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IMPACTS OF A SEVERE DROUGHT ON GRASSLAND BIRDS IN WESTERN NORTH DAKOTA[1]

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Abstract. We studied the effect of a severe drought on the population dynamics and community structure of grassland birds in western North Dakota. During the spring and summer of 1988 the northern Great Plains suffered one of the warmest, driest periods in its recorded history. We compared the changes in bird populations and nesting productivity over a 3-yr period before, during, and after the drought. Total grassland bird density declined 61% ($P < .05$) between June 1987 and June 1988. Densities of six of eight common species declined significantly during the drought. Populations of all but two species recovered in 1989 and total bird density in June 1989 did not differ significantly from June 1987. Species richness and species diversity both declined significantly during the drought and recovered to predrought levels in 1989. Species richness declined more on fair condition than on good condition range during the drought.

Vesper Sparrow (*Pooecetes gramineus*) hatching success, number of young fledged per successful nest, and nesting success were significantly lower in 1988 than either 1987 or 1989. Clutch size did not differ among the three years. The decline in nesting success in 1988 was primarily due to nest abandonment during incubation. Nesting of Vesper Sparrows, Horned Larks (*Eremophila alpestris*), and Western Meadowlarks (*Sturnella neglecta*) ended abruptly in mid-June 1988 during a period of extremely hot weather. In 1987 and 1989, nesting continued into July.

Despite substantial reductions in bird density and productivity during the drought, many species recovered to predrought levels 1 yr following the drought. This suggests that year-to-year fluctuations in densities of some of these species may not be tightly linked to short-term changes in local productivity. However, sequential years of low productivity may have more substantial effects on these short-lived species. Thus, if drought conditions in North American grasslands become more frequent, as some climate models predict, there could be related changes in the avifauna of the region.

Key words: density changes; drought; grassland bird community; nesting phenology; nesting productivity; North Dakota; Pooecetes; *range condition.*

INTRODUCTION

Grassland bird communities are characterized by large temporal and spatial variation in breeding densities (Giezentanner 1970, Wiens 1973, 1974, 1977, Kantrud 1981, Dale 1984). Wiens (1974, 1977, 1986) has suggested that these fluctuations are driven in part by the extreme variability in climatic conditions during the breeding season, leading to "ecological crunches" that greatly reduce density or productivity and may have profound effects on bird community structure. Despite this emphasis on the effects of climatic variability on the structure of grassland bird communities, there has been little documentation of the community response to severe climatological events during the breeding season.

Variation in temperature and precipitation may affect bird populations either indirectly, through habitat changes, or directly, through heat stress or water restriction (Immelmann 1971, Wiens 1974, Smith 1982, Morrison 1986). Vegetation coverage and physiognomy may change drastically in response to drought conditions in grassland habitats (Weaver and Albertson 1956). Many studies have shown that densities of grassland bird species are influenced by the structure and coverage of vegetation (Cody 1968, Wiens 1969, Rotenberry and Wiens 1980*a*, Bock and Webb 1984). In addition, arthropod abundance may decline in response to severe drought in arid (Seely and Louw 1980) and mesic environments (Smith 1982). A decline in arthropod abundance may reduce the nesting productivity of omnivorous bird species that require animal food for nestlings.

The drought of 1988 in the northern Great Plains was one of the most severe on record. The months of May–July 1988 were both the hottest and driest on record for the 1931–1988 period for most of Montana, North Dakota, and Minnesota (USDA/NOAA 1988). This was a consequence of below normal spring precipitation and record high temperatures in June and July throughout the northern Great Plains. Furthermore, much of this region had been suffering from

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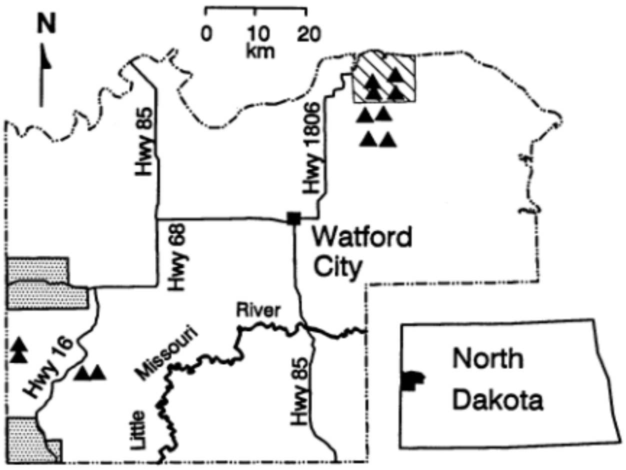

FIG. 1. Location of bird census transects (▲) and grasshopper treatment areas (▨ *Nosema locustae*; ▒ malathion) in McKenzie County, North Dakota.

below normal precipitation since the early 1980s. Several climate models predict that the northern Great Plains will become hotter and drier in the next several decades (Schneider 1989). Understanding the effects of drought on the dynamics of bird populations (Peters 1988) can be helpful when considering the impacts of climate change on bird communities in this region. In this paper we report the effects of a severe drought on grassland bird density, productivity, and community patterns in western North Dakota.

STUDY AREA AND METHODS

Our study was conducted in and adjacent to the Little Missouri National Grasslands in western North Dakota. The vegetation of the area is mixed-grass prairie dominated by *Bouteloua gracilis* with a diverse layer of taller grasses (including *Stipa comata, Agropyron smithii,* and *Koeleria cristata*) and sedges (*Carex* spp.) (Weaver and Albertson 1956). Draws (shallow ravines) usually are dominated by shrubs (*Symphoricarpos occidentalis, Artemisia cana,* and *Shepherdia argentea*) or trees (*Populus deltoides, Fraxinus pennsylvanica, Juniperus scopulorum,* and *Ulmus americana*). The Little Missouri National Grasslands is one of two demonstration areas for the Grasshopper Integrated Pest Management Project of the United States Department of Agriculture's (USDA) Animal Plant Health Inspection Service (APHIS). This is a long-term project to develop integrated grasshopper control methods that have minimal impacts on nontarget plant and animal populations.

Temperature and precipitation data were obtained from the Watford City weather station, near the center of the study area (Fig. 1). Precipitation and temperature data were available for a 37-yr period (1953–1989).

Bird censuses and range condition.—Birds were censused using a line-transect method (Emlen 1977). Transects were established in June 1987 in areas that were treated with *Nosema locustae* spores in bran bait (a biological control agent for grasshoppers) or with the pesticide malathion (0.65 kg/ha). In addition, control transects were established in similar habitat adjacent to the treatment areas. The transects in the malathion treatment areas were not included in the following analyses because the treatments may have affected bird populations in these areas (T. L. George et al., *unpublished data*). There was no significant reduction in grasshopper densities in the *Nosema* treatment area (N. Foster, *personal communication*) and the bait contained no toxic chemicals. When the *Nosema* transects were excluded from the analyses the patterns were identical, but some of the differences were nonsignificant because of low statistical power. Therefore, transects in the *Nosema* treatment area were included in the analyses. All transects were placed in relatively uniform grassland or grass–shrub vegetation; wooded draws were avoided because the bird species composition in these draws differed greatly from the grasslands. Transects were at least 400 m apart.

Four 1500-m transects were established in the *Nosema* treatment area, and four control transects of equal length were established 2–10 km south of the treatment area (Fig. 1). Four 1000-m transects were established 5–10 km from the malathion treatment areas (Fig. 1). Thus, 12 transects were used in these analyses. Each transect was marked at 100-m intervals and flags were placed perpendicular to the transect route 10 and 25 m from some transect markers to aid in estimation of bird distances from the transect line. Birds were censused from ≈15 min prior to sunrise (≈0545) until 0830–0900. Each transect was censused independently by two observers on the same morning. The distance of each bird that was seen or heard and the manner in which the bird was detected (singing, visual, calling, both visual and auditory, or flying over) were recorded as the observer slowly walked the transect (≈2 km/h). Distances were grouped into categories: 0–10 m, 11–25 m, 26–50 m, 51–100 m, 101–150 m, and 151–200 m. Transects were censused in late May and late June in each season except 1987, when they were censused only in June. The May censuses (23–28 May 1988, and 26–31 May 1989) coincided with beginning of the nesting season for most species (Fig. 2). The June censuses (19–28 June 1987, 25–26 June 1988, 25–29 June 1989) coincided with the peak of the renesting period. Only the control transects (those outside of the *Nosema* treatment area in 1987) were censused in June 1988.

Observations of the 15 following grassland bird species (species that nest or forage primarily in grassland vegetation) commonly observed along the transects were combined to estimate grassland bird density: Sharp-tailed Grouse (*Tympanuchus phasianellus*), Upland Sandpiper (*Bartramia longicauda*), Mourning Dove (*Zenaida macroura*), Eastern Kingbird (*Tyrannus tyrannus*), Horned Lark (*Eremophila alpestris*), Sprague's Pipit (*Anthus spragueii*), Clay-colored Sparrow (*Spi-*

zella pallida), Field Sparrow (*S. pusilla*), Vesper Sparrow (*Pooecetes gramineus*), Lark Sparrow (*Chondestes grammacus*), Baird's Sparrow (*Ammodramus bairdii*), Grasshopper Sparrow (*A. savannarum*), Western Meadowlark (*Sturnella neglecta*), Brewer's Blackbird (*Euphagus cyanocephalus*), and Brown-headed Cowbird (*Molothrus ater*). Lark Buntings (*Calamospiza melanocorys*) were observed very rarely along the transects (nine times in 3 yr) and were not included in the analyses.

We computed a relative density index by selecting a detection distance for each species following Reynolds et al. (1980) and dividing the area sampled by the number of detections. Species richness was the number of species detected along the transect. Species diversity was calculated as the inverse of Simpson's index, $N_2 = 1/\Sigma\ (p_i)^2$, where p_i is the proportional density of species i. As suggested by Hill (1973), species evenness was calculated using the formula $E = N_2/N_1$, where $N_1 = \exp(-\Sigma\ p_i \ln\ p_i)$.

The condition of the vegetation along the bird census transects was obtained from the United States Forest Service. Range condition was rated by Forest Service personnel as good, fair, or poor, based on soil type and ocular estimates of the cover of dominant grasses. All of the pastures where the bird transects were located were rated as good ($N = 9$), fair-to-good ($N = 2$), or fair ($N = 1$). We pooled pastures rated as fair-to-good and fair for analysis.

Nesting success.—Nests were located by dragging a heavy rope between two observers and searching where birds flushed; nests were also found incidentally while conducting field work. Each nest was checked at 1–4 d intervals until the young fledged or the nest failed. We monitored nests of all species we encountered; however, sample sizes for statistical comparison of nesting parameters between years were sufficient only for Vesper Sparrows. Nests in areas treated with malathion in 1987 or with carbaryl in 1988 were excluded from the analyses because these treatments may depress nesting success (T. L. George et al., *unpublished data*).

Nesting success was estimated using the Mayfield (1961, 1975) method. Estimates of daily survivorship were calculated separately for the incubation and nestling periods and nesting success was calculated as the product of the survivorship estimates for the two periods (following Hensler 1985). The variance of the estimate was calculated following Hensler (1985).

In addition to nesting success, we tabulated clutch size, percent of eggs hatched, number of young fledged per successful nest, and number fledged per nesting attempt. Clutch size was the maximum number of eggs in a nest if the clutch was complete. A clutch was considered complete when the number of eggs was constant for two consecutive visits to the nest. The percent of eggs hatched was calculated as the proportion of young that hatched from eggs that were present in the nest during the visit prior to hatching. When a nest was abandoned during incubation, percent hatched was recorded as zero. The number of young fledged was the number of young in the nest on day 7–9 post-hatching. All comparisons were made using the number of young fledged from successful nests (nests in which at least one young fledged). The number of young fledged per nesting attempt was calculated as the product of nesting success and the number of young fledged per successful nest.

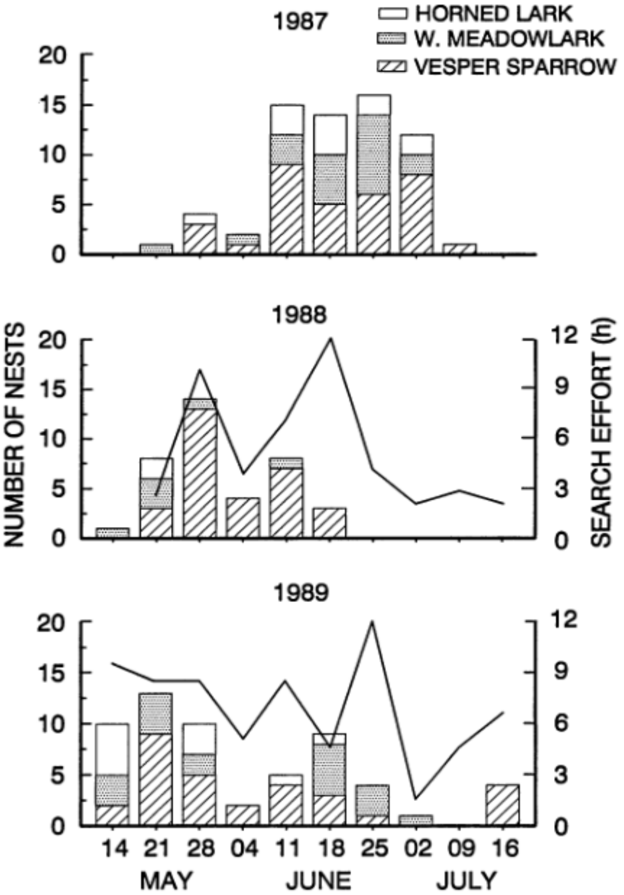

FIG. 2. Number of nests of Horned Larks, Western Meadowlarks, and Vesper Sparrows initiated during 7-d intervals in 1987, 1988, and 1989 (histogram bars, left ordinate). Dates are midpoints of intervals. Curves show nest search time (h).

Nesting phenology.—Nesting phenology was estimated for the three most common nesting species: Horned Larks, Vesper Sparrows, and Western Meadowlarks. The date of initiation of incubation was assumed to be the day the last egg in a clutch was laid, a common pattern in passerines (Gill 1990). This was estimated based on laying sequence, hatch date, or the age of the young (assuming an incubation period of 12 d for Horned Larks and Vesper Sparrows and 14 d for Western Meadowlarks [Harrison 1984]). If the nest was destroyed before the young hatched and the nest had not been found during laying, the date of nest initiation for Horned Larks and Vesper Sparrows was assumed

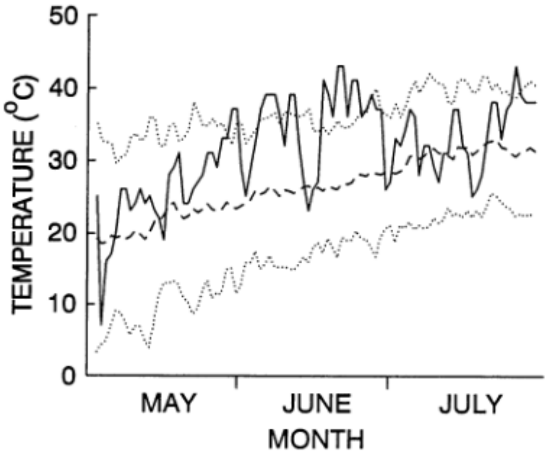

FIG. 3. Daily high temperatures in 1988 at Watford City, North Dakota (——), mean high temperature (– – –) for period 1953–1987, 1989, and upper and lower 95% confidence limits around mean (· · · · ·) for same years.

to be 6 d prior to the midpoint of the period when the nest was active; 7 d were assumed for Western Meadowlarks. The number of hours we searched for nests using the rope-dragging technique was recorded in 1988 and 1989.

Analyses

Weather data.—We calculated $\bar{X} \pm 1$ SD of daily high temperatures of 1953–1987, 1989 during the principal nesting period (May–July) and compared this to the temperatures recorded in 1988. June 1988 was abnormally hot (USDA/NOAA 1988), so we compared the average daily highs in June 1987–1989 with the other years. April–July precipitation provides most of the moisture used by native plants and is highly correlated with vegetative productivity in the northern Great Plains (Rogler and Haas 1947). We compared April–July precipitation in 1987–1989 with the long-term mean (1953–1986).

Bird census data.—Total bird density, densities of the eight most common bird species, and community measures (species richness, diversity, and evenness) were compared between years and months (May vs. June) using a two-way ANOVA with census period and transect number as the effects. In this model there is no replication, and therefore the test of the effect of census period assumes no interaction between census period and transect number (Sokal and Rohlf 1981: 344). The data were tested for equality of variance using Hartley's test (Neter and Waserman 1974:512–513). If the variances were equal and the effect of census period was significant in the ANOVA, differences between census periods were compared using Ryan's Q multiple range test (following the recommendations of Day and Quinn 1989). If the equality of variance assumption was not met, the effect of census period was tested using a paired multiple random permutation procedure (MRPP; Mielke and Berry 1982). The MRPP test makes no assumptions about the underlying distribution of the data or equality of variances, and therefore is appropriate for these kinds of comparisons (Biondini et al. 1988). Software (BLOSSOM) for the MRPP procedure was obtained from Brian Cade (United States Fish and Wildlife Service, National Ecology Research Center). The effects of range condition on bird density and community measures were tested with a repeated-measures ANOVA. Differences in means on fair and good rangeland sites between the first census period (June 1987) and subsequent periods were compared with linear contrasts. All parametric statistical tests were done with PC-SAS using a fixed effects model (SAS 1988).

Nesting parameters.—Clutch size generally decreases during the season in passerines (Klomp 1970), and we noted a significant decline in clutch size of Vesper Sparrows over the season ($F_{3,34} = 5.44$, $P = .026$). To control for seasonal decreases, clutch size was compared between years using analysis of covariance (ANCOVA) with day of year as the covariate. There was no significant effect of day of year on percent hatched or number fledged from successful nests, and these variables were not normally distributed; therefore, differences in these parameters were tested using a nonparametric Kruskal-Wallis test (Sokal and Rohlf 1981: 429–432). Nesting success was compared using a z test. The variance estimate for number of young fledged per nest attempt was calculated using the exact formula for calculating the variance of a product (Goodman 1960), and differences between means were compared using a z test.

RESULTS

Weather.—Daily high temperatures were above normal for most of May and June 1988 and were well above the 95% confidence intervals in late June (Fig. 3). Average high temperatures during June 1988 were 4.7 standard deviations above the 34-yr mean (Fig. 4). Temperatures were above average in June 1987 and 1988 (2.0 and 0.2 SD above the mean, respectively). However, the deviations in 1987 and 1989 did not approach the extreme high temperatures recorded in June 1988. April–July precipitation in 1988 was 1.6 standard deviations below the 34-yr mean (Fig. 4). While precipitation during this period was below normal in 1987 and 1989, it was closer to the long-term mean (1.0 and 0.3 SD below the mean, respectively). April–July precipitation in Watford City had been at or below normal since 1979. Thus the area was suffering a long-term precipitation deficit before the 1988 drought started.

Bird density and diversity.—Total grassland bird density declined 35% between June 1987 and May 1988 and decreased an additional 37% from May to June 1988, resulting in a 61% decline between June 1987 and June 1988 (Fig. 5). Densities increased be-

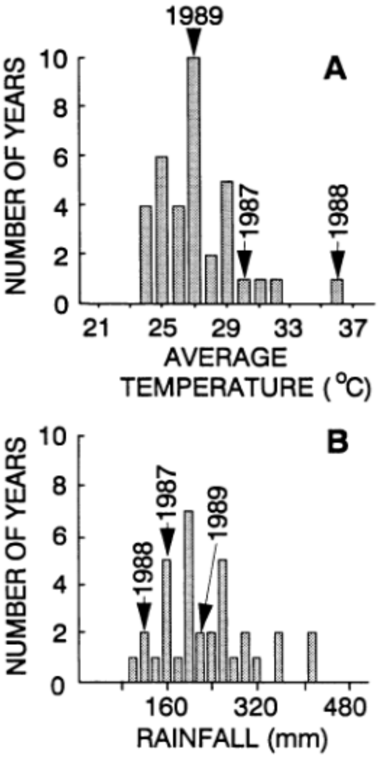

FIG. 4. Average daily high temperatures during June and total April–July rainfall in Watford City, North Dakota for years 1953–1989. Numbers on the x axis are the upper bounds on the intervals.

tween June 1988 and June 1989, and by the latter date were not significantly different from June 1987.

Densities of the eight most common grassland bird species fluctuated greatly during the period (Fig. 6). Horned Lark densities declined between June 1987 and June 1988, but increased to 64% higher in June 1989 than June 1987. Horned Larks were the only species that showed an overall increase during the study. Western Meadowlark densities did not vary significantly over the course of the study. Vesper Sparrows declined monotonically between June 1987 and May 1989. They increased slightly in June 1989, but were still 52% lower than June 1987 ($P < .05$). Densities of Baird's Sparrows and Sprague's Pipits declined sharply between June 1987 and May and June 1988, followed by partial recovery in 1989. Grasshopper Sparrows showed a decline similar to the previous species between 1987 and 1988, but recovered completely in 1989. Clay-colored Sparrows gradually declined between June 1987 and June 1989, although there was a nonsignificant increase in June 1988. The density of Clay-colored Sparrows in June 1989 was 78% lower than in June 1987 ($P < .05$); this was the greatest decrease of any species over this period. Field Sparrows declined 66% between June 1987 and June 1988, but returned to predrought numbers by June 1989.

Both species richness and diversity declined significantly between June 1987 and June 1988 and recovered to predrought levels by June 1989 (Fig. 7). Evenness increased slightly in 1988 and then declined to 1987 levels in 1989. The decline in species richness between 1987 and 1988 was largely a result of the absence of Sprague's Pipits, Baird's Sparrows, and Grasshopper Sparrows from many of the transects. The parallel decline in species diversity during this period was due to the decline in richness of the community; evenness was slightly higher in 1988.

Range condition had a significant effect only on Vesper Sparrow density, which was significantly lower on the fair than the good condition range (Table 1). However, the response of bird density and diversity to the drought is more appropriately tested by analyzing the interaction between period and condition and the contrasts between the first census period and subsequent periods. The period × condition interaction was significant for species diversity, but none of the linear contrasts between the first period and subsequent periods were significant ($P > .07$ for all comparisons). Although there was no significant interaction for species richness, there was a significant decline in richness ($F_{1,6} = 9.18$, $P = .023$) on the fair relative to the good condition sites between June 1987 and May 1988 (Fig. 8). The relative decline in Vesper Sparrow density was greater on the good than fair condition sites in May 1988, and May and June 1989 ($F_{1,6} = 7.51$, $P = .034$; $F_{1,6} = 30.26$, $P = .002$; $F_{1,6} = 26.23$, $P = .002$, respectively). Horned Lark density was significantly higher on the fair relative to the good sites in May 1989 ($F_{1,6} = 8.83$, $P = .025$).

Nesting success.—Clutch size did not differ significantly among the three years when seasonal changes in incubation date were included in the ANCOVA model (Table 2). Percent hatched, number of young fledged, and nesting success were all significantly lower in 1988 than either 1987 or 1989. The decline in percent hatched in 1988 was primarily due to nest abandonment. If abandoned nests are eliminated from the analysis, hatching success in 1988 was only slightly

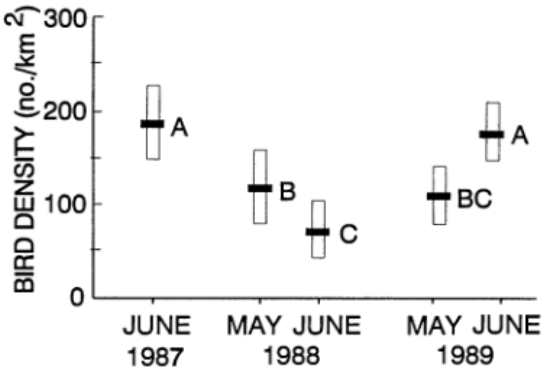

FIG. 5. Total grassland bird density on census transects 1987–1989. Means (horizontal solid lines; rectangles are ±2 SE) with different letters differ significantly ($P < .05$, Ryan's Q). Effect of census period was tested with ANOVA ($F_{4,40} = 19.41$, $P = .0001$).

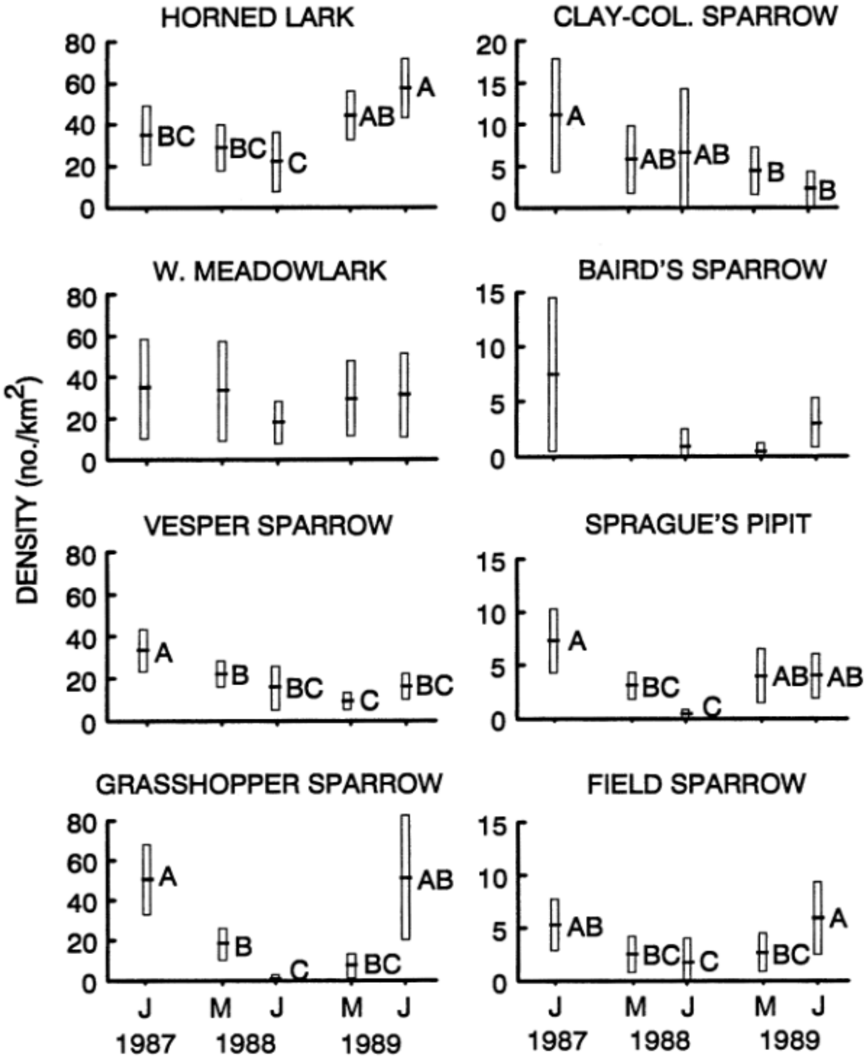

FIG. 6. Relative density of individual bird species along census transects 1987–1989. Means (horizontal lines; rectangles are ±2 SE) with different letters differ significantly ($P < .05$). Effect of census period was tested with ANOVA for Horned Lark ($F_{4,40} = 10.10$, $P < .0001$), Western Meadowlark ($F_{4,40} = 6.15$, $P = .0006$), Vesper Sparrow ($F_{4,40} = 9.90$, $P < .0001$), Clay-colored Sparrow ($F_{4,40} = 5.85$, $P = .0008$), Sprague's Pipit ($F_{4,40} = 5.35$, $P = .002$), and Field Sparrow ($F_{4,40} = 4.27$, $P = .006$). Ryan's Q test was used for multiple comparisons with the ANOVA tests. Differences in means for the other species were compared using a paired multiple random permutation procedure (MRPP) (Mielke and Berry 1982). Alpha levels for the MRPP were protected for multiple comparisons using a Bonferroni adjustment.

below the other two years and did not differ significantly (82.0, 70.7, 83.5% for 1987, 1988, 1989, respectively; $P > .1$ for all comparisons). The decline in nesting success in 1988 was largely a result of low success during incubation. The proportion of nests surviving the incubation period was 0.47 in 1987, 0.22 in 1988, and 0.60 in 1989 ($P = .008$ between 1988 and 1989). There were no significant differences in daily survivorship during the nestling period between any of the years. The number of young fledged per nest attempt was much greater in 1987 than 1988, but the difference was not significant ($z = 1.48$, $P = .14$) due to the large variance associated with the 1987 estimate. Number of young fledged per nest attempt was significantly higher in 1989 than in 1988; there was no difference between 1987 and 1989.

There were insufficient numbers of nests of Horned Larks and Western Meadowlarks to make statistical tests of nesting success between years, but nesting productivity appeared to be low in 1988 for both of these species. Only 2 Horned Lark nests were found in 1988 while 10 and 11 were found in 1987 and 1989, respectively. Similarly, we found 19 Western Meadowlark nests in 1987 and 1989 and 6 in 1988.

Nesting phenology.—Nest initiation of Horned Larks, Western Meadowlarks, and Vesper Sparrows ended abruptly during the last week of June in 1988, but continued into early July in both 1987 and 1989 (Fig.

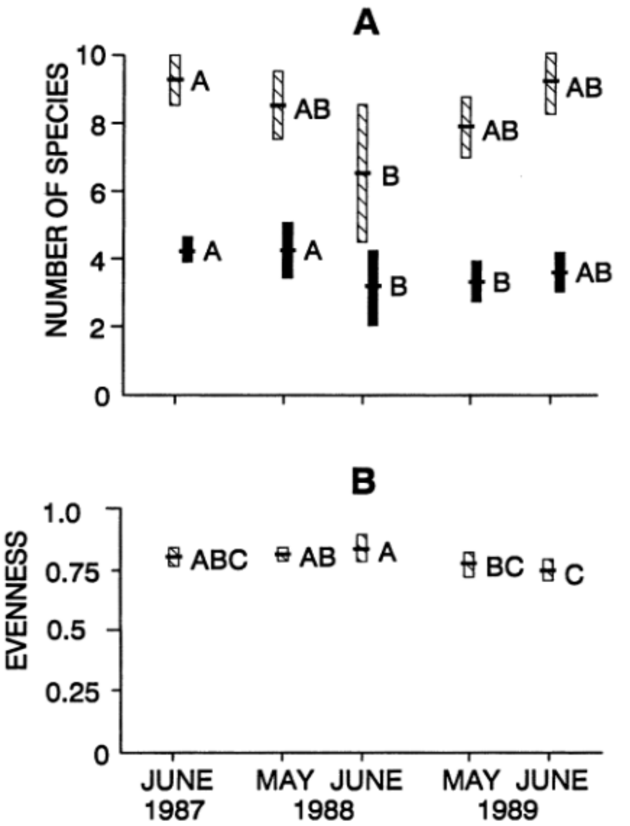

FIG. 7. Species richness (hatched bars), and species diversity (solid bars) (A) and evenness (B) of grassland birds 1987–1989. Means (horizontal lines; rectangles are ±2 SE) with different letters differ significantly ($P < .05$, Ryan's Q). Effect of census period for species richness ($F_{4,40} = 6.5$, $P = .0004$), species diversity ($F_{4,40} = 4.62$, $P = .004$), and species evenness ($F_{4,40} = 3.70$, $P = .012$) was tested with ANOVA.

2). The absence of recorded nests in late June and July 1988 was not due to a lack of searching effort. We continued rope dragging until the second week in July in 1988, but failed to find any nests in the last week of June or the first two weeks of July (Fig. 2). In 1987, we did not begin dragging for nests until 12 June, which accounts for the low number of early nests in that year.

DISCUSSION

The grassland bird community in western North Dakota was severely impacted by the drought of 1988. The large decline in total bird density and the reduction in nesting productivity of the common grassland species suggest that the drought produced an "ecological crunch" on the community. The recovery of total bird density in 1989 shows that many species can rapidly rebound from such crunches. Some species, however, did not recover, indicating that species differed in their "tracking inertia" (Wiens 1986). Thus, these kinds of environmental changes may leave an imprint on the bird community after the event.

Changes in community parameters during and after the drought were the result of different responses by the species. The decline in species richness and diversity during the drought was largely due to decreases in one common species, the Grasshopper Sparrow, and several less common species (Sprague's Pipit, Clay-colored Sparrow, and Baird's Sparrow). This was coupled with relatively little change of two other common species, Horned Larks and Western Meadowlarks. Thus, the community shifted from a relatively diverse assemblage of both common and uncommon species to one dominated by fewer, widespread, common species. This kind of shift in community composition has been observed in other grassland bird communities in response to dry weather (Dale 1984, Cody 1985) and is similar to the changes associated with heavy grazing in semi-arid grasslands (Ryder 1980, Kantrud 1981, Bock and Webb 1984).

TABLE 1. Effect of range condition on bird density and community measures.

	Condition		Period × Condition	
Variable	F	P	F	P
Horned Lark	0.02	.88	1.59	.37
Vesper Sparrow	42.68	.0006	7.74	.062
W. Meadowlark	5.69	.054	6.75	.073
Total density	0.89	.38	1.03	.51
Species richness	1.42	.28	2.38	.25
Species diversity	1.14	.33	86.6	.002
Species evenness	0.51	.50	2.17	.28

The greater decline in species richness on fair relative to good condition range during the drought suggests that managing for good condition range may ameliorate the effects of drought on some grassland bird populations. Unfortunately, there is little information on

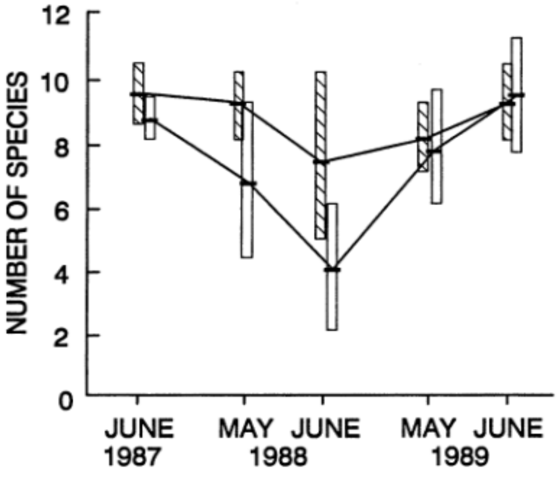

FIG. 8. Species richness on good (hatched bars) and fair (open bars) condition range 1987–1989 (horizontal lines are means; rectangles are ±2 SE). Effect of condition ($F_{1,6} = 1.42$, $P = .28$), period ($F_{4,3} = 7.92$, $P = .06$), and period × condition ($F_{4,3} = 2.38$, $P = .25$) was tested with ANOVA. Species richness significantly declined on poor relative to good condition range in May 1988 ($F_{1,16} = 9.18$, $P = .023$, linear contrast between June 1987 and May 1988).

TABLE 2. Reproductive parameters for Vesper Sparrows 1987–1989. Means followed by different superscript letters differ significantly ($P < .05$).* Differences in clutch size were tested using ANCOVA with year and date of incubation as the main effects. Nesting success and number of young fledged per nesting attempt were compared between years with z tests.

	Clutch size		Percent hatched		Number fledged		Nesting success†		Number fledged/attempt
Year	$\bar{X} \pm 2$ SE	N	$\bar{X} \pm 2$ SE	N	$\bar{X} \pm 2$ SE	N	$\bar{X} \pm 2$ SE	N	$\bar{X} \pm 2$ SE
1987	3.5 ± 0.26	21	75.7 ± 18^{a}	13	3.0 ± 0.7^{a}	11	0.32 ± 0.26^{a}	21	0.96 ± 1.10^{ab}
1988	4.1 ± 0.22	16	33.0 ± 21^{b}	15	1.4 ± 0.8^{b}	5	0.10 ± 0.10^{b}	25	0.14 ± .24^{a}
1989	4.0 ± 0.32	13	71.0 ± 16^{a}	20	3.2 ± 0.5^{a}	13	0.36 ± 0.20^{a}	29	1.15 ± .90^{b}

* The effect of year on clutch size was not significant ($F_{2,42} = 0.92$, $P = .41$). The effect of year was significant for both percent hatched ($\chi^2 = 9.21$, df = 2, $P = .01$) and number of young fledged ($\chi^2 = 7.73$, df = 2, $P = .02$), Kruskal-Wallis tests.

† Nesting success (proportion of nests fledging one or more young) was estimated using the Mayfield method (Mayfield 1975).

the interaction between drought and range condition on grassland bird communities. Dale (1984) found that species richness declined more on heavily grazed than on ungrazed pasture during a drought in mixed-grass prairie in Saskatchewan. Wiens and Dyer (1975), on the other hand, found no consistent relationship between yearly changes in bird numbers and grazing intensity over a 3-yr period (which included a drought year) on short-grass and mixed-grass prairie sites. However, the increase in bird density on the grazed plots was largely due to increases in Horned Larks. Thus, adjustment of grazing intensity to maintain rangelands in good condition may benefit most grassland bird species during drought conditions.

Drought conditions may cause decreases, increases, or no changes in bird populations in semi-arid environments. Rotenberry and Wiens (1980*b*) found no significant differences in bird density between a dry year (1977) and two normal years (1978, 1979) at 14 shrub-steppe sites in the northern Great Basin of North America despite substantial changes in the coverage of forbs and grasses. However, the sites that had the highest turnover in bird species composition had higher grass cover and total plant cover than those sites with low turnover, suggesting that bird densities in grassier habitats fluctuate more than those in shrub-dominated sites. Wiens (1986) also examined temporal variation in bird densities at several sites in southern Oregon and northern Nevada over a 7-yr period. Despite differences in growing season precipitation of 700% among years, he found little consistent variation in bird numbers over the sites. Maurer (1985) found that total bird density and biomass were higher but diversity was lower during a wet year than a year of normal precipitation in grassland habitat in southern Arizona. Cody (1985) suggested that the relationship between spring rainfall and bird density at a mixed-grass prairie site in east-central North Dakota depended on the habitat affinities of a particular species. Densities of species associated with wetter habitats tended to be positively correlated with spring rainfall at the site, while those associated with drier habitats were generally negatively correlated. Thus, the response of grassland bird communities to drought is quite variable and may depend on the severity of the drought, the bird species in the community, and the climate and vegetation of a particular site.

Changes in bird densities between and within years may be due to a variety of factors, including variation in recruitment, survival, productivity, and local movement after breeding (Knopf and Sedgwick 1987, Temple and Wiens 1989, DeSante 1990). The decline of Sprague's Pipits, and Vesper, Baird's, and Grasshopper sparrows between June 1987 and May 1988 probably was not due to low productivity the previous year, as April–July precipitation at Watford City was close to the 37-yr average in 1987 and nesting productivity of Vesper Sparrows was high. Likewise, precipitation in 1987 was normal over most of the northern Great Plains (USDA/NOAA 1987*a, b*). It is more likely that the decline was due to reduced recruitment of individuals to our study area in the spring of 1988, possibly in response to the poor condition of the vegetation. The precipitation deficit began in early 1988 and continued through the summer. Vegetation productivity and height at 20 sites within the Little Missouri National Grasslands declined 65 and 27%, respectively, between 1987 and 1988 (D. Uresk, *personal communication*). Many grassland bird species respond to the structure and coverage of vegetation (Cody 1968, Wiens 1969, 1973), and much of the habitat, therefore, may have appeared unsuitable to some species in the spring of 1988.

The lack of a decline in total bird density between May 1988 and May 1989 was unexpected given the low productivity in 1988 and the low annual survival of passerine birds (usually 0.4–0.6, Lack 1966). Furthermore, declines in density have been observed in other bird populations following severe climatological events (Knopf and Sedgwick 1987). The absence of a decline between years suggests that local productivity in one year had little impact on recruitment in the following year. The lack of an effect may be due to local populations being supplemented by recruitment from larger areas, by a surplus of nonbreeding individuals, or by density-dependent effects on survival (Temple and Wiens 1989). A decoupling of local productivity and year-to-year changes in bird populations has been observed in other bird communities that are dominated by migratory species (DeSante 1990). However, several sequential years of below-normal productivity may have a significant impact on the populations of these short-lived species (Temple and Wiens 1989).

The sharp decline in nesting productivity of Vesper Sparrows in 1988 was largely due to nest abandonment. Several proximate factors may contribute to nest abandonment, including energy constraints on the incubating female, heat stress, or egg inviability. Schartz and Zimmerman (1971) found that the proportion of time spent resting by male Dickcissels (*Spiza americana*) was linearly related to temperature and humidity above 34°C in eastern Kansas. They concluded that the early termination of breeding that they observed in one year was directly related to heat stress. Termination of breeding, however, may also be related to food availability (DeSante and Baptista 1989). Most of the nest abandonment and the early termination of breeding on our study area in 1988 coincided with the extremely high temperatures in late June, suggesting that heat stress may have played a role. However, grasshopper numbers also were declining during June and July (Fowler et al. 1991), and therefore energy constraints may also have been involved. It is likely that a combination of heat stress and declining food availability contributed to the increased nest abandonment and the termination of breeding in 1988.

Although the relationship between precipitation and nesting productivity in arid environments is well documented (Immelmann 1971, Serventy 1971), the situation is less clear in semi-arid and mesic environments. Rotenberry and Wiens (1989) found that the number of young fledged was correlated with precipitation for Brewer's Sparrows (*Spizella breweri*) and Sage Sparrows (*Amphispiza belli*) in central Oregon. Clutch size was also correlated with precipitation in Brewer's Sparrows but not Sage Sparrows. Sage Thrashers (*Oreoscoptes montanus*) showed no correlation with precipitation for any reproductive parameters. DeSante and Guepel (1987) found that productivity of birds in coastal scrub habitat in northern California was related to precipitation in a nonlinear fashion. Productivity increased with precipitation to a maximum in years of high or slightly above-average rainfall, and then dropped during years of heavy rainfall. Thus, the relationship between breeding productivity and precipitation is complex and may depend on the species, the climate of a particular site, and the timing and severity of drought.

Management recommendations

Given that drought conditions are a natural part of the mixed-grass prairie environment, what recommendations can we make regarding management of these grasslands? First, because bird species respond differently to drought conditions, monitoring programs should include as many species as possible. Closely monitoring one or a few "indicator" species may not provide reliable information on the whole bird community. This will become more important as native grassland continues to dwindle and if drought conditions become more frequent in this region, as some climate models predict. Second, livestock grazing should be managed in a manner that assists recovery of degraded rangeland and maintains good condition range where it exists.

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