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Factors Affecting Attwater's Prairie-Chicken Decline on the Attwater Prairie Chicken

Michael E. Morrow
Attwater Prairie Chicken National Wildlife Refug

Robert S. Adamcik
Attwater Prairie Chicken National Wildlife Refug

Jenny D. Friday
Attwater Prairie Chicken National Wildlife Refug

Lloyd B. McKinney
Texas A&M University, College Station

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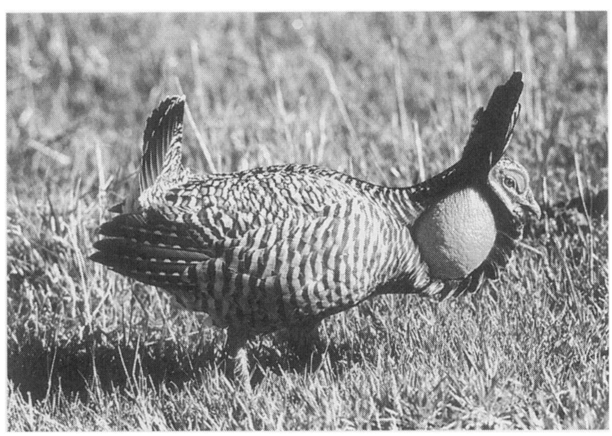
Michael E. Morrow, Robert S. Adamcik, Jenny D. Friday, and Lloyd B. McKinney

Abstract We examined the association between changes in the number of Attwater's prairie-chicken (*Tympanuchus cupido attwateri*) on the Attwater Prairie Chicken National Wildlife Refuge from 1972 to 1993 and changes in refuge management practices (burning and grazing). We also examined the relationship of prairie-chicken population increases and decreases on the refuge to rainfall and off-refuge prairie-chicken populations. Burning within the prairie-chicken's core habitat on the refuge and variability in grassland structure were directly correlated ($P < 0.05$) with increases and declines in prairie-chicken populations. Refuge population increases and declines were inversely correlated ($P < 0.1$) with average April rainfall/event, May absolute departure from long-term average rainfall, May number of rainfall events, annual absolute departure of rainfall from the long-term average, and the annual number of rainfall events. Refuge population increases and declines were directly correlated ($P < 0.1$) with off-refuge populations, although the off-refuge population decline began 4 years earlier than on-refuge.

Key words burning, grazing, land use, management, prairie-chicken, precipitation

The Attwater's prairie-chicken (*Tympanuchus cupido attwateri*) is a subspecies of prairie-chicken endemic to prairies along the Gulf of Mexico (Bendire 1894). Historically, Attwater's populations approached 1 million individuals on an estimated 2.4 million ha of prairie habitat (Lehmann 1968). By 1937, populations had declined to an estimated 8,700 individuals and have continued to decline. Our 1994 census estimated that 158 Attwater's prairie chickens remained in the wild (Attwater Prairie Chicken Natl. Wildl. Refuge, unpubl. data). It is listed as endangered by the State of Texas and the U.S. Fish and Wildlife Service.

Loss of prairie habitat has been the primary factor influencing the decline of the Attwater's prairie-chicken.



Attwater's prairie-chicken

Address for Michael E. Morrow and Jenny D. Friday: Attwater Prairie Chicken National Wildlife Refuge, PO Box 519, Eagle Lake, TX 77434, USA. Robert S. Adamcik was with the Attwater Prairie Chicken National Wildlife Refuge during this research. Current address for Robert S. Adamcik: Division of Refuges, U.S. Fish and Wildlife Service, 4401 N. Fairfax Drive, Arlington, VA 22203, USA. During this research, Lloyd B. McKinney was with the Department of Rangeland Ecology and Management at Texas A&M University, College Station. Current address for Lloyd B. McKinney: Illinois Natural History Survey, Center for Wildlife Ecology, 607 E. Peabody Drive, Champaign, IL 61820, USA.

These losses have resulted from agricultural conversion, urban and industrial expansion, overgrazing, and invasion of prairies by woody species (Lehmann 1941, Jurries 1979, Lawrence and Silvy 1980). The Attwater Prairie Chicken National Wildlife Refuge (APCNWR) was established in 1972 to protect and manage prairie habitats for the Attwater's prairie-chicken.

Numbers of prairie-chickens on the refuge have varied since establishment (Fig. 1). In general, prairie-chicken populations exhibited an upward trend to 222 through spring 1987 and then began declining despite intensified management. By 1993, the population had declined to an estimated 34 individuals (APCNWR, unpubl. data). Similar trends were observed in prairie-chicken populations off the refuge, although these declines began 4 years prior to the decline on APCNWR (Fig. 1).

The purpose of this study was to examine increases and declines in prairie-chicken populations from 1973 through 1993 on APCNWR in relation to changes in refuge management practices (grazing and prescribed burning). We also examined changes in abundance of prairie-chickens on the refuge with respect to rainfall and off-refuge prairie-chicken populations. Specifically, we hypothesized that prairie-chicken population increases and decreases were related to changes in:

1. stocking rates for refuge grazing,
2. refuge acreages managed with prescribed fire,
3. vegetation structure as influenced by management practices,
4. amount and frequency of rainfall during key periods of the prairie-chicken's life history, and
5. prairie-chicken population levels in areas surrounding the refuge.

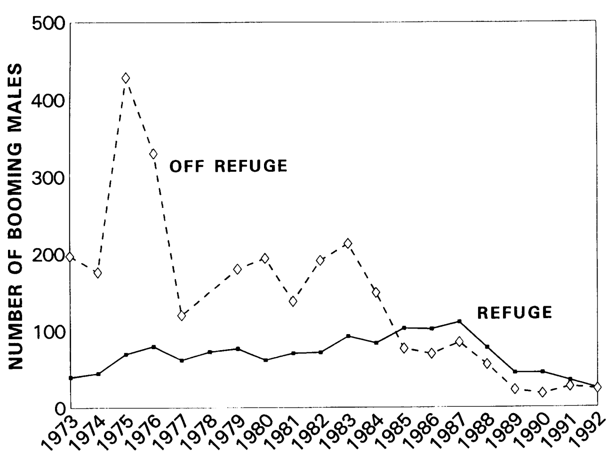


Fig. 1. Population trends of Attwater's prairie-chicken on the Attwater Prairie Chicken National Wildlife Refuge and in surrounding Austin and Colorado counties, Texas, 1973–1992.

Study area

The 3,240-ha APCNWR is located in the gulf prairies and marshes ecoregion of Texas (Gould 1975), about 120 km inland from the Gulf of Mexico. Approximately 2,295 ha are prairie grasslands dominated in the climax community by little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*). Loamy prairie, sandy prairie, and coarse sand range sites predominate, occupying 31, 26, and 18% of the refuge, respectively. These range sites are interspersed with lowland and claypan range sites of <1 to several ha. Approximately 35% of the refuge has been cultivated in the past, with 97 ha cultivated as food plots.

Currently, range condition on refuge grasslands as defined by Dyksterhuis (1949) varies from poor on formerly cultivated areas to good on unbroken prairie. The refuge is bounded on the east by the San Bernard River and is bisected by Coushatta Creek. Both of these drainages support robust stands of woody vegetation dominated by live oaks (*Quercus virginiana*), black willow (*Salix nigra*), sycamore (*Platanus occidentalis*), yaupon (*Ilex vomitoria*), and Macartney rose (*Rosa bracteata*). Slopes on the refuge vary from 1% to 3%, resulting in poor drainage during periods of heavy rainfall. Numerous roads and fences constructed to facilitate management have altered natural drainage patterns (Fig. 2).

Not all refuge habitats are equally well suited to all phases of prairie-chicken life history. Prairie-chicken habitat, especially nesting habitat, has generally been concentrated in the center of the refuge on loamy and sandy prairie range sites (Fig. 2). Morrow (1986) observed only 1 of 26 prairie-chicken nests outside of these pastures in 3 years. Of 131 prairie-chickens observed in 1987, 125 were in this area (APCNWR, unpubl. data). Plots of booming males since 1974 also show booming grounds concentrated in the same central pastures (APCNWR, unpubl. data). Therefore, this 1,077-ha core-use area was the focus of our analyses.

Refuge management is directed at providing clumped bunchgrass communities characteristic of the climax grasslands required by prairie-chickens (Lehmann 1941, Cogar et al. 1977, U.S. Fish and Wildl. Serv. 1993). Integral to this management are controlled grazing (Kessler 1978) and prescribed fire (Chamrad and Dodd 1972). Grazing regimes in the past consisted of a combination of continuous grazing and deferred rotation, although continuous grazing at 5.3-5.7 ha/animal units (AU)/year has been considered a typical stocking rate. Prescribed burns typically have been conducted during December–February,

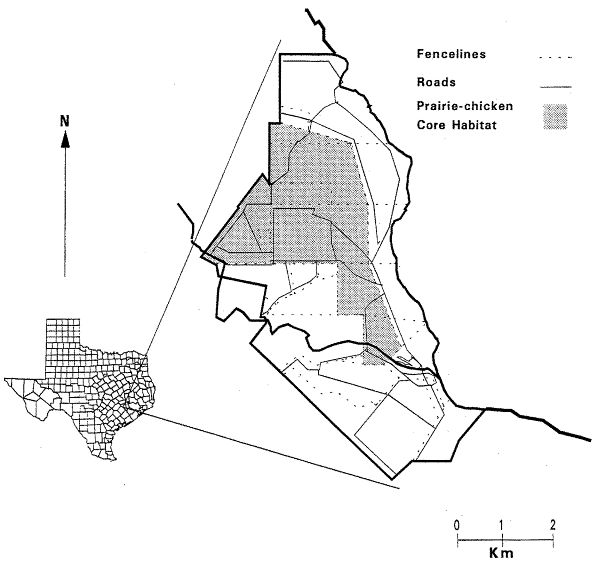


Fig. 2. Attwater's prairie-chicken core habitat on the Attwater Prairie Chicken National Wildlife Refuge, Colorado County, Texas, 1973–1992.

with green-up beginning in early to mid-March. Shredding, both strips and blocks, is used to provide habitat diversity and to reduce biomass accumulation in those years when grass growth exceeds optimal height and density. Herbicides are used to control invasion of Macartney rose and other woody species when prescribed fire alone fails to control their spread.

Methods

Population changes of grouse are driven by changes in breeding success (Bergerud 1988*b*:693, Peterson and Silvy 1994). Therefore, we hypothesized that increases and declines in the refuge prairie-chicken population were correlated with changes in 3 factors affecting habitat quality for reproduction: grazing, burning, and rainfall.

Annual increases or declines (%) in the number of refuge prairie-chickens were estimated from spring counts of booming males. Adult male prairie-chickens captured with drop nets on booming grounds were banded and weighed during 1983–1985 and 1991–1992 (Morrow 1986, APCNWR unpubl. data). A Mann-Whitney test (SAS Inst., Inc. 1988*b*) was used to test the hypothesis that male weights were similar from the 2 time periods. Since prairie-chicken young are capable of independent survival by 1 July (Lehmann 1941:19), grazing, burning, and rainfall data were summarized by 12-month periods beginning with 1 July to correspond with the annual prairie-chicken life cycle.

Grazing and burning analyses

Cattle stocking rates (ha/AU/yr) and the amount of prescribed burning (ha burned) within the refuge core area were determined for each year of the study by examining refuge records. Relationships between prairie-chicken population increases and declines and changes in grazing and burning were tested with correlation analyses.

Rainfall analyses

The peak in initiation of incubation occurs in April, and the peak in hatch occurs during May (Lehmann 1941). Therefore, we hypothesized that amount of rainfall during April and May would affect reproductive success and, as a result, the relative change in annual population size. We also hypothesized that yearly rainfall (1 Jul–30 Jun) would affect survival and the quality of habitat for reproduction.

Lehmann (1941:34) suggested the nature of rains were important in interpreting the effects of rainfall on reproductive success. We examined the absolute departure of rainfall from long-term average amounts, the average rainfall/event, and the number of rainfall events during the 3 time periods. Rainfall data were obtained from the Texas Agricultural Experiment Station farm located approximately 11 km southwest of APCNWR.

Simple correlation was used to test the relationship between the 12 rainfall parameters (total rainfall, absolute departure from long-term average, $\bar{x}$ rainfall/event, and the number of rainfall events, during Apr, May, and 1 Jul–30 Jun) and % annual population change. One-tailed hypotheses (H_0: $r \geq 0$ vs. H_A: $r < 0$) were tested for all rainfall parameters except total rainfall, which was tested using a 2-tailed hypothesis (H_0: $r = 0$ vs. H_A: $r \neq 0$). Where H_0 was rejected, we subjected the data to Mann-Whitney analyses (Daniel 1978) to test the hypothesis that the rainfall parameter differed between the period when the refuge population was increasing (1976–1986) versus those years when the population declined (1987–1992; Fig. 1).

Vegetation structure analyses

Vegetation obstruction of vision (OV) values (Robel et al. 1970) were collected during October–December of 1983–1984 and 1988–1992 to quantify structural habitat characteristics. OV data were collected on transects of variable length and location, but were consistently located in representative habitats within pastures. The October–December period was chosen for analysis of OV data because vegetation structure during this period reflected the impacts of management through the end of the growing season, and because this period permitted the maximum number of year-to-year comparisons.

We assumed these OV data provided an indicator of vegetation structure during the earlier March–June nesting and brooding period. OV data were subjected to Friedman's 2-way analysis for block designs (SAS Inst., Inc. 1985), using OV as the response variable, year as the classification variable, and pastures as blocks. Means were separated using Tukey's studentized range test to control the maximum experimentwise error rate (SAS Inst., Inc. 1988*b*). Simple correlation was used to test the hypothesis that changes in OV coefficient of variation (CV) were related to increases and declines in the refuge prairie-chicken population.

Off-refuge analysis

On the assumption that the refuge population is not independent of surrounding populations, increases and declines in refuge prairie-chicken populations were also examined in relation to changes in off-refuge land use. Data on land use within a 56,000-ha area of Austin and Colorado counties, Texas, and approximately centered on APCNWR, were derived from high-altitude aerial photography (1:62,500) for calendar years 1952, 1964, 1982, and 1990. Aerial photos were classified to level II categories of urban, cropland, grassland (rangeland and tame pasture), and commercial and industrial use (Anderson et al. 1976) and transferred to a base map. Base maps were hand-digitized into the ARC/INFO geographic information system for data analysis. To explore the possibility that loss of prairie-chicken populations off-refuge was contributing to the refuge decline, we tested the relationship between population changes on the refuge and off-refuge using simple correlation.

Statistical considerations

Data were tested for normality using the Shapiro-Wilk statistic (SAS Inst., Inc. 1988*a*). Data sets meeting the normality assumption were analyzed using Pearson's simple linear correlation; otherwise Spearman's rank correlation was used (Zar 1974). Power analyses (Cohen 1977, Kraemer 1987) were conducted for all Pearson correlation analyses to evaluate the relative risk of incorrectly accepting the null hypothesis (Type II error). A power analysis was also conducted for the Friedman's 2-way analysis of the OV data.

Results

Power of statistical tests

Power of the Pearson product-moment correlation analyses at $\alpha_{(1\text{-tailed})} = 0.10$ and $n = 17$ was calculated at 47% and 81% for r values of 0.3 and 0.5, respectively. Power of 2-tailed analyses for the same α, n, and values of r were 33% and 69%, respectively. These r values represent medium and large effect sizes according to Cohen (1977). Power efficiency of the Spearman rank correlation analysis is 91% of the Pearson product-moment, when both tests are applied under the assumptions of the Pearson product-moment test (Daniel 1978:304). Power of the Friedman's analysis on OV data was calculated at > 99.5% for $\alpha = 0.01$,7 year classes, $n = 1{,}037$, $n' = 148$, and critical effect size > 0.25 (Cohen 1977).

Prairie-chicken weights

Median weights of 27 males captured on spring booming grounds from 1983 to 1985 was 975 g compared to 925 g for 8 males captured from 1991 to 1992. The hypothesis that male weights were similar during both periods was rejected (Mann-Whitney U = 176.5, $P < 0.01$).

Grazing and burning

Records on use of prescribed fire were available from July 1976 to June 1992. During those years, hectares burned within the core prairie-chicken habitat ranged from 0 to 367 ha (Table 1). No burning was conducted during 6 of these 16 years. Only 16 ha were burned from July 1985 to June 1988.

Grazing records were examined only for the period following refuge acquisition (1980). Complete grazing records were available for July 1981-June 1992 (Table 1). Core habitat grazing levels were constant at 2,180 animal unit-months (AUM; 5.9 ha/AU/yr) from July 1982 to June 1988. In 1988-1989, grazing levels were reduced to 891 AUM (14.5 ha/AU/yr) in response to drought conditions (rainfall -37% and -20% of long-term average in 1987-1988 and 1988-1989, respectively), with cattle completely removed from some pastures. Cattle were restocked in 1989-1990 to 2,895 AUM (4.5 ha/AU/yr). Reduced grazing levels (1,786 and 2,021 AUM, respectively) occurred again in 1990-1991 and 1991-1992 because high spring rainfall damaged refuge fences.

No association ($P > 0.1$) existed between grazing level or area burned and prairie-chicken population increases and declines when all data were considered. However, for the years when grazing was constant (Table 1), area burned was correlated with percent population change ($r_s = 0.81$, $n = 7$, $P < 0.03$).

Vegetation structure

OV data for October-December of 1983-1984 and 1988-1992 are presented in Table 2. These measurements were generally consistent with expected changes in vegetation resulting from burning and grazing practices and changes in precipitation levels during previous growing seasons (Table 1). OV means

Table 1. Rainfall, prescribed burning, grazing, and Attwater's prairie-chicken (APC) population change (%) on the Attwater Prairie Chicken National Wildlife Refuge, Texas, July 1976–June 1992.

Year[a]	Rainfall departure (cm)[b]	Burning (ha)	Grazing (AUM)[c]	APC population change (%)[d]
1976–1977	5.0	238	n/a	+18
1977–1978	–23.0	0	n/a	+6
1978–1979	23.8	74	n/a	–20
1979–1980	–8.4	78	n/a	+14
1980–1981	–6.9	0	n/a	+1
1981–1982	1.1	332	2,180	+29
1982–1983	7.0	155	2,180	–10
1983–1984	–8.9	290	2,180	+23
1984–1985	26.7	0	2,180	–1
1985–1986	–7.8	16	2,180	+9
1986–1987	22.2	0	2,180	–30
1987–1988	–37.2	0	2,180	–42
1988–1989	–20.0	0	891	0
1989–1990	–32.8	298	2,895	–22
1990–1991	–6.2	184	1,786	–29
1991–1992	65.4	363	2,021	–32

[a] Data were collected 1 July–30 June to correspond with the APC life cycle. Nesting and brooding occurs March–June.
[b] Departure from the long-term average rainfall.
[c] Animal-unit-month.
[d] Population change (%) was determined by comparing counts of booming males during March within a year to those of the next year. This comparison permitted evaluation of reproductive success during the indicated year.

were different ($P \leq 0.05$) among all years except 1983, 1991, and 1992, and for 1990 and 1991 (Table 2). The only prairie-chicken population increase observed during the 7 years for which OV data were available was in 1983-1984 (reproduction during 1984) when the mean OV was the lowest ($P \leq 0.05$; Tables 1,2).

OV CV was positively correlated with prairie-chicken population change ($r = 0.79$, $n = 7$, $P = 0.03$). With the exception of 1990, OV CV was consistently lower during 1988-1992 as compared to 1983-1984. The greatest prairie-chicken population decline observed during the 7 years for which we had OV data (-42%) occurred during 1987-1988 (reproduction during 1988) when OV CV was the least (Tables 1,2). Conversely, the only population increase occurred when OV CV was greatest.

Refuge-independent factors

Precipitation. Rainfall, especially during the reproductive period has long been considered an important factor in influencing prairie-chicken reproductive success (Lehmann 1941). Our analyses suggest that the average rainfall/event in April ($r = -0.40$, $n = 17$, $P < 0.06$), the May absolute departure from the long-term average ($r_s = -0.43$, $n = 17$, $P < 0.04$) and the May number of events ($r = -0.52$, $n = 17$, $P < 0.03$) were factors which were inversely correlated with reproductive success (Table 3). Similarly, the annual absolute departure of rainfall from the long-term average ($r_s = -0.64$, $n = 17$, $P = 0.004$) and the annual number of events ($r_s = -0.46$, $n = 17$, $P < 0.04$) were also inversely correlated with annual population increases and declines. The number of rainfall events during May and the absolute departure of rainfall from the long-term average for the year were greater ($P < 0.1$) during the 1987-1992 declining period as compared to 1976-1986 (Table 4).

Off-refuge habitat. Grassland habitat off-refuge has declined 83% in historic times (Fig. 3). A 30% loss of grasslands occurred between 1982-1990; even more important was the dramatic increase in habitat fragmentation during this period (Fig. 3). These habitat losses, coupled with the other factors discussed here affecting refuge birds, led to a dramatic decline in prairie-chicken populations off-refuge (Fig. 1). By 1992, the closest booming ground was approximately 8 km from the nearest refuge booming ground. As a result, interchange of individ-

Table 2. Vegetation obstruction of vision (OV) measurements taken from transects on Attwater Prairie Chicken National Wildlife Refuge, Colorado County, Texas, October–December, 1983–1992.

Year	$\bar{x}$[a] (dm)	SD	CV (%)
1983	1.8 A	0.9	50
1984	1.0 B	0.6	60
1985	—	—	—
1986	—	—	—
1987	—	—	—
1988	2.6 C	1.0	38
1989	4.1 D	1.7	41
1990	1.4 E	0.7	50
1991	1.5 A E	0.6	40
1992	1.8 A F	0.7	39

[a] Means joined by a common letter are not different ($P > 0.05$) as determined by Tukey's studentized range test.

Table 3. Simple correlation analyses of Attwater's prairie-chicken population changes on the Attwater Prairie Chicken National Wildlife Refuge, Colorado County, Texas, with rainfall variables potentially affecting reproduction, 1976–1992.

Time period	Rainfall variable	r	P[a]
Apr	Total precipitation	−0.38 (s)[b]	0.13
	Abs. depart. from LTA[c]	−0.20	0.22
	Average/event	−0.40	0.06
	Number of events	−0.16	0.28
May	Total precipitation	−0.16	0.54
	Abs. depart. from LTA	−0.43 (s)	0.04
	Average/event	+0.27	0.14
	Number of events	−0.52	0.03
1 Jul–30 Jun	Total precipitation	−0.15	0.58
	Abs. depart. from LTA	−0.64 (s)	0.004
	Average/event	+0.17 (s)	0.27
	Number of events	−0.46 (s)	0.04

[a] Total precipitation = P (2-tailed), all other variables = P (1-tailed).

[b] Spearman rank correlation coefficients.

[c] Absolute departure from long-term average.

uals between refuge and non-refuge populations has been severely restricted if not eliminated.

Increases and declines in the refuge prairie-chicken population were correlated with increases and declines in off-refuge populations ($r_s = 0.40$, $n = 19$, $P < 0.09$). However, the off-refuge population decline began 4 years earlier than that on-refuge (Fig. 1), resulting in the relatively weak observed correlation. Increases and declines in both populations were strongly correlated once the refuge population began declining in 1988 ($r_s = 0.83$, $n = 6$, $P < 0.04$).

Table 4. Results of Mann–Whitney tests on selected rainfall parameters observed at the Texas Agricultural Experiment Station farm, Eagle Lake, Colorado County, Texas, during periods of increasing (1976–1986) ($n = 11$) and decreasing (1987–1992) ($n = 6$) prairie-chicken populations on the Attwater Prairie Chicken National Wildlife Refuge, Colorado County, Texas.

		$\bar{x}$ parameter value		
Period	Parameter	1976–1986	1987–1992	P
Apr	Average/event (cm)	1.0	1.2	0.61
May	Abs. depart. from LTA[a] (cm)	5.2	8.2	0.36
	Number of events	7.7	12.0	0.08
1 Jul–30 Jun	Abs. depart. from LTA (cm)	11.9	30.6	0.09
	Number of events	90.4	107.8	0.14

[a] Absolute departure from the long-term average.

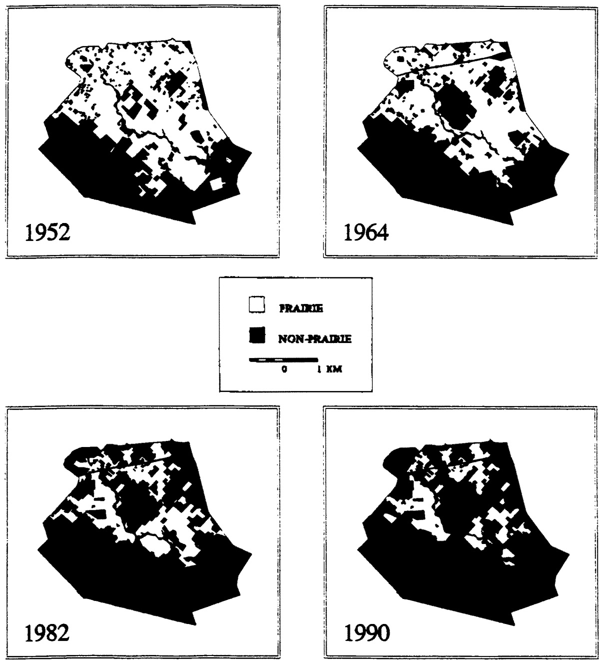


Fig. 3. Grassland habitat availability in a 56,000-ha area of Austin and Colorado counties, Texas, from 1952–1990. Grasslands comprised 52%, 43%, 24%, and 17% of the total area in 1952, 1964, 1982, and 1990, respectively.

Discussion

Grazing, burning, and vegetation structure

The importance of burning in prairie-chicken management has been recognized by several investigators (e.g., Chamrad and Dodd 1972, Westemeier 1972, Kessler 1978, Kobriger et al. 1988). An interaction between burning and grazing may mask the effects of either variable when considered alone in simple correlation analyses, unless the other variable is held constant. Multi-variate techniques would be more appropriate for the type of analyses needed, but our sample sizes ($n \leq 16$) preclude their use.

Prairie-chicken nests are typically located in clumps of grass with OV's averaging 2.1-2.8 dm at the nest site (Cogar et al. 1977, Lutz 1979, Svedarsky 1979, Lawrence 1982, Morrow 1986, Manske and Barker 1988). However, it is important that grass cover between these clumps be open enough to allow for movement by adults and young chicks. Cogar et al. (1977) found that OV in preferred habitat averaged 2.74 ± 1.27 dm. Similarly, Manske and Barker (1988) found that OV within 4 m of greater prairie-chicken (*T. c. pinnatus*) nests averaged 2.5 ± 1 dm. Our data lead us to believe that the mean OV is less important than the variability in structure associated with that mean.

Our analyses suggest that inadequate interspersion of open areas within the grassland structure may have contributed to population declines in recent years. Given that grazing is used as a tool to increase habitat heterogeneity for prairie-chickens (U.S. Fish and Wildl. Serv. 1993), insufficient grazing may have resulted in this condition. Cattle numbers were drastically reduced or totally removed from many pastures in fall 1988 in response to rainfall deficits during summer 1988 (Table 1). However, OV data collected in 1988 (Table 2) just prior to cattle removal do not suggest an overgrazed situation within the core habitat, especially when the structural characteristics of preferred nesting habitat are considered. Rather, we think that vegetation existing in 1988, which was in the preferred range reported by Cogar et al. (1977) and Manske and Barker (1988), became too dense by 1989 as a result of cattle removal. This situation was aggravated further by 4 years of essentially no burning (Table 1).

Refuge-independent factors

Precipitation. Lehmann (1941:33) indicated that rainfall during March, April, or June had little impact on reproductive success. However, our data indicate that reproductive success may be affected by nest flooding as suggested by the inverse correlation with rainfall/event in April (Table 3). Schwartz (1945:67) found that heavy rains destroyed many greater prairie-chicken nests. Lawrence (1982:68) documented Attwater's nest abandonment as a result of flooding. While, as Lehmann (1941) pointed out, nests flooded in April may be rebuilt, such renesting attempts are typically less successful and contain fewer eggs/clutch (Robel 1970). Bergerud (1988*a*,*b*) stated that grouse density is primarily dependant upon nesting success.

Lehmann (1941:33) suggested that reproductive success was directly related to the relative lack of rainfall in May, i.e., the drier weather was in May when compared to the long-term average, the greater the reproductive success. But, the results of our correlation of prairie-chicken population change with absolute departure (i.e., < or >) from average rainfall in May suggest that dry years as well as wet years were associated with reduced reproductive success (Table 3). Bergerud (1988*a*) and Peterson and Silvy (1994) also suggested that drought conditions during May might lead to reduced reproductive success due to adverse impacts on brood-rearing habitat. Conversely, Lawrence (1982:68) documented the adverse impacts of excessive rainfall on Attwater's broods. Furthermore, our observed correlation with annual rainfall's absolute departure from long-term averages suggests possible adverse impacts to habitat from drought or excessive rainfall throughout the year. This parameter was greater ($P < 0.1$) during the 1987-1992 declining period for refuge prairie-chickens (Table 4).

Our data show that frequency of rain as indicated by the correlation of population change with the number of rainfall events during May is more important than the total amount of precipitation (Table 3). Lehmann (1941:34) suggested that chilling caused by frequently occurring, light rains might be an important factor affecting juvenile mortality. Moss (1985) found that the number of days it rained and the amount of rain during the early brooding period were inversely correlated with capercaillie (*Tetrao urogallus*) survival. Moss (1985) speculated that this relationship was due to chicks being unable to forage for insects during rainfall events. Such nutritional stress may have contributed to the lower weights observed in adult male prairie-chickens captured on APCNWR during 1991-1992 as compared to those captured in 1983-1985. The number of May rainfall events was greater during the 1987-1992 declining period for APCNWR prairie-chickens (Table 4). Schwartz (1945:67), Svedarsky (1979:46), and Gross (1963: 242-243) found that the effect of rain on prairie-chickens is most serious when it occurs shortly after hatching. Gross (1963:242) suggested that weather condition (i.e., amount and frequency of rain in combination with ambient temperature) is frequently the determining factor in successful production of prairie-chicken young.

Off-refuge habitat. Hamerstrom et al. (1957) found greater prairie-chicken densities were correlated with the proportion of permanent grassland available in an area. A "low lingering" population was found in an area with as little as 10-15% permanent grassland (Hamerstrom et al. 1957:86). Since the potential prairie habitat in Figure 3 includes tame-grass pastures of minimal benefit to prairie-chickens, it is likely that the amount of prairie habitat remaining by 1990 had dropped below the minimum threshold capable of sustaining a prairie-chicken population.

While it is likely that common factors have affected prairie-chicken populations on- and off-refuge, loss of contiguous off-refuge populations probably contributed to the decline on APCNWR. Such a relationship is suggested by the time-lag in onset of the refuge decline. Population isolation may have created a mortality sink for dispersing juveniles, or lack of genetic interchange may have led to heterozygosity below biologically viable levels (LaCava and Hughes 1984). We do not have sufficient data to establish a relationship between on- and off-refuge populations. However, we do suggest that research is badly needed regarding size and distribution of habitat blocks necessary to support minimally viable prairie-chicken populations and to quantify ingress and egress of prairie-chickens within habitat blocks.

Summary and management implications

No single factor has caused the dramatic prairie-chicken decline observed on APCNWR in recent years; rather, it was likely the result of interactions among several factors. Small sample sizes precluded the use of statistical analyses that might have quantified these interactions. Due to small sample sizes, the power of the correlation analyses we used was mediocre at best. Therefore, although significant associations were not detected for some of the parameters we hypothesized to be associated with increases and declines in prairie-chicken populations, we do not conclude that no association exists. Larger data sets will be needed to test these hypotheses more rigorously. Other factors not yet tested also may have contributed to the decline.

We identified factors associated with rainfall (April average rainfall/rainfall event, yearly and May departure from long-term average, and frequency of May and yearly rainfall) which were inversely correlated with prairie-chicken population increases and declines. Unfortunately, managers cannot realistically control the impacts of detrimental weather conditions. The *r*-selected species are often subjected to catastrophic, density-independent mortality factors such as adverse weather conditions (Pianka 1970) which may lead to extinction of small populations (Roughgarden 1979:377).

Our analyses also identified management practices that appeared to be related to changes in the number of prairie-chickens on APCNWR. The amount of burning in the prairie-chicken's core habitat on the refuge and the amount of variability in its grassland structure as influenced by grazing were directly correlated with increases and declines in prairie-chicken populations. Management can and must optimize these factors on prairie-chicken habitat. Data presented here were collected at 1 location; relationships identified here should be tested on other prairie-chicken populations. Additionally, as suggested by Potts and Robertson (1994), manipulative experiments with burning and grazing on prairie-chicken habitat are needed to fully evaluate their impacts on prairie-chicken populations.

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Literature cited

Anderson, J. R., E. E. Hardy, J. T. Roach, and R. E. Witmer. 1976. A land use and land cover classification system for use with remote sensor data. U.S. Geol. Surv. Prof. Pap. No. 964. 28pp.

Bendire, C. E. 1894. *Tympanuchus americanus attwateri* Bendire. Attwater's or southern prairie hen. Auk 11:130–132.

Bergerud, A. T. 1988*a*. Population ecology of North American grouse. Pages 578–685 *in* A. T. Bergerud and M. W. Gratson, eds. Adaptive strategies and population ecology of northern grouse. Univ. Minnesota Press, Minneapolis.

Bergerud, A. T. 1988*b*. Increasing the numbers of grouse. Pages 686–731 *in* A. T. Bergerud and M. W. Gratson, eds. Adaptive strategies and population ecology of northern grouse. Univ. Minnesota Press, Minneapolis.

Chamrad, A. D., and J. D. Dodd. 1972. Prescribed burning and grazing for prairie chicken habitat manipulation in the Texas coastal prairie. Proc. Tall Timbers Fire Ecol. Conf. 12:257–276.

Cogar, V. F., J. D. Horkel, and N. J. Silvy. 1977. Vegetation type preference of Attwater's prairie chicken in coastal prairie. Proc. Southeastern Assoc. Fish Wildl. Agencies. 32:41–50.

Cohen, J. 1977. Statistical power analyses for behavioral sciences. Academic Press, New York, N.Y. 474pp.

Daniel, W. W. 1978. Applied nonparametric statistics. Houghton Mifflin Co., Dallas, Tex. 510pp.

Dyksterhuis, E. J. 1949. Condition and management of range land based on quantitative ecology. J. Range Manage. 2:104–115.

Gould, F. W. 1975. Texas plants—a checklist and ecological summary. Texas Agric. Exp. Stn. Publ. MP-585. 121pp.

Gross, A. O. 1963. *Tympanuchus cupido americanus* (Reichenbach) — greater prairie chicken. Pages 242–264 in A. C. Bent, Life histories of North American gallinaceous birds. Dover Publ., Inc., New York, N.Y.

Hamerstrom, F. N., Jr., O. E. Mattson, and F. Hamerstrom. 1957. A guide to prairie chicken management. Wisconsin Conserv. Dep. Tech. Wildl. Bull. 15. 128pp.

Jurries, R. W. 1979. Attwater's prairie chicken. F. A. Series No. 18. Texas Parks and Wildl. Dep., Austin. 36pp.

Kessler, W. B. 1978. Attwater's prairie chicken ecology in relation to agricultural and range management practices. Ph.D. Thesis, Texas A&M Univ., College Station. 158pp.

Kobriger, J. D., D. P. Vollink, M. E. McNeill, and K. F. Higgins. 1988. Prairie chicken populations of the Sheyenne Delta in North Dakota, 1961–1987. Pages 1–7 *in* A. J. Bjugstad, ed. Prairie chickens on the Sheyenne National Grasslands. U.S. For. Serv. Gen. Tech. Rep. RM-159. 73pp.

Kraemer, H. C. 1987. How many subjects? Statistical power analysis in research. Sage Publ., Newbury Park, Calif. 120pp.

LaCava, J. and J. Hughes. 1984. Determining minimum viable population levels. Wildl. Soc. Bull. 12:370–376.

Lawrence, J. S. 1982. Effect of predator reduction on the reproductive success of Attwater's prairie chicken. M.S. Thesis, Texas A&M Univ., College Station. 105pp.

Lawrence, J. S., and N. J. Silvy. 1980. Status of the Attwater's prairie chicken—an update. Pages 29–33 *in* P. A. Vohs, Jr. and F. L. Knopf, eds. Proc. prairie grouse symposium, Oklahoma State Univ., Stillwater.

Lehmann, V. W. 1941. Attwater's prairie chicken, its life history and management. U. S. Fish and Wildl. Serv., North Am. Fauna Series 57. 65pp.

Lehmann, V. W. 1968. The Attwater prairie chicken, current status and restoration opportunities. Trans. North Am. Wildl. Conf. 33:398-407.

Lutz, R. S. 1979. The response of Attwater's prairie chicken to petroleum development. M.S. Thesis, Texas A&M Univ., College Station. 82pp.

Manske, L. L., and W. T. Barker. 1988. Habitat usage by prairie grouse on the Sheyenne National Grasslands. Pages 8-20 *in* A. J. Bjugstad, ed. Prairie chickens on the Sheyenne National Grasslands. U.S. For. Serv. Gen. Tech. Rep. RM-159. 73pp.

Morrow, M. E. 1986. Ecology of Attwater's prairie chicken in relation to land management practices on the Attwater Prairie Chicken National Wildlife Refuge. Ph.D. Thesis, Texas A&M Univ., College Station. 100pp.

Moss, R. 1986. Rain, breeding success and distribution of capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix* in Scotland. Ibis 128:65-72.

Peterson, M. J., and N. J. Silvy. 1994. Spring precipitation and fluctuations in Attwater's prairie-chicken numbers: hypotheses revisited. J. Wildl. Manage. 58:222-229.

Pianka, E. R. 1970. On *r*- and *K*-selection. Am. Nat. 104:592-597.

Potts, G. R., and P. A. Robertson. 1994. Gamebird research in North America and Europe: the way forward, a critique and a plea. Trans. North Am. Wildl. and Nat. Resour. Conf. 59:415-420.

Robel, R. J. 1970. Possible role of behavior in regulating greater prairie chicken populations. J. Wildl. Manage. 34:306-312.

Robel, R. J., J. N. Briggs, J. J. Cebula, N. J. Silvy, C. E. Viers, and P. G. Watt. 1970. Greater prairie chicken ranges, movements, and habitat usage in Kansas. J. Wildl. Manage. 34:286-306.

Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. Macmillan Publ. Co., New York, N.Y. 634pp.

SAS Institute, Inc. 1985. SAS user's guide: statistics, version 5 ed. SAS Inst., Inc., Cary, N.C. 957pp.

SAS Institute, Inc. 1988*a*. SAS procedures guide, release 6.03 ed. SAS Inst., Inc., Cary, N.C. 441pp.

SAS Institute, Inc. 1988*b*. SAS/STAT user's guide, release 6.03 ed. SAS Inst., Inc., Cary, N.C. 1028pp.

Schwartz, C. W. 1945. The ecology of the prairie chicken in Missouri. Univ. Missouri Stud. 20:1-99.

Svedarsky, W. D. 1979. Spring and summer ecology of female greater prairie chickens in northwestern Minnesota. Ph.D. Thesis, Univ. North Dakota, Grand Forks. 166pp.

U. S. Fish and Wildlife Service. 1993. Attwater's prairie chicken recovery plan. U. S. Fish and Wildl. Serv., Albuquerque, N.M. 48pp.

Westemeier, R. L. 1972. Prescribed burning in grassland management for prairie chickens in Illinois. Proc. Tall Timbers Fire Ecol. Conf. 12:317-338.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, N.J. 620pp.

Michael (Mike) E. Morrow received his B.S. from Kansas State University and an M.S. and Ph.D. from Texas A&M University. He is a Wildlife Biologist with the U.S. Fish and Wildlife Service at the Attwater Prairie Chicken National Wildlife Refuge (APCNWR), where he participates in habitat management and recovery activities for the Attwater's prairie-chicken. His professional interests include endangered species, small populations management, and upland game birds. ***Robert (Bob) S. Adamcik*** is a Wildlife Biologist with the U.S. Fish and Wildlife Service, Division of Refuges in Washington, D.C., where he is responsible for coordinating biological program initiatives, policy, and research needs associated with the National Wildlife Refuge System. Bob was formerly an Assistant Refuge Manager at APCNWR and Kern National Wildlife Refuge, and was a Fish and Wildlife Service Environmental Liaison to the U.S. Navy on Vieques Island, Puerto Rico. He received a B.S. from Texas A&M University and an M.S. from the University of Wisconsin at Madison. His professional interests include predator ecology, endangered species, and nongame issues. ***Jenny D. Friday*** recently left a Wildlife Biologist position at APCNWR. She received a B.S. from Texas A&M University. ***Lloyd (Tony) B. McKinney*** is an Assistant Research Scientist with the Illinois Natural History Survey. He received an M.S. degree (Dec 1996) from the Department of Rangeland Ecology and Management, Texas A&M University, where he conducted a project on land-use changes within the range of the Attwater's prairie-chicken. Tony's professional interests are landscape ecology, wildlife habitat modeling, and the integration of global positioning system technology with ecological data to map spatially explicit wildlife populations.

Associate Editor: Brennan