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DENSITY-INDEPENDENT FACTORS AFFECTING THE AVIAN DIVERSITY OF THE TALLGRASS PRAIRIE COMMUNITY

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ABSTRACT.—The low species richness in grassland bird communities has been hypothesized to result from competition in a simplistic, saturated habitat (Cody) or to result from the periodic occurrence of climatic extremes that prevent drought-susceptible species from perennial settlement (Wiens). Predictions based on these two hypotheses were evaluated using June population estimates on burned and unburned tallgrass prairie over the decade, 1981–1990, on the Konza Prairie Research Natural Area, Kansas. The results of these analyses support the notion that drought tolerance is the primary factor that determines membership in the tallgrass prairie community. When drought and fire are coincidental, however, the community does respond in a manner commensurate with the saturation hypothesis by a reduction in bird abundances but not a decrease in species richness. *Received 9 May 1991, accepted 10 Sept. 1991.*

The avian community of the North American tallgrass prairie, like those of grasslands throughout the world, is not diverse, less than ten species being the norm (Cody 1966). Furthermore, the number of breeding species is not only small but relatively constant (Wiens 1973). While "the species occupying these grasslands are optimally adapted to present environmental conditions and are comprised of the best selection of the species potentially available for habitat occupancy" (Cody 1968:136), there is disagreement as to the definitive factors that provide this "best selection."

Cody (1966, 1968) considers these communities to be saturated, with the component species having divided up the limited resources available in the single-stratum vegetative substrate to the degree that there is no opportunity for exploitation by any additional species. Knopf et al. (1990) have suggested that birds inhabiting grassland-shrubsteppe use the vigor of the vegetation as a critical predictor of food availability, implying that food availability is an important dimension of their niches. This suggests to me, at least, that food is limiting and that competition does affect the structure of the community.

Wiens (1974), on the other hand, notes that the participation of birds in grassland ecosystem energy flow is minuscule (1.0–2.5 kcal/m^2 per season) and that there is no resource partitioning (Rotenberry and Wiens 1980), concluding that grassland communities are not saturated and hence competition cannot explain the low species richness. Rather, his analysis

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suggests that the paucity of grassland species results from periodic climatic extremes which, acting like a bottleneck, have permitted only a few species to survive and be successful during those times of environmental stress. As evidenced by the considerable annual variation in grassland bird densities (Wiens and Dyer 1975), populations then blossom during the intervening benign periods of more than adequate resources. Ricklefs (1987) also considers competition and niche theory to be inadequate in explaining local community diversity, since this notion excludes the effects of regional and evolutionary history as well as the impact of unique events and circumstances.

As part of the continuing NSF-supported Long-term Ecological Research effort at The Nature Conservancy's 3500-ha Konza Prairie Research Natural Area in Riley and Geary counties, Kansas, grassland bird populations have been measured during June for the past decade. Fire, imposed on watershed-sized areas at intervals from annually to every 20 years, is a major aspect of the experimental and management plan at Konza Prairie and provides a mechanism to investigate these contrasting explanations for grassland bird species diversity.

METHODS

During the first two weeks of June from 1981 through 1990, variable distance transects (Burnham et al. 1980) were completed over a distance of 1.58 km in burned prairie and from 3.27 to 6.83 km in unburned prairie on a set of permanently marked routes. The transects in burned prairie were located in two watersheds that had been burned in early April every year since either 1972 or 1978 and continued to be annually burned throughout the course of this study. The unburned transects were in seven watersheds that had not been burned since at least 1971, although 2.6 km of the total transect length had been affected by a wildfire in late April 1980. During the course of the study, however, no fires occurred, although total transect length had to be decreased as certain of the watersheds were shifted to other burning treatments in 1988 and 1989.

Although perpendicular distances of bird sightings are available in the data sets, numbers of records were insufficient to provide absolute density values for individual species. These data do provide annual, but unreplicated, measures of species richness and relative abundances in birds/km. Species seen only once in this decade were excluded from this analysis as were raptors, swallows, and the lekking Greater Prairie-Chickens (*Tympanuchus cupido*), taxa that are not adequately quantified by this method. While comparisons based on single-year censuses at different locations should be approached with skepticism (Wiens 1981), there are situations, such as annually repeated observations at the same locations, for which this approach is satisfactory (Kantrud 1981).

Precipitation data have been collected continuously on site since 1983. March soil moisture has been shown by Briggs and Knapp (pers. comm.) to be the best predictor of above-ground primary productivity, and these values were obtained at a depth of 25 cm with neutron probes and are based on a mean of two tubes per watershed and averaged across seven watersheds. Soil moisture data have been collected only since 1984.

Species recorded on unburned prairie were divided into core-species (recorded in all years) and erratics (recorded between 20% and 90% of the years). This restrictive definition for core-species was purposefully conservative so that any ambiguity resulting from the actual absence of a species or its apparent absence because of the limitations of the methodology would be circumvented, although it has been my experience that over these transect distances species that were present during a particular breeding season were seldom missed on the June transect. The core-species, in turn, were divided into those dependent on grassland habitats and those requiring significant presence of woody vegetation. The Brown-headed Cowbird (*Molothrus ater*), a core species, parasitizes hosts in all habitats and is classified as habitat independent. These same assignments were used for birds in burned prairie, although many of the core species were not perennial in that habitat.

RESULTS AND DISCUSSION

As is to be expected (see Risser et al. 1981), the diversity among the grass-dependent species is low, and most species (71%) are present only during the breeding season. Of these summer residents, 60% winter within the north temperate zone while the remainder winter in the neotropics or south temperate zone (Table 1, A.O.U. 1983).

Are grassland bird communities saturated?—Unburned prairie is spatially heterogeneous, presenting a mosaic of standing dead vegetation, C3 and C4 grasses, forbs, and woody vegetation. Annually burned prairie is more homogeneous, being floristically and structurally simple, since fire eliminates standing dead vegetation and ground litter and reduces coverage by C3 grasses, forbs, and woody vegetation (Gibson 1989). Thus fire results in a reduction in plant species richness. Fire also reduces evenness in the plant community by encouraging the dominance of the warm-season (C4) grasses, primarily big bluestem (*Andropogon gerardii*) (Collins and Gibson 1990). Fire also increases subsequent primary productivity (Knapp and Seastedt 1986), increasing energy resources available to consumer species (Evans 1988).

If grassland bird communities are saturated within limits imposed by the simplicity of the vegetative substrate, fire should reduce the number of bird species even more by further simplifying the vegetative structure of the community, yet increase the abundances of the remaining species by augmentating the energy resource base. When all species were considered (Table 2), there was a significant decrease in species richness with burning (Student's $t = 12.50$, df = 18, $P < 0.01$). This results primarily from the low coverage of woody vegetation on burned prairie and its unsuitability to woody-dependent core-species and most erratics. If just the grass-dependent core-species were considered, there was also a significant decrease in species richness (Student's $t = 11.36$, df = 18, $P < 0.01$). This latter result accrues from the preemptive impact of removal of litter and standing dead on Henslow's Sparrows (*Ammodramus henslowii*) (Zimmerman 1988) and the virtual elimination of Common Yellowthroats (*Geothlypis trichas*) on burned prairie, which is probably also

TABLE 1

MEAN (±SE) RELATIVE ABUNDANCES (BIRDS/KM) OF SPECIES RECORDED FROM 1981 THROUGH 1990 ON TRANSECTS IN UNBURNED AND BURNED TALLGRASS PRAIRIE ON THE KONZA PRAIRIE RESEARCH NATURAL AREA, KANSAS. (RAPTORS, PRAIRIE-CHICKENS, SWALLOWS EXCLUDED)

	Unburned	Burned
Core-species, present every year		
Grass-dependent species		
Ring-necked Pheasant, *Phasianus colchicus*	1.0 ± 0.16	0.2 ± 0.10[a]
Upland Sandpiper, *Bartramica longicauda*	2.9 ± 0.46	5.2 ± 0.70
Mourning Dove, *Zenaida macroura*	4.0 ± 0.39	2.2 ± 0.45
Common Yellowthroat, *Geothlypis trichas*	3.1 ± 0.39	0.2 ± 0.17[a]
Dickcissel, *Spiza americana*	13.9 ± 0.90	12.3 ± 1.86
Grasshopper Sparrow, *Ammodramus savannarum*	8.3 ± 0.67	6.8 ± 0.90
Henslow's Sparrow, *A. henslowii*	2.8 ± 0.59	0
Red-winged Blackbird, *Agelaius phoeniceus*	1.6 ± 0.22	3.8 ± 0.37
Eastern Meadowlark, *Sturnella magna*	8.0 ± 0.41	6.8 ± 0.80
Woody-dependent species		
Northern Bobwhite, *Colinus virginianus*	3.0 ± 0.47	1.2 ± 0.44[a]
Eastern Kingbird, *Tyrannus tyrannus*	1.4 ± 0.18	1.5 ± 0.19
House Wren, *Troglodytes aedon*	1.3 ± 0.29	0
Brown Thrasher, *Toxostoma rufum*	2.8 ± 0.23	0.7 ± 0.18[a]
Bell's Vireo, *Vireo bellii*	2.3 ± 0.52	0
Field Sparrow, *Spizella pusilla*	2.8 ± 0.45	0
Northern Oriole, *Icterus galbula*	0.4 ± 0.09	0.3 ± 0.10[a]
American Goldfinch, *Carduelis tristis*	2.3 ± 0.55	0
Habitat-independent species		
Brown-headed Cowbird, *Molothrus ater*	8.4 ± 0.51	6.1 ± 1.24
Erratic species, present 20–90% of years		
Grass-dependent species		
Killdeer, *Charadrius vociferus*	0.4 ± 0.03	0
Common Nighthawk, *Chordeiles minor*	0.3 ± 0.10	1.0 ± 0.36
Lark Sparrow, *Chondestes grammacus*	0.1 ± 0.03	0
Woody-dependent species		
Yellow-billed Cuckoo, *Coccyzus americanus*	0.6 ± 0.13	0
Red-headed Woodpecker, *Melanerpes erythrocephalus*	0.3 ± 0.06	0
Red-bellied Woodpecker, *M. carolinus*	0.1 ± 0.05	0
Northern Flicker, *Colaptes auratus*	0.7 ± 0.15	0.2 ± 0.10
Eastern Phoebe, *Sayornis phoebe*	0.1 ± 0.07	0
Great Crested Flycatcher, *Myiarchus crinitus*	0.2 ± 0.06	0
Blue Jay, *Cyanocitta cristata*	0.3 ± 0.08	0
Black-capped Chickadee, *Parus atricapillus*	0.1 ± 0.05	0
Tufted Titmouse, *P. bicolor*	0.1 ± 0.04	0
Eastern Bluebird, *Sialia sialis*	0.4 ± 0.24	0

TABLE 1

CONTINUED

	Unburned	Burned
American Robin, *Turdus migratorius*	0.2 ± 0.05	0.1 ± 0.08
Gray Catbird, *Dumetella carolinensis*	0.2 ± 0.08	0
Loggerhead Shrike, *Lanius ludovicianus*	0.2 ± 0.15	0
European Starling, *Sturnus vulgaris*	0.3 ± 0.12	0
Warbling Vireo, *Vireo gilvus*	0.1 ± 0.03	0
Yellow Warbler, *Dendroica petechia*	0.1 ± 0.03	0
Northern Cardinal, *Cardinalis cardinalis*	0.3 ± 0.10	0
Blue Grosbeak, *Guiraca caerulea*	0.1 ± 0.05	0
Rufous-sided Towhee, *Pipilo erythrophthalmus*	0.6 ± 0.56	0
Common Grackle, *Quiscalus quiscula*	0.1 ± 0.02	0.8 ± 0.28
Orchard Oriole, *Icterus spurius*	0.1 ± 0.09	0

[a] Present less than every year in burned prairie.

a result of the loss of litter. While both of these responses are in the direction predicted by the saturation hypothesis, the reductions are not due to competitive exclusion. Rather they are due to the eradication of critical niche dimensions by the alteration of the physical structure of the habitats.

Relative abundances were not modified in the expected direction, significantly decreasing rather than increasing when all species were considered (Student's $t = 4.46$, df = 18, $P < 0.01$) and not changing when just the grass-dependent core-species (exclusive of Henslow's Sparrows and Common Yellowthroats) were compared (Student's $t = 0.60$, df = 18, $P > 0.05$). The former results from the elimination of so many core and erratic species dependent upon woody vegetation. The absence of a difference in relative abundances of the grass-dependent core-species common to both treatments suggests that these populations are not at resource-imposed saturation levels, that indeed, the resource base of this bird community is not actually critical. Food resources are sufficient in unburned prairie, and the increases in both primary production and primary consumer populations in response to burning have no effect on the numbers of birds in the community. Indeed, resources appear sufficient, if not even superabundant.

Does a climatic bottleneck select species in the grassland bird community?—Precipitation is the variable that imposes the characteristic life form to grasslands from the mesic tallgrass prairie on the eastern edge of the rainshadow of the Rocky Mountains to the xeric short-grass plains that ascend to the foothills and spill over into the inter-mountain parks. Furthermore, precipitation is highly variable; abnormally wet or dry years

TABLE 2

ANNUAL SPECIES RICHNESS AND TOTAL RELATIVE ABUNDANCE (BIRDS/KM) IN BURNED AND UNBURNED TALLGRASS PRAIRIE

	All species[a]		Grass core-species		Woody core and erratic species	
Year	No.	Birds/km	No.	Birds/km	No.	Birds/km
Unburned prairie						
1981	26	52.4	9	34.1	16	11.0
1982	32	57.3	9	36.2	22	14.1
1983	35	69.2	9	44.1	25	18.5
1984	31	84.1	9	50.0	21	24.8
1985	34	76.8	9	47.2	24	21.0
1986	32	89.2	9	56.5	22	23.3
1987	33	98.5	9	54.0	23	33.5
1988	26	82.0	9	46.4	16	25.0
1989	23	71.6	9	45.9	13	19.9
1990	26	75.6	9	41.6	16	25.7
Mean	29.8	75.7	9	45.6[b]	19.8	21.7
SE	1.32	4.41	0	2.24	1.32	2.01
Burned prairie						
1981	12	48.7	6	38.6	5	5.7
1982	10	33.4	6	27.2	3	2.5
1983	10	44.3	7	32.3	2	1.9
1984	11	44.3	6	34.2	4	5.7
1985	11	41.8	6	34.8	4	3.2
1986	12	46.8	6	38.6	5	6.3
1987	14	74.7	8	55.1	5	7.0
1988	13	58.2	7	37.3	5	8.9
1989	15	41.8	7	27.8	7	9.5
1990	13	62.0	6	50.6	6	8.2
Mean	12.1	49.6	6.5	37.6	4.6	5.9
SE	0.53	3.81	0.22	2.84	0.40	0.75

[a] Includes Brown-headed Cowbird, hence is greater than the sum of the other two categories.

[b] This mean reduced to 39.7 for comparison with burned value by excluding totals for Henslow's Sparrow and Common Yellowthroat.

occur in tallgrass prairie about once every four years (Wiens 1974). If bird populations are affected by precipitation, there should be a correlation between their numbers and the amount of moisture available. The analysis of product-moment coefficients for a number of ways of expressing this variable on an annual basis correlated with the total relative abundances of birds per year in unburned and burned prairie revealed that March soil moisture is the only variable that was significantly correlated with both unburned ($r = 0.77$, $N = 7$, $P < 0.05$) and burned ($r = 0.80$, $N = 7$, $P < 0.05$) grassland bird numbers (Table 3).

TABLE 3

PEARSON PRODUCT-MOMENT CORRELATION COEFFICIENTS BETWEEN BIRDS/KM AND THE FOLLOWING VARIABLES

	Unburned	Burned
March soil moisture	0.77[a]	0.80[a]
Previous year's precipitation	0.81[a]	0.39
Current year's precipitation	0.31	−0.30
Current March–June precipitation	0.34	−0.20

[a] $P < 0.05$.

The saturation hypothesis was not supported by the effects of burning on species richness and relative abundance, but moisture availability provides a mechanism to not only again test that hypothesis, but the bottleneck hypothesis as well. If the saturation hypothesis for grass-dependent core-species is true, there should be a positive correlation between abundances and soil moisture, since soil moisture is positively correlated with aboveground productivity and hence a more structurally complex and energetically richer habitat. If the bottleneck hypothesis is true, however, there should be no correlation between the relative abundances of the grass-dependent core-species and soil moisture, since these species are present because they have been affected by previous selective impacts of climatic extremes. These species tolerate these extremes, and March soil moisture, for example, should be irrelevant to their abundance.

The woody-dependent core-species as well as the erratics are not grassland species in the strict sense (see Mengel 1970), but have invaded the tallgrass prairie through the forest-prairie mosaic to the east. Thus they have not been influenced in their evolution by the assumed bottleneck of climatic extremes. As a control comparison, the relative abundances of these two species groups have been combined and similarly related to March soil moisture. In habitats where periodic aridity is not a characteristic of the environment, drought does markedly decrease breeding densities (Smith 1982). I expected, therefore, that these numbers should be positively correlated with soil moisture.

When this analysis was completed for populations on unburned prairie, the results support the bottleneck hypothesis. The correlation for the grass-dependent core-species was not significant ($r = 0.40$), whereas that for the woody-dependent core-species and erratics was positive and significant ($r = 0.86$, $N = 7$, $P < 0.01$). When the same analysis was done for burned prairie, however, the relationships were reversed. The numbers of grass-dependent core-species were significantly correlated with March soil moisture ($r = 0.94$, N = 7, $P < 0.01$), but those of the woody-dependent core-species and erratics were not ($r = 0.10$).

The lack of significance for this latter group is arithmetic. Their abundances are so low in burned prairie (Table 2) that they do not generate the necessary differences in products that are part of the computation. The interesting question, of course, is why there is a significant correlation of the relative abundances of the grass-dependent core-species with soil moisture in burned prairie, even though the bottleneck hypothesis predicts that this relationship should not exist, as it did not in unburned prairie.

I suggest that in the tallgrass prairie, the appropriate species are indeed few because they are the hardy few that can withstand the periodic occurrence of climatic severity, and their populations are not affected by these extremes as long as the structural complexity of the habitat has not fallen below some threshold level. In normal and wet years, above-ground plant biomass is usually greater on burned prairie than it is on unburned prairie (Hulbert 1988), but in drought years the primary productivity of burned prairie drops below that of unburned prairie (Briggs et al. 1989). Fire induces a reduction in the structural complexity of the prairie, but on average, this change does not significantly depress relative abundances among the grass-dependent core-species when moisture is sufficient. When drought inhibits the above-ground productivity of burned prairie to a level below an acceptable threshold, however, fire does affect these bird populations.

The controversy regarding the factors that affect bird diversity in grasslands appears to be a function of whether the biotic factors (vegetative structure and food resources) result in saturation and the ensuing interspecific competition involved in their utilization determines species richness or whether it is the abiotic factors (climatic instability) that select for a set of "bottleneck-tolerant" species without the operation of competition. My analysis suggests that adaptation to periodic drought imposes the primary requirement for membership by the grass-dependent core-species in the tallgrass prairie community. The low species richness reflects the reality that few species have this ability. Since the North American grassland biome is a relatively young assemblage of species, perhaps few species actually have had the time to evolve this tolerance (F. Knopf, pers. comm.). Fire has a direct structural impact on the community and eliminates certain species by affecting critical dimensions of their niches, not as a result of competitive resource partitioning, but rather by obliterating species-appropriate resource space. In average and wet years, fire does not increase bird abundance concomitant with an increase in trophic resources as would be expected if the community were saturated. When drought is coupled with periodic fire, however, the community does reach a state of biotic saturation so that even these drought-adapted species suffer a decrease in abundance, although no species drops out entirely from the community. Wiens (1974) had speculated that this could occur.

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