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Influence of Local and Landscape Characteristics on Avian Richness and Density in Wet Playas of the Southern Great Plains, USA

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Abstract Playa wetlands (shallow, circular, depressional wetlands) in the Southern Great Plains are essential to the maintenance of regional biodiversity. However, the relative importance of habitat characteristics for maintaining avian species richness and density in playas is unknown. We examined influences of local- and landscape-scale characteristics on avian communities in wet playas. We conducted biweekly avian surveys on 80 playas (40 playas/year) from summer 2003 through spring 2005. Avian species richness was positively related to playa area and hydroperiod. More avian species and greater densities of birds were found at wetlands when water depths were intermediate (30–80 cm) during fall, winter and spring. Increased cultivation in playa watersheds increased total-, native-, and exotic-avian species richness.

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However, unsustainable sediment accumulation caused by cultivation can fill the playa basin and result in the loss of playa function, which will not benefit future bird populations. Landscape variables generally were less consistent with avian communities among seasons compared to local variables. Playas with greater numbers of other playas within 1 and 10 km had lower bird densities than those with fewer surrounding playas, likely due to the increase of habitat availability. Larger playas within predominantly uncultivated watersheds, that have an intermediate water depth, longer hydroperiod (within a season), and 26–50% vegetation cover are likely to maximize seasonal native avian richness. However, manipulating static water depths and maintaining long hydroperiods over extended periods will not meet avian objectives over the long term because playas must go through natural wet/dry fluctuations between years to maintain the desired plant community and productivity that supports diverse avian populations.

Keywords Avian Community · Hydroperiod · Playas · Southern Great Plains

Introduction

Environmental characteristics within a wetland (e.g., water depth and vegetation) are generally good predictors of avian diversity and abundance (Elphick and Oring 1998). Because wetlands are closely linked to their surrounding watersheds, activities beyond the wetland boundary at the landscape level can also influence wetland function (Gleason and Euliss 1998; Houlahan and Findlay 2003; Smith et al. 2008). For example, agricultural practices surrounding a

wetland that result in erosion can change wetland hydrology (Euliss and Mushet 1996; van der Kamp et al. 2003) and affect wetland avian communities. While avian species have different responses to environmental change (Mason and Macdonald 2000), the ability to understand how avian communities respond to local (i.e., within boundary) and landscape (i.e., beyond boundary) characteristics is key to providing useful conservation plans.

Agricultural influences are often hypothesized as one of the main causes of avian population declines in North America including wetland birds (Bethke and Nudds 1995; Rodenhouse et al. 1995). Wetlands with uncultivated watersheds normally support high avian abundance as opposed to those surrounded by cultivation (Shutler et al. 2000). Through runoff, agriculture alters the quality and quantity of water and wetland productivity (Donald et al. 2001; Knoll et al. 2003), which influences the avian community by affecting food resources and available habitat (Freemark and Boutin 1995; Hoffmann and Dodson 2005). Agricultural runoff may also change wetland function through sediment accumulation, thereby, reducing seedling and invertebrate emergence (Gleason et al. 2003) and shortening hydroperiods (Luo et al. 1997; Tsai et al. 2007, 2010). Vertebrate species can also be affected by agriculture. For example, more exotic avian species are generally found in habitats surrounded by cultivation due to many factors including fragmentation (Smallwood 1994). However, knowledge of how land use influences community composition of native vs. exotic avian species is generally lacking.

Water depth, vegetation composition and structure, and wetland size are important local characteristics determining wetland bird composition (Elphick and Oring 1998; Riffell et al. 2001; Guadagnin et al. 2009). Deep water not only directly restricts wetland use by shorebirds due the limitation of leg length (Isola et al. 2000), but also influences prey accessibility (Nagarajan and Thiyagesan 1996; Gawlik 2002). Vegetation cover and interspersion patterns also influence avian diversity and abundance (Moreno-Mateos et al. 2009). For example, patchy emergent vegetation is associated with increased diversity and abundance of breeding (Murkin et al. 1997), migrating (Webb et al. 2010), and wintering waterfowl (Smith et al. 2004). Generally, larger wetlands have more species than smaller wetlands (e.g., Craig and Beal 1992; Rosenzweig 1995; Guadagnin et al. 2009; but see Oertli et al. 2002), likely because the number of habitat types and niches increase in larger areas (Williams 1964) or, alternatively, larger areas contain more species simply because they have more individuals than smaller areas (Connor and McCoy 1979). These hypotheses are not mutually exclusive and may collectively have an important influence on the species-area relationship.

Landscape characteristics can also explain relationships between habitat and avian community composition (Pearson 1993; Cunningham and Johnson 2006). Because wetland birds may use multiple wetlands in a season, amount of wetland habitat in the landscape can influence species richness (Farmer and Parent 1997; Fairbairn and Dinsmore 2001). Moreover, landscape structure and pattern affect species distributions by potentially influencing avian movements among patches (Fernandez-Juricic 2000) and habitat occupancy (Wiens et al. 1997).

The >25 000 playa wetlands in the Southern Great Plains (SGP) are essential for maintaining biodiversity in the region because they provide the primary habitat available for aquatic species on an otherwise arid landscape (Haukos and Smith 1994). Most studies in this region have focused on game birds (e.g., waterfowl and gallinaceous birds; but see Davis and Smith 1998; Conway et al. 2005) and their relationships with local habitat requirements (e.g., Smith et al. 2004). Information on how local and landscape environmental variables influence playa use by avian communities is lacking for effective conservation planning. We examined influences of local- and landscape-scale characteristics associated with playa wetlands on avian species richness and density.

Methods

Study Area

The SGP encompasses playas with an average size of 6.3 ha (Guthery and Bryant 1982) that cover approximately 2% of this landscape (Haukos and Smith 1994). Playa basins are identified by hydric soil (e.g., Randall clay) surrounded by upland sandy and loamy soils (Allen et al. 1972). Precipitation occurs irregularly, primarily in late spring/early summer and early autumn (Bolen et al. 1989), averaging 47.2 cm (1911–2005) (NOAA 2006). However, annual precipitation during our study was 39.8 cm (June 2003–May 2004) and 75.0 cm (June 2004–May 2005) (NOAA 2006). Playas are inundated by precipitation and runoff with water loss occurring via evapotranspiration and recharge to the Ogallala Aquifer (Osterkamp and Wood 1987). Because of irregular rainfall and high rates of evapotranspiration, playas generally are not flooded year round (Smith 2003).

Data Collection

In each year (June–May; 2003 and 2004), we selected 40 playas (80 total, no overlap between years) following

significant precipitation events in 14 counties using ground and aerial surveys and maps. Because playas frequently do not fill with water every year, we could not choose playas completely random but selected playas from a pool that fit three criteria: inundated to the visual edge (determined by vegetation and slope changes; Luo et al. 1997), minimal anthropogenic modifications within the basin (e.g., pits, roads), and immediately surrounded by >75% cropland or native grassland. This approach did not affect the interpretation of our results because sampled playas were flooded to the visual edge within a short period of time. With different initial water depths (3.3–178.7 cm) and playa sizes (1.4–47.2 ha), our sample accounted for the variation in the population. Additionally, visually choosing playas surrounded by >75% cropland or native grassland bolstered our ability to understand the influence of land use. Although our results may not be applicable to all playas on the SGP, we could apply the inference to playas that filled during the same rainfall period, which fit the playa inundation cycle.

We conducted avian ground surveys once every 2 weeks for a year to include all seasons as long as playas retained water from June 2003 to May 2004 and from June 2004 to May 2005. We used binoculars and spotting scopes to identify species within each playa. We chose a vantage point from which to scan for birds in the open water. To ensure consistent sampling effort for playas of different sizes, we followed Naugle et al. (2001) and set two observation locations in playas <5 ha, three locations in playas 5–10 ha, and four locations in playas >10 ha. Then we proceeded around the playa to these predetermined locations near the playa edge and remained at each location for 6 min to record additional species and also estimate the number of each species in the playa. In most cases, we were able to count all species from vantage points and confirm the recorded species and number at survey locations. However, sometimes in more densely vegetated or larger playas, we could only detect species at survey locations. We kept track of the location of birds detected to minimize double counting. We also recorded species observed during travel between these locations. Species flying over playas were excluded from analyses, but birds constantly feeding over the playa (i.e., swallows, terns) were counted (Rivers and Cable 2003). The number of birds counted in each playa was treated as minimum number of birds and we did not correct for variability in detectability among playas. We terminated surveys when a playa dried (i.e., no longer contained surface water and the topsoil did not have enough moisture to form and maintain a soil ball), but resumed surveys once the playa was re-inundated. We separated avian data into four seasons to match patterns of bird appearance: summer (June-August), fall (September-November), winter (December-February),

and spring (March-May) for analyses. We used total number of species observed during each survey for species richness and calculated minimum density using the total number of individuals observed during each survey divided by playa area.

During each avian survey, we visually estimated percent vegetated area within playas following Naugle et al. (2000) into seven categories: <1%, 1–5%, 6–25%, 26–50%, 51–75%, 76–95%, and >95%. As an additional measure of vegetation, we visually estimated the number of emergent plant species that individually comprised >10% of the vegetated wetland area as an index of wetland vegetation heterogeneity (Naugle et al. 2001). We measured water depth after each avian survey. Measurements in the basin were recorded at three poles evenly spaced along a transect that spanned the diameter of each playa. We averaged the three water depth measurements of each survey because the elevation of the basin floor changes little in playas (Luo et al. 1997). We defined hydroperiod as the number of consecutive days a playa had measureable water (≥1 cm) within a season. We measured sediment depth (from the top of the sediment to the point with more than 50% hydric soil), basin elevation, and determined hydric soil edge location similar to Luo et al. (1997) as defined in Tsai et al. (2007). Hydric soil edge was determined by taking a series of soil cores along a transect perpendicular to the visual edge (details see Tsai et al. 2007). We calculated percent volume loss following Tsai et al. (2007). The calculation of volume loss was based on hydric soil of each playa, which provides a standardized way to compare the influence of sediment on playa volume. Because playas are located in the bottom of closed depressions with isolated watersheds, their hydric soils can be completely covered in sediment and thus playas lose more than 100% of their original volume.

We measured the visual edge of each playa to estimate playa area with a Global Positioning System. We digitized and verified land use cover in 10-km radius (31,416 ha) areas from the center of each playa using Digital Orthophoto Quarter Quadrangle aerial photographs (TNRIS 2006) in ESRI® ArcGIS and from the Farm Service Agency of the U. S. Department of Agriculture following Tsai et al. (2007). We classified land uses as native grassland, cropland, Conservation Reserve Program (CRP), playa, urban area, and other (e.g., reservoir). We quantified landscape structure within 1-, 5-, and 10-km radii. We chose 1-, 5-, and 10-km radii as landscape scales considering mobility and behavior of species (Wiens et al. 1986). For example, nearly 90% of the movements of migratory shorebirds were restricted to <10 km at stopover sites (Farmer and Parent 1997) whereas dabbling ducks normally fly <5 km from feeding sites to roosting sites on a daily basis (Cox and Davis 2002). Within each radii we used FRAGSTATS*ARC® to

determine number of playas (NP), percent cover of playas (PP), and interspersion and juxtaposition index (IJI; measure of differences in land use of adjacent patches) to quantify isolation and density of playas (McGarigal and Marks 1995). We calculated landscape complexity indices: landscape shape index (LSI), Shannon diversity index (SHDI) of land use (hereafter, diversity of land use), Shannon evenness index of land use (SHEI), edge density (m edge/ha, ED), and mean edge contrast index (MECI; degree of contrast between a land use type and its immediate neighbors) (McGarigal and Marks (1995). Finally, we determined each study playa watershed using a digitized United States Geological Survey contour map (TNRIS 2006). We followed Tsai et al. (2007) to calculate tilled index as:

$$\text{Tilled Index} = (\text{Tilled landscape} - \text{Untilled landscape})/$$
$$(\text{Tilled landscape} + \text{Untilled landscape}),$$

where tilled area included cropland and CRP and untilled area included native grass within watershed. The tilled index ranged from −1 (100% native grass) to 1 (100% tilled).

Data Analyses

We calculated variance inflation factors (VIF) on our initial 33 biologically relevant variables (i.e.,% vegetation cover, number of species >10%, water depth, playa area, hydro-period, sediment depth, volume loss, tilled index, and eight landscape variables [NP, PP, IJI, LSI, SHDI, SHEI, ED, MECI] within 1-, 5-, and 10-km radii) to assess collinearity (Belsley et al. 1980; Kutner et al. 2004) and excluded those with VIF >2 (Graham 2003). The 16 remaining variables (Table 1) were used for building models. To test the polynomial relationship between birds and water depth, we included a quadratic term as well as the linear term for water depth (Gawlik 2002). If a quadratic term for water depth is included in the model, a linear form for water depth is required for inclusion in the model (Freund and Littell 1991; Freund and Wilson 1993). Because waterfowl species richness and density are often greater in wetlands with 50% emergent vegetation compared to wetlands with dense or sparse vegetation (Weller and Fredrickson 1974), we also included a quadratic term to test for a polynomial relationship between birds and vegetation cover. We used the mid-point value of each vegetation category in the analyses.

We constructed 84 generalized linear models to describe each response variable (i.e., avian species richness and density) in each season separately using combinations of the 16 variables. We started with single-variable models of each independent variable, local variables only, and landscape variables only. We then expanded the model sets by adding combinations of variables based on knowledge of richness and density from the literature and professional judgment

based on experience and field observations. We tested models by using PROC GENMOD in SAS (SAS Institute, Inc., Cary, NC) which can incorporate various link functions to model non-normal data (e.g., Poisson and negative binomial distributions) without transformation (Littell et al. 2002). We used GENMOD and a Poisson distribution with a log-link function to model species richness and density. However, overdispersion was high (i.e., deviance/degrees of freedom [df]>25) for density models. Therefore, we used GENMOD and a negative binomial distribution with a log-link function to model density (deviance/df=1.2). We combined the data from 2 years and created models for each season because habitat requirements of bird species differ among seasons.

To determine whether exotic species played an important role in influencing richness, we excluded exotic species (see Appendix 1) from total species and used GENMOD to model native species richness. To further clarify the relationship between exotics and land use, we calculated the percentage of exotic species by using the number of exotic species divided by the number of all species within a year for each playa. We then related the percentage of exotic species to tilled index. We used GENMOD assuming a binomial distribution and incorporated a logit-link function to account for the non-normal nature of binomial data.

We treated surveys within a season in each experimental unit (i.e., playa) as repeated measures in analyses and used generalized estimating equation (GEE) approach in GENMOD to account for temporal autocorrelation (Hardin and Hilbe 2003). Because GEE is not a likelihood-based method, we used the quasi-likelihood criterion (QIC_u) (Pan 2001), where QIC_u replaced the likelihood in Akaike's Information Criterion, to evaluate and rank models. We calculated ΔQIC_u values for all other candidate models (relative to the lowest QIC_u value) and QIC_u weights (w_i) for each candidate model, considering models with $\Delta QIC_u < 2$ as plausible given the data (Burnham and Anderson 2002).

Species richness and density models present relationships between dependent variable and environmental variables but do not provide management recommendations. To further elucidate the relationship between water depth and avian community and provide management applications, we plotted the effect of water depth on species richness and density within a season while holding all other variables constant at their median values (Shaffer and Thompson 2007). Because GENMOD does not provide an R^2 value, we used multiple least-squares regression analysis to obtain an adjusted R^2 value for each model with a $\Delta QIC_u < 2$.

Results

We conducted 1,045 avian surveys from June 2003 through May 2005. We observed a total of 212 651 individuals from

Table 1 Median, mean, standard error (SE), minimum (Min), and maximum (Max) of variables measured for wet playas (*n*=80) in the Southern Great Plains, USA, in June 2003 to May 2005

Variables	*n*	Median	Mean	SE	Min	Max
Survey level						
Water depth (cm) (WD)	1045	30.0	37.4	1.0	0.0	249.0
Percent vegetation cover (%) (VEC)	1045	15.0	32.9	5.7	0.5	97.5
Number of plant species>10% (NS)	1045	1.00	0.99	0.03	0.00	4.00
Seasonal level						
Hydroperiod (HYDRO) in summer	80	86.0	77.1	1.7	32.0	92.0
Hydroperiod in fall	58	83.0	69.7	3.5	6.0	91.0
Hydroperiod in winter	44	90.0	73.3	3.6	14.0	90.0
Hydroperiod in spring	56	65.0	59.2	4.0	8.0	92.0
Playa level						
Playa area (ha) (AR)	80	9.5	11.1	0.9	1.4	47.2
Tilled Index [a] (TI)	80	0.76	0.51	0.07	−1.00	1.00
Sediment depth (cm) (SD)	80	18.9	27.1	2.9	0.9	104.9
Percent volume loss (%) (VL)	80	52.4	109.7	17.8	1.4	951.3
Landscape level						
Number of playas within 1 km (NP_01)	80	2.0	2.7	0.3	1.0	16.0
Number of playas within 10 km (NP_10)	80	143.0	155.2	9.9	28.0	380.0
Interspersion and juxtaposition of playas within 1 km (%) (IJI_01)	80	40.8	34.7	3.6	0.0	100.0
Interspersion and juxtaposition of playas within 10 km (%) (IJI_10)	80	64.7	60.6	1.7	1.0	85.2
Shannon diversity index of land use within 1 km (SHDI_01)	80	0.76	0.76	0.04	0.12	1.39
Shannon diversity index of land use within 10 km (SHDI_10)	80	1.12	1.08	0.02	0.61	1.36
Edge density within 10 km (m/ha) (ED_10)	80	22.4	22.4	0.6	12.7	35.9
Mean edge contrast index within 10 km (MECI_10)	80	44.1	43.7	0.3	36.2	49.2

[a] Tilled Index = (Tilled landscape − Untilled landscape)/(Tilled landscape + Untilled landscape)

122 species (Appendix 1). The surrounding watershed ranged from 100% grassland to 100% cropland, however, the mean tilled index was close to 0.5, indicating a dominance of cropland in the watersheds. Mean volume loss was 110%, suggesting that our study playas have lost their original volume. Mean water depth was 37.4 cm (Table 1).

Playa area, water depth, hydroperiod, tilled index, percent vegetation cover, and number of plant species >10% were included in the best-fit models of species richness for at least one season. Playa area had a positive influence on richness in the best-fit models for all seasons (Table 2). Water depth was an important predictor appearing in the best-fit models for species richness for spring with a positive linear and a negative

Table 2 Generalized estimating equation models using Poisson distribution for species richness in wet playas in the Southern Great Plains, USA, from June 2003 to May 2005 (seasons pooled between years) with mean number of parameters (*K*), delta quasi-likelihood criterion (ΔQIC_u), QIC_u weight (w_i), overdispersion (deviance/degrees of freedom [df]) and adjusted R² (Adj R²). Adjusted R² of top models were calculated using a multiple least-squares regression analysis. Only models with ΔQIC_u<2 were presented for each season

| Season	Model[a]	K[b]	ΔQIC_u	w_i	Deviance/df	Adj R²
Summer	AR + HYDRO + TI	4	0.00	1.00	1.83	0.38
Fall	AR + HYDRO + VEC - VEC*VEC + NS	6	0.00	0.99	2.75	0.34
Winter	AR + HYDRO + TI	4	0.00	0.95	2.17	0.34
Spring	AR + WD - WD*WD - VEC + NS	6	0.00	0.53	1.33	0.45
	AR + WD - WD*WD + VEC - VEC*VEC + NS	7	0.23	0.42	1.33	0.44

[a] Explanation of abbreviated variables are presented in Table 1

[b] Number of parameters including the intercept

Fig. 1 The effect of water depth on species richness with 95% confidence intervals in wet playas in the Southern Great Plains, USA, from June 2003 to May 2005 (seasons pooled between years)
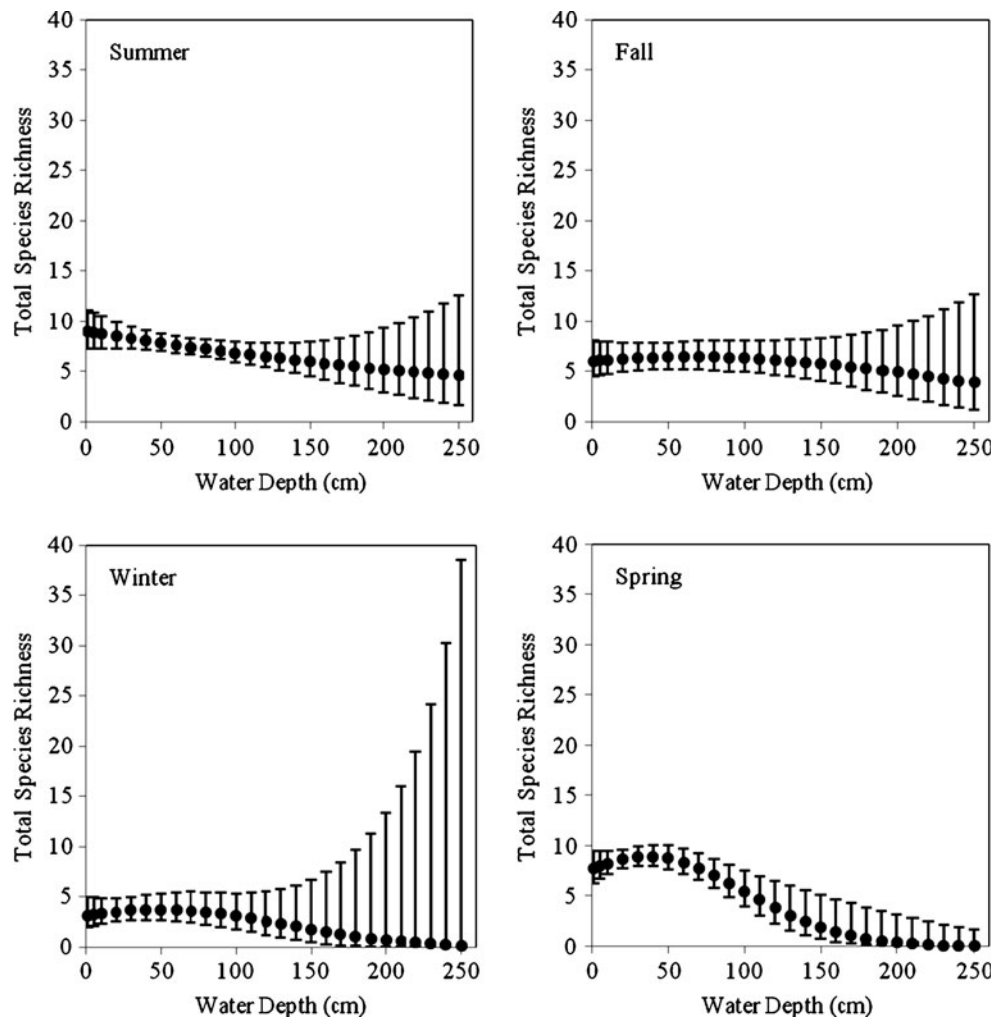
quadratic term. Species richness peaked when water depth ranged from 50 to 80 cm in fall, 40–60 cm in winter and 30–50 cm in spring (Fig. 1). There was no obvious species richness peak within the water depth ranges observed in summer. Hydroperiod had a positive relationship with species richness in the best-fit models in summer, fall, and winter. Tilled index had a positive influence on richness in the best-fit models for summer and winter (Table 2). Percent vegetation cover showed a polynomial relationship with species richness in the best-fit models in fall and spring. Percent vegetation cover had a negative influence on richness in spring. Number of plant species >10% had a positive influence on richness in fall and spring. Models had the best fit in spring ($R^2=0.45$) and poorest fit in fall and winter ($R^2=0.34$) (Table 2).

Table 3 Generalized estimating equation models using negative binomial distribution for bird density in wet playas in the Southern Great Plains, USA, from June 2003 to May 2005 (seasons pooled between years) with number of parameters (K), delta corrected quasi-likelihood criterion (ΔQIC_u), QIC_u weight (w_i), overdispersion (deviance/degrees of freedom [df]), and adjusted R^2 (Adj R^2). Adjusted R^2 of top models were calculated using a multiple least-squares regression analysis. Only models with $\Delta QIC_u < 2$ were presented for each season

Season	Model[a]	K[b]	ΔQIC_u	w_i	Deviance/df	Adj R^2
Summer	- AR + HYDRO - NP_10 [c]	4	0.00	1.00	1.08	0.30
Fall	HYDRO - NP_01	3	0.00	1.00	1.17	0.12
Winter	AR + WD - WD*WD + TI	5	0.00	1.00	1.14	0.25
Spring	- ED_10 + SHDI_01	3	0.00	1.00	1.13	0.09

[a] Explanation of abbreviated variables are presented in Table 1

[b] Number of parameters including the intercept.

Fig. 2 The effect of water depth on bird density with 95% confidence intervals in wet playas in the Southern Great Plains, USA, from June 2003 to May 2005 (seasons pooled between years)
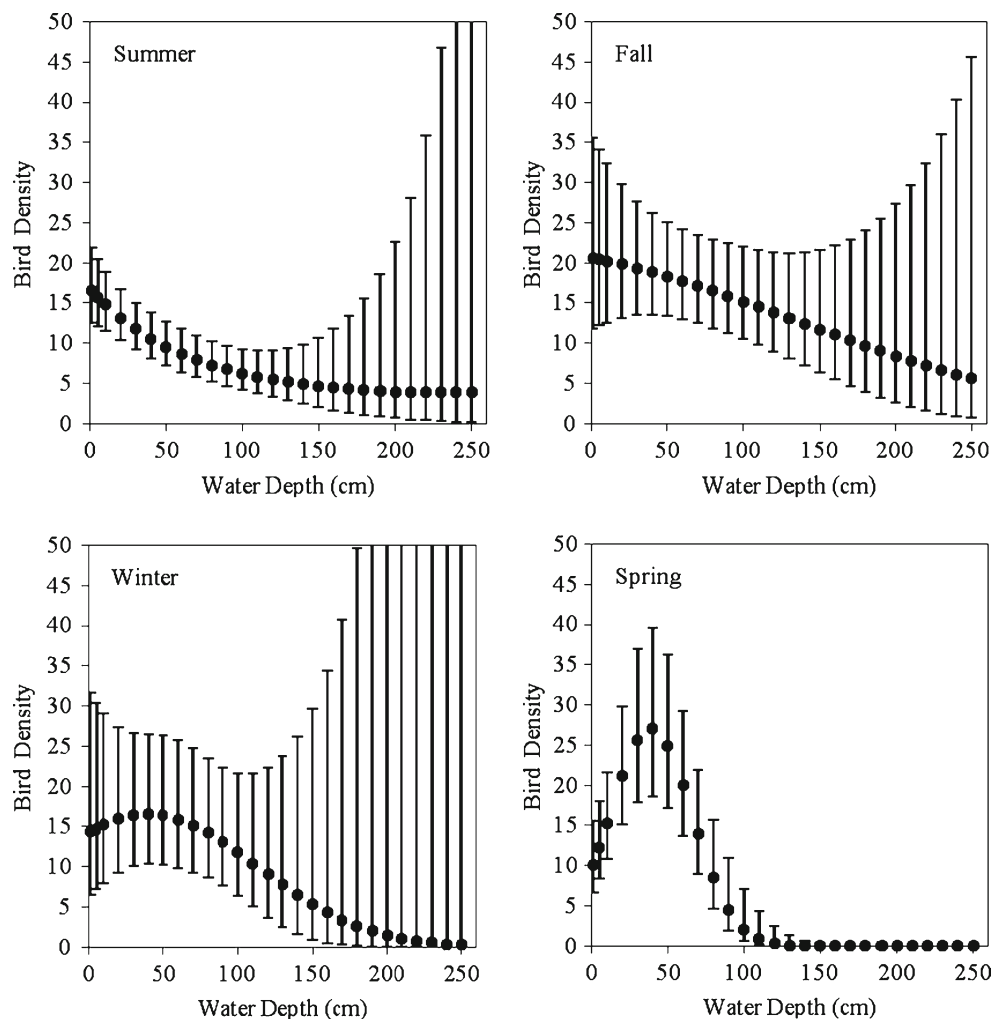
Each season had only one best-fit model for avian density (Table 3). Playa area did not have a consistent influence on density in the best-fit models, being negative in summer and positive in winter. Water depth appeared in the best-fit model for winter, with polynomial responses. A positive linear and a negative quadratic term indicated that bird density increased as water depth increased, richness initially increased, reached a peak, and then decreased. Bird density peaked when water depth ranged from 30 to 50 cm in both winter and spring (Fig. 2). However, there was no obvious density peak within the water depth ranges observed in summer and fall. Hydroperiod was positively correlated to density in summer and fall. Tilled index had a positive influence on density only for winter, indicating that density was greater in playas surrounded by a cultivated landscape (Table 3). Diversity of land use within 1 km was positively correlated to density in spring. Mean edge contrast index within 10 km had a negative influence on density in best-fit models for spring. The number of playas within 1 and 10 km had negative influences on density in the best-fit models for fall and summer, respectively. This indicated that total density per playa decreased as number of playas in the landscape increased. Models had the best fit in summer ($R^2=0.30$) and poorest fit in spring ($R^2=0.09$) (Table 3).

The best fit models describing native species richness were essentially identical to those when exotic species were included. When tilled index increased, the percentage of exotic species increased ($\chi^2=4.23$, df=1, $P=0.04$), indicating that playas dominated by cultivated landscape (i.e., tilled index>0) had a greater percentage of exotic species than did playas surrounded by native grassland (i.e., tilled index<0). The mean percentage of exotic species was 1.53% and 0.74% in playas with tilled index greater and smaller than mean tilled index (i.e., 0.51), respectively.

Discussion

Our results provide systematic insight into influences of local- and landscape-scale characteristics on avian communities in wet playas. By modeling species richness and density, we can understand the variation and rapid turnover

of avian communities in playa wetlands and their associations with environmental variables. Variables in species richness models were more consistent compared to variables in density models, and variations were likely the outcome of changes in avian community composition and their needs across seasons (Wiens 2001). Therefore, season-specific considerations are critical in successful playa conservation planning. From a management perspective, local variables such as vegetation cover, water depth, and hydroperiod are applicable in informing what type of conservation/manipulation to use for managing avian communities in this semi-arid region, whereas, landscape variables are useful for prioritizing habitat conservation.

We found that playa area was positively associated with species richness. Species-area relationships have been documented in wetland systems in different regions (Brown and Dinsmore 1986; Webb et al. 2010), with some exceptions (Fairbairn and Dinsmore 2001). More species can be found in larger areas than smaller areas because of greater habitat diversity (Williams 1964) and/or number of individuals in a larger area (Connor and McCoy 1979). As playa area increases, there are still only two types of habitat, edge and basin (Smith and Haukos 2002). Therefore, avian richness in playas is likely affected more by the number of individuals rather than habitat diversity. The species-area relationship was also supported by the model explaining bird density in winter, which showed that playa area had a positive influence on density in winter. Therefore, as playa area increased, number of individuals increased, which contributed to richness. In contrast, playa area was not a significant predictor for richness in dry playas for any season (Tsai 2007). Wet playas provide a unique habitat compared to upland semi-arid environments, serving as habitat islands (Whited et al. 2000). Non-wetland species were not restricted to dry playas and thus could use playas or additional nearby upland environments.

Species richness was greatest at water depths from 30 to 80 cm which is deeper than optimal depths (10–20 cm) suggested (Elphick and Oring 1998; Colwell and Taft 2000; Bolduc and Afton 2004). However, comparisons between studies may not be appropriate as resource availability and abundance can be confounded with water depth in different wetland types (Bolduc and Afton 2008). Also, we measured depth in the basin bottom not on the playa edge where many species were likely foraging. When we estimated the range of optimal depths at which density is maximal by fitting quadratic models, the right-skewed distribution of water depth may have overestimated water depth.

Percent vegetation cover was also an important influence on richness and density, which has been found in other studies of breeding (Weller and Spatcher 1965; Murkin et al. 1982) and migrating bird richness (Webb et al. 2010) and wintering waterfowl (Smith et al. 2004). The

intermediate level of vegetation cover can provide more food resources, increase visual isolation between breeding pairs, and increase habitat diversity (Kaminski and Prince 1981; Murkin et al. 1982; Smith et al. 2004). Playas must go through natural hydrological fluctuations to achieve this vegetation pattern unless they are intensively managed for moist-soil plant production (Haukos and Smith 1993).

Within-season hydroperiod consistently had a positive effect on species richness. This possibly was related to greater prey availability as longer hydroperiods may allow more time for invertebrates to colonize (Batzer and Resh 1992), especially in the summer and fall, thus supporting more avian species in greater abundance. However, prolonged hydroperiods can also modify aquatic invertebrate species composition by increasing predator–prey interactions and competition, thus decreasing overall biomass (Snodgrass et al. 1999; Babbitt et al. 2003). Although playas with longer hydroperiods may benefit avian communities because of greater food availability or simply by providing reliable habitat and increasing the number of days that playas can be used by birds in different seasons, playas must dry for a period of time to maintain productivity (Smith et al. 2008).

We hypothesized that species richness should be negatively correlated with tilled index. However, tilled index was positively related to richness in playas for summer and winter. This result is not solely due to exotic avian species since the percentage of exotic species in the avian community and native species richness were both positively related to tilled index. In Canada, species richness was higher in wetlands surrounded by grassland than in wetlands surrounded by cropland because some species preferred areas with fewer disturbances (Shutler et al. 2000). Different crop types (e.g., corn and sorghum) may contribute to this relationship by providing food resources, especially during winter. Annual plant species in the playas that were associated with cropland watershed (Tsai et al. 2012) can also provide additional food sources. However, agriculture activities were not randomly distributed across the landscape and may be associated with soil quality and water availability. Therefore, the direct effect of land use on avian communities is not easy to measure, and knowledge about how land use influences avian communities will require more research focused on fitness.

In studies of grassland birds (Cunningham and Johnson 2006; Winter et al. 2006) and wetland birds (Webb et al. 2010), neither local nor landscape variables alone explained the distribution and composition of bird assemblages. We also found that both categories of variables were important in predicting avian communities in playas, but more so for local variables compared to landscape variables. For example, landscape variables generally did not appear in the best-fit models for all seasons, indicating that species with

different life history require different landscape characteristics dependent on the season. Additionally, previous studies indicate that the amount of wetlands in the surrounding landscape has an important influence on avian species richness and density in a single wetland (Brown and Dinsmore 1986; Fairbairn and Dinsmore 2001). In our study, we found that number of playas within 1 and 10 km were negatively related to density in fall and summer, respectively. This may be because local birds tended to disperse to other playas when other wet playas with diverse habitat were available. The importance of landscape variables suggested that it is necessary to consider variables beyond individual playas in managing avian community in playas.

Wet playas provide essential habitats for avian communities throughout the year. Tsai (2007) found that wet playas support twice as many species and six times as many individuals as do dry playas. However, dry playas are also important to regional diversity because they provide habitat for non-wetland species. A wetland must go through wet/dry fluctuations to maintain productivity essential for wetland dependent birds during the next wet phase (Euliss et al. 2008). Thus, the natural cycle of wetting and drying is important to maintain avian diversity on the landscape. However, anthropogenic influences such as unsustainable sedimentation have changed the natural wet/dry cycle in playas (Tsai et al. 2007). Modifications in the playa basin (e.g., ditches and pits) concentrate water in a small area for prolonged period. These changes may also facilitate biological invasion of introduced or exotic species (Shay et al. 1999). Therefore, studies focused on how changes of the wet/dry cycle influence species assemblage and playa function are needed.

Playas are resilient ecosystems that can continue to support avian species when subject to anthropogenic impacts affecting hydroperiod and impairing ecological function. Even though most of our study playas were surrounded by cropland watersheds and accumulated unsustainable levels of sediment, they currently continue to provide habitat for avian species, which is reflected in the recorded species richness. However, continued sediment accumulation will result in the physical loss of playas (Johnson 2011), which will no longer support the observed species richness. To avoid this condition, conservation of playas with grassland watersheds should be a high priority for sustainability of future species richness. Playas with cropland watersheds should be managed to minimize sediment transport into the wetland to prolong the functional life of the playa.

Conclusion

State, federal, and nongovernmental conservation groups have conserved few playa habitats in the SGP in the last 2 decades (Smith 2003; Smith et al. 2011). If conserving playa habitat becomes a priority, our data suggests that purchasing and obtaining easements on larger playas would maximize native avian species diversity assuming that other conditions are equivalent. Intermediate water depths ranging from 30 to 80 cm and percent vegetation cover from 26% to 50% cover in playas should maximize species richness and density in winter and spring. For short term management, water level and vegetation conditions can be maintained through moist-soil management by drawdown or pumping water according to specific timeline (Haukos and Smith 1993). However, these methods can only be implemented on a local scale. Because playas must go through natural wet/dry fluctuations to sustain productivity, holding water level at a constant depth indefinitely will not benefit the avian community for the long term (Euliss et al. 2008). As playas go through wet and dry periods, changing water levels through time provides the necessary habitat requirements for a diversity of birds. Vegetation cover will also respond naturally to the changing water levels. Therefore, preserving hydrology is critical to maintaining normal playa function and playas in native grassland settings will likely allow the natural cycle to occur more often.

Continued erosion of cultivated watersheds and subsequent sedimentation has reduced playa volume and hydroperiod (Luo et al. 1997; Tsai et al. 2007, 2010). Although a higher tilled index results in a shorter hydroperiod (Tsai et al. 2007), species richness was greater in playas with higher tilled index. For example, a playa with a tilled index of 0.5 (i.e., three times as much cropland as grassland) holds water 29.5 fewer days than a playa with tilled index of −0.5 (i.e., three times as much grassland as cropland), but the playa with the tilled index of 0.5 would generally have 0.34 more species. At the same time, the percentage of exotic avian species also increased. Although exotic species were not the only cause of higher species richness in playas with a higher tilled index (native species richness was also positively correlated with tilled index), land use surrounding playas should be considered an important criterion for prioritizing playas for conservation in the future. A buffer zone with native grass around playas should reduce erosion and provide more natural hydroperiods (Skagen et al. 2008). However, more information is needed to specify buffer zone size and type.

Appendix

Table 4 Birds occurring in wet playas in the Southern Great Plains, USA, from June 2003 to May 2005. Symbol "V" means bird was found in that year and numbers appearing in parentheses represented the number of playas in each year in which the bird species was detected. Nomenclature follows the American Ornithologists' Union (1998)

Family	Scientific name	Common name	2003–2004 (n=40)	2004–2005 (n=40)	Exotic species
Anatidae	*Anser albifrons*	Greater White-fronted Goose		V (3)	
	Chen caerulescens	Snow Goose	V (1)	V (6)	
	Branta spp.	Canada/Cackling Goose	V (3)	V (11)	
	Aix sponsa	Wood Duck	V (2)	V (1)	
	Anas strepera	Gadwall	V (18)	V (25)	
	Anas americana	American Wigeon	V (18)	V (29)	
	Anas platyrhynchos	Mallard	V (38)	V (38)	
	Anas discors	Blue-winged Teal	V (34)	V (33)	
	Anas cyanopetera	Cinnamon Teal	V (18)	V (22)	
	Anas clypeata	Northern Shoveler	V (23)	V (30)	
	Anas acuta	Northern Pintail	V (24)	V (29)	
	Anas crecca	Green-winged Teal	V (23)	V (32)	
	Aythya valisineria	Canvasback	V (2)	V (4)	
	Aythya americana	Redhead	V (20)	V (19)	
	Aythya collaris	Ring-necked Duck	V (1)	V (5)	
	Aythya affinis	Lesser Scaup	V (4)	V (12)	
	Bucephala albeola	Bufflehead	V (1)	V (6)	
	Oxyura jamaicensis	Ruddy Duck	V (5)	V (13)	
	Lophodytes cucullatus	Hooded Merganser		V (2)	
Phasianidae	*Phasianus colchicus*	Ring-necked Pheasant	V (3)	V (3)	V
Podicipedidae	*Podilymbus podiceps*	Pied-billed Grebe	V (1)	V (7)	
	Podiceps auritus	Horned Grebe	V (1)	V (2)	
	Podiceps nigricollis	Eared Grebe	V (4)	V (7)	
Phalacrocoracidae	*Phalacrocorax auritus*	Double-crested Cormorant		V (2)	
Ardeidae	*Ardea herodias*	Great Blue Heron	V (16)	V (20)	
	Ardea alba	Great Egret	V (1)	V (3)	
	Egretta thula	Snowy Egret		V (3)	
	Egretta caerulea	Little Blue Heron		V (1)	
	Bubulcus ibis	Cattle Egret	V (16)	V (14)	
	Nycticorax nycticorax	Black-crowned Night-Heron	V (27)	V (22)	
	Butorides virescens	Green Heron		V (1)	
Threskiornithidae	*Plegadis chihi*	White-faced Ibis	V (20)	V (16)	
	Platalea ajaja	Roseate Spoonbill	V (1)		
Cathartidae	*Cathartes aura*	Turkey Vulture	V (1)		
Accipitridae	*Circus cyaneus*	Northern Harrier	V (5)	V (8)	
	Buteo swainsoni	Swainson's Hawk		V (3)	
	Buteo regalis	Ferruginous Hawk	V (1)		
	Accipiter striatus	Sharp-shinned Hawk		V (1)	
Falconidae	*Falco sparverious*	American Kestrel	V (2)		
	Falco peregrinus	Peregrine Falcon	V (1)		
Rallidae	*Laterallus jamaicensis*	Black Rail	V (1)		
	Porzana carolina	Sora	V (3)	V (1)	
	Fulica americana	American Coot	V (15)	V (20)	

Table 4 (continued)

Family	Scientific name	Common name	2003–2004 (n=40)	2004–2005 (n=40)	Exotic species
Gruidae	*Grus canadensis*	Sandhill Crane	V (6)	V (5)	
	Pluvialis squatarola	Black-bellied Plover	V (1)	V (3)	
	Charadrius vociferous	Killdeer	V (40)	V (39)	
	Charadrius montanus	Mountain Plover	V (1)		
Recurvirostridae	*Himantopus mexicanus*	Black-necked Stilt	V (18)	V (15)	
	Recurvirostra americana	American Avocet	V (38)	V (36)	
Scolopacidae	*Tringa melanoleuca*	Greater Yellowlegs	V (28)	V (29)	
	Tringa flavipes	Lesser Yellowlegs	V (22)	V (27)	
	Tringa solitaria	Solitary Sandpiper	V (20)	V (17)	
	Catoptrophorus semipalmatus	Willet	V (4)	V (4)	
	Actitis macularia	Spotted Sandpiper	V (14)	V (18)	
	Bartramia longicauda	Upland Sandpiper	V (19)	V (13)	
	Numenius americanus	Long-billed Curlew	V (17)	V (13)	
	Limosa haemastica	Hudsonian Godwit	V (1)		
	Limosa fedoa	Marbled Godwit	V (1)	V (3)	
	Calidris canutus	Red Knot	V (2)		
	Calidris alba	Sanderling	V (1)		
	Calidris pusilla	Semipalmated Sandpiper	V (7)	V (10)	
	Calidris mauri	Western Sandpiper	V (15)	V (13)	
	Calidris minutilla	Least Sandpiper	V (11)	V (13)	
	Calidris fuscicollis	White-rumped Sandpiper	V (3)	V (1)	
	Calidris bairdii	Baird's Sandpiper	V (15)	V (21)	
	Calidris melanotos	Pectoral Sandpiper	V (1)	V (2)	
	Calidris alpina	Dunlin	V (1)		
	Calidris himantopus	Stilt Sandpiper	V (4)	V (5)	
	Limnodromus spp.	Dowitcher	V (17)	V (10)	
	Gallinago delicata	Wilson's Snipe	V (2)	V (15)	
	Phalaropus tricolor	Wilson's Phalarope	V (21)	V (22)	
	Tryngites subruficollis	Buff-breasted Sandpiper		V (1)	
Laridae	*Larus philadelphia*	Bonaparte's Gull	V (1)		
	Larus pipixcan	Franklin's Gull		V (1)	
	Sterna forsteri	Foster's Tern		V (1)	
	Chlidonias niger	Black Tern	V (1)		
	Larus delawarensis	Ring-billed Gull	V (1)	V (4)	
Columbidae	*Columba livia*	Rock Pigeon	V (2)	V (1)	V
	Streptopelia decaocto	Eurasian Collared-Dove		V (1)	V
	Zenaida macroura	Mourning Dove	V (30)	V (31)	
Cuculidae	*Geococcyx californianus*	Greater Roadrunner		V (1)	
Strigidae	*Athene cunicularia*	Burrowing Owl	V (2)		
Caprimulgidae	*Chordeiles minor*	Common Nighthawk	V (1)		
Alcedinidae	*Ceryle alcyon*	Belted Kingfisher		V (1)	
Tyrannidae	*Sayornis phoebe*	Eastern Phoebe		V (1)	
	Sayornis saya	Say's Phoebe	V (2)	V (1)	
	Tyrannus verticalis	Western Kingbird	V (15)	V (8)	
	Tyrannus forficatus	Scissor-tailed Flycatcher	V (3)	V (10)	
Corvidae	*Corvus brachyrhynchos*	American Crow	V (4)	V (4)	
	Corvus cryptoleucus	Chihuahuan Raven		V (1)	
Alaudidae	*Eremophila alpestris*	Horned Lark	V (36)	V (29)	

Table 4 (continued)

Family	Scientific name	Common name	2003–2004 (n=40)	2004–2005 (n=40)	Exotic species
Hirundinidae	*Tachycineta bicolor*	Tree Swallow		V (6)	
	Stelgidopteryx serripennis	Northern Rough-winged Swallow	V (3)		
	Riparia riparia	Bank Swallow	V (1)		
	Petrochelidon pyrrhonota	Cliff Swallow	V (11)	V (10)	
	Hirundo rustica	Barn Swallow	V (38)	V (35)	
Mimidae	*Mimus polyglottos*	Northern Mockingbird	V (2)		
Sturnidae	*Sternus vulgaris*	European Starling	V (3)	V (1)	V
Motacillidae	*Anthus rubescens*	American Pipit	V (14)	V (11)	
Emberizidae	*Aimophila cassinii*	Cassin's Sparrow		V (1)	
	Spizella passerina	Chipping Sparrow	V (2)		
	Spizella pallida	Clay-colored Sparrow	V (1)	V (1)	
	Pooecetes gramineus	Vesper Sparrow	V (6)	V (5)	
	Chondestes grammacus	Lark Sparrow	V (6)	V (14)	
	Calamospiza melanocorys	Lark Bunting	V (3)	V (1)	
	Passerculus sandwichensis	Savannah Sparrow	V (10)	V (17)	
	Ammodramus savannarum	Grasshopper Sparrow	V (15)	V (4)	
	Zonotrichia leucophrys	White-crowned Sparrow	V (2)	V (1)	
	Calcarius mccownii	McCown's Longspur	V (7)	V (11)	
	Calcarius lapponicus	Lapland Longspur	V (2)		
	Calcarius ornatus	Chestnut-collared Longspur	V (6)		
Cardinalidae	*Passerina caerulea*	Blue Grosbeak	V (2)	V (3)	
	Spiza americana	Dickcissel	V (2)	V (2)	
Icteridae	*Agelaius phoeniceus*	Red-winged Blackbird	V (37)	V (32)	
	Sturnella spp.	Meadowlark	V (36)	V (34)	
	Xanthocephalus xanthocephalus	Yellow-headed Blackbird	V (14)	V (10)	
	Euphagus cyanocephalus	Brewer's Blackbird	V (9)	V (4)	
	Quiscalus quiscula	Common Grackle	V (12)	V (12)	
	Quiscalus mexicanus	Great-tailed Grackle	V (22)	V (20)	
	Molothrus ater	Brown-headed Cowbird	V (9)	V (9)	
	Icterus bullockii	Bullock's Oriole	V (1)	V (1)	
Passeridae	*Passer domesticus*	House Sparrow	V (1)	V (1)	V

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