THE SOUTHWESTERN NATURALIST 31(4):493-501 NOVEMBER 10, 1986

THE RELATIONSHIP OF PLANT SPECIES HETEROGENEITY TO SOIL VARIATION IN BUFFALO WALLOWS

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ABSTRACT—"Buffalo wallows" are depressions formed in North American grasslands by the trampling and dust-bathing of bison (*Bison bison*). Plant species composition and resource availability within these concave depressions differ from that of the surrounding grassland. The vegetation and soil characteristics of wallows still subject to bison activity were examined in order to possibly relate plant species heterogeneity to edaphic factors.

Ordination analysis demonstrated that species cover and composition differed among wallows. Vegetational heterogeneity among wallows was related to differences in several edaphic parameters. Regression analyses indicated that differences in vegetational composition were most consistently correlated with differences in soil texture, ammonium-nitrogen and sodium. These differences, together with probabilistic events in species establishment and recurrent disturbances, produce the diverse vegetation of wallows. The heterogeneous species assemblages of wallows enhance grassland species diversity primarily because wallows increase habitat diversity.

Natural disturbances are a common feature in most ecosystems (White, 1979). Disturbance was shown to affect such community characteristics as diversity (Collins and Uno, 1983), species composition (White, 1979), and resource availability (Chapin, 1983). Studies of natural disturbances in grasslands addressed the impacts of fire (Daubenmire, 1968; Vogl, 1974; Kucera, 1981) and, to a lesser extent, the grazing, trampling and mound building activities of native herbivores (Platt, 1975; Bonham and Lerwick, 1976; Coppock et al., 1983a,b). Only recently, however, have "buffalo wallows" received attention as natural disturbance sites in grasslands (Collins and Uno, 1983). These depressions, formed in the North American grasslands by the trampling and dust-bathing of bison (*Bison bison*), were a common feature of the North American prairie in pre-European times (England and DeVos, 1969). Wallows still exist in unplowed grasslands in central Oklahoma, where they support populations of wetland plants within a matrix of upland vegetation (Barkley and Smith, 1934; Collins and Uno, 1983; Polley and Collins, 1984). Polley and Collins (1984) investigated seasonal changes of vegetation and edaphic factors along a gradient from prairie to wallow interior. Vegetational differences along the gradient corresponded to differences in soil texture, soil moisture, available phosphorus and pH.

This study was undertaken to examine in greater detail the vegetation and soils within wallows still subject to bison visitation. The degree of plant species heterogeneity among these disturbed patches was more precisely evaluated. Edaphic factors that were potentially responsible for differences in species composition among wallows were also investigated.

STUDY AREA—The buffalo wallows sampled in this study were in the 23,885 ha Wichita Mountains Wildlife Refuge, in Comanche County, southwest Oklahoma (latitude 34°44′N, longitude 98°43′W). Since the removal of domestic livestock in 1937, the area has been grazed by a managed population of approximately 625 bison, along with 300 longhorn cattle (*Bos taurus*), 500 elk (*Cervus canadensis*), and 1200 deer (*Odocoileus virginianus*) (U.S. Fish and Wildlife Service, 1978). Mean annual precipitation in the refuge is 714.7 mm (30 year record), of which 398.3 mm falls during the five-month period from April through August (NOAA, 1980). The total for the same five-month period in 1982, when this study was conducted, was 523.5 mm (NOAA, 1982).

METHODS—The four wallows chosen for this study were representative of the natural range of wallow vegetation and soils previously encountered (Polley and Collins, 1984). The number of wallows was reduced to allow more extensive investigation of edaphic parameters potentially responsible for differences in species composition. All wallows sampled were in mixed-grass prairie (Crockett, 1964). The wallows, which ranged from 3.0 to 10.0 m in diameter, were underlain by deep brown to reddish-brown loam to clay loam Mollisols (USDA, 1960). Vegetation cover values within wallows were recorded in contiguous 0.5 m^2 quadrats along a belt transect that bisected the long axis of each wallow. At two sample periods (18 -20 May and 17-22 August 1982), all species rooted in each quadrat were visually assigned cover values according to the methods of van der Valk and Bliss (1971): + for <1% cover, 1 for 1-5%, 2 for 6-15%, 3 for 16-25%, 4 for 26-50%, 5 for 51-75%, 6 for 76-95% and 7 for 96-100%. Plant nomenclature followed Waterfall (1979).

The following ten chemical and physical factors were quantified within each wallow: soil water potential, soil texture, pH, NO_3-N, NH_4-N, available phosphorus (P), K, Na, Ca and Mg. Texture and chemical analyses were performed on composite samples of three subsamples (5 to 15 cm depth) taken from every third quadrat along the contiguous transect. Soil cores (7 cm diam.) were taken from every third quadrat at 5 to 15 cm and 15 to 25 cm depths. Water content was quantified gravimetrically and soil water potential determined from moisture retention curves using a pressure membrane extractor. Points of the moisture retention curves were averages of two measurements.

Soil samples were air dried, passed through a 2 mm sieve and stored in sealed plastic bags until analysis. Percent gravel (>2 mm) was determined as the percentage of total sample dry weight. Mechanical analysis (Day, 1965) was run on the 2 mm fraction. Soil pH was measured with a glass electrode in a 1:1 soil:distilled water suspension (Peech, 1965). Soil textural and moisture percentages were transformed using an arcsine transformation prior to statistical analyses.

Exchangeable NH_4-N and NO_3-N were ascertained in 2*N* KCl (5 ml/g soil) extracts of soil using the MgO-Devarda alloy steam-distillation procedure (Bremner, 1965). Available soil phosphorus was measured in ammonium fluoride-hydrochloric acid soil extracts (Bray and Kurtz, 1945) using the ascorbic acid procedure of John (1970). Potassium, Na, Ca and Mg were determined in 1*N* ammonium acetate extracts at pH 7.0 by atomic absorption spectrophotometry (Anonymous, 1971). Values recorded for each quadrat represent averages of duplicate measurements on the composite soil samples in the case of mechanical analysis and triplicate measurements for pH and the remaining soil chemical factors. Values of pH were transformed to the antilog before averaging and further statistical analyses.

Species encountered in fewer than 5% of sampled quadrats during each sample period were omitted from the multivariate analyses, but all species were included in calculations of diversity. Cover-class values for species were converted to percentages by using the midpoints of cover classes. Untransformed vegetation cover values from 40 quadrats were ordinated for each sample period with detrended correspondence analysis (DCA) (Hill, 1979; Hill and Gauch, 1980).

Samples were compared among wallows by ANOVA (Helvig and Council, 1979) and Duncan's multiple range test. Stepwise multiple regressions were run to ascertain how plant cover inside wallows correlated with various edaphic parameters. Diversity in each wallow was estimated as the antilogarithm of H′, the Shannon-Wiener index (Peet, 1974):

$$H' = -\Sigma\, p_i \ln p_i$$

where p_i is the proportion (total cover) of species *i* in each wallow. Richness was the number of species present per wallow.

RESULTS—Species composition and diversity differed between wallows and varied seasonally within individual wallows. *Eleocharis* spp. (spikerush) and *Coreopsis tinctoria* (tick-seed) were the most common species (Table 1).

TABLE 1—Average percent cover of major species, total percent cover, richness and diversity for four wallows (1-4) in May and August. Species cover values within each row and month are not significantly different at P = 0.05 by Duncan's multiple range test when followed by the same letter. Dashes indicate 0.0 percent cover.

	May				August			
Species	1	2	3	4	1	2	3	4
Alopecurus carolinianus	6.7^{a}	0.2^{a}	0.1^{a}	0.1^{a}	—^{a}	—^{a}	—^{a}	—^{a}
Ambrosia psilostachya	—^{a}	—^{a}	0.5^{a}	2.7^{a}	—^{a}	—^{a}	0.3^{a}	0.2^{a}
Aster ericoides	—^{a}	—^{a}	0.3^{a}	1.1^{a}	—^{a}	0.1^{a}	0.2^{a}	0.3^{a}
Coreopsis tinctoria	9.8^{b}	39.0^{a}	38.6^{a}	5.5^{b}	2.9^{a}	10.4^{a}	32.8^{a}	1.6^{a}
Cyperus acuminatus	—^{a}	0.2^{a}	0.1^{a}	0.2^{a}	0.2^{a}	2.9^{a}	8.2^{a}	2.9^{a}
Echinochloa crusgalli	—^{a}	—^{a}	—^{a}	—^{a}	—^{b}	—^{b}	—^{b}	5.9^{a}
Eleocharis spp.	20.7^{a}	5.8^{a}	1.9^{a}	0.7^{a}	75.7^{a}	71.7^{a}	21.0^{b}	1.9^{b}
Grindelia squarrosa	—^{b}	—^{b}	—^{b}	3.8^{a}	—^{a}	—^{a}	—^{a}	0.1^{a}
Hordeum pusillum	—^{a}	5.5^{a}	0.3^{a}	0.4^{a}	—^{a}	0.1^{a}	—^{a}	—^{a}
Juncus interior	—^{c}	0.1^{c}	0.5^{c}	3.1^{a}	—^{a}	—^{a}	0.7^{a}	0.8^{a}
Krigia oppositifolia	—^{b}	—^{b}	0.3^{a}	—^{b}	—^{a}	—^{a}	—^{a}	—^{a}
Marsilea mucronata	—^{a}	—^{a}	—^{a}	—^{a}	0.3^{a}	—^{b}	—^{b}	—^{b}
Plantago elongata	—^{b}	—^{b}	—^{b}	9.0^{a}	—^{a}	—^{a}	—^{a}	—^{a}
Plantago virginiana	—^{a}	—^{a}	0.9^{a}	0.8^{a}	—^{a}	—^{a}	.05^{a}	0.1^{a}
Tridens albescens	—^{a}	0.8^{a}	5.1^{a}	—^{a}	—^{b}	1.3^{b}	17.3^{a}	—^{b}
Other species	0.0	1.0	5.6	7.2	0.0	1.2	1.1	2.6
Total	37.2	52.6	54.2	34.6	79.1	87.7	82.1	16.4
Richness	3	15	24	28	4	9	16	18
Diversity	2.68	2.52	3.64	11.85	1.22	1.96	4.33	7.68

These were the only species encountered in all wallows at each of the sample periods. Of the total flora recorded (44 species), only two other species were found to occur in all wallows at least once during the sample periods (*Alopecurus carolinianus, Cyperus acuminatus*). *Plantago elongata* (plantain), *Grindelia squarrosa* (curly-cup gumweed), and *Tridens albescens* (white tridens) had high percent cover in individual wallows in May, while *Echinochloa crusgalli* (barnyard grass) had the highest cover in wallow 4 in August. Species richness and diversity were greatest in wallows 3 and 4 in both May and August. Diversity was lower in wallows 1 and 2 due to the consistently high percent cover of *Coreopsis tinctoria* and *Eleocharis* spp. (Table 1).

The heterogeneity of wallow vegetation was also reflected in the ordination results. Samples from the four wallows were generally separated along Axis 1 of the May data ordination (Fig. 1A). However, samples from wallows 2 and 3 occurred together near the center of the ordination figure and were more similar in species composition than were samples from wallows 1 and 4. This pattern reflected the high cover of *Eleocharis* spp. and *Alopecurus carolinianus* (foxtail) in wallow 1 and their lower cover in wallows 2, 3, and 4 (Table 1). The distinction of wallow 4 in the May ordination was largely attributable to the significantly greater cover of *Plantago elongata, Juncus interior,* and *Grindelia squarrosa* in this wallow (Table 1).

Significant differences among wallows in soil texture, moisture, pH, NH_4-N, Na and Mg were apparent in May (Table 2). Multiple linear

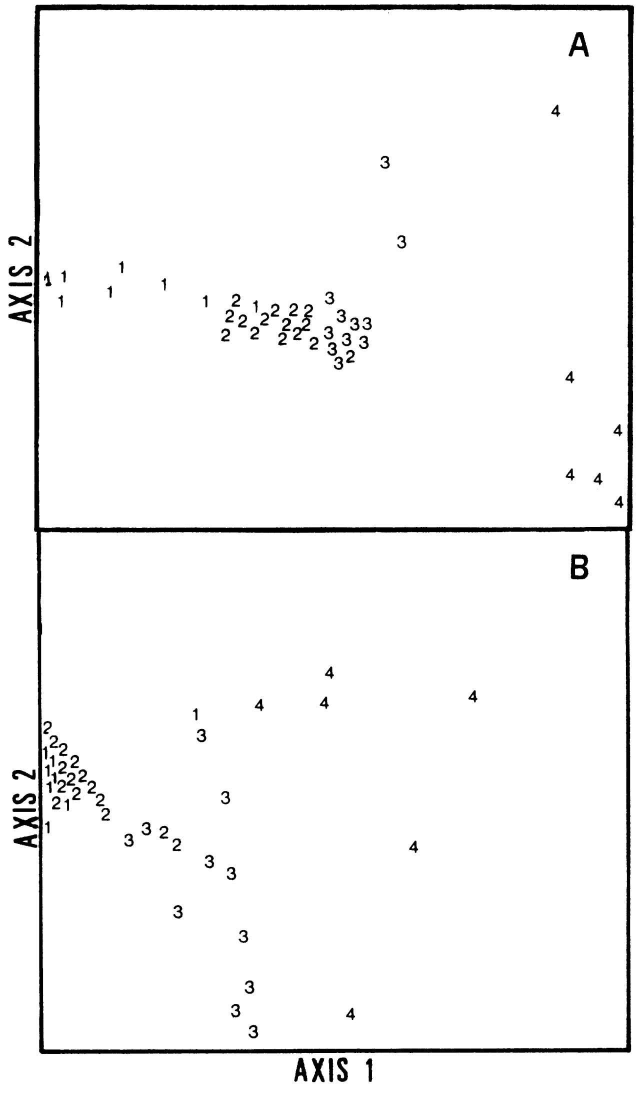

FIG. 1—Two-dimensional ordination by detrended correspondence analysis of samples from buffalo wallows in May (A) and August (B) 1982. Numerals (1, 2, 3, 4) denote different wallows.

regression analyses relating species cover to edaphic parameters indicated that all significant edaphic parameters except pH and % clay were correlated to cover of one or more wallow species in May (Table 3). Available P and NO_3-N were also related to species cover.

Differences in species composition between the four wallows were also evident from the August ordination (Fig. 1B). Samples from wallows 3 and 4 were distinctly separated along Axis 1 of the August ordination. This pattern reflected the significantly lower abundance of *Eleocharis* spp. and greater importance of *Tridens albescens* in these wallows than in wallows

TABLE 2—Means of edaphic parameters inside four wallows (1-4) in May and August. Significance was determined for each month using ANOVA and Duncan's multiple range test on quadrats for which edaphic data were collected. Values within each row and month are not significantly different at $P = 0.05$ by Duncan's multiple range test when followed by the same letter. Dashes indicate no data collected.

	May				August			
Edaphic parameter	1	2	3	4	1	2	3	4
NH_4-N ($\mu g \cdot g^{-1}$)	13.0^{ab}	11.6^{b}	11.1^{b}	14.9^{a}	7.0^{a}	7.7^{a}	4.8^{b}	6.9^{ab}
NO_3-N ($\mu g \cdot g^{-1}$)	5.3^{a}	6.5^{a}	5.6^{a}	2.1^{a}	4.6^{ab}	2.4^{c}	3.4^{bc}	5.7^{a}
P ($\mu g \cdot g^{-1}$)	13.8^{a}	8.0^{a}	13.0^{a}	9.5^{a}	23.7^{a}	8.8^{b}	6.1^{b}	7.5^{b}
K ($\mu g \cdot g^{-1}$)	283.3^{a}	276.7^{a}	281.9^{a}	299.3^{a}	309.8^{a}	255.8^{a}	245.4^{a}	307.3^{a}
Na ($\mu g \cdot g^{-1}$)	181.0^{b}	32.1^{c}	105.5^{bc}	655.0^{a}	99.6^{b}	36.3^{b}	72.0^{b}	511.5^{a}
Ca ($\mu g \cdot g^{-1}$)	1168.4^{a}	1664.0^{a}	1048.0^{a}	1447.0^{a}	1136.6^{a}	1249.4^{a}	1068.8^{a}	1574.8^{a}
Mg ($\mu g \cdot g^{-1}$)	546.6^{a}	396.9^{bc}	340.2^{c}	851.2^{a}	388.6^{b}	266.0^{c}	273.6^{c}	794.1^{a}
Sand (%)	60.6^{a}	54.0^{a}	59.2^{a}	54.9^{a}	—	—	—	—
Silt (%)	14.9^{b}	20.2^{a}	19.6^{a}	12.9^{b}	—	—	—	—
Clay (%)	24.5^{b}	24.9^{b}	21.2^{b}	32.2^{b}	—	—	—	—
Gravel (%)	2.3^{b}	2.0^{b}	1.7^{b}	10.3^{a}	—	—	—	—
Moisture (5-15 cm) (MPa)	-0.10^{a}	-0.18^{a}	-0.20^{a}	-0.23^{a}	-4.87^{a}	-4.15^{a}	-5.05^{a}	-2.95^{a}
Moisture (15-25 cm) (MPa)	$-.15^{ab}$	-0.19^{a}	-0.024^{b}	-0.025^{b}	—	—	—	—
pH	5.78^{b}	5.95^{b}	5.41^{b}	6.59^{a}	5.05^{b}	4.99^{b}	5.27^{b}	6.36^{a}

1 and 2 (Table 1). The distinction between samples from wallows 1 and 2 in August was less clear than in May due to a reduction in species number and the overwhelming cover of *Eleocharis* spp. in these wallows at the end of the rainy season.

Significant differences among wallows in NH_4-N, NO_3-N, Na, Mg, pH and available P were evident in August (Table 2). Means and significance of % sand, silt, clay and gravel among wallows were based on single samples collected in May (Table 2). Multiple linear regression analyses identified NH_4-N, Na, % silt and % clay among significant edaphic parameters and available P among remaining parameters as important in defining cover of certain wallow species in August (Table 3).

TABLE 3—Significant multiple linear regression equations relating wallow species cover to edaphic parameters in May and August. Coefficients of determination (r^2) and levels of significance (P) are shown. The edaphic parameters are: NH_4 = ammonium-nitrogen, NO_3 = nitrate-nitrogen, P = available phosphorus, Na = sodium, Mg = magnesium, silt = silt content, clay = clay content, grav = gravel (>2 mm), moist = moisture (15-25 cm).

Species	Equation	r^2	P
	May		
Alopecurus carolinianus	$= 2.72\ NH_4 - 0.028\ Na - 106.81\ silt - 7.53$	0.75	0.009
Coreopsis tinctoria	$= 754.7\ silt - 6.03\ NO_3 - 73.6$	0.75	0.005
Eleocharis spp.	$= 2.10\ P - 9.24\ moist - 24.2$	0.57	0.025
Grindelia squarrosa	$= 53.1\ grav - 0.91$	0.37	0.050
Juncus interior	$= 37.32\ grav - 0.565$	0.65	0.005
Plantago elongata	$= 34.1\ grav + 0.018\ Na - 0.0019\ Mg - 1.37$	0.95	0.001
	August		
Coreopsis tinctoria	$= 270.4\ silt - 36.3$	0.38	0.050
Echinochloa crusgalli	$= 0.268\ NH_4 + 0.0143\ Na - 0.0475\ P - 2.10$	0.98	0.001
Eleocharis spp.	$= 10.79\ NH_4 - 0.117\ Na - 7.93$	0.58	0.025
Tridens albescens	$= -4.68\ NH_4 - 108.34\ Clay + 64.16$	0.70	0.004

TABLE 4—Mean values of edaphic parameters from inside and outside four wallows in May and August. Means within each row and month are not significantly different at P = 0.05 when followed by the same letter. Dashes indicate no data were collected.

	May		August	
Edaphic parameter	Inside	Outside	Inside	Outside
NH_4-N ($\mu g \cdot g^{-1}$)	11.9^a	15.6^b	7.4^a	6.0^b
NO_3-N ($\mu g \cdot g^{-1}$)	7.3^a	4.8^b	3.0^a	2.5^a
P ($\mu g \cdot g^{-1}$)	11.4^a	9.3^a	8.8^a	5.0^b
K ($\mu g \cdot g^{-1}$)	283.9^a	254.1^a	258.2^a	239.8^a
Na ($\mu g \cdot g^{-1}$)	57.4^a	52.1^a	51.3^a	40.5^a
Ca ($\mu g \cdot g^{-1}$)	1582.1^a	1130.9^a	1310.1^a	1315.8^a
Mg ($\mu g \cdot g^{-1}$)	399.4^a	277.3^b	281.4^a	263.3^a
Sand (%)	57.4^b	69.9^a	—	—
Silt (%)	17.8^a	17.6^a	—	—
Clay (%)	24.8^a	12.5^b	—	—
Gravel (%)	2.0^a	0.8^a	—	—
Moisture (5-15 cm) (MPa)	-0.14^a	-0.08^a	-3.96^a	-9.10^b
Moisture (15-25 cm) (MPa)	-0.11^a	-0.09^a	—	—
pH	5.89^a	6.53^a	4.98^b	6.06^a

Wallow soils differed substantially from those of the surrounding grassland, both in absolute terms and in variation among sites. The mean value of NH_4-N was higher in grassland than in wallow soils in May (Table 4). The reverse was true in August, however, possibly due to retarded mineralization of organic soil N under the prevailing low-moisture conditions of the grassland soils (Mengel and Kirby, 1982). Average soil texture, NO_3-N, available P, Mg, moisture and pH also varied between grassland and wallow samples. Wallow soils were also more heterogeneous than those outside wallows. Analysis of edaphic parameters from outside the four wallows revealed that only % sand and pH differed significantly ($P = 0.05$) among the four grassland sites in either May or August.

DISCUSSION—Many previous studies on natural disturbances in grasslands focused on the ecosystem or community level (England and DeVos, 1969; Vogl, 1974; Kucera, 1981; Coppock et al., 1983a,b). Beyond the recognition that no two disturbance events are alike, little attention has been given to the heterogeneity of plant assemblages or physical sites between disturbed patches in grasslands. Our results demonstrated variation in species importance and composition among wallows only a few kilometers apart. These differences were correlated most strongly with differences in soil texture, NH_4-N and Na.

While the occurrence and distribution of some wallow species were correlated to edaphic factors, the feasibility of generalizing strict relations of species to soil characteristics from these limited results seems remote. It appears, instead, that differences in edaphic factors among wallows interact with probabilistic events and recurrent disturbances to produce heterogeneous plant assemblages. Unpredictable events may include time of wallow creation, proximity of seed sources, seed dispersal, seed dormancy, and microsite conditions for seed germination and seedling establishment. Species composition of wallows is further complicated by abiotic disturbances, including water level fluctuations and frequency or intensity of fire. Thus, many biotic and abiotic factors combine to increase species heterogeneity and soil variability in buffalo wallows.

Evidence from other studies documents the overriding effects of water level fluctuation on species composition in wetlands (Kadlec, 1962; Harris and Marshall, 1963; van der Valk, 1975). For instance, standing water is detrimental to the establishment of many species, while water level change may allow other species to become established (Holland and Jain, 1977; van der Valk, 1981). Therefore, wallow species must be able to exploit favorable moisture regimes as well as survive adverse conditions of drought or flooding.

The frequency and magnitude of recurrent animal disturbances, particularly the trampling and wallowing activities of bison, also affect species composition (Collins and Uno, 1983). In wallows frequently revisited by bison, ruderal species are abundant. Where the impacts of wallowing and trampling are diminished, perennial plants (i.e., *Eleocharis* spp., *Tridens albescens*, and *Juncus interior*) become established. In the latter situations, competitive replacement, as modified by soil factors, may become an important process determining species composition.

The ecological significance of highly variable environments within the grassland ecosystem is not clearly understood. Wallows are unique in that they constitute ephemeral pool habitats that support a number of wetland species (e.g., *Alopecurus carolinianus, Bacopa rotundifolia, Heteranthera limosa*,and *Marsilea mucronata*) not typically found on other naturally disturbed sites within grasslands (Platt, 1975; Coppock et al., 1983a). It has been suggested that wallows served as disturbance safe-sites for ruderal and wetland species within mature grassland vegetation and that regional species diversity in grasslands is increased by the vegetation of wallows (Collins and Uno, 1983). Our findings demonstrated the heterogeneous nature of wallow plant assemblages. Overall, this heterogeneity is induced by the concomitant effects of biotic factors, abiotic disturbances and the diverse and distinctive nature of wallow soils. The variability in species importance and composition among wallows, together with the variability of vegetation within single wallows during the growing season (Collins and Uno, 1983; Polley and Collins, 1984), contribute to an increased regional species diversity in grasslands.

We express our appreciation to Scott L. Collins, Raymond E. Phillips, and Forrest L. Johnson for valuable guidance and assistance throughout the study and to Gorden E. Uno and James K. Detling for constructive comments on the manuscript. Thanks also are extended to the staff of the Wichita Mountains Wildlife Refuge for access to study areas.

The financial support of a National Science Foundation Graduate Fellowship to the senior author and that provided by the University of Oklahoma are gratefully acknowledged.

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