A LANDSCAPE-LEVEL EVALUATION OF THE LESSER PRAIRIE-CHICKEN

By

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PREFACE

Historically, ecosystems in the southern Great Plains were shaped by natural disturbances such as fire and herbivory. In the late nineteenth century, much of the region was settled, and currently, the region is dominated by cropland and pastures, interspersed with tracts of native rangeland. Lesser prairie-chickens (*Tympanuchus pallidicinctus*) are gallinaceous birds indigenous to the region. In 1980, it was estimated that the overall range and population had declined by 92% and 97%, respectively. I evaluated the influence of landscape-level factors on long-term population trends. This thesis includes two manuscripts formatted for submission to *The American Midland Naturalist* (Chapter 1) and *Ecological Applications* (Chapter 2).

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ABSTRACT.—Distribution and abundance of the lesser prairie-chicken (*Tympanuchus pallidicinctus*) have declined by >90%. Lesser prairie-chickens possess large home ranges that include up to several thousand hectares and several habitat types. Seasonal and diurnal activities of birds are concentrated around leks (traditional display grounds). A geographic information system (GIS) was used to relate spatial and temporal changes in vegetation and land use to population trends of lesser prairie-chickens in Oklahoma, Texas, and New Mexico. We quantified landscape-level changes in vegetation around lesser prairie-chicken leks and examined relationships between those changes and long-term population trends. Population trends were estimated 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 to specific cover types were not as important as the total amount of change occurring on landscapes. In general, lesser prairie-chickens were influenced more by alteration of habitat patterns than by any particular type of land use at the landscape-level.

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 remained stable (Copelin, 1963; Hoffman, 1963; Crawford and Bolen, 1976). In Oklahoma from 1960 to 1980, populations of lesser prairie-chickens declined by 55%, and their distribution declined by 50% from historic levels (Taylor and Guthery, 1980b). In 1980, it was estimated that the overall range and population had declined by 92% and 97%, respectively (Taylor and Guthery, 1980b).

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). Size of home range varies and can cover several thousand hectares (Taylor and Guthery, 1980a). Typical home ranges include at least one lek and a number of grassland and shrubland communities that are essential for food and cover (Copelin, 1963; Donaldson, 1969). Leks exhibit characteristics that maximize visibility during breeding displays (Jones, 1963). Nest sites are selected for height (> 50 cm) and density (25 – 40%) of residual vegetation (Copelin, 1963; Haukos and Smith, 1989, Riley *et al.*, 1992; Giesen, 1994). Females select brood and foraging habitat for its provision of concealment cover while simultaneously not restricting mobility (Riley and Davis, 1993; Riley *et al.*, 1993). Descriptions of nesting, lekking and brood-rearing habitats suggest that an interspersion of grasses, shrubs and forbs is advantageous to lesser prairie-chickens (Copelin, 1963; Jones, 1963; Riley and Davis, 1993).

It has been proposed that the cultivation of rangelands was primarily responsible for lesser prairie-chicken declines prior to 1980 (Crawford and Bolen, 1976; Taylor and Guthery, 1980b). Further speculation has proposed that other factors like grazing pressure, drought, excessive harvest and landscape-level patterns of vegetation may contribute to population declines (Hoffman, 1963; Crawford and Bolen, 1976; Applegate and Riley, 1998; Giesen, 1998). Landscape ecology has become increasingly used to address critical issues wildlife conservation (McGarigal and Marks, 1995; Burke, 2000). Recent research has quantified effects of habitat patterns at the landscape-level on greater prairie-chickens (*Tympanuchus cupido*), capercaille (*Tetrao urogallus*) and other species (McGarigal and Marks, 1995; Storch, 1997; Ryan *et al.*, 1998; Niemuth, 2000). Also, avian abundance and distribution in western riparian zones may be more influenced by landscape composition than by patch-level characteristics (Farina, 1997; Saab, 1999). Lesser prairie-chicken habitat research has been 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.

Landscape structure (configuration of habitat) may be important to lesser prairie-chickens because they depend on several habitat types and possess large home ranges. However, landscape structure may not adequately explain abundance of a species just as local habitat structure may not be adequate, especially with species that exhibit high site fidelity such as lesser prairie-chickens (Weins et al 1986; McGarigal and McComb, 1995; Tewksbury *et al.*, 1998). Several studies have indicated that changes in landscape structure are 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 the lesser prairie-chicken. Our objectives were to 1) estimate long-term population trends for 13 lesser prairie-chicken populations, 2) quantify landscape-level composition and change for landscapes surrounding each lek and 3) determine if landscape-level composition and change of landscapes surrounding leks were related to population trends.

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 Texas and Oklahoma and adjacent lands in eastern New Mexico. Five study sites were located in Oklahoma within Harper, Ellis and Texas counties; five study sites were located in Texas within Hemphill, Wheeler and Lipscomb counties; and three study sites were located in New Mexico within Chaves, Roosevelt and Lea counties. Elevation ranges from 460 to 1,525 m above mean sea level, and the topography is characterized by rolling, open plains with gentle slopes (U.S. Department of Agriculture Soil Conservation Service (SCS), 1981). Rainfall across the region is erratic, 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 (SCS, 1981, Sala *et al.*, 1988).

Historically, landscapes were comprised of native prairie and shrublands, but currently, landscapes contain mosaics plant communities in which grasses and forbs are usually most abundant (Vankat, 1974; Dhillion, *et al.*, 1994). Shortgrasses, characteristic of western regions, are dominated by blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*) (Kuchler, 1964). Shortgrass, midgrass, and tallgrass species like blue grama, little bluestem (*Schizachyrium scoparium*), sideoats grama (*B. curtipendula*) and big bluestem (*Andropogon gerardii*) cover the central and eastern regions (Kuchler, 1964). Shrubs 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 interannual precipitation (Vankat, 1974). 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. 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; Moses and Rabinowitz, 1990). To account for low and variable populations, spring lek counts were transformed by:

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

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 (residual = y_{ij} (actual) - y_{ij} (predicted)) (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 (SAS Institute, 1985). Leks with trends less than zero ($\alpha \leq 0.05$) were classified as "declining," and leks with trends not less than zero 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) pre-dated 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. A t-test ($\alpha \leq 0.05$) was used to examine differences in mean population trends between declining and not-declining leks.

Landscape composition.—Vegetation within a 4.8-km radius of a centrally located lek at each site (map extent = 7,238 ha) was mapped from interpretation of black and white aerial photographs taken between 1959 and 1996 at a scale of 1:7,920. Inter-lek distances ranged between one and several 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 photointerpretation 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 years. 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 actual distance, respectively.

Landscape composition of each map was summarized into 17 cover types (Table 1). Also, cover types were grouped into seven collective categories of general vegetation properties and land use to evaluate broader relationships between changes in landscape composition and population trends (Table 1). Mean historic landscape composition was calculated for each site by averaging sequential values across time, and historic landscape composition data were averaged according to state to examine regional differences in vegetation and land use.

Changes in landscape composition were computed for each site as:

$$[\Delta A_i / t]$$

where ΔA_i was the change in area (most recent composition minus initial historic composition) of each cover type and group i and t was the period of time 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):

$$LCI = \frac{1}{2} \sum_i |\Delta A_i / t|$$

The LCI quantified total change in vegetation and land use at the landscape-level for each site by combining the average historic changes of all cover types into one value. The LCI included a factor of one-half because summing absolute values of landscape change essentially doubled the index. Historic landscape composition (mean across time) and changes in landscape composition were analyzed using ANOVA ($\alpha \leq 0.10$) to examine differences in means using state as the treatment variable (SAS Institute, 1985).

Population-habitat relationships.—Historic landscape composition may be confounded by time because intervals between sequential aerial photographs were not of leks. Further analyses of landscape structure are needed to better understand if landscapes characteristics (e.g., mean patch size, mean patch shape and average arrangements of patches) are critical to lesser prairie-chicken populations, and if so at what scales.

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LIST OF FIGURE CAPTIONS

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).

Fig 2. Relationship between landscape change index (LCI) and long-term population trends for thirteen lesser prairie-chicken populations in Oklahoma, Texas and New Mexico.

Fig 3. Relationship between population trend (Table 2) and rate of change in landscape composition of shrublands (ha / decade) for 13 landscapes containing lesser prairie-chicken populations in Oklahoma, Texas and New Mexico.

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.

Classification	Description of Dominant Features
Cover Type	
Lek	Traditional display ground
Water	Tanks, ponds, or streams
Bare ground	Roads, oil pads, and pipelines
Shortgrass prairie	Shortgrass prairie species (e.g., *Bouteloua gracilis*)
Midgrass prairie	Midgrass prairie species (e.g., *Schizachyrium scoparium*)
LD-Shinnery oak (Low density)	Shinnery oak (*Quercus havardii*) <15%, and prairie grass species
MD-Shinnery oak (Moderate density)	Shinnery oak 15-75%, and prairie grass species
HD-Shinnery oak (High density)	Shinnery oak >75%, and prairie grass species
LD-Mixed shrubland[a] (Low density)	Sand sagebrush (*Artemesia filifolia*) <15%, and prairie grass species mixed with other shrubs
HD-Mixed shrubland[a] (High density)	Sand sagebrush >15%, and prairie grass species mixed with other shrubs
Pasture	Introduced pasture (e.g., Old-world bluestem) or heavily manipulated pasture (e.g., brush-hog)
Cultivation	Cultivated fields
Windbreak	Windbreak
Riparian	Riparian vegetation
Development	Farm houses, yards, buildings, and railroads
HD-Eastern redcedar (High density)[b]	Eastern redcedar (*Juniperus virginana*) >15% and prairie grass species
HD-Mesquite (High density)[c]	Mesquite (*Prosopis glandulosa*) >15% and prairie grass species
Grouped Categories	
Native vegetation	Native prairie grass and shrub species (Includes: 1, 4-10, 14, 16, and 17)
Native prairie	Native short- and midgrass prairie species (Includes: 4 and 5)
LD-Shrubland (Low density)	Shinnery oak and mixed shrubs <15% (Includes: 6 and 9)
HD-Shrubland (High density)	Shinnery oak and mixed shrubs >15% (Includes: 7, 8, and 10)
Total Shrubland	Total shinnery oak and mixed shrubs (Includes: 6 – 10)
Tree	Windbreaks, mesquite, and cedar breaks (Includes: 13, 16, and 17)
Upland Prairie-Shrubland	Native prairie grass species, shinnery oak <15%, and mixed shrubs <15% (Includes: 4 – 6, and 9)
Landscape Change Index (LCI)	Total landscape change in land use and habitat (Includes: all cover types)

[a] Includes shinnery oak, Chickasaw plum (*Prunus angustifolia*), sumac (*Rhus* spp.), and others
[b] In Harper County, Oklahoma only
[c] In New Mexico only

Table 2. – Summary of 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 $P \leq 0.05$.

Lek Name	Range of Dates	Population Trend (β)	Coefficient of Variation (CV)	Coefficient of Determination (r^2)	Percentage Change (per decade)	Population Status
OK1	1980 - 1996	-0.11‡	31.4	0.50	-92.1	Declining
OK2	1965 - 1996	-0.01	41.0	0.01	-30.9	Not declining
OK3	1970 - 1996	-0.14‡	63.5	0.44	-96.2	Declining
OK4[a]	1959, 1996					Declining
OK5	1988 - 1996	-0.20‡	10.3	0.79	-94.1	Declining
TX1	1959 - 1996	0.00	30.5	0.00	-12.7	Not declining
TX2	1959 - 1996	-0.03‡	20.3	0.20	-61.3	Declining
TX3	1959 - 1996	0.00	37.0	0.00	2.7	Not declining
TX4	1959 - 1996	0.01‡	6.1	0.25	32.9	Not declining
TX5	1959 - 1996	-0.03	34.7	0.11	-51.4	Not declining
NM1	1970 - 1985	-0.07	45.1	0.09	-75.9	Not declining
NM2	1970 - 1985	0.04	18.0	0.16	90.1	Not declining
NM3	1970 - 1985	-0.01	24.9	0.00	-12.2	Not declining

[a] Current surveys indicate population not sustained beyond 1959.

Table 3.— Comparison of historic and current landscape compositions (ha) for landscapes associated with lesser prairie-chicken populations in terms of 17 basic cover types. Mean changes in historic landscape composition (ha per decade) are also shown. Comparisons were made between landscapes in which populations declined (n=5) and landscapes 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 Historic Landscape Composition			
	Historic				Current							
	Declining		Not Declining		Declining		Not Declining		Declining		Not Declining	
Classification	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Lek	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
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
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
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
Midgrass 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
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
MD-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
HD-Shinnery oak	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
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
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
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
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
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
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
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
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
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

Table 3 Continued.—Comparison of historic and current landscape compositions (ha) for landscapes associated with lesser prairie-chicken populations in terms of 7 grouped categories. Mean changes in historic landscape composition (ha per decade) are also shown. Comparisons were made between landscapes in which populations declined (n=5) and landscapes 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 Historic Landscape Composition			
	Historic				Current							
	Declining		Not Declining		Declining		Not Declining		Declining		Not Declining	
Classification	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Native Vegetation	5790.4	347.6	6557.6	379.4	5757.0	326.5	6544.7	376.8	-1.4	72.7	-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	-134.1	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

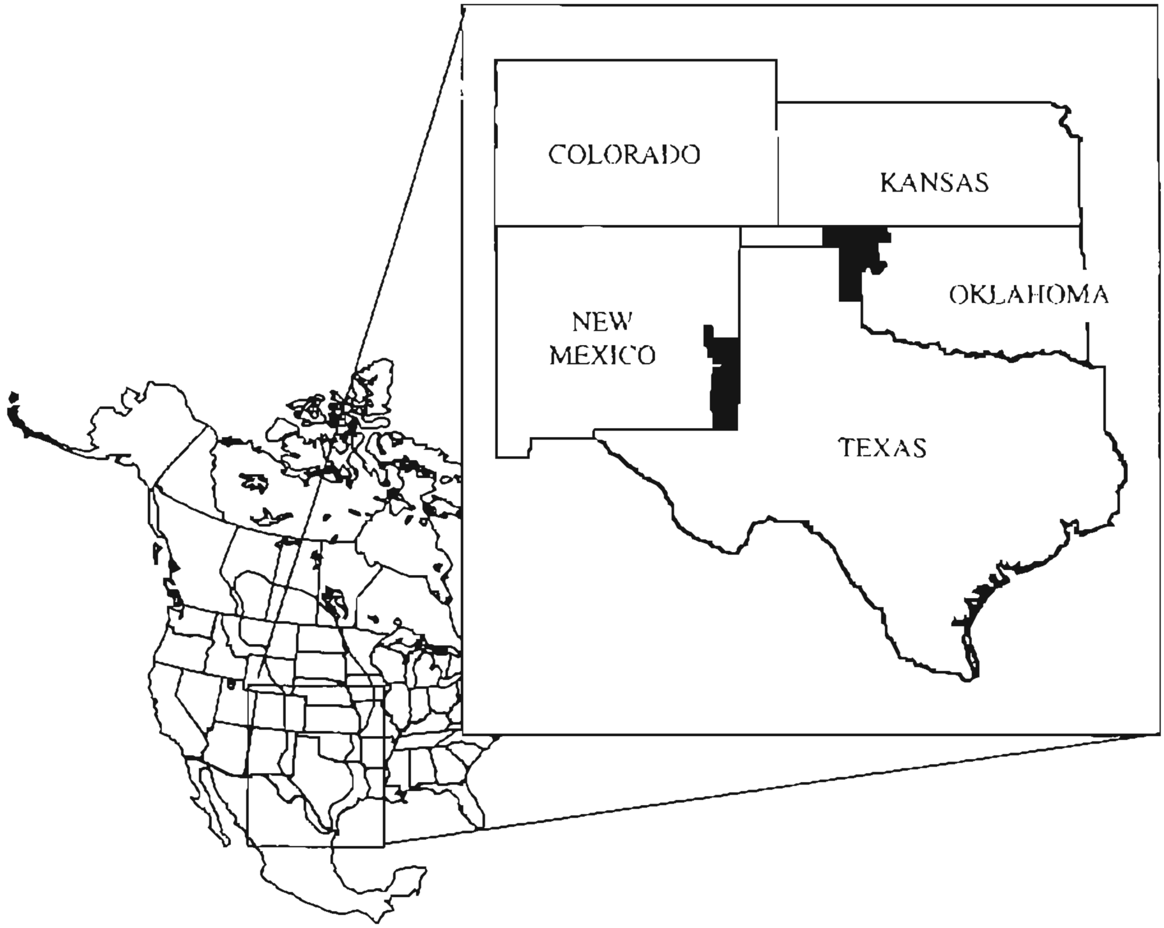

Fig 1.- Map of study region located within the southern Great Plains of the United States, illustrating 13 study sites within Oklahoma (n = 5), Texas (5) and New Mexico (3) (counties containing study sites shaded).

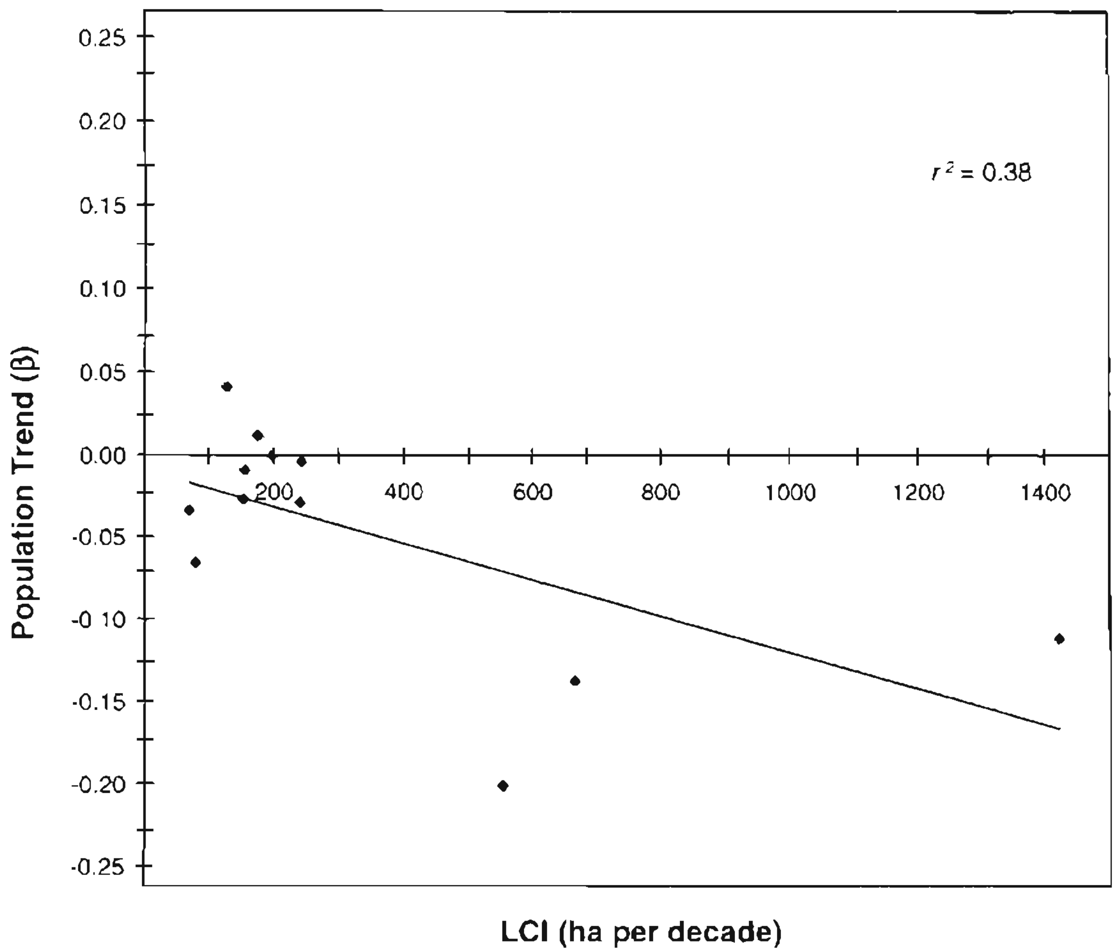

Fig 2.—Relationship between landscape change index (LCI) and long-term population trends for thirteen lesser prairie-chicken populations in Oklahoma, Texas and New Mexico.

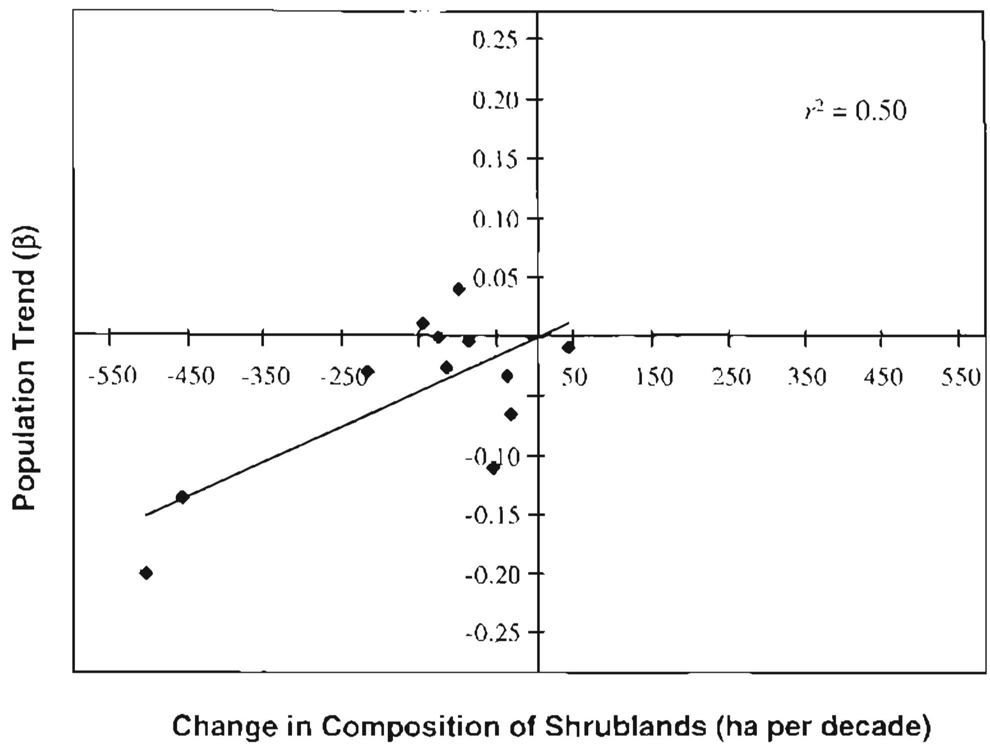

Fig 3.-- -Relationship between population trend (Table 2) and rate of change in landscape composition of shrublands (ha / decade) for 13 landscapes containing lesser prairie-chicken populations in Oklahoma, Texas and New Mexico.

A MULTI-SCALE ANALYSIS OF THE LESSER PRAIRIE-CHICKEN

Abstract.—Recent theories propose that landscape structure and change are scale-dependent landscape characteristics, wildlife populations respond to landscape structure and change, and relationships between populations and landscape structure and change are best studied at broad scales. Population levels and range for the lesser prairie-chicken (*Tympanuchus pallidicinctus*) have declined by > 90% over the past 100 years, making it a species of concern. Our objective was to use a multi-scale approach to examine scale-dependent relationships between landscape structure and change and long-term trends for lesser prairie-chicken populations in the southern Great Plains. We used a geographic information system to quantify landscape structure and change at multiple scales for fragmented agricultural landscapes surrounding 10 lesser prairie-chicken leks. Trend analysis of long-term population data for the populations was used to classify each population and landscape (declined, sustained). We analyzed 9 landscape structure and change metrics using a repeated measures analysis of variance to determine significant effects ($\alpha = 0.10$) between declining and sustained landscapes. Five metrics of landscape structure and change (landscape change index, percent cropland, increases in tree-dominated cover types, and changes in edge density) contained significant interactions between population status and scale, indicating different scaling effects of landscape structure and change on declining landscapes. Main effects of status were significant for one metric of landscape change (change in largest patch index), which indicated that landscapes with declining leks lost greater proportions of large, continuous patches than landscapes with sustained leks. Main effects of scale were significant for several landscape metrics (variability of patch size, change in variability of patch size, largest patch index, patch richness, change in patch richness, interspersion / juxtaposition index, and percentages of nonhabitat, tree, and low-density shrubland) indicating that landscape patterns were scale-dependent. The importance of landscape change as a critical factor in wildlife population-habitat relationships has largely been deemphasized by approaches that impose a static view on landscapes. However, multi-scale analyses of relationships between landscape structure and change and wildlife populations may provide the most robust analyses by incorporating landscape and population dynamics.

Key words: Scale; landscape dynamics; geographic information system; lesser prairie-chicken; landscape structure; landscape change; fragmentation; southern Great Plains (USA).

INTRODUCTION

Ecology is a scale-dependent science (Schneider 1994), and much of the historical work has been conducted at fine scales (Wiens 1989). For example, uncertainty in the effects of local habitat variability or short-term environmental fluctuations on avian populations and communities is fairly well understood. However, ecological systems may possess complexity at broad spatial (km^2) and temporal scales (>10 years) that obscure fine-scale ecological relationships (O'Neill et al. 1986). There are numerous examples where critical issues facing conservationists and ecologists are at least partially the consequence of broad-scale alterations of landscapes adjacent to or encompassing the habitat of interest (Burke 2000). Distribution and abundance of a variety of avian species in riparian ecosystems were influenced more by the landscape-level vegetation matrix than by local-level habitat variables (Saab 1999). Landscape-level loss and fragmentation of habitat affect distribution and nest success of greater prairie-chickens (*T. cupido*) in midwestern prairies (Ryan et al. 1998, Niemuth 2000) and the capercaille (*Tetrao urogallus*) in western Europe (Storch 1997).

From a landscape perspective, habitat is a multi-scale organization of biotic and abiotic components required by an organism that result from ecological processes operating over a range of spatio-temporal scales (O'Neill et al. 1986). Landscape structure and change are emergent properties of habitat at coarse scales delineated by the inherent scaling of landscape elements and the biological interactions within the landscape (Forman and Godron 1986, Levin 1992). Wildlife species possess traits that determine scales at which they adapt to and use habitats, thereby partially determining their response to landscape structure and change (Levin 1992, Wiens et al. 1993). Research over the past decade has shown that wildlife responds to landscape structure at multiple spatial scales (McGarigal and McComb 1995, Murrow et al. 1996, Miller et al. 1997, Turner et al. 1997, Burke and Goulet 1998, Law and Dickman 1998, Bergin et al. 2000) and landscape structure and change are scale-dependent (Addicott et al. 1987, Milne et al. 1989, Turner et al. 1989, Cullinan and Thomas 1992). Coarse-scale changes in landscape-level patterns alter flows of resources and energy into and out of local habitat patches and affect movements of organisms within landscapes depending on the scale-dependent landscape patterns and life-history traits of the species (Gardner et al. 1987, Wiens and Milne 1989, Saunders et al. 1991, Pulliam et al. 1992, Wiens et al.

1993, Knopf and Samson 1994, Turner et al. 1995, Law and Dickman 1998). The result is a dynamic, multifaceted relationship between wildlife populations and their habitat in which multiple variables and multiple scales are interrelated.

Population levels and range for the lesser prairie-chicken (*Tympanuchus pallidicinctus*) have declined by >90 % from historic levels (Crawford 1980, Taylor and Guthery 1980a, Giesen 1994b). Lesser prairie-chickens are a species of grouse endemic to the southern Great Plains of the United States that are closely associated with the prairies and shrublands of the region (Aldrich 1963). Much work has been done to quantify local-level habitat factors (Doerr and Guthery 1980, Haukos and Smith 1989, Olawsky and Smith 1991, Riley et al. 1992, Riley and Davis 1993), but little effort has been focused on the landscape-level. Lesser prairie-chickens depend on a variety of habitat components (Donaldson 1969), and descriptions of different vegetation types important to lesser prairie-chickens suggest the importance of habitat mosaics (Jones 1963, Giesen 1998). Dominant cocks and hens possess a high degree of site fidelity to habitat surrounding or adjacent to leks, and home ranges can include several thousand hectares (Taylor and Guthery 1980b, Riley et al. 1993, Giesen 1994a, Riley et al. 1994). Several authors have speculated that 1,024-7,238 ha of continuous habitat may be required to sustain a population (Davison 1940, Copelin 1963, Taylor and Guthery 1980b), suggesting that populations may be associated with landscape-level structure and change (Crawford and Bolen 1976, Chapter 1). However, it is not known how spatial arrangements, composition and change of habitat within home ranges may influence lesser prairie-chicken populations (Jones 1963, Crawford 1980) or the importance of scaling effects in agricultural landscapes.

A complete understanding of relationships between wildlife populations and landscape structure and change requires a multi-scale analysis because landscapes exhibit complexity at a number of spatio-temporal scales (Saab 1999). A multi-scale analysis of landscape structure and change is critical to understanding this imperiled species because lesser prairie-chickens possess large home ranges, high site fidelity, and respond to variable fine-scale habitat factors (Taylor and Guthery 1980a) within landscapes that have been highly fragmented by agriculture (Fuhlendorf et al. *in press*). Our objective was to use a multi-scale approach to examine scale-dependent relationships between landscape structure and change and long-term trends for lesser prairie-chicken populations in the southern Great Plains.

STUDY REGION AND METHODS

Study region

This study was conducted on the southern Great Plains in western Oklahoma and northeastern Texas. Historically, the region supported lesser prairie-chickens in abundance, but over the past century populations have declined by >90 % (Taylor and Guthery 1980a) and much of the original prairies have been altered by agriculture (Samson and Knopf 1994). Currently, the region supports some of the last remaining large, stable populations of lesser prairie-chickens. Five study sites were located in Harper, Ellis, and Texas counties of Oklahoma, and five in Hemphill, Wheeler, and Lipscomb counties in Texas. Elevations are typically less than 1500 m (above sea level), and the topography is characterized by rolling, open plains with gentle slopes (Dhillion et al. 1994). Climate is continental and semiarid, with much of the annual rainfall occurring between May and October (41 cm average). Average annual temperatures range from 13 °C to 18 °C (Dhillion et al. 1994).

Prior to settlement, landscapes were composed of contiguous tracts of native prairie and shrublands, but currently landscapes contain a patchwork of rangeland, cropland, and pasture (Fuhlendorf et al. *in press*). Grasses and forbs are most abundant on landscapes, although specific compositions of plant communities vary depending on the history of the landscape (Fuhlendorf et al. *in press*). Species like blue grama (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths), sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash.), big bluestem (*Andropogon gerardii* Vitman), western ragweed (*Ambrosia psilostachya* DC.), annual buckwheat (*Eriogonum annum* Nutt.), and broom snakeweed (*Gutierrezia* spp.) can be found throughout the region (Vankat 1974). Sand sagebrush (*Artemisia filifolia*) and shinnery oak (*Quercus havardii*) are important shrub species, and other shrubs include sand plum (*Prunus angustifolia* Marsh.), sumac (*Rhus* spp. L.), and mesquite (*Prosopis* spp. L.) (Vankat 1974).

Landscape structure and change

Landscapes were mapped from interpretation of black and white aerial photographs taken between 1959 and 1996 at a scale of 1:7920. Dates for aerial photography across the region did not occur sequentially at regular time periods but corresponded to intervals of five or ten years. Accuracy of photo-interpretation was verified by comparing classified landscapes to the vegetation at each site. Landscapes were constructed with ARC/INFO software using topographic quadrangle maps (scale =

1:24,000) for geo-registration (Environmental Systems Research Institute, Inc. 1995). Landscapes were originally delineated into 17 cover types and were reclassified into 8 for this analysis (Chapter 1). Minimum resolution (grain) and mapping unit (accuracy) corresponded to 2 m and 20 m actual distance, respectively.

Because landscapes are heterogeneous and dynamic, numerous methods exist for quantifying physical aspects of landscapes and their elements (Turner and Gardner 1991). Usually, landscape characteristics are quantified in terms of a number of landscape metrics—a set of variables that measure physical aspects of landscapes or landscape elements in terms of number, distance, area, or ratio of measures (FRAGSTATS; McGarigal and Marks 1995). We quantified landscape composition, structure, and change in terms of eight cover types and eight landscape metrics (Table 1) at different distances from leks within each landscape. Observations of radiocollared lesser prairie-chickens indicate a strong tendency for birds to concentrate within 4.8-km of leks (Taylor and Guthery 1980b, Giesen 1994a, Riley et al. 1994), so leks were used as central points on each landscape. Landscape structure and change were measured at five scales based on 1.2, 1.7, 2.4, 3.4, and 4.8 km radii, corresponding to 452-, 905-, 1,810-, 3,619-, and 7,238-ha landscape extent, respectively (Fig. 1). We were most concerned with relationships between observed landscape patterns (e.g., landscape structure) and lesser prairie-chicken population trend, so 'scale' refered to the operational scale, or the spatial extent, over which populations may respond to landscape structure and change (Jenerette and Wu 2000).

All landscape metrics quantifying landscape structure were computed using FRAGSTATS (McGarigal and Marks 1995, Ritters et al. 1995). Formulas and algorithms used in all computations are listed in Appendix 3 of the FRAGSTATS manual except for the Landscape Change Index (see Chapter 1). Landscape change and the Landscape Change Index (LCI) were computed following methods used in Chapter 1 because lesser prairie-chicken population trends were found to be inversely correlated with landscape change at the single scale of 7,238-ha. Change in a landscape metric is denoted by a "Δ" preceding the acronym (e.g., change in MPS is represented as ΔMPS), for all landscape metrics except the LCI. Landscape change and LCI were standardized to a per decade basis because the temporal extent of the data was not the same for all landscapes. LCI was defined as one-half the sum of the absolute values of the average landscape change across all habitat types (i.e., percentage of landscape area subject to change per decade) (Chapter 1).

Multi-scale relationships

Trends for 10 lesser prairie-chicken population were calculated in Chapter 1 using data obtained from the Oklahoma Department of Wildlife Conservation and Texas Parks and Wildlife (Table 2). Inter-lek distances ranged from one to several hundred kilometers, and there was no indication of autocorrelation of population trend with inter-lek distance suggesting that populations at each lek were as independent samples. Status was assigned to each population and landscape corresponding to long-term population trends using simple linear regression methods used in Chapter 1. Similar methods have been used to estimate long-term avian population trends and abundance (Collins, 1990; Moses and Rabinowitz, 1990). Landscapes in which population trends significantly declined were classified as "declined," and landscapes in which population trends did not significantly decline were classified as "sustained."

Landscape patterns may be scale-dependent, and because landscape metrics are not independent among scales, landscape metrics were analyzed using auto-regressive models in a repeated measures analysis of variance to account for the high degree of correlation between metric values among the different scales (PROC MIXED, Littell et al. 1996). Metrics of landscape structure and change were tested ($\alpha \leq 0.10$) to determine if they contained an interaction of status and scale. Metrics that contained an interaction were examined to determine simple effects of scale and status within the interaction using the SLICE option (PROC MIXED, Littell et al. 1996). A supportive analysis was conducted on metrics that contained an interaction of status and scale by correlating means with population trend across scales (SAS Institute Inc. 1985). In addition, because landscape change (LCI) was important to lesser prairie-chickens (Chapter 1), changes in cover types (Δlek) were correlated with LCI across scales to determine which cover types contributed to the change index.

Landscapes were examined to determine effects of scaling for all structure and change metrics that did not contain an interaction of status and scale. Means were tested using autoregressive models in a repeated measures analysis of variance to determine main effects of status and scale ($\alpha \leq 0.10$, PROC MIXED, Littell et al. 1996). Multiple comparison of means across scales was conducted using Fisher's Least Significant Difference test.

RESULTS

Quantification of landscape structure and change indicated that landscapes associated with lesser prairie-chicken populations were variable in space and time (Table

3). Percent Cropland ($F = 2.57$, $P = 0.0567$), ΔTree ($F = 3.06$, $P = 0.0613$), the Landscape Change Index (LCI, $F = 7.11$, $P = 0.0003$), and ΔEdge Density (ΔED, $F = 2.08$, $P = 0.1069$) contained significant interactions between status and scale (Fig. 2). Percent Cropland increased with scale on declining landscapes ($F = 8.13$, $P = 0.0001$) and was similar across scales on sustained landscapes ($F = 0.48$, $P = 0.7523$), resulting in significantly more Cropland on declining landscapes at the 7,238-ha scale ($F = 3.29$, $P = 0.0789$). ΔTree increased with scale in declining landscapes ($F = 5.54$, $P = 0.0017$) and was similar across all scales in sustained landscapes ($F = 0.04$, $P = 0.9972$) with a significantly greater increase in ΔTree on declining landscapes at the 7,238-ha scale ($F = 7.85$, $P = 0.0086$). LCI increased with scale in declining landscapes ($F = 23.53$, $P < 0.0001$) and was similar across scales within sustained landscapes ($F = 1.36$, $P = 0.2680$), with significant differences occurring at 3,619- ($F = 3.71$, $P = 0.0630$) and 7,238-ha ($F = 24.21$, $P < 0.0001$) scales between declining and sustained landscapes. Differences in the LCI indicated that changes in composition were greater within declining landscapes and that effects of landscape change were most important at 3,619- and 7328-ha scales. ΔED varied across scales but, unlike the LCI, differences between declining and sustained landscapes occurred at 452-, 905-, and 1,810-ha scales ($F \geq 3.08$, $P \leq 0.100$). No other metrics contained significant interactions of status and scale, but main effects of status were significant for ΔLPI ($F = 15.83$, $P = 0.0043$, Fig. 3). Reductions of ΔLPI were more negative for declining landscapes (-6.0 % per decade ± 0.7) than sustained landscapes (-0.5 % per decade ± 0.4), which meant that reductions to large continuous patches were greater on declining landscapes.

Correlations between population trends and landscape metrics supported results of the repeated measures analyses that relationships were scale-dependent, even though those correlations were independent of population status. Relationships between Percent Cropland, ΔTree, the LCI and population trends were inverse and increased in strength with scale. At the 3,619-ha scale, ΔTree ($r = -0.85$, $P = 0.0035$) and the LCI ($r = -0.62$, $P = 0.0739$) were correlated with population trends (Fig. 4). Those relationships were more significant at the 7,238-ha scale ($r = -0.84$, $P = 0.0043$; $r = 0.95$, $P = 0.0001$) and less significant at scales less than 3,619-ha. The correlation between Cropland and population trends was only significant ($r = -0.76$, $P = 0.0185$) at the 7,238-ha scale. ΔED was significant at all scales and was the only landscape metric that was significant at the three smaller scales.

Changes in cover types that were correlated with LCI were scale-dependent. ΔLD-Shrubland was correlated with LCI at smaller scales but became decreasingly correlated with LCI as scale increased (Table 4). ΔLek, ΔTree, ΔPrairie, ΔPasture, and ΔCropland became increasingly correlated with LCI as scale increased (Table 4). Correlations between ΔPasture and ΔCropland with LCI reflect landscape changes resulting from conversion of Cropland to Pasture.

For many landscape metrics that did not contain an interaction of status and scale, main effects of scale were significant (Table 5). Variability of Patch Size (VAR-PS), ΔVAR-PS, LPI, Patch Richness (PR), ΔPR, Interspersion / Juxtaposition Index (IJI), Nonhabitat, Tree, and LD-Shrubland ($F \geq 2.25$, $P \leq 0.100$) contained significant scaling effects. VAR-PS, PR, and IJI increased with scale indicating that greater amounts of landscape heterogeneity were sampled at larger scales. However, ΔVAR-PS and ΔPR decreased as scale increased suggesting that VAR-PS and PR approached maximum values at the 7,238-ha scale. Nonhabitat and Tree increased and LD-Shrubland decreased with scale. Mean Patch Size (MPS), ED, Mean Shape Index (MSI), Fractal Dimension (FD), ΔMPS, ΔMSI, ΔFD, ΔIJI, ΔLek, ΔPrairie, ΔPasture, and ΔHD-Shrubland were similar across scales (Table 3).

DISCUSSION

Current landscape structure and historic change are important, scale-dependent factors influencing wildlife populations (Miller et al. 1997, Turner et al. 1997, Law and Dickman 1998, Saab 1999, Bergin et al. 2000, Niemuth 2000). Numerous investigations into the role of scale in ecology have described the intrinsic scaling of ecological phenomena and demonstrated the importance of scaling properties (Brown and Allen 1989, Wiens 1989, Levin 1992, Horne and Schneider 1995, Fuhlendorf and Smeins 1996, 1999, Biessonette 1997). Relationships between wildlife populations and landscape structure and change may be confounded when 1) problems (declining populations) are perceived at scales inappropriately fine or coarse (Gardner et al. 1987, McGarigal and Marks 1995) or 2) conclusions at a particular scale (the importance of a certain factor) are inappropriately applied at other scales (Addicott et al. 1987, Turner 1990). Frequently, information is limited on relationships between scale and factors influencing wildlife populations, and many studies are conducted at arbitrary scales. An alternative to studies at single, arbitrary scales is an analysis that evaluates factors at multiple scales (Wiens et al. 1987, Turner et al. 1989). Our multi-scale analysis of landscapes with declining populations of lesser prairie-chickens and landscapes with sustained populations indicated differences in landscape structure and change in five variables of which four of the five exhibited scale-dependency.

Importance of landscape change

Rarely has landscape change been addressed as an important habitat factor to which wildlife populations may respond. Traditional approaches to describing temporal changes in wildlife species typically emphasize either population dynamics (Pulliam et al. 1992, Wiens et al. 1993) or effects of habitat (local and landscape) features on populations or communities (Miller et al. 1997, Otto 1996). Both approaches assume that dispersal is random and complete and that all available habitat is occupied (Milne et al. 1989). However, if there is a lag in the response of a population to changes in habitat structure, then the state of the habitat and a population may appear to be unrelated. Species that exhibit high site fidelity may be associated with lag times longer than species that do not exhibit site fidelity (Knick and Rotenberry 2000). In such cases, an understanding of factors important to the species may be obscured because the habitat was considered as a static entity, and the potential importance of lag effects were not acknowledged (Wiens et al. 1986).

The importance of historical landscape change to lesser prairie-chicken populations was thought to be limited to the cultivation of native rangelands and the concomitant increase in cropland that occurred prior to the start of this study (Copelin 1963, Jackson and DeArment 1963, Crawford and Bolen 1976, Taylor and Guthery 1980a, Cannon and Knopf 1981). Our data indicated that historical cultivation is important to the current status of lesser prairie-chicken populations (percentages of cropland were 2.5 times greater on declining landscapes than on sustained) but also suggested that reductions in cultivated land may not benefit populations. Much of the marginal cropland within the region was converted to pasture in response to government subsidies offered to control soil erosion and reduce commodity surplus (Giesen 1998). The potential for habitat improvement for lesser prairie-chickens through establishment of perennial grasses on marginal cropland has been debated (Copelin 1963, Kirsch 1974). Our data actually indicated that this change had a negative effect on populations.

The importance of the landscape change index (LCI) suggests that any change on landscapes with long-term populations may have negative effects. The LCI is a generic indicator of the overall change occurring on a landscape that considers the sum of the changes in all cover types. Measures of overall change were 2-4.5 times greater on declining landscapes and had strong negative relationships with population trend. Specific cover types that had strong negative relationships with lesser prairie-chicken populations were cropland and tree dominated cover types. Increases in trees were the result of either intentional plantings for windbreaks adjacent to cropland or pasture, or the unintentional encroachment of woody plants (*Juniperus* spp.) onto prairies and shrublands. Concern for the encroachment of woody species onto prairies and shrublands is global (Archer 1994) and has implications for management of prairie bird species (Bergin et al 2000, Niemuth 2000). Lesser prairie-chickens select lower-statured vegetation for feeding and roosting (Jones 1963) and alteration of structure by woody plants may result in changes in species composition, reduced visibility, and creation of perch sites and cover for predators. These cover types increased largely at the expense of native prairies and shrublands that are critical to lesser prairie-chickens. While these cropland were 2.5 times greater on declining landscapes than on sustained) but also suggested that reductions in cultivated land may not benefit populations. Much of the marginal cropland within the region was converted to pasture in response to government subsidies offered to control soil erosion and reduce commodity surplus (Giesen 1998). The potential for habitat improvement for lesser prairie-chickens through establishment of perennial grasses on marginal cropland has been debated (Copelin 1963, Kirsch 1974). Our data actually indicated that this change had a negative effect on populations.

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Changes in the spatial arrangement of cover types within landscapes also influence wildlife populations (McGarigal and McComb 1995, Burke and Goulet 1998, Ryan et al. 1998, Saab 1999, Bergin et al. 2000, Niemuth 2000). Our data indicated that changes in ΔLPI and ΔED were greater on declining landscapes over the past 10-35 years. This was important to lesser prairie-chickens because they depend on broad, continuous tracts of habitat (Copelin 1963, Jones 1963). Changes in edge density result from alteration of patch sizes and shapes. Greater values on declining landscapes at the three smallest scales indicate that increase in edge within close proximity of leks was greater on declining landscapes than on sustained landscapes. Traditionally, edge has been thought to benefit game birds (Leopold 1933). Edges at the local-level may indicate mosaics of habitat that lesser prairie-chickens respond positively to, such as heterogeneity of grass and shrub dominance within native prairie. These mosaics and their associated edges are typically nested within individual cover types at the landscape-level (Forman and Godron 1986, O'Neill et al. 1986). However, edges at the landscape-level may represent fragmentation of critical cover types, such as the edges created by the cultivation of rangeland. Our results suggested that increases in edge density at the landscape-level were highly correlated with population declines over the past several decades.

Landscape change is probably a critical habitat factor for lesser prairie-chicken populations because of several spatially dependent traits that suggest high site fidelity

(Knick and Rotenberry 2000). Specifically, individuals show a strong tendency to remain within 4.8 km of leks (Taylor and Guthery 1980b), hens tend to nest within 2.0 km of leks (Giesen 1994a), and cocks establish and defend specific territories on leks (Copelin 1963). Also, dynamics of isolated populations on highly fragmented landscapes may be more dependent on landscape-level habitat stability and less dependent on immigration and emigration than less isolated populations suggesting that there may be a synergistic effect associated with landscape fragmentation and change.

Importance of scale

Over the past several decades, with the development of computer technology, and the fields of landscape ecology and conservation biology, many critical issues involving populations and habitat structure have been resolved using GIS and broad-scale approaches. Multi-scale approaches are necessary for determining which factors and scales are most important because the multivariate effects of spatially and temporally variable habitat on wildlife populations are scale-dependent. Yet most studies have addressed the importance of landscape structure on wildlife populations while being restricted to analyses at capriciously selected single scales and have failed to account for scale-dependency in observed landscape structure and relationships. The LCI, occurrence of cropland, and increases in trees were much more important to populations of lesser prairie-chickens at broad scales because home ranges typically include up to several thousand hectares. The importance of reductions to large patches on declining landscapes supports the conclusion that lesser prairie-chickens depend on continuous native vegetation across multiple scales. However, effects of current landscape structure and historic change on populations within proximity of species' pools may be obscured by immigration and emigration (MacArthur and Wilson 1967), and persistence of isolated populations may depend more on internal disturbance regimes and landscape dynamics (Pickett and Thompson 1978). Significance of the LCI, percent cropland, and ΔTree at the largest scale suggests that fragmentation of rangeland has occurred and some local populations are becoming more isolated as a result of increases in cover types either detrimental to or not usable by lesser prairie-chickens. A larger (coarse) scale study than ours could address the degree of fragmentation and isolation of landscapes surrounding lesser prairie-chicken leks.

Care should be taken in selecting scales and metrics that are not irrelevant to a process or organism of interest because landscape structure and change are inherently scale-dependent and observation of factors and relationships impose observer-dependent scales (Turner et al. 1989, Wiens 1989, Kolasa and Pickett 1991). ΔED was the only landscape metric significant and highly correlated with population trend at the three smallest scales. Yet the other significant measures of landscape structure and change (LCI, cropland, ΔTree) were not important at these smaller scales, suggesting that populations are sensitive to changes in landscape structure and change across a range of scales and illustrated how changing the scale of an analysis may produce conclusions that may appear to contradict conclusions at other scales (Fuhlendorf and Smeins 1999). Effects of scale may strongly bias conclusions of an ecological study because scale is such a fundamental component of ecology, and science in general (Levin 1992).

Ecological studies are highly dependent on scaling principles. Our data supported emerging ecological theories governing relationships between wildlife populations and habitat structure and change—specifically that many relationships are often best evaluated across multiple spatial and temporal scales because factors most important at one scale may not be important at other scales (Turner et al. 1989, Fuhlendorf and Smeins 1999, Saab 1999, Bergin et al. 2000, Niemuth 2000). Studies conducted at multiple scales produce a greater understanding of the factors most important to a population because of the inherent scaling of biotic and abiotic (environmental) factors present in ecological systems and because of the scaling associated with species-specific life-history traits. Lesser prairie-chicken populations are a good example of the complexity that occurs across multiple spatio-temporal scales because they possess a number of traits (high site fidelity, large home ranges) that influence scales at which they respond to changes in habitat structure. Our data suggested that landscapes with declining populations were more fragmented and consequently more isolated than landscapes with sustained populations. Fragmentation and isolation reduce immigration and emigration among landscapes (Fahrig 1997). We propose that for this reason, populations with declining landscapes were more dependent on the stability of the landscape within 4.8 km of the lek and therefore critically affected by landscape change.

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LIST OF FIGURE CAPTIONS

FIG 1. Illustration of five spatially nested landscapes corresponding to 452-, 905-, 1,810- 3,619-, and 7,238-ha, respectively surrounding lesser prairie-chicken leks in Oklahoma and Texas.

FIG 2. Mean percentage of cropland (a), mean change in tree cover (b), the landscape change index (LCI) (c), and changes in edge density (d) across five spatial scales for landscapes surrounding lesser prairie-chicken leks. * Indicates significant interactions between population status (Table 2) and scale ($\alpha = 0.10$).

FIG. 3. Mean changes in largest patch index (LPI) for declining and sustained landscapes surrounding lesser prairie-chicken leks in Oklahoma and Texas (1959 - 1996).

FIG 4. Scatter plot of Pearson's correlation coefficients for correlations between lesser prairie-chicken population trends (Table 2) and amounts of cropland, change in amounts of tree cover, the landscape change index (LCI), and change in edge density at five spatial scales within landscapes surrounding leks in Oklahoma and Texas (1959 - 1996). Circles indicate significant correlations ($\alpha = 0.10$).

TABLE 1. Descriptions of metrics used to quantify landscape structure and change for landscapes containing lesser prairie-chicken populations in Oklahoma and Texas (1959 - 1996).

	METRIC	DESCRIPTION[B]	UNITS STRUCTURE	UNITS CHANGE[A]
MPS	MEAN PATCH SIZE	Mean patch size of all patches on a landscape.	ha	ha/decade
VAR-PS	VARIABILITY OF PATCH SIZE	Mean variability of patch sizes on a landscape.	1000 ha^2	1000 ha^2/decade
LPI	LARGEST PATCH INDEX	Largest patch size on a landscape, expressed as the percent of landscape area.	%	%/decade
ED	EDGE DENSITY	Mean amount of patch perimeter on a landscape per hectare.	m/ha	m/ha/decade
MSI	MEAN SHAPE INDEX	Ratio of patch perimeter to area divided by a factor of 2π	-	-
FD	FRACTAL DIMENSION	Twice the log of patch perimeter divided by the product of the log of patch area and total number of patches on a landscape.	-	-
PR	PATCH RICHNESS	Number of different patch types on a landscape.	-	-
IJI	INTERSPERSION / JUXTAPOSITION INDEX	Degree to which similar patch types are uniformly distributed and mixed across a landscape		
	COVER TYPE			
	LEK	Lesser prairie-chicken breeding site (booming ground)	%	% / decade
	NONHABITAT	Open water, bare ground, and development (farm houses, yards, buildings, and railroads	%	% / decade
	TREE	Tall, woody vegetation (riparian, windbreaks, *Juniperus* spp.)	%	% / decade
	PRAIRIE	Native short- and midgrass prairie species	%	% / decade
	PASTURE	Introduced pasture or heavily manipulated pasture (e.g. mechanical control of woody species)	%	% / decade
	CROPLAND	Cultivated fields	%	% / decade
	LD-SHRUBLAND	Low-density (<15%), shinnery oak (*Quercus havardii*) and other mixed shrubs	%	% / decade
	HD-SHRUBLAND	High-density (>15%) shinnery oak and other mixed shrubs	%	% / decade
LCI	LANDSCAPE CHANGE INDEX	Total landscape change in land use and vegetation (Includes: all cover types)	N / A	% / decade

[A] Change in metrics are represented by a "Δ" preceding the abbreviation listed (e.g. 'change in MPS' = ΔMPS and 'change in Lek' = ΔLek).

[B] Descriptions of landscape metrics taken from McGarigal and Marks 1995.

[C] Includes sand sagebrush (*Artemisia filifolia*), Chickasaw plum (*Prunus angustifolia*), sumac (*Rhus* spp.), and others.

TABLE 2. Summary of trend analysis for ten lesser prairie-chicken populations. Trends are regression slopes in the log scale, units are expressed as natural logarithm of the lek count per year. ‡ Indicates observed significance level ≤ 0.05. Taken from Chapter 1.

LEK NAME	POPULATION TREND (β)	PERCENTAGE CHANGE (PER DECADE)	POPULATION STATUS
OK1	-0.11‡	-92.1	DECLINED
OK2	-0.01	-30.9	SUSTAINED
OK3	-0.14‡	-96.2	DECLINED
OK4[a]			DECLINED
OK5	-0.20‡	-94.1	DECLINED
TX1	0.00	-12.7	SUSTAINED
TX2	-0.03‡	-61.3	DECLINED
TX3	0.00	2.7	SUSTAINED
TX4	0.01‡	32.9	SUSTAINED
TX5	-0.03	-51.4	SUSTAINED

[a] Current surveys indicate population not sustained.

TABLE 3. Summary statistics for metrics of landscape structure and change for landscapes surrounding lesser prairie-chicken leks in Oklahoma and Texas. Changes in structure metrics and composition were measured between 1959 and 1996. Significant effects are listed next to means ($\alpha = 0.10$).

	STRUCTURE					CHANGE[B] (Δ)				
	EFFECT[A]	MEAN	SE	MIN	MAX	EFFECT[A]	MEAN	SE	MIN	MAX
METRIC										
MPS	-	39.3	1.4	23.0	75.8	-	-8.9	1.9	-52.6	8.4
VAR-PS	SCALE	51.4	7.7	5.2	239.6	SCALE	-17.2	4.3	-146.2	14.1
LPI	SCALE	67.2	3.0	17.3	97.6	STATUS	-3.2	0.6	-15.1	4.9
ED	-	19.0	0.9	7.9	34.5	INTERACT	3.4	0.8	-2.4	21.4
MSI	-	1.4	0.0	1.2	1.6	-	0.0	0.0	-0.2	0.5
FD	-	1.4	0.0	1.3	1.7	-	0.0	0.0	-0.2	0.1
PR	SCALE	6.0	0.2	4.0	8.0	SCALE	0.0	0.0	-0.6	0.8
IJI	SCALE	49.0	2.7	6.6	80.7	-	-2.0	1.1	-29.8	15.6
LCI	N / A	-	-	-	-	INTERACT	2.2	0.5	0.0	18.1
COVER TYPE										
LEK	-	0.0	0.0	0.0	0.0	-	0.0	0.0	0.0	0.0
NONHABITAT	SCALE	0.9	0.1	0.0	3.0	-	0.0	0.0	-1.1	0.4
TREE	SCALE	2.0	0.8	0.0	30.5	INTERACT	0.3	0.2	-0.8	6.4
PRAIRIE	-	9.9	2.2	0.4	73.8	-	1.2	0.3	-2.2	6.9
PASTURE	-	5.9	1.4	0.0	37.4	-	0.8	0.3	-2.8	9.4
CROPLAND	INTERACT	3.4	0.7	0.0	20.1	-	-0.4	0.3	-11.4	2.6
LD-SHRUBLAND	SCALE	66.6	3.2	25.2	97.6	-	-0.8	0.7	-8.6	17.6
HD-SHRUBLAND	-	11.3	2.7	0.0	64.3	-	-1.1	0.6	-18.4	6.0

[A] INTERACT = interaction between STATUS {declined, sustained} and SCALE {452, 905, 1810, 3619, 7238 ha} was significant.
STATUS = main effects of STATUS were significant.
SCALE = main effects of SCALE were significant.

[B] Change in metrics are represented by a "Δ" preceding the abbreviation listed (e.g. 'change in MPS' = ΔMPS and 'change in Lek' = ΔLek).

TABLE 4. Summary of Pearson's correlation coefficients between mean change in landscape composition and the landscape change index (LCI) across five spatial scales for landscapes surrounding lesser prairie-chicken leks in Oklahoma and Texas (n=10). † Indicates $0.10 \geq P > 0.05$ and ‡ indicates $P < 0.05$.

	SCALE				
COVER TYPE	452 ha	905 ha	1810 ha	3619 ha	7238 ha
Δ LEK	0.12	0.06	-0.24	-0.85 ‡	-0.80 ‡
Δ NONHABITAT	0.40	0.24	0.11	-0.73 ‡	-0.34
Δ TREE	0.12	0.10	-0.23	0.17	0.30
Δ PRAIRIE	0.07	0.07	-0.06	0.17	0.58 †
Δ PASTURE	0.08	0.17	-0.01	0.69 ‡	0.66 ‡
Δ CROPLAND	-0.14	-0.29	-0.16	-0.79 ‡	-0.77 ‡
Δ LD-SHRUBLAND	0.69 †	0.51	0.62 †	-0.03	-0.44
Δ HD-SHRUBLAND	-0.77 ‡	-0.66 †	-0.60 †	0.10	0.39

TABLE 5. Means (standard error) of landscape metrics (of structure and change) containing significant scaling effects for landscapes surrounding lesser prairie-chicken leks (n=10) at five spatial scales in Oklahoma and Texas. Capital letters in the same row represent multiple comparison of means across scales (α = 0.10).

	452		905		1810		3619		7238	
METRIC[1]	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE	MEAN	SE
VAR-PS	9.9 A	1.2	21.4 A	3.5	39.3 B	6.4	71.4 C	13.0	115.1 D	24.3
ΔVAR-PS	-7.5 C	3.8	-18.9 B	13.5	-22.7 A	15.6	-47.5 A	20.6	-87.4 A	29.2
LPI	77.7 D	4.8	73.6 C	6.0	68.6 B	6.5	63.1 A	6.8	53.0 A	7.9
PR	4.8 A	0.3	5.4 B	0.5	6.2 C	0.4	6.5 C	0.4	7.0 D	0.4
ΔPR	0.3 D	0.3	0.3 D	0.3	-0.2 C	0.2	-0.5 B	0.2	-0.5 A	0.2
IJI	36.1 A	5.2	45.4 B	4.8	49.7 C	4.8	54.8 D	5.9	59.1 E	7.0
NONHABITAT	0.5 A	0.1	0.8 AB	0.2	1.0 B	0.2	1.0 B	0.2	1.3 BC	0.3
TREE	0.0 A	0.0	0.3 A	0.2	0.8 A	0.5	2.9 AB	1.9	6.2 BC	3.1
LD-SHRUBLAND	72.9 D	7.2	70.8 C	7.4	68.2 B	7.4	63.6 AB	7.2	57.4 A	7.5

[1] VAR-PS = variability of patch size; ΔVAR-PS = change in variability of patch size; LPI = largest patch index; PR = patch richness; ΔPR = change in patch richness; IJI = interspersion / juxtaposition index (Table 1).

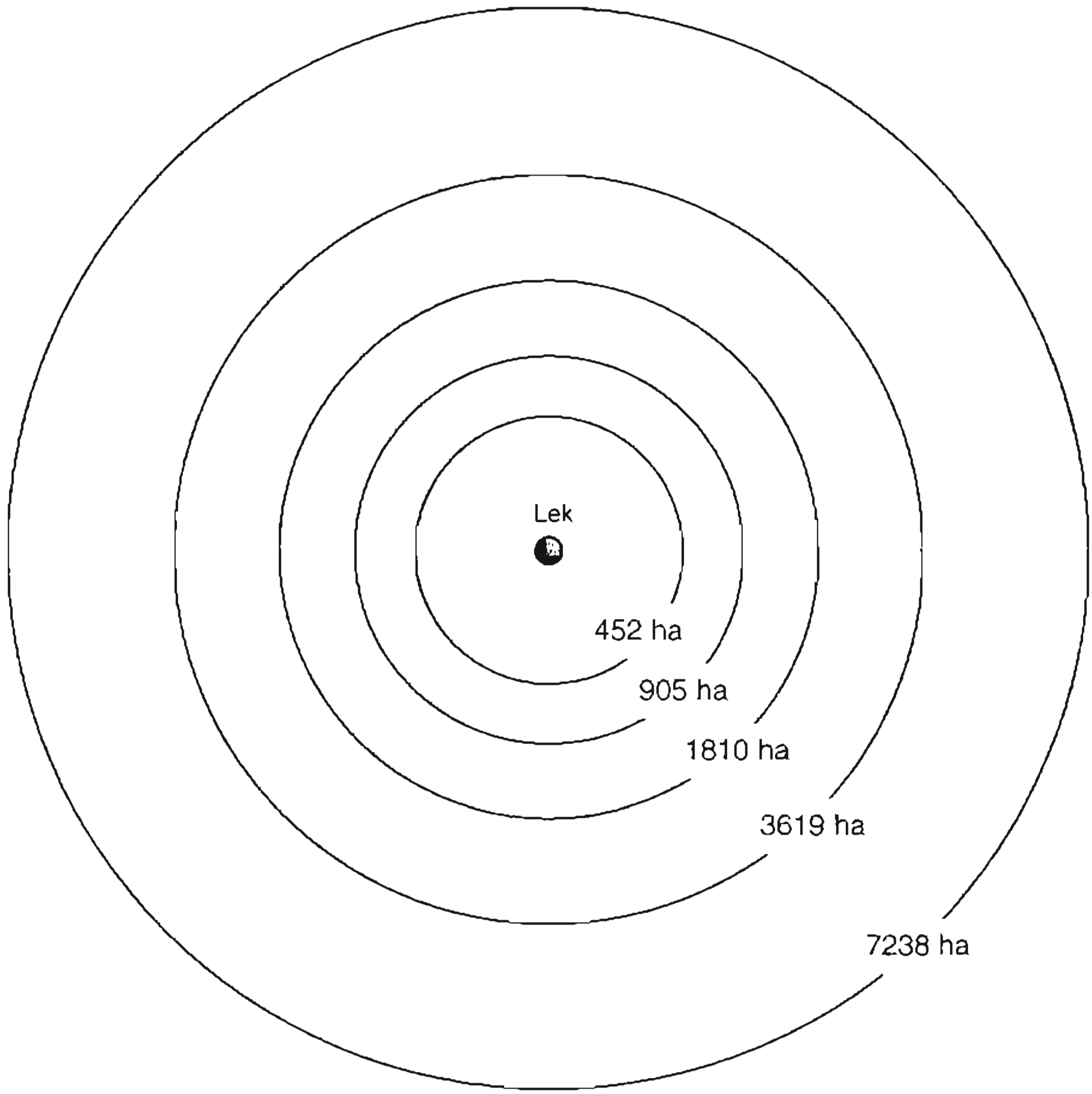

FIG 1. Illustration of five spatially nested landscapes corresponding to 452-, 905-, 1,810-, 3,619-, and 7,238-ha, respectively surrounding lesser prairie-chicken leks in Oklahoma and Texas.

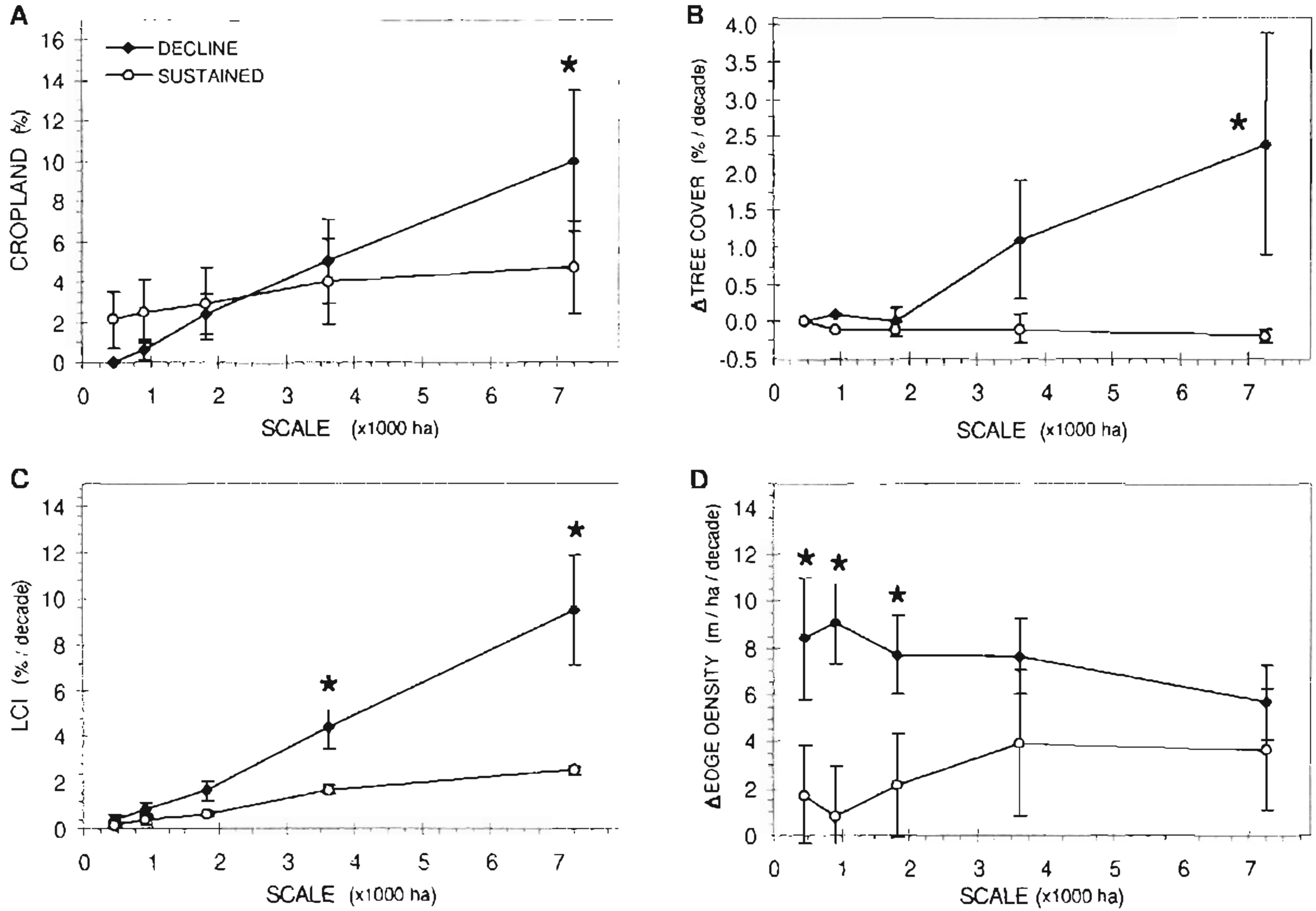

FIG 2. Mean percentage of cropland (a), mean change in tree cover (b), the landscape change index (LCI) (c), and changes in edge density (d) across five spatial scales for landscapes surrounding lesser prairie-chicken leks. * Indicates significant interactions between population status (Table 2) and scale ($\alpha = 0.10$).

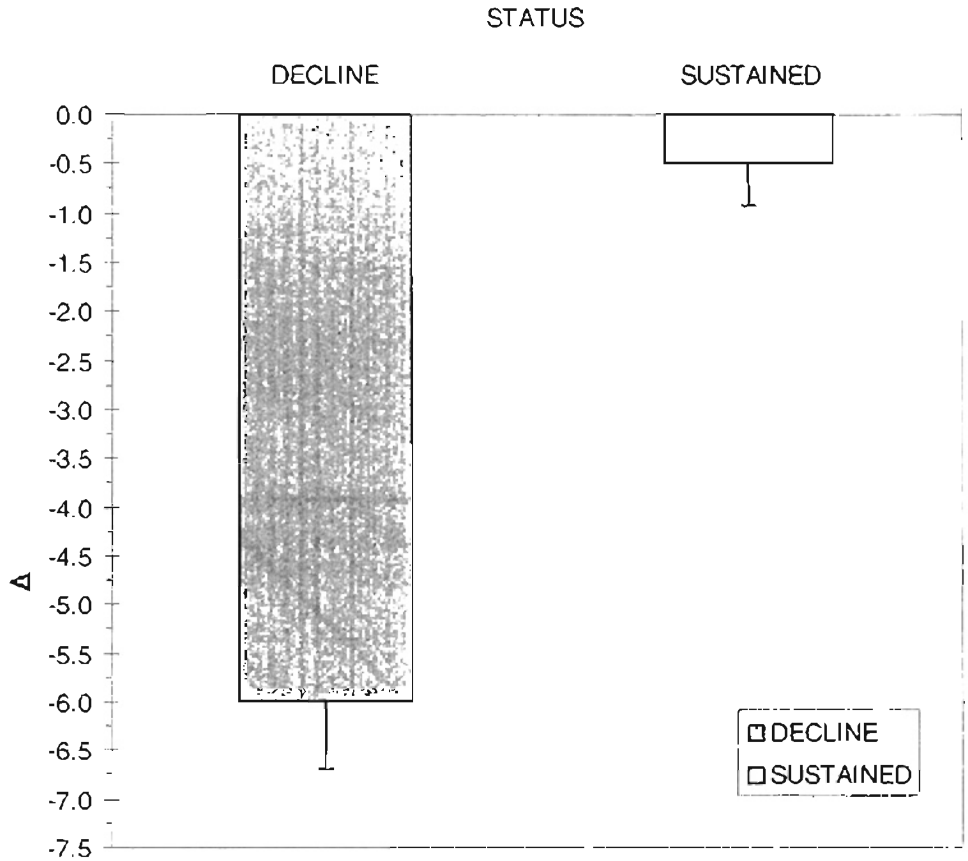

FIG. 3. Mean changes in largest patch index (LPI) for declining and sustained landscapes surrounding lesser prairie-chicken leks in Oklahoma and Texas (1959 - 1996).

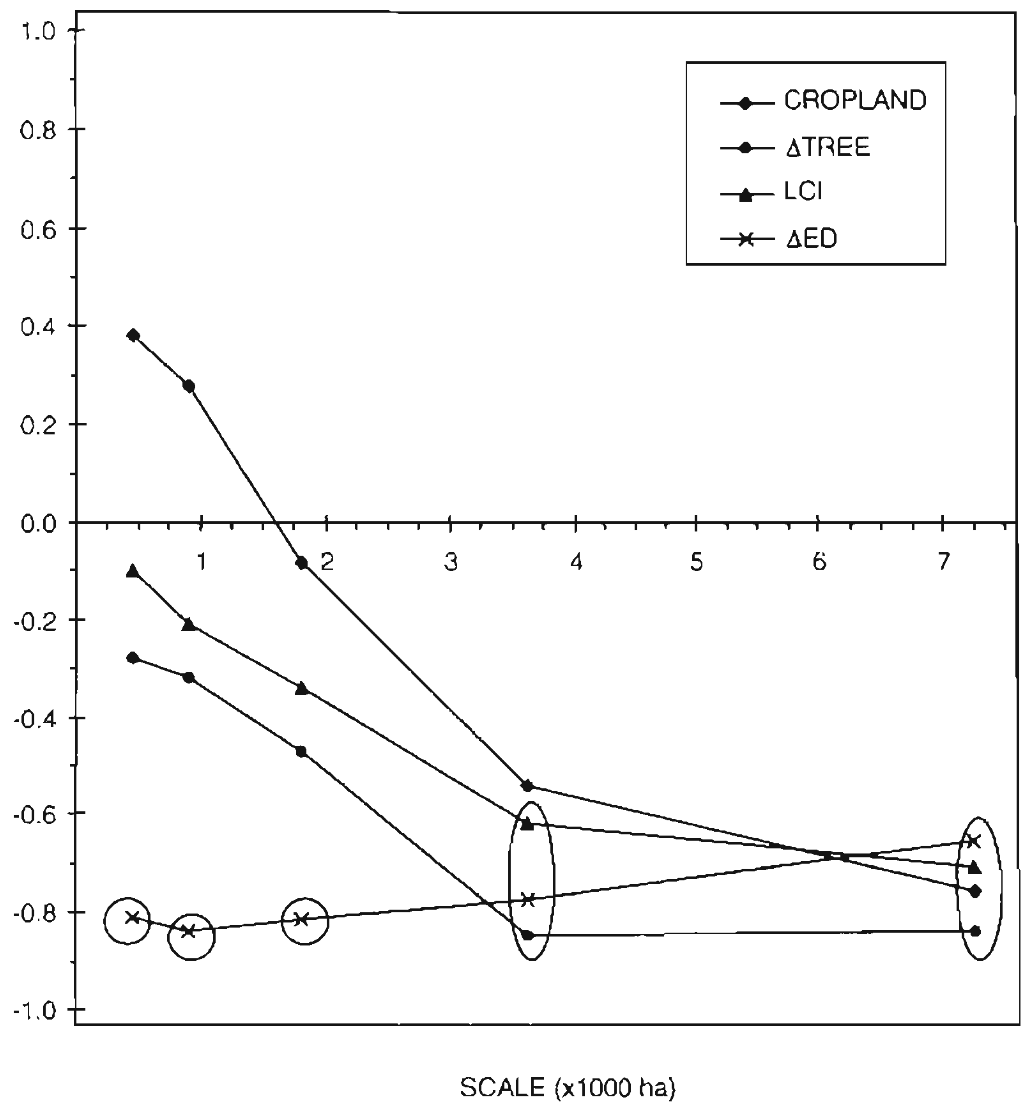

FIG 4. Scatter plot of Pearson's correlation coefficients for correlations between lesser prairie-chicken population trends (Table 2) and amounts of cropland, change in amounts of tree cover, the landscape change index (LCI), and change in edge density at five spatial scales within landscapes surrounding leks in Oklahoma and Texas (1959 - 1996). Circles indicate significant correlations ($\alpha = 0.10$).

VITA

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