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INFLUENCE OF GRAZING AND AVAILABLE MOISTURE ON BREEDING DENSITIES OF GRASSLAND BIRDS IN THE CENTRAL PLATTE RIVER VALLEY, NEBRASKA

DANIEL H. KIM,[1,4] WESLEY E. NEWTON,[2] GARY R. LINGLE,[1,3] AND FELIPE CHAVEZ-RAMIREZ[1]

ABSTRACT.—We investigated the relationship between grassland breeding bird densities and both grazing and available moisture in the central Platte River Valley, Nebraska between 1980 and 1996. We also compared species richness and community similarity of breeding birds in sedge (*Carex* spp.) meadows and mesic grasslands. Densities of two species had a significant relationship with grazing and six of seven focal species had a significant relationship with available moisture. Bobolink (*Dolichonyx oryzivorus*) and Brown-headed Cowbird (*Molothrus ater*) densities were lower in grazed plots compared to ungrazed plots, whereas Red-winged Blackbird (*Agelaius phoeniceus*) densities were greater in sedge-meadow plots compared to mesic grassland plots. Bobolink, Dickcissel (*Spiza americana*), and Brown-headed Cowbird were negatively associated with available moisture with breeding densities peaking during the driest conditions. Our results suggest that wet conditions increase species richness for the community through addition of wetland-dependant and wetland-associated birds, but decrease densities of ground-nesting grassland birds in wet-meadow habitats, whereas dry conditions reduce species richness but increase the density of the avian assemblage. We propose that wet-meadow habitats serve as local refugia for grassland-nesting birds during local or regional droughts. *Received 9 October 2007. Accepted 21 March 2008.*

Grassland birds have experienced greater population declines over the past 40 years than any other avian group in North America (Askins 1993, Sauer et al. 2005). These declines in the Midwest and Great Plains have been attributed to loss of grasslands in breeding areas (Knopf 1994, Herkert 1995). Many recent studies of grassland birds have examined the effects of habitat loss and fragmentation on avian occurrence and abundance (e.g., Herkert et al. 2003). Several studies also have examined the impacts of natural ecological drivers, such as burning and grazing, but only a few studies have evaluated the dynamic wet-dry cycles associated with grasslands and their influence on avian densities or nest success (Cody 1985, George et al. 1992, Zimmerman 1992, Igl and Johnson 1999, Fuhlendorf et al. 2006).

The dominant historical ecological factors were fire and grazing in the eastern mesic tallgrass prairies (Steinauer and Collins 1996), while the historical ecological drivers in the shortgrass prairies in the western Great Plains were climate and grazing (Bragg and Steuter 1996). The mixed-grass prairie ecosystem represents the integration of the characteristics of the tallgrass and shortgrass prairies as influenced by climate and soils (Bragg and Steuter 1996). As the climate becomes more arid from the eastern tallgrass prairies to the western shortgrass plains, drought supersedes fire as the primary ecological factor.

Vegetation structure may be the most important aspect of habitat selection and suitability for grassland birds (Wiens 1969, 1973; Cody 1981; George et al. 1992; Winter et al. 2005). The forb component in mixed-grass systems, which is responsible for the majority of the structural variation, is directly affected by precipitation (Bragg and Steuter 1996). Grassland bird populations respond quickly to and are relatively tolerant of changes in vegetation structure resulting from natural (e.g., drought, wildfire) and anthropogenic disturbances (e.g., mowing, prescribed fire) (Dechant et al. 2003a, b, c; Herkert 2003). In addition, fluctuations in precipitation affect food resource availability through reductions in insect biomass during drought years (Wittenberger 1980, George et al. 1992).

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Vegetation structure within the Platte River Valley of south-central Nebraska is influenced by both vegetation association and management practices. Vegetation associations in riparian wet-meadow pastures in this region vary from wetland emergent vegetation to dry-ridge grasslands based on elevation above the water table (Henszey et al. 2004). Sedge (*Carex* spp.) meadows and mesic tallgrass prairies are the dominant plant communities in native and restored areas within the riparian corridor and provide patches of suitable habitat for grassland birds in a mosaic of crop fields with strips of gallery forests.

We evaluated the influence of grazing and available moisture on breeding densities of grassland birds in mesic prairies and sedge meadows. We had two major objectives: (1) document differences in avian assemblages between sedge-meadow and mesic prairie plots using community metrics (richness and similarity), and (2) examine the impacts of grazing and fluctuating wet-dry cycles on the density of seven grassland bird species.

METHODS

Study Area and Management.—Research occurred on lands owned and managed by the Platte River Whooping Crane Maintenance Trust Inc. (hereafter ''the Trust''). The Trust owns and manages >4,000 ha of cropland, wet-meadow grasslands, and gallery forests in Hall, Buffalo, and Phelps counties along the Platte River in central Nebraska. The study area was Mormon Island Crane Meadows in Hall County, Nebraska (40° 48′ N, 98° 26′ W). Wet meadows were managed using a three-pasture grazing rotation. Each pasture was grazed either in the early season (May–late Jun), mid season (late Jun–mid Aug) or late season (mid Aug–mid Oct). Rotation order changed annually (Table 1), and management included periodic prescribed burns to discourage woody plant encroachment (Currier et al. 1985). We categorized pastures as grazed only if cattle were present in the early grazing season (i.e., before or during the bird censuses).

Four permanent 16-ha plots were established on Mormon Island Crane Meadows (MICM) in Hall County, Nebraska and classified as either sedge meadow or mesic prairie following recommendations of Henszey et al. (2004). Plots 1 and 2 were classified as mesic prairie and had greater topographic relief, raising them above the water table and resulting in greater densities of goldenrod (*Solidago* spp.), Maximilian sunflower (*Helianthus maximiliani*), and yellow sweetclover (*Melilotus officinalis*). Plots 3 and 4 were classified as sedge meadow, were 15–60 cm closer to the water table, and included expansive seasonal wetland habitat. Plots 3 and 4 were characterized by intermittent relic channels dominated by aquatic sedge (*Carex aquatilis*), which formed hummocks as a result of grazing and the presence of indigo bush (*Amorpha fruticosa*) near sloughs and relic channels. All plots occurred within the largest contiguous tract (>1,000 ha) of wet-meadow habitat in the central Platte River Valley (Lingle 1981). Spatially, no plot was further than 2.0 km from any other plot and all plots occurred within the same landscape. The plots do not represent true replicates, but they were on different grazing schedules.

TABLE 1. Study design and classification of Palmer Drought Severity Index (PDSI) into five categories. Grazing treatments included grazing (1) and no grazing (0). No data (ND) were collected in 1991 and 1992 or in sedge plot 4 in 1981.

Year	PDSI (Aug)	PDSI category (midpoint)	Mesic plots		Sedge plots	
			1	2	3	4
1980	−1.89	A (−0.91)	1	1	1	1
1981	1.42	B (1.06)	1[a]	0	1	ND
1982	2.54	C (3.03)	0	0	0	1
1983	3.74	C (3.03)	1	0[a]	1[a]	1
1984	4.59	D (4.99)	1[a]	1[a]	0	1
1985	4.20	D (4.99)	1[a]	0[a]	0	1
1986	3.24	C (3.03)	0	0[a]	0	1
1987	4.10	D (4.99)	0[a]	0	0[a]	1
1988	1.64	B (1.06)	0	1[a]	0[a]	1[a]
1989	0.60	B (1.06)	1	0	0[a]	1[a]
1990	0.54	B (1.06)	0	1	0	0
1991	ND	ND	ND	ND	ND	ND
1992	ND	ND	ND	ND	ND	ND
1993	7.94	E (6.96)	1	0	0	1
1994	4.23	D (4.99)	0[a]	1	0	0[a]
1995	−0.59	A (−0.91)	0	0[a]	0	0
1996	2.21	C (3.03)	0	1[a]	0	0

[a] Indicates that plot was burned during spring. Most prescribed fire resulted in patchy burns resulting in no detectable affects of fire to species density in this study.

Palmer Drought Severity Index.—We downloaded Palmer Drought Severity Index (PDSI) data for central Nebraska (State Cli-

TABLE 2. Densities (males/10 ha) of species detected during breeding bird censuses at Mormon Island Crane Meadows in Hall County, Nebraska, 1980-1996. Densities are by plot and averaged across years. Plots 1 and 2 represent mesic mixed-grass prairie, and plots 3 and 4 represent sedge-meadow grasslands.

Species	Plot 1	Plot 2	Plot 3	Plot 4
Least Bittern (*Ixobrychus exilis*)	0.000	0.000	0.042	0.021
Wood Duck (*Aix sponsa*)	0.000	0.000	0.000	0.021
Mallard (*Anas platyrhynchos*)	0.000	0.000	0.250	0.417
Northern Pintail (*A. acuta*)	0.000	0.000	0.000	0.000
Blue-winged Teal (*A. discors*)	0.125	0.042	0.323	0.313
Virginia Rail (*Rallus limicola*)	0.000	0.000	0.000	0.042
Ring-necked Pheasant (*Phasianus colchicus*)	0.042	0.000	0.000	0.000
Northern Bobwhite (*Colinus virginianus*)	0.021	0.042	0.000	0.000
Killdeer (*Charadrius vociferous*)	0.229	0.000	0.313	0.477
Upland Sandpiper (*Bartramia longicauda*)	1.615	1.500	1.302	1.208
Wilson's Snipe (*Gallinago delicata*)	0.000	0.000	0.063	0.042
Wilson's Phalarope (*Phalaropus tricolor*)	0.000	0.000	0.438	0.813
Mourning Dove (*Zenaida macroura*)	0.094	0.125	0.198	0.510
Sedge Wren (*Cistothorus platensis*)	0.208	0.000	0.146	0.271
Common Yellowthroat (*Geothlypis trichas*)	0.000	0.000	0.000	0.063
Grasshopper Sparrow (*Ammodramus savannarum*)	1.823	3.208	0.792	1.052
Swamp Sparrow (*Melospiza georgiana*)	0.000	0.000	0.000	0.083
Dickcissel (*Spiza americana*)	2.354	1.396	3.031	1.271
Bobolink (*Dolichonyx oryzivorus*)	5.313	4.938	5.677	4.969
Red-winged Blackbird (*Agelaius phoeniceus*)	1.333	0.167	7.323	7.208
Eastern Meadowlark (*Sturnella magna*)	0.083	0.167	0.083	0.021
Western Meadowlark (*S. neglecta*)	1.729	1.573	0.948	1.271
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	0.000	0.000	0.000	0.083
Brown-headed Cowbird (*Molothrus ater*)	1.917	1.542	2.563	2.625
Focal species density	16.083	14.323	21.640	19.604
Mean species richness	6.8	6.1	8.1	10.0
Species richness	14	11	16	21

mate Division 5) from the National Climate Data Center web site (http://www.ncdc.noaa.gov/oa/climate/research/monitoring.html). The PDSI is a long-term drought index calculated monthly and incorporates both precipitation and temperature data (Palmer 1965). The PDSI expresses the severity of a wet (positive values) or dry (negative values) period by factoring in both past and present conditions. More specifically, values of zero to −0.5 indicate normal moisture conditions, −0.5 to −1.0 indicate incipient drought, −1.0 to −2.0 indicate mild drought, −2.0 to −3.0 indicate moderate drought, −3.0 to −4.0 indicate severe drought, and less than −4.0 indicate extreme drought. Similar adjectives are associated with positive values and wet periods. Each state is divided into climate regions and PDSI values are calculated independently for each region. We evaluated the relationship between PDSI values from each month in the breeding season (May–Aug) and annual breeding bird abundances using simple correlation coefficients for each individual species and all focal species combined. PDSI values from August had the highest correlations with all species except Grasshopper Sparrow (scientific names of birds are in Table 2), which was more highly correlated with PDSI values from May. We used PDSI values from August for further evaluation of species response to climatic factors with August values representing cumulative conditions through the breeding season.

Avian Surveys.—We conducted spot map surveys on each of the four 16-ha wet-meadow plots following standard Breeding Bird Census techniques (Van Velzen 1972). We systematically walked each plot on a minimum of eight mornings during the breeding season. Each territorial male present, its behavior, and the location of all nests found were mapped. Only female Brown-headed Cowbirds were counted, except in 1980, when they were present but not counted. Eight surveys for each plot were conducted annually between 0505 and 1059 hrs CST from 23 May to 25 June from 1980 to 1990, and from 1993 to 1996 for a total of 15 years of data on plots 1–3. Plot 4 had 14 years of data, because no data were collected in that plot in 1981. Annual reports for these study sites were published in *American Birds* and *Journal of Field Ornithology* (Hay and Lingle 1982; Lingle and Whitney 1983a, b; 1991a, b; Lingle and Haugh 1984a, b; Lingle and Bedell 1989a, b; 1990a, b; Lingle et al. 1994a, b; Lingle 1995a, b; 1996a, b).

Statistical Analyses.—We report species richness for each plot for all 15 years and averaged across years. We compared avian communities using Morisita's (1959) Similarity Index, which ranks community similarity from 0.0 (no species overlap) to 1.0 (complete overlap). We calculated densities for each species on each plot (males/10 ha). We selected seven focal species (Upland Sandpiper, Grasshopper Sparrow, Dickcissel, Bobolink, Red-winged Blackbird, Western Meadowlark, and Brown-headed Cowbird) that were either obligate grassland nesting birds or strongly associated with grassland habitats and which occurred consistently across all four plots.

We used analysis of variance (ANOVA) to assess the effects of PDSI and grazing on the density of each bird species and overall avian diversity. We considered the design structure to be in the form of a strip-plot (Milliken and Johnson 1984). Given that PDSI is completely aliased with year (i.e., regional PDSI values are unique to each year but the same for all plots within a year), we first placed PDSI values into five categories (0–20, 21–40, 41–60, 61–80, and 81–100 percentiles). We considered these five levels of PDSI to be applied across each of the four plots simultaneously as ''strips'' with grazing applied randomly within each plot by PDSI combination. The results of this categorization and randomization varied (Table 1) with midpoint values of each PDSI category indicating reasonable spread and randomness of each factor level across years. We considered each of the four plots as random blocks for each PDSI by grazing level combination. Multiple occurrences of each PDSI category by grazing level combination were considered as sub-samples in time (Steel and Torrie 1980). We used PROC MIXED (SAS Institute Inc. 2004) to conduct the ANOVAs by considering three error terms and by computing Type III sums-of-squares using the most appropriate *F*-tests based on expected mean squares (Littell et al. 2006). We used Fisher's protected LSD test for pairwise comparisons between means for significant main effects and interactions at $P = 0.05$ (Milliken and Johnson 1984). All means reported are least squares means (lsmeans) with standard errors. We performed a similar analysis for prescribed burns and PDSI, but no significant associations were found. Thus, we do not report means or statistics for burn effects.

RESULTS

Plot Similarity and Species Richness.—Species richness (s) was greater for sedge-meadow plots ($s = 18.5$) compared to mesic-grassland plots ($s = 12.5$) (Table 2). Mesic-prairie plots were more similar to each other ($C_\lambda = 0.83$) than to sedge-meadow plots ($0.72 > C_\lambda > 0.51$) using Morisita's Similarity Index (C_λ); however, sedge-meadow plots had the greatest similarity ($C_\lambda = 0.90$).

PDSI Values.—Moisture conditions varied over the 15 years of study from mild drought (PDSI = -1.89) to extremely wet (PDSI = 7.94, flooded fields with only patches of dry ground available for nesting). Many of the bird species commonly associated with wet meadows and wetlands were detected only during extremely wet or flood conditions. For example, Virginia Rail, Wilson's Snipe, and most waterfowl species were detected only on wet-meadow plots during relatively wet seasons (PDSI > 3.0).

Bird Densities.—ANOVA results indicated the main effects of grazing and available moisture (i.e., PDSI), and their interaction, varied for each focal species and for all focal species combined (Table 3, Fig. 1). Data for all focal species combined indicated a significant relationship with PDSI main effect but with no grazing or interaction effects. The densities for all focal species combined, averaged across PDSI levels, were similar between ungrazed plots (32.1 ± 4.00 males/10 ha) and grazed plots (28.5 ± 3.92 males/10 ha). The densities of all focal species combined, averaged across the two grazing re-

TABLE 3. Analysis of variance assessing effects of grazing and available moisture (Palmer Drought Severity Index) on species densities.

Species	Grazing[a] F_{df}-test[b]	PDSI F_{df}-test[b]	Interaction F_{df}-test[b]
Focal species	$F_{1,3}$ = 7.34	$F_{4,8}$ = 30.52**	$F_{4,8}$ = 0.13
Upland Sandpiper	$F_{1,3}$ = 9.49	$F_{4,8}$ = 9.31**	$F_{4,8}$ = 5.59*
Grasshopper Sparrow	$F_{1,3}$ = 3.56	$F_{4,8}$ = 3.81	$F_{4,8}$ = 3.18
Dickcissel	$F_{1,3}$ = 0.03	$F_{4,8}$ = 68.21**	$F_{4,8}$ = 2.15
Bobolink	$F_{1,3}$ = 15.33*	$F_{4,8}$ = 8.82**	$F_{4,8}$ = 1.51
Red-winged Blackbird	$F_{1,3}$ = 0.73	$F_{4,8}$ = 8.88**	$F_{4,8}$ = 0.96
Western Meadowlark	$F_{1,3}$ = 5.77	$F_{4,8}$ = 32.15**	$F_{4,8}$ = 3.82
Brown-headed Cowbird	$F_{1,3}$ = 11.62*	$F_{3,5}$ = 13.31**	$F_{3,5}$ = 0.63

[a] Grazed fields had cattle in the plots during spot mapping; fallow fields were not grazed during the census period.
[b] Significance level: * $P < 0.05$; ** $P < 0.01$.

gimes, declined with increasing PDSI from 41.9 ± 4.78 males/10 ha at the lowest level of PDSI (−0.91) to 14.0 ± 8.15 males/10 ha at the highest level of PDSI (6.96).

Bobolink and Brown-headed Cowbird densities indicated significant main effects for grazing and PDSI but no interaction between the two effects. Bobolink densities, averaged across all PDSI levels, were higher on ungrazed plots (11.5 ± 1.06 males/10 ha) than on grazed plots (5.3 ± 1.08 males/10 ha). Bobolink densities, averaged across the two grazing regimes, declined from 11.8 ± 1.15 males/10 ha at the lowest level of PDSI (−0.91) to 6.4 ± 1.50 males/10 ha at the highest level of PDSI (6.96). Brown-headed Cowbird patterns paralleled those of Bobolink. Densities were higher on ungrazed plots (4.3 ± 0.61 females/10 ha) than on grazed plots (2.6 ± 0.59 females/10 ha) and tended to decline with increasing levels of PDSI (3.9 ± 0.59 females/10 ha at PDSI 1.51 to 3.0 ± 0.99 females/10 ha at PDSI 6.96).

Upland Sandpiper had a significant grazing by PDSI interaction. Their densities on grazed plots were near constant with a mean of 2.9 ± 0.34 males/10 ha across the PDSI levels. Densities on ungrazed plots peaked at intermediate levels of PDSI (2.6 ± 0.99 males/10 ha) with low densities at both the lowest PDSI level (0.6 ± 0.58 males/10 ha) and at the highest PDSI level (0.0 ± 0.76 males/10 ha).

Dickcissel, Western Meadowlark, and Red-winged Blackbird densities varied significantly with PDSI with no indication of grazing main effects or grazing by PDSI interactions. Dickcissel densities declined with increasing PDSI levels when averaged across both grazing treatments from 5.9 ± 1.05 males/10 ha (PDSI -0.91) to 0.3 ± 1.60 males/10 ha (PDIS 6.96). Western Meadowlark densities were low (all <4.0 males/10 ha) with no significant interaction occurring between PDSI and grazing, but Western Meadowlark experienced the most erratic patterns in densities across PDSI levels. Western Meadowlark declined significantly across the PDSI levels from 2.8 ± 0.29 males/10 ha (PDSI −0.91) to 2.0 ± 0.53 males/10 ha (PDSI 6.96). Red-winged Blackbird densities varied significantly with PDSI but had no grazing effects; the species declined only slightly from 8.6 ± 3.30 males/10 ha to 5.2 ± 3.60 males/10 ha with increasing PDSI.

Grasshopper Sparrow had non-significant increases in densities under grazed treatments for the lowest PDSI level (−0.91), but had no difference between grazing treatments or across PDSI levels. Grasshopper Sparrow mean density was 2.76 ± 0.37 males/10 ha across all levels of PDSI and the two grazing treatments.

DISCUSSION

All study plots were in close proximity, but small variations in elevation (at the decimeter scale) influenced the vegetative communities (Henszey et al. 2004) and, concomitantly, avian communities. Sedge-meadow pastures had a higher water table and were more susceptible to flooding. Thus, sedge-meadow plots had greater species richness due to wetland-associated and -dependant bird species using inundated fields during wet periods (Table 1). The extent of inundation depended on both local precipitation and river flood stage; in

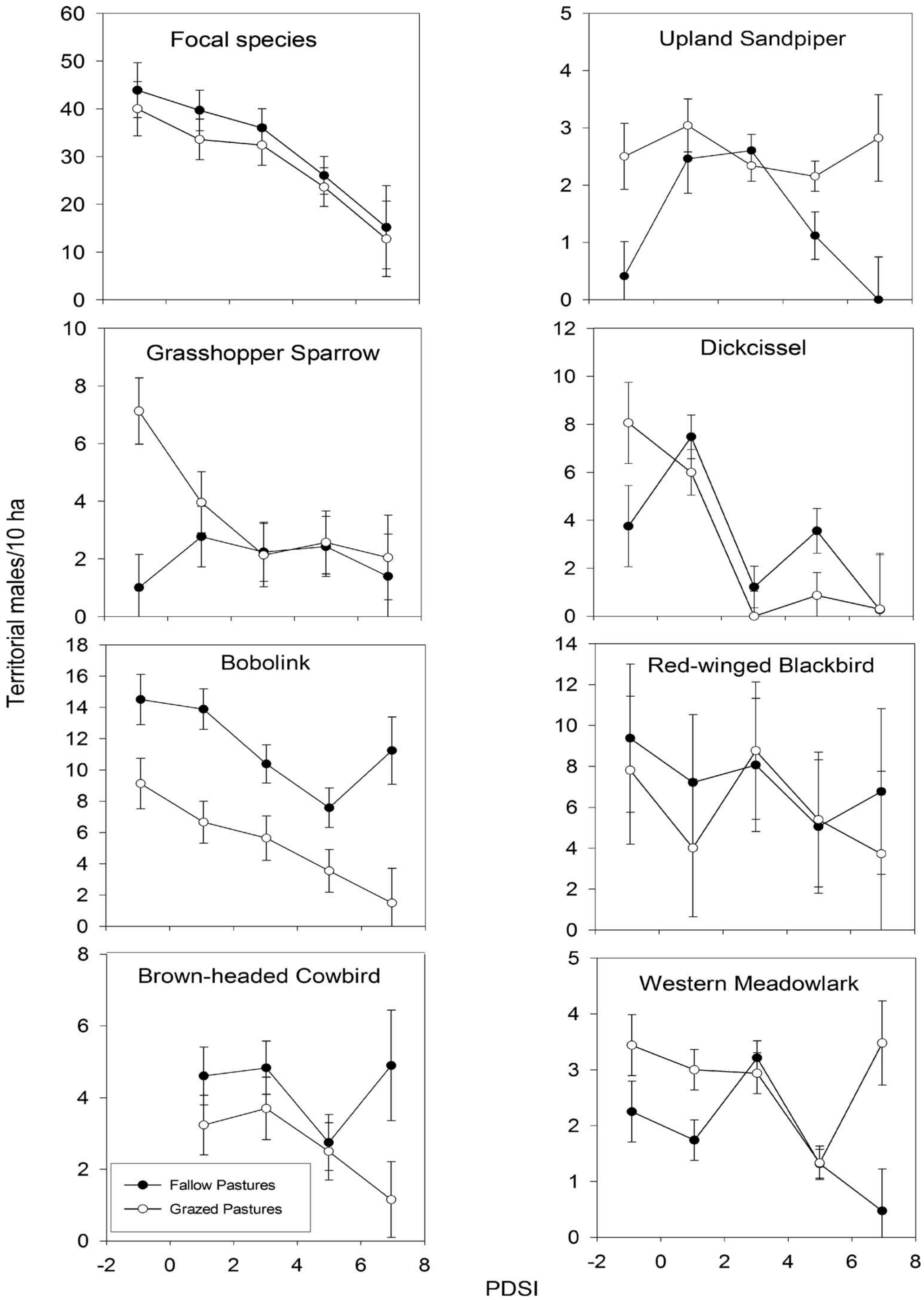

FIG. 1. Effects of moisture availability (Palmer Drought Severity Index or PDSI) on density of grassland birds. Open circles represent grazed plots, and closed circles represent ungrazed plots. The PDSI ranges from −2 (drier than normal, minimal standing water) to 8 (very wet, plots flooded).

some years, inundation may result from upstream releases from reservoirs on the Platte River rather than local precipitation patterns.

The Bobolink's predilection for ungrazed pastures is supported by findings from other studies (Bollinger 1995, Fritcher et al. 2004, Winter et al. 2005), and likely reflects this species' preference for moderate to tall, dense vegetation (Dechant et al. 2003b). The negative relationship between Bobolink densities and PDSI suggests that nest sites may be limited during wet years or there are moisture-related movements of Bobolink between riparian and upland grasslands. Some studies of banded Bobolink populations noted site fidelity increases with habitat quality in stable environments (Bollinger and Gavin 1989, Fletcher et al. 2006). Grazing and climatic fluctuations might remove predictability from riparian grasslands at our study sites, potentially facilitating movements at the patch scale.

We did not find a strong relationship between grazing and densities of Grasshopper Sparrow, Western Meadowlark, and Upland Sandpiper. Previous studies have reported these three species breed in actively managed (burned, grazed or hayed) grasslands (Dechant et al. 1999, 2003a, d), but the low overall densities for all three species limited the statistical power to detect a strong grazing-treatment effect. Upland Sandpipers typically are associated with early seral stages in grasslands, and Western Meadowlarks display intermediate habitat preferences with regional variation in their responses to disturbances (e.g., associated with recent disturbance in tallgrass prairie, associated with rested pastures in shortgrass prairie; Renfrew and Ribic 2001, Fritcher et al. 2004). The Upland Sandpiper was the only species that had an interaction between grazing and PDSI; however, the species had minimal variation in densities on grazed plots compared to ungrazed plots. Standing water on the ungrazed plots may have reduced suitability of ungrazed plots during extremely wet years for Upland Sandpipers or resulted in their movements to upland grasslands

Dickcissel and Red-winged Blackbird also displayed negative relationships with PDSI. Vegetation associations for Red-winged Blackbird appear more important than environmental conditions during selection of breeding habitat (Fletcher and Koford 2004). The association with PDSI may result from potential fluctuations in habitat suitability or in nest-site or prey availability while Dickcissels may respond to environmental conditions at either patch or regional scales. Drought conditions have been implicated as a proximate cause of Dickcissel irruptions in some areas (Taber 1947, Igl 1991). In addition, Dickcissel densities during dry or average PDSI years may be affected by interspecific interactions with Red-winged Blackbirds. To our knowledge, no studies have reported direct behavioral dominance of Red-winged Blackbirds over Dickcissels (Yasukawa and Searcy 1995, Temple 2002), although both species share similar nest-site selection (i.e., above ground nesters in grasslands). Dickcissels in the Platte River Valley initiate nesting 2–3 weeks after Red-winged Blackbirds, and the larger blackbird males often chase Dickcissel males from their territories (D. H. Kim, unpubl. data).

Cowbird densities in our study were higher in ungrazed plots compared to grazed plots, which is counter to information in the literature (e.g., Kostecke et al. 2003). Possible explanations include (1) regional cowbird densities are near capacity (Jensen and Cully 2005), (2) the spatial proximity of grazed pastures to ungrazed plots (<2 km) exert no energetic costs on female cowbirds moving among breeding and feeding areas (Goguen and Mathews 2001), or (3) host species' densities declined with grazing, offsetting the increased foraging opportunities for cowbirds. In our system, cowbird densities tracked Dickcissel and Red-winged Blackbird densities, but especially Bobolink densities, suggesting cowbirds may exploit the most common host species in the study area or that these four species share similar habitat preferences in this region

Available moisture may have profound effects on the avian community in sedge meadows and mesic grasslands. Declining species richness associated with drier conditions was consistent with other grassland bird studies (George et al. 1992, Zimmerman 1992), but declining densities with higher PDSI values suggests that sedge meadows and mesic grasslands may be less suitable for grassland birds during wet conditions. The pattern of increasing density associated with drought conditions in the Platte River Valley appears opposite of other reported studies (e.g., Igl and Johnson 1999). Individual species have different habitat requirements; therefore, changes in vegetation structure and amount of standing water should affect species individually. For example, Igl and Johnson (1999) found abundance of Le Conte's Sparrow (*Ammodramus leconteii*) increased with moisture availability in grasslands enrolled in the Conservation Reserve Program in the northern Great Plains. This unexpected pattern from our study could result from riparian wet-meadow grasslands acting as a refugia for species escaping drier conditions in regional upland areas. Dry conditions may cause birds to move from upland sites as vegetation structure and habitat suitability deteriorates with drought conditions. During dry years, wet-meadow habitats should remain suitable longer during the breeding season given the higher water table and greater soil moisture compared to upland sites.

Van Horne (1983) cautioned against using density as an indicator of habitat quality, especially in disturbed habitats. Additional research focusing on reproductive success over several years will be required to measure the importance of both climate and grazing on reproductive success for all seven species. For example, in Oregon, drought lowered annual reproductive success for Bobolinks (Wittenberger 1982). Dry conditions also may limit food availability for adults and young. Although some insects, such as orthopterans, may increase during dry conditions, the availability and biomass of lepidopteran larvae may decrease, restricting growth rates for young nestlings unable to efficiently process chitonous prey. In either case, birds may be able to assess the potential of food or nest-site availability based on the condition of grasslands at the beginning of the breeding season (early May in Nebraska) and to adjust their breeding densities accordingly.

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