Am. Midl. Nat. 145:261–274

Influence of Landscape Composition and Change on Lesser Prairie-chicken (Tympanuchus pallidicinctus) Populations

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ABSTRACT.—Home ranges of lesser prairie-chickens (*Tympanuchus pallidicinctus*) include up to several thousand ha of several habitat types that are concentrated around leks (traditional display grounds). A geographic information system (GIS) was used to relate changes in vegetation and land use to population trends of lesser prairie-chickens in Oklahoma, Texas and New Mexico. We quantified changes in vegetation within 4.8 km of lesser prairie-chicken leks and examined relationships among those changes and long-term population trends based on the number of displaying males per lek. Five of 13 populations declined between 1959 and 1996. Landscapes in which populations of lesser prairie-chickens declined were characterized by greater rates of landscape change and greater loss of shrubland cover types than landscapes in which populations did not decline. Changes of specific cover types were not as important as the total amount of change occurring on landscapes. Conservation of lesser prairie-chickens should focus on stability of vegetation and land use and specifically attempt to maintain continuity of shrublands within 4.8 km of existing leks.

INTRODUCTION

Lesser prairie-chickens (*Tympanuchus pallidicinctus*) are indigenous to rangelands of the southern Great Plains, inhabiting parts of Colorado, Kansas, Oklahoma, Texas and New Mexico (Aldrich, 1963). Anecdotal evidence suggests that lesser prairie-chickens were plentiful at the time of settlement of the region (Bent, 1963). Reports of population declines were first noted in the 1930s (Duck and Fletcher, 1944; Hoffman, 1963; Jackson and DeArment, 1963). Between 1940 and 1960 populations in Colorado and Texas continued to decline, but populations in Oklahoma were stable (Copelin, 1963; Hoffman, 1963; Crawford and Bolen, 1976). In Oklahoma populations of lesser prairie-chickens declined by 55% from 1960 to 1980 and their distribution declined by 50% from historic levels (Taylor and Guthery, 1980b). In 1980, Taylor and Guthery (1980b) estimated that the overall range and population had declined by 92% and 97%, respectively. It has been suggested that heavy grazing, drought, excessive harvest and cultivation of rangelands may have contributed to these declines (Hoffman, 1963; Crawford and Bolen, 1976; Taylor and Guthery, 1980b; Applegate and Riley, 1998; Giesen, 1998).

Landscape ecology has become increasingly useful in addressing critical issues in wildlife conservation, and recent research has quantified landscape-level effects on greater prairie-chickens (*Tympanuchus cupido*), capercaille (*Tetrao urogallus*) and other species (McGarigal and Marks, 1995; Storch, 1997; Ryan *et al.*, 1998; Burke, 2000; Niemuth, 2000; Farina, 1997;

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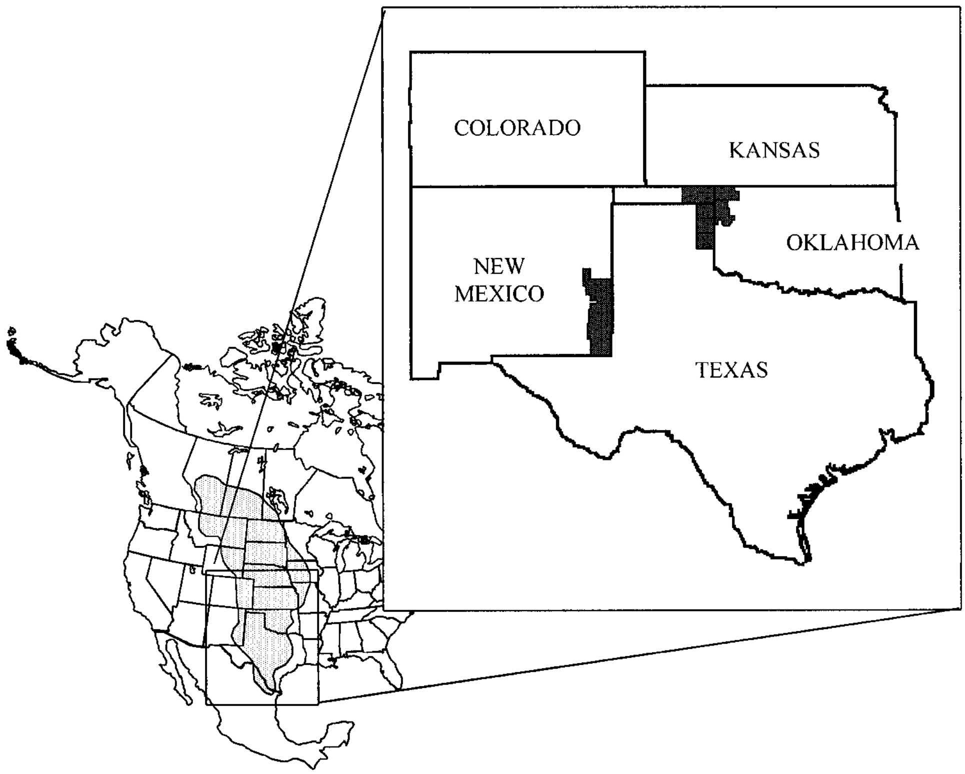

FIG. 1.—Map of study region located within the southern Great Plains of the United States, illustrating 13 study sites within Oklahoma (n = 5), Texas (5) and New Mexico (3) (counties containing study sites shaded)

Saab, 1999). Lesser prairie-chicken habitat research has been primarily limited to short-term, patch-level (*e.g.*, species composition and habitat physiognomy) studies and management of habitat for populations has been implemented without regard for long-term, landscape-level patterns and dynamics. Large home ranges and a dependence on many different habitat types suggest that an analysis of landscape composition may be critical in understanding lesser prairie-chicken population dynamics. Several studies have also indicated that landscape change is important and may be more important than current landscape structure (Dunn *et al.*, 1991; Knick and Rotenberry, 2000). We evaluated the importance of landscape-level composition and change to long-term population trends for lesser prairie-chickens. Our objectives were to: (1) estimate long-term population trends for 13 lesser prairie-chicken leks, (2) quantify landscape-level composition and change of landscapes surrounding each lek and (3) determine if composition and change of landscapes surrounding leks were related to population trends estimated from lek counts.

METHODS

Study area.—Our study was conducted on the southern Great Plains in western Oklahoma, northern Texas and eastern New Mexico (Fig. 1). The study region included the High Plains and Rolling Plains physiographic provinces of the panhandle of Texas, western Oklahoma and eastern New Mexico. Five study sites were located in Oklahoma in Harper, Ellis and Texas counties; five study sites were located in Texas in Hemphill, Wheeler and Lipscomb counties; and three study sites were located in New Mexico in Chaves, Roosevelt and Lea counties. Elevation ranged from 460 to 1525 m above mean sea level, and the topography was characterized by rolling open plains with gentle slopes (U.S. Department of Agriculture Soil Conservation Service (USDA-SCS), 1981). Rainfall across the region was erratic, mainly occurring between late spring and autumn. Average annual precipitation and temperature ranged from 38 cm and 13 C in the west to 76 cm and 18 C in the east (USDA-SCS, 1981; Sala *et al.*, 1988).

Historically, these landscapes were comprised of a mosaic of native prairies and shrublands (Vankat, 1974; Dhillion *et al.*, 1994). Shortgrasses, such as blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*), are dominant grass species on western portions of the study area (Kuchler, 1964). Midgrasses and tallgrasses are more dominant on eastern and central prairies and shrublands of the study area and include little bluestem (*Schizachyrium scoparium*), sideoats grama (*B. curtipendula*) and big bluestem (*Andropogon gerardii*) (Kuchler, 1964). Dominant shrubs throughout the study area include sand sagebrush (*Artemisia filifolia*), shinnery oak (*Quercus havardii*), sand plum (*Prunus angustifolia*), sumac (*Rhus* spp.) and mesquite (*Prosopis* spp.). A multitude of forbs occur within the region, with dominance depending on management and recent precipitation patterns (Vankat, 1974). Currently, tracts of cultivation and introduced pasture occur extensively throughout the region (Dhillion *et al.*, 1994).

Population status.—Population data (spring lek counts of displaying males) for the 13 sites were obtained from the Oklahoma Department of Wildlife Conservation, Texas Parks and Wildlife Department and the Bureau of Land Management in New Mexico (*see* Table 2 for sampling dates). Use of population trends rather than population sizes was more appropriate due to missing data and an unbalanced sampling design among states. Similar methods have been used to estimate abundance and avian population trends (Collins, 1990; Geissler and Sauer, 1990; Moses and Rabinowitz, 1990). To account for low and variable populations, spring lek counts were transformed by:

$$z_{ij} = \ln(y_{ij} + c) \tag{1}$$

where z_{ij} was the transformed count, y_{ij} was the spring lek count for site i in year j and c = 0.5 (transformation constant) (Collins, 1990; Steele *et al.*, 1997). To choose a transformation constant, data were back-transformed so that a comparison of residual values could be computed ($\text{residual}_{ij} = \text{actual}_{ij} - \text{predicted}_{ij}$) (Collins, 1990); residuals were minimized for $c = 0.5$. For 12 of the sites simple linear regression of transformed data (z_{ij}) against time was performed to determine the population trend for each site as the estimate of the slope of the regression (β) (SAS Institute, 1985). Leks with trends significantly less than zero ($\alpha \leq 0.05$) were classified as "declining" and all other leks were classified as "not-declining." For one site in Oklahoma (OK4), simple linear regression could not be used to determine a population trend because lek counts (mean = 17) predated aerial photography. Surveys of the lek in 1995, 1996, 1997 and 1998 indicated the population was not sustained, and the population was classified as "declining."

Landscape composition and change.—Seasonal and diurnal movements of radio-collared lesser prairie-chickens indicate differential use of habitats and a tendency for birds to concentrate activities within 4.8 km of leks (display grounds) (Giesen, 1994; Riley *et al.*, 1994). Therefore, vegetation within a 4.8-km radius of a centrally located lek (map extent = 7238 ha) was mapped from interpretation of black and white aerial photographs taken between 1959 and 1996 at a scale of 1:7920. Inter-lek distances ranged between one and several

TABLE 1.—Descriptions of cover types and grouped categories used to interpret aerial photography (1959–1996) for classification of landscapes containing lesser prairie-chicken populations in Oklahoma, Texas, and New Mexico

Class	Classification	Description of dominant features
Cover Type		
1	Lek	Traditional display ground
2	Water	Tanks, ponds, or streams
3	Bare ground	Roads, oil pads, and pipelines
4	Shortgrass prairie	Shortgrass prairie (e.g., *Bouteloua gracilis*)
5	Mixed grass prairie	Mixed grass prairie (e.g., *Schizachyrium scoparium*)
6	LD-Shinnery oak (Low density)	Shinnery oak (*Quercus havardii*) ł5%, and mixed grass prairie
7	HD-Shinnery oak (High density)	Shinnery oak −15%, and mixed grass prairie
8a	LD-Mixed shrubland (Low density)	Sand sagebrush (*Artemesia filifolia*) and other shrubs <15%, and mixed grass prairie
9a	HD-Mixed shrubland (High density)	Sand sagebrush and other shrubs >15%, and mixed grass prairie
10	Pasture	Introduced pasture (e.g., Old-world bluestem) or heavily manipulated pasture (e.g., mechanical shrub reduction)
11	Cultivation	Cultivated fields
12	Windbreak	Windbreak
13	Riparian	Riparian vegetation
14	Development	Farm houses, yards, buildings and railroads
15	HD-Eastern redcedar (High density)	Eastern redcedar (*Juniperus virginana*) >15% and mixed grass prairie
16	HD-Mesquite (High density)	Mesquite (*Prosopis glandulosa*) >15% and mixed grass prairie
Grouped categories		
	Native vegetation	Native prairie and shrubland (Includes 1, 4–9, 13, 15 and 16)
	Native prairie	Native short- and mixed grass prairies (Includes: 4 and 5)
	LD-Shrubland (Low density)	Shinnery oak and mixed shrubs <15% (Includes: 6 and 8)
	HD-Shrubland (High density)	Shinnery oak and mixed shrubs >15% (Includes: 7 and 9)
	Total Shrubland	Total shinnery oak and mixed shrubs (Includes: 6–9)
	Tree	Windbreaks, *Prosopis glandulosa, Juniperus spp.* (Includes 12, 15 and 16)
	Upland Prairie-Shrubland	Native prairie, shinnery oak <15%, and mixed shrubs <15% (Includes: 4–6, and 8)

[a] Includes shinnery oak, Chickasaw plum (*Prunus angustifolia*), sumac (*Rhus* spp.) and others

TABLE 2.—Summary of sampling dates and population trend analysis of lesser prairie-chickens at 13 sites in Oklahoma, Texas and New Mexico. Population trends are regression slopes in the log scale, units are expressed as the natural logarithm of the lek count per year. ‡ indicates populations that are significantly declining ($P \leq 0.05$)

Lek name	Years of population data	Years of aerial photography	Population trend (β)	Coefficient of variation (CV)	Coefficient of Determination (r^2)	Percentage change (per decade)	Population Status
OK1	1980–1996	1983, 1995	−0.11‡	31.4	0.50	−92.1	Declining
OK2	1965–1996	1965, 1973, 1981, 1990	−0.01	41.0	0.01	−30.9	Not declining
OK3	1970–1996	1975, 1985, 1995	−0.14‡	63.5	0.44	−96.2	Declining
OK4[a]	1959–1996	1959, 1995					Declining
OK5	1988–1996	1990, 1995	−0.20‡	10.3	0.79	−94.1	Declining
TX1	1959–1996	1959, 1967, 1972, 1981, 1996	0.00	30.5	0.00	−12.7	Not declining
TX2	1959–1996	1959, 1967, 1972, 1981, 1996	−0.03‡	20.3	0.20	−61.3	Declining
TX3	1959–1996	1959, 1970, 1979, 1991	0.00	37.0	0.00	2.7	Not declining
TX4	1959–1996	1959, 1970, 1979, 1991	0.01	6.1	0.25	32.9	Not declining
TX5	1959–1996	1959, 1970, 1979, 1991	−0.03	34.7	0.11	−51.4	Not declining
NM1	1970–1985	1973, 1983	−0.07	45.1	0.09	−75.9	Not declining
NM2	1970–1985	1973, 1983	0.04	18.0	0.16	90.1	Not declining
NM3	1970–1985	1973, 1983	−0.01	24.9	0.00	−12.2	Not declining

[a] Current surveys indicate population not sustained beyond 1959

hundred kilometers and there was no indication of autocorrelation of population trends and inter-lek distance suggesting that populations at each lek were independent. All photo-interpretation was done by J. S. Shackford, and its accuracy was verified by site visits comparing classified landscapes to actual vegetation. Dates for aerial photography across the region did not occur sequentially at regular time periods but corresponded to intervals of 5–10 y during the lesser-prairie chicken population sampling period (*see* Table 2). Topographic quadrangle maps (scale = 1:24,000) were used for geo-registration. Landscapes were constructed using ARC/INFO software (Environmental Systems Research Institute, Inc., 1995). Minimum resolution (grain) and mapping unit (accuracy) correspond to about 2 m and 20 m, respectively.

Landscape composition of each map was classified into 17 cover types (Table 1). Cover types were grouped into seven categories of general vegetation properties and land use to evaluate broader relationships between changes in landscape composition and population trends of lesser prairie chickens (Table 1). Mean landscape composition was calculated for each site by averaging sequential values across time.

Changes in landscape composition were computed for each site as:

$$\Delta A_i / t \tag{2}$$

where ΔA_i was the change in area (most recent composition minus initial historic composition) of each cover type and grouped category (Table 1); t was the time (reported in decades) corresponding to photographic data. A landscape change index (LCI) was calculated for each site by multiplying a factor of one-half by the sum of the absolute values of average changes of all cover types (equation 2 above):

$$\text{LCI} = \frac{1}{2} \sum_i (\Delta A_i / t) \tag{3}$$

LCI quantified total change in vegetation and land use at the landscape-level for each site by combining the absolute average changes of all cover types into one value. Summing absolute values of landscape change essentially doubled the index so the LCI included a factor of one-half to more accurately reflect the actual area of change. Mean landscape composition (across time) and changes in landscape composition were analyzed using ANOVA ($\alpha \leq 0.10$) to examine differences in means among states (SAS Institute, 1985).

Population-habitat relationships.—Analyses were conducted on landscape composition of most recent map years (1996 for Texas and Oklahoma and 1985 for New Mexico) and the average of all map years for each site to determine the relative importance of "current" and mean landscape compositions. Relationships between landscape composition and lek trends were analyzed with analysis of variance (ANOVA, $\alpha \leq 0.10$) in which differences were evaluated between declining and not declining landscapes (lek status). Correlation analyses were also conducted to identify linear relationships between population trends and landscape change without considering lek status. Analyses were conducted on mean landscape composition, current landscape composition and changes in landscape composition.

RESULTS

Population status.—Population trends of lesser prairie-chickens ranged from −0.20 to 0.04 (Table 2). Analyses of population trends indicated that five populations declined (OK1, OK3, OK4, OK5 and TX2) from 1959 to 1996. Four populations (OK2, TX5, NM1 and NM3) had negative trends but relationships were not significant so populations were classified as 'not declining'. The remaining four populations did not have negative trends resulting in a total of eight populations classified as 'not declining'. Mean trend for populations that declined was −0.10 (SE = 0.02).

Landscape composition.—Landscape composition was variable among sites, but there were consistent patterns of vegetation and land use. Landscapes were composed of a matrix of native vegetation and included a variety of patch types. On average, landscapes contained 86.5% native vegetation (6263 ha, SE = 280), 5.9% pasture (429 ha, SE = 170), 6.1% cultivation (441 ha, SE = 158) and small amounts (<1%) of development, windbreaks, bare ground and open water. Of the native vegetation, 87.2% (5462 ha, SE = 364) was shrubland and of the total shrubland 88.2% (4819 ha, SE = 504) was low-density shrubland. Over the past 40 y native vegetation decreased by 0.1% (10 ha, SE = 29) per decade, pasture has increased by 0.9% (65 ha, SE = 48) per decade and cultivation has decreased by 0.9% (66 ha SE = 63) per decade (Table 3). Total low-density shrubland decreased by 1.6% (113 ha, SE = 79) per decade; total high-density shrubland decreased by 0.6% (43 ha, SE = 61) per decade.

Mean composition of landscapes varied among states. Landscapes in Oklahoma contained an average of 79.6% (5761 ha, SE = 359) native vegetation, which was significantly less than landscapes in New Mexico (99%; 7185 ha, SE = 10) but not landscapes in Texas (85.8%; 6210 ha, SE = 543). Shrubland dominance ranged from 92.6% (6703 ha, SE = 186) in New Mexico to 78.1% (5656 ha, SE = 455) in Texas and 62.5% (4524 ha, SE = 598) in Oklahoma. Mean changes in landscape composition differed among states for two groups: total shrubland ($F = 4.63$, $P = 0.090$) and the landscape change index ($F = 9.30$, $P = 0.012$). Loss of total shrubland was 1.0% (55 ha, SE = 22) per decade for landscapes in New Mexico, 2.0% (137 ha, SE = 22) per decade for landscapes in Texas and 3.0% (220 ha, SE = 10) per decade for landscapes in Oklahoma. Rates of landscape change based on LCI were 1.2% (90 ha, SE = 18) per decade for landscapes in New Mexico, 2.8% (201 ha, SE = 18) per decade for landscapes in Texas and 11.2% (810 ha, SE = 223) per decade for landscapes in Oklahoma.

Population-habitat relationships.—Landscapes in which populations declined were compositionally different than landscapes in which populations did not decline (Table 3). Current and mean landscapes in which populations declined contained less low-density mixed shrubland ($P < 0.05$), less total low-density shrublands ($P < 0.01$) and less upland prairie-shrubland ($P < 0.01$) than landscapes in which populations did not decline. Current landscape composition (based on most recent photographs) of declining landscapes had less total shrubland ($P < 0.01$) than not-declining landscapes.

Means of LCI were greater for landscapes in which lesser prairie-chicken populations declined (827, SE = 221) than for landscapes in which populations did not decline (149, SE = 21; $P = 0.04$). That relationship was supported by a correlation between trends at lesser prairie-chicken leks and the LCI ($r = 0.63$, $P = 0.028$; Fig. 2). Landscapes in which populations declined lost total shrubland at a greater rate (3.8% or 272 ha, SE = 89) per decade than landscapes in which populations did not decline (1% or 74 ha per decade, SE = 22; $P = 0.09$). A correlation between lesser prairie-chicken trends and rates of decline of total shrublands supported this relationship ($r = 0.71$, $P = 0.008$). Correlations between change in other cover types and lesser prairie-chicken trends were not significant.

DISCUSSION

A previous comparison of eight landscapes in western Texas indicated that a minimum of 63% rangeland (or maximum of 37% cultivation) was necessary to sustain populations of lesser prairie-chickens for 2 y and suggested that cultivation of rangelands has contributed

TABLE 3.—Comparison of mean and current landscape compositions (ha) of 16 basic cover types and 7 grouped categories for landscapes associated with lesser prairie-chicken populations. Mean changes in landscape composition (ha per decade) are also shown. Comparisons were made between landscapes in which populations declined (n = 5) and landscape in which populations did not decline (n = 8) and capital letters indicate differences ($P \leq 0.10$) within the same row for each method of calculating landscape composition

		Landscape composition								Mean change in Landscape composition			
		Mean				Current							
		Declining		Not declining		Declining		Not declining		Declining		Not declining	
Class	Classification	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE	x̄	SE
2	Water	5.6	3.5	6.1	4.8	2.9 B	0.9	0.9 A	0.5	−3.7	4.3	−1.3	1.5
3	Bare ground	41.6	12.7	33.1	5.8	39.7	13.7	41.6	9.2	−11.0	12.1	12.4	11.3
4	Shortgrass prairie	50.4	8.6	39.9	7.5	84.6	18.0	64.2	15.1	42.9	19.6	10.4	6.5
5	Mixed grass prairie	427.2	301.8	389.2	90.7	471.7	317.9	373.2	80.2	94.6	51.8	60.5	24.1
6	LD-Shinnery oak	1527.7	753.6	405.6	405.6	1454.7	623.2	318.3	318.3	−57.0	166.3	−9.6	9.6
7	HD-Shinnery oak	1430.6	1008.1	124.4	124.4	1388.0	783.7	200.6	200.6	−47.5	166.4	−6.0	6.0
8	LD-Mixed shrubland	1748.1 A	1049.1	5377.5 B	832.6	1671.5 A	981.3	5412.3 B	833.0	−191.1	145.7	−18.7	21.5
9	HD-Mixed shrubland	0.0	0.0	27.2	14.6	0.0	0.0	0.0	0.0	0.0	0.0	−34.1	18.3
10	Pasture	521.6	258.7	371.0	235.9	632.3	288.4	380.6	243.0	142.5	120.6	16.9	21.8
11	Cultivation	802.0	305.1	215.3	132.2	718.8	249.9	211.0	118.1	−149.3	165.0	−14.5	17.6
12	Windbreak	13.9	7.1	9.6	6.2	14.9	7.5	13.2	8.3	1.1	0.9	1.8	1.2
13	Riparian	445.6	231.8	122.0	85.3	452.2	237.1	107.1	86.9	62.4	87.1	−12.0	6.5
14	Development	45.7	30.2	24.5	12.5	55.7	38.0	28.0	14.6	9.7	8.6	1.0	0.9
15	HD-Eastern redcedar	160.7	160.7	0.0	0.0	234.4	234.4	0.0	0.0	106.6	106.6	0.0	0.0
16	HD-Mesquite	0.0	0.0	71.8	41.6	0.0	0.0	69.0	39.4	0.0	0.0	−5.6	7.3
Grouped categories													
	Native Vegetation	5790.4	347.6	6557.6	379.4	5757.0	326.5	6544.7	376.8	−1.4	72.1	−15.1	22.2
	Native Prairie	477.6	307.9	429.1	96.7	556.3	333.2	437.4	91.9	−10.7	171.6	−20.0	51.2
	LD-Shrubland	3275.8 A	595.0	5783.0 B	484.3	3126.2 A	428.7	5730.5 B	550.5	−114.1	180.8	−112.1	75.6
	HD-Shrubland	1430.6	1008.1	151.7	121.4	1388.0	783.7	200.6	200.6	−74.3	166.6	−23.3	11.9
	Total Shrubland	4706.5	588.1	5934.7	404.0	4514.1 A	571.0	5931.2 B	400.9	−271.6 B	89.3	−73.7 A	21.9
	Tree	174.6	157.8	81.4	39.7	249.3	231.3	82.2	36.9	107.8	106.4	−3.9	7.6
	Upland Prairie-Shrubland	3753.4 A	565.6	6212.1 B	514.0	3682.4 A	363.3	6168.0 B	582.5	−110.7	173.6	42.5	33.1
	Landscape Change Index									827.0 B	221.4	148.8 A	20.8

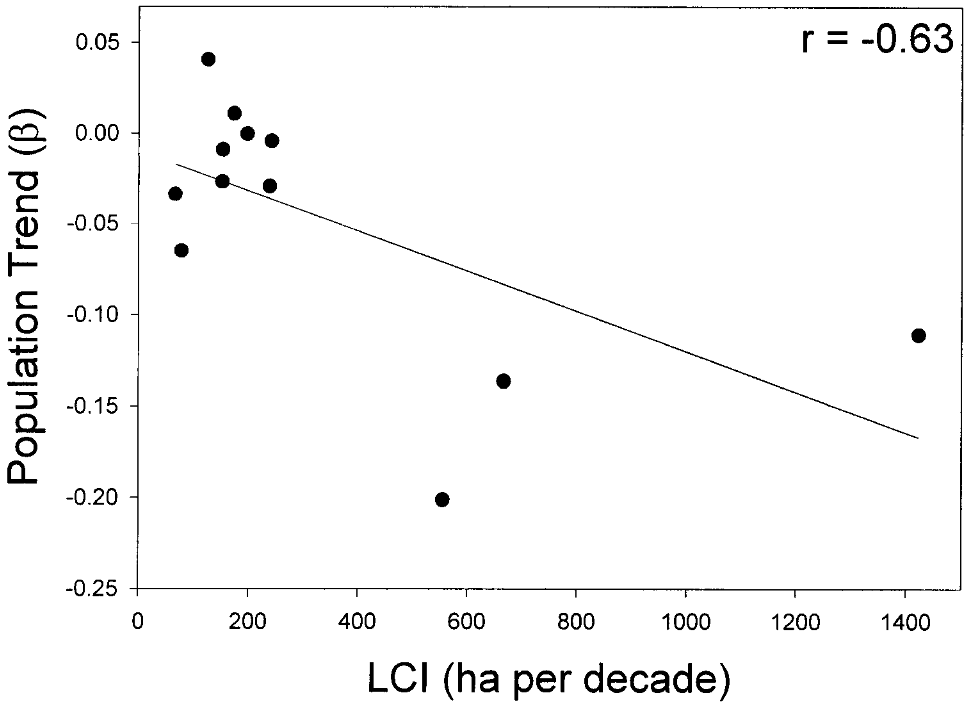

FIG. 2.—Relationship between landscape change index (LCI) and long-term population trends for 12 lesser prairie-chicken populations in Oklahoma, Texas and New Mexico. Lek OK4 is not shown because of insufficient data to calculate the population trend. Lek OK4 was declining and the landscape change index was 1252 ha per decade

to observed population declines (Crawford and Bolen, 1976). In our study analysis of spring lek counts for 13 populations of lesser prairie-chickens indicated that 5 populations declined between 1959 and 1996. Quantification of landscape-level composition and change within 4.8-km of leks indicated significant relationships between landscape-level changes in vegetation and lesser prairie-chicken population trends. Declining populations were associated with landscapes characterized by greater rates of total landscape change (11% per decade) and loss of shrubland cover types (3.8% per decade) compared with landscapes in which populations did not decline (2% and 1% per decade, respectively). Amount of cultivation was not associated with population trends for these 13 populations.

Spring lek counts for lesser prairie-chickens varied considerably from year to year; however, regression analyses were useful to determine population trends (Geissler and Sauer, 1990). Variability of spring lek counts may be caused by a number of factors. Short-term cyclic variability may be influenced by methodological, demographic and environmental uncertainties like unbalanced sex ratios, variable clutch size, mortality due to predation, drought, timing of spring precipitation, frequency of winter storms, movement of birds among leks and sampling personnel and protocol (Pollock *et al.*, 1990; Stacy and Taper, 1992; Murrow *et al.*, 1996; Guthery, 1997). Long-term population trends may be affected by genetic factors (such as reduced genetic diversity, reduced allelic diversity and bottle-

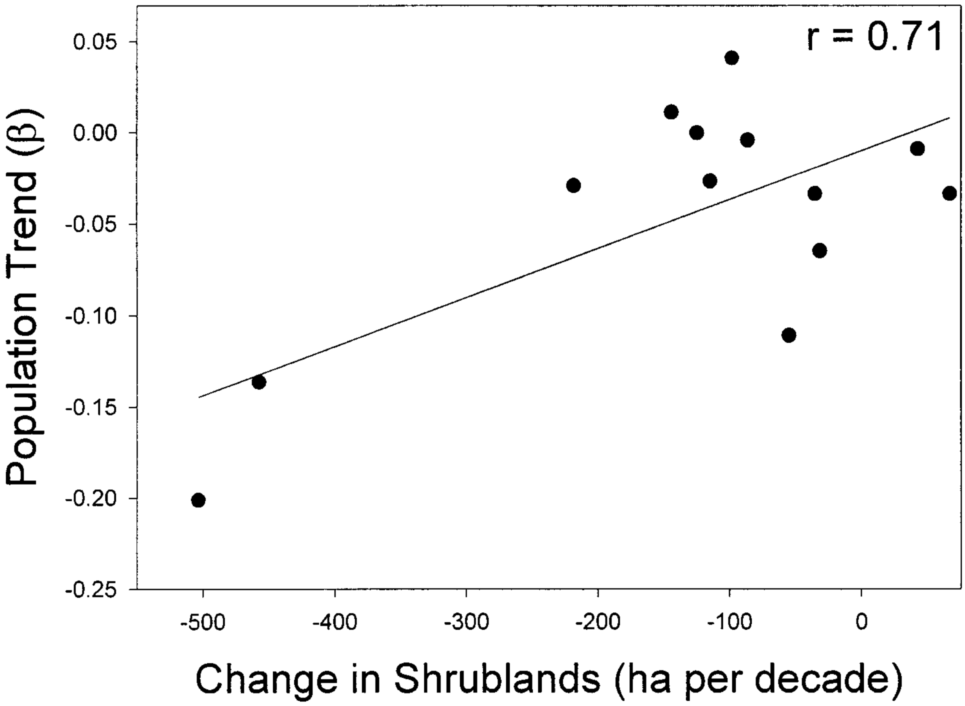

FIG. 3.—Relationship between population trend (Table 2) and rate of change in of shrublands (ha/decade) for 13 landscapes containing lesser prairie-chicken populations in Oklahoma, Texas and New Mexico. Lek OK4 is not shown because of insufficient data to calculate the population trend. The lek was declining and the change in shrublands was −124 ha per decade

necks) and landscape patterns of vegetation and land use (Hedrick and Miller, 1992; Wiens *et al.*, 1993).

Population trends for lesser prairie-chickens were related to the rate at which land was converted from one vegetation type or land use to another (landscape change) (Fig. 2). The landscape change index (LCI) suggested that 44% of the area had cover types that changed in landscapes with declining lesser prairie-chicken populations, and only 8% of the area changed in landscapes in which populations did not decline over the past four decades (Table 3). The LCI can over-estimate total area affected by change when change is calculated over multiple time steps because repeated changes on the same sites are not considered. However, the index does accurately measure the relative relationship between the amount of change on individual landscapes and population trends. Overall, the average landscape change for landscapes in which populations declined was more than five times the average change for landscapes in which populations did not decline.

Rates of landscape change can be highly variable depending upon the spatio-temporal scale, pattern-driving processes and socio-economics of a region (Turner, 1989; Dunn *et al.*, 1991; Licht, 1997). A critical factor in the southern Great Plains affecting rates of change is the variable patterns of ownership that are remnants of historical settlement patterns. Landscapes in Oklahoma were divided into homesteads of 64 ha about 100 y ago, but most landscapes in Texas and New Mexico retained relatively large (ca. >250 ha), more continuous parcels of rangeland (Samson and Knopf, 1994). Therefore, management practices in Texas and New Mexico were applied more extensively and consistently than management practices in Oklahoma. Smaller ownership tracts in Oklahoma increased the potential for more variable management and greater amounts of change. The landscape change index for Oklahoma landscapes suggested changes at a rate of 11% per decade compared with 1% in New Mexico and 3% in Texas. Four of the five populations that declined occurred in Oklahoma. The relationship between landscape change and lesser prairie-chicken declines in these states suggests that historical settlement patterns may be an important consideration in understanding long-term population trends for lesser prairie-chickens.

The relative importance of historic landscape change and current landscape structure is dependent on a species' site fidelity (Dunn *et al.*, 1991; Knick and Rotenberry, 2000). Permanency of leks, territoriality of cocks on leks from year to year, the tendency of hens to nest within 2.0 km of leks and seasonal movements that are concentrated within 4.8-km of leks are indications that lesser prairie-chicken populations have high site fidelity and may be dependent upon landscapes with minimal change (Copelin, 1963; Giesen, 1994). Stability of shrublands appears to be particularly important to lesser prairie-chickens. The average decline in total shrubland during this study was nearly four times greater on landscapes with declining populations than on landscapes where populations did not decline (Table 3). Shrubland communities provide a year-round source of food and cover and are influenced less than herbaceous dominated communities by other factors that could influence habitat, such as cattle grazing and periodic drought. Past management that alters herbaceous communities on these landscapes may have increased the importance of shrublands for lesser prairie-chickens.

There were no well-defined relationships between population trends of lesser prairie-chickens and cultivation or native vegetation as suggested by previous studies (Crawford and Bolen, 1976; Taylor and Guthery, 1980b). Our analyses were limited to landscapes dominated by native vegetation and changes that occurred over the past 10–35 y, and most of the conversion of rangeland to cropland on these landscapes occurred before 1959 (Licht, 1997). In fact, during our study cultivated land declined on average, while pasture (introduced forages) and tree dominated cover types increased (HD-Eastern Redcedar, Riparian, Windbreak) (Table 3). The increase in pasture is similar in proportion to the decline in cropland and can be primarily attributed to the Conservation Reserve Program that converted marginal cropland into perennial vegetation cover during the 1980s (Fuhlendorf *et al., in press*). Increases in tree dominated landscapes are associated with encroachment of *Juniperus virginiana* on rangelands, increased trees along riparian areas and intentional plantings of windbreaks. Separately these changes were not significant to lesser prairie-chicken populations, but collectively they contributed to the significantly greater landscape change on landscapes with declining populations.

Structure and stability of the Great Plains rangelands have been greatly altered over the past century including regions occupied by lesser prairie-chickens (Samson and Knopf, 1994). Understanding the importance of landscape composition and change is critical to the conservation of many species, especially those with high site fidelity, such as the lesser prairie-chicken (Saunders *et al.*, 1991; Pulliam *et al.* 1992; Wiens *et al.*, 1993; Miller *et al.*, 1997; Law and Dickman, 1998; Ryan *et al.*, 1998; Knick and Rotenberry, 2000; Niemuth, 2000). For the lesser prairie-chicken, shrubland communities were the most critical landscape component, but composition and change of specific cover types were no more important than the total amount of change occurring on landscapes. Landscapes that have undergone the most rapid change over the past several decades also had the most intensive settlement patterns resulting in smaller land holdings. These settlement patterns and concomitant changes in landscape structure may have set the stage for many of the population trends we are currently observing. Management of stable lesser prairie-chickens populations should focus on maintaining stability of land use and should seek to sustain continuity of shrublands within 4.8-km of active leks. Further analyses of landscape structure are needed to better understand spatial scales and landscapes characteristics (*e.g.*, mean patch size, mean patch shape and average arrangements of patches) that are critical to lesser prairie-chicken populations.

Acknowledgments.—This manuscript is approved for publication by the Director, Oklahoma Agricultural Experiment Station. Research was a Federal Aid Wildlife Restoration Act under project AP-96-201W supported by the Oklahoma Department of Wildlife Conservation and Oklahoma State University through the Oklahoma Cooperative Fish and Wildlife Research Unit (Okla. Dep. Wildl. Conserv., Okla. State Univ., U.S. Geol. Surv. Biol. Resour. Div. and Wildl Manage. Inst., cooperating). Additional support was provided by the Oklahoma Agricultural Experiment Station, Oklahoma State University. We thank the Oklahoma Department of Wildlife Conservation, Texas Parks and Wildlife Department and the Bureau of Land Management for sharing data from their lek counts, Dr. Fred Guthery and Dr. M. Woodward for manuscript reviews, Dr. Mark Payton for statistical assistance, Mark Gregory, Lori Gallimore, Shane Feirer, Champe Greene, and D. Williams for technical support.

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SUBMITTED 22 JUNE 2000 ACCEPTED 4 DECEMBER 2000