchus cinerascens</i>)	65	60	61	41	88	79	100	17	13	61	273
White-winged Dove (<i>Zenaida asiatica</i>)	60	80	61	86	6	26	43	33	6	43	243
Summer Tanager (<i>Piranga rubra</i>)	75	60	100	82	47	56	86	0	13	64	241
Blue Grosbeak (<i>Passerina caerulea</i>)	65	60	43	27	65	85	86	33	50	59	225
Song Sparrow (<i>Melospiza melodia</i>)	40	60	86	73	12	10	0	17	0	36	225
Cassin's Kingbird (<i>Tyrannus vociferans</i>)	30	40	68	64	6	18	14	33	75	40	209
Common Yellowthroat (<i>Geothlypis trichas</i>)	45	60	79	100	0	26	29	33	0	44	204
Vermilion Flycatcher (<i>Pyrocephalus rubinus</i>)	45	60	75	64	53	28	14	0	38	46	203
Bell's Vireo (<i>Vireo bellii</i>)	55	20	18	27	53	28	71	0	0	30	195
Gila Woodpecker (<i>Melanerpes uropygialis</i>)	25	60	68	59	24	21	86	33	0	38	181
Mourning Dove (<i>Zenaida macroura</i>)	55	40	46	68	18	38	86	50	56	48	162
House Finch (<i>Carpodacus mexicanus</i>)	35	100	50	50	71	31	57	33	0	42	133
Black-throated Sparrow (<i>Amphispiza bilineata</i>)	5	40	11	9	35	64	43	17	0	27	126
Brown-crested Flycatcher (<i>Myiarchus tyrannulus</i>)	35	10	46	55	24	31	43	0	13	33	106
Lesser Goldfinch (<i>Carduelis psaltria</i>)	5	40	75	68	6	21	29	17	13	33	105
Verdin (<i>Auriparus flaviceps</i>)	10	0	7	5	82	56	71	0	0	29	103
Black-chinned Hummingbird (<i>Archilochus alexandri</i>)	50	60	43	50	29	44	57	33	13	41	100
Bullock's Oriole (<i>Icterus bullockii</i>)	60	20	18	50	12	5	0	0	0	21	74
Northern Cardinal (<i>Cardinalis cardinalis</i>)	30	0	14	32	47	38	57	0	6	28	73
Ladder-backed Woodpecker (<i>Picoides scalaris</i>)	0	60	39	36	24	28	43	0	6	26	66
Gambel's Quail (<i>Callipepla gambelii</i>)	15	40	14	0	18	15	43	0	0	13	59
Northern Flicker (<i>Colaptes auratus</i>)	10	20	36	41	6	5	43	0	0	18	47
Western Wood-Pewee (<i>Contopus sordidulus</i>)	0	0	43	36	0	0	0	33	0	14	45
Bushtit (<i>Psaltriparus minimus</i>)	5	0	14	5	0	10	29	0	0	8	44
Botteri's Sparrow (<i>Aimophila botterii</i>)	0	0	0	5	0	0	14	50	69	10	40
Common Ground-Dove (<i>Columbina passerine</i>)	10	20	25	18	6	18	14	67	6	18	39
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	0	20	36	32	0	0	0	0	0	11	36
Western Kingbird (<i>Tyrannus verticalis</i>)	20	20	11	23	0	8	14	33	0	12	30
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	0	20	25	45	6	18	14	0	0	17	29
Black Phoebe (<i>Sayornis nigricans</i>)	0	20	29	27	0	0	0	0	0	9	26
Canyon Towhee (<i>Pipilo fuscus</i>)	15	0	11	0	18	21	14	17	0	12	26
Great Blue Heron (<i>Ardea Herodias</i>)	0	0	11	50	0	3	0	0	0	9	25
Northern Beardless-Tyrannulet (<i>Camptostoma imberbe</i>)	20	0	4	18	12	13	29	0	0	11	25
Northern Rough-winged Swallow (<i>Stelgidopteryx serripennis</i>)	20	0	7	5	12	3	0	0	6	7	24
Phainopepla (<i>Phainopepla nitens</i>)	10	0	18	0	24	5	29	0	0	9	22
Chihuahuan Raven (<i>Corvus cryptoleucus</i>)	5	20	4	9	6	5	0	17	0	6	18
Bridled Titmouse (<i>Baeolophus wollweberi</i>)	0	0	4	27	0	3	0	0	0	5	16
Northern Mockingbird (<i>Mimus polyglottos</i>)	0	20	0	9	6	13	0	0	19	8	16
Gray Hawk (<i>Buteo nitidus</i>)	0	20	11	27	0	5	0	0	0	8	15
Great Horned Owl (<i>Bubo virginianus</i>)	0	0	14	14	0	0	0	0	0	4	15
Eastern Meadowlark (<i>Sturnella magna</i>)	0	0	0	0	0	0	0	17	44	5	15
Turkey Vulture (<i>Cathartes aura</i>)	0	0	0	9	6	0	14	0	0	3	13
Mallard (<i>Anas platyrhynchos</i>)	0	0	7	32	0	0	0	0	0	6	12

(Continued)

APPENDIX. (Continued)

Species	Salt cedar		Cottonwood		Mesquite			Grassland		All	n
	EPH	INT	INT	PER	EPH	INT	PER	INT	PER		
American Kestrel (<i>Falco sparverius</i>)	10	0	4	5	0	0	14	0	13	4	11
Scaled Quail (<i>Callipepla squamata</i>)	0	0	0	0	0	3	29	17	13	4	10
Common Raven (<i>Corvus corax</i>)	15	0	0	0	12	8	0	0	0	5	9
Cassin's Sparrow (<i>Aimophila cassinii</i>)	0	0	0	0	0	8	0	17	19	4	9
Killdeer (<i>Charadrius vociferous</i>)	0	0	7	5	0	3	0	17	0	3	8
European Starling (<i>Sturnus vulgaris</i>)	0	0	4	0	0	0	14	0	0	1	8
Crissal Thrasher (<i>Toxostoma crissale</i>)	5	0	0	0	6	10	14	0	0	4	8
Say's Phoebe (<i>Sayornis saya</i>)	0	0	0	0	6	8	0	33	0	4	6
Rufous-crowned Sparrow (<i>Aimophila ruficeps</i>)	0	0	0	0	0	10	14	0	6	4	6
Varied Bunting (<i>Passerina versicolor</i>)	10	0	0	0	6	5	0	0	0	3	6
Cactus Wren (<i>Campylorhynchus brunneicapillus</i>)	0	0	0	0	6	0	0	17	13	3	5
Pyrrhuloxia (<i>Cardinalis sinuatus</i>)	5	0	4	5	0	5	0	0	0	3	5
Hooded Oriole (<i>Icterus cucullatus</i>)	5	0	4	14	0	0	0	0	0	3	5
Barn Swallow (<i>Hirundo rustica</i>)	0	0	0	0	0	3	0	0	13	2	4
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	0	0	4	5	0	0	0	17	0	2	4
Greater Roadrunner (<i>Geococcyx californianus</i>)	5	0	0	0	0	3	14	0	0	2	3
Curve-billed Thrasher (<i>Toxostoma curvirostre</i>)	0	0	0	5	0	3	0	0	6	2	3
Cooper's Hawk (<i>Accipiter cooperii</i>)	5	0	0	0	0	0	0	17	0	1	2
Purple Martin (<i>Progne subis</i>)	0	0	0	5	0	0	14	0	0	1	2
Green Heron (<i>Butorides virescens</i>)	0	0	0	5	0	0	0	0	0	1	1
Swainson's Hawk (<i>Buteo swainsoni</i>)	0	0	4	0	0	0	0	0	0	1	1
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	0	0	4	0	0	0	0	0	0	1	1
Lesser Nighthawk (<i>Chordeiles acutipennis</i>)	0	0	0	0	0	3	0	0	0	1	1
Common Nighthawk (<i>Chordeiles minor</i>)	5	0	0	0	0	0	0	0	0	1	1
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	0	0	0	0	0	0	0	0	6	1	1
Black-tailed Gnatcatcher (<i>Polioptila melanura</i>)	0	0	0	0	6	0	0	0	0	1	1
House Sparrow (<i>Passer domesticus</i>)	0	0	4	0	0	0	0	0	0	1	1
Total number of species detected	44	34	54	53	42	54	42	31	28	76	
Number of sites	5	3	9	7	5	8	4	2	3	23	
Number of points	20	5	28	22	17	39	7	6	16	160	
Average visits per point	8	7	10	10	8	9	11	9	8	8	