



Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains

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Abstract

Large-scale patterns of land use and fragmentation have been associated with the decline of many imperiled wildlife populations. Lesser prairie-chickens (*Tympanuchus pallidicinctus*) are restricted to the southern Great Plains of North America, and their population and range have declined by > 90% over the past 100 years. Our objective was to examine scale-dependent relationships between landscape structure and change and long-term population trends for lesser prairie-chicken populations in the southern Great Plains. We used a geographic information system (GIS) to quantify landscape composition, pattern and change at multiple scales (extents) for fragmented agricultural landscapes surrounding 10 lesser prairie-chicken leks. Trend analysis of long-term population data was used to classify each population and landscape (declined, sustained). We analyzed metrics of landscape structure and change using a repeated measures analysis of variance to determine significant effects ($\alpha = 0.10$) between declining and sustained landscapes across multiple scales. Four 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 on landscapes with declining and stable populations. Any single spatial scale that was evaluated would not have given complete results of the influences of landscape structure and change on lesser prairie-chicken populations. The smallest spatial scales (452, 905, and 1,810 ha) predicted that changes in edge density and largest patch size were the only important variables, while large-scale analysis (7,238 ha) suggested that the amount of cropland, increase in trees (mostly *Juniperus virginiana*), and general landscape changes were most important. Changes in landscape structure over the past several decades had stronger relationships with dynamics of lesser prairie-chicken populations than current landscape structure. Observed changes suggest that these local populations may be appropriately viewed from a metapopulation perspective and future conservation efforts should evaluate effects of fragmentation on dispersal, colonization, and extinction patterns.

Introduction

Although the role of scale in ecology has been discussed extensively over the past three decades (Kershaw 1957; Stommel 1963; Wiens 1989; Levin 1992), many investigations are still conducted at arbitrary

spatial and temporal scales (Bissonette 1997). Failure to account for scale-dependent patterns has confused and confounded ecological synthesis and led to many improper extrapolations of research results (Wiens 1989; Costanza and Maxwell 1994; Gardner 1998). Dynamic patterns of plants and animals often are in-

fluenced by different processes at different spatio-temporal scales resulting in variable patterns when observed across multiple scales (Carlile et al. 1989; O'Neill et al. 1986; Wiens 1989; Menge and Olson 1990). No single scale exists to completely describe population, community, and landscape patterns (Greig-Smith 1983; Wiens 1989; Levin 1992). Therefore, analyses of multiple scales are necessary to accurately describe relationships between organisms and their environment (Sugihara and May 1990; Glenn et al. 1992; Fuhlendorf and Smeins (1996, 1999)). Both theoretical and empirical approaches have demonstrated relationships between spatial scale and spatial pattern (Wiens 1989; Turner 1990; Costanza and Maxwell 1994), but few studies have examined the interactive relationship between scale and population trends (Bissonette 1997).

Wildlife habitat can be considered from this multi-scale perspective as a hierarchically nested organization of conditions and resources required by an organism, where all habitat units are composed of subunits within larger subunits (Kolasa and Waltho 1998). A fundamental difference among species is that they perceive their environment at different spatio-temporal scales. The appropriate scale to evaluate wildlife habitat is dependent upon species' life-history traits and behavioral activities, such as dispersal, food acquisition, and predator avoidance (Levin 1992; Wiens et al. (1993, 1995)). Because each activity may occur at a different scale, it is likely that landscape structure and change may influence wildlife populations across a range of spatio-temporal scales (Miller et al. 1997; Turner et al. 1997; Law and Dickman 1998; Saab 1999; Bergin et al. 2000; Niemuth 2000). Most studies are conducted at arbitrary scales because it is usually difficult to identify important scales *a priori*. Such studies could lead to incomplete or even misleading results. Therefore, it is critical that investigators use multi-scale approaches in evaluating responses of wildlife populations to changes in habitat or landscape pattern (Bissonette 1997).

Lesser prairie-chickens (*Tympanuchus pallidicinctus*) are a species of grouse endemic to the prairies and shrublands of the southern Great Plains of North America (Aldrich 1963). Population levels and range have declined by > 90% from historic levels (Crawford 1980; Taylor and Guthery 1980a; Giesen 1994b). Previous research was focused primarily on local-level habitat and has demonstrated that lesser prairie-chickens require a mosaic of prairie and shrubland habitats dispersed across the landscape, albeit the na-

ture of such dispersion is unknown (Jones 1963; Riley et al. 1992; Riley and Davis 1993; Giesen 1998). Lesser prairie-chickens possess a high degree of site fidelity to habitat surrounding or adjacent to their breeding display grounds (leks), and home ranges can be several thousand ha (Taylor and Guthery 1980b; Giesen 1994a; Riley et al. 1994). Several authors have speculated that 1,024-7,238 ha of unfragmented habitat (native grasslands and shrublands) may be required to sustain a population, suggesting that populations may be associated with landscape-level structure and stability (Davison 1940; Crawford and Bolen 1976; Taylor and Guthery 1980b; Woodward et al. 2001). However, it is not known how spatial arrangements, composition, and change of habitat within home ranges may influence lesser prairie-chicken populations across multiple spatial scales.

Numerous studies have evaluated effects of large-scale land use patterns and fragmentation on wildlife populations with variable results (e.g., Debinski and Holt (2000)). However, few studies have evaluated effects of landscape changes on wildlife populations across multiple spatial scales or described the relationships between scale and population trends (Bissonette 1997). The lesser prairie-chicken is an excellent case study for evaluating these relationships because many previous studies have reported sensitivity to fine-scale habitat, as well as landscape-level features, suggesting that examining amount and spatial arrangement of habitat across scales may be particularly relevant for this species. Lesser prairie-chickens have a large home range that suggests the need for an extensive study area. Although a previous evaluation indicated that change in landscape composition was an important factor for lesser prairie-chicken populations, it did not evaluate multiple scales or landscape metrics that describe shape and configuration (Woodward et al. 2001). Therefore, our goal was to examine the influence of spatial scaling on the relationship between lesser prairie-chicken population dynamics and landscape structure (composition, shape and spatial arrangement) and change. Our specific objectives were to determine effect of structure, and change of landscape elements on population dynamics of the lesser prairie-chicken; and quantify effects of variable spatial extents on relationships between landscape structure and lesser prairie-chicken populations.

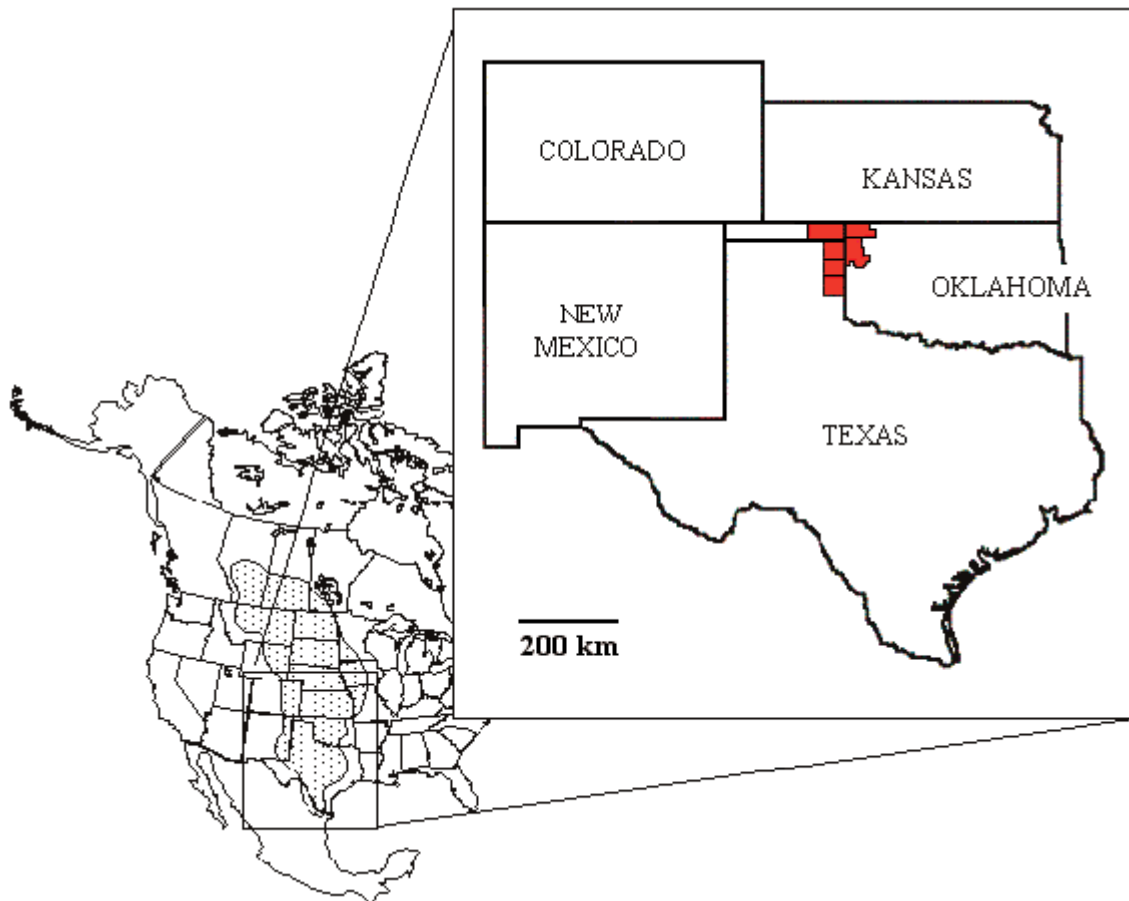


Figure 1. Map of study region located within the southern Great Plains of North America, illustrating 10 study sites within Oklahoma ($n = 5$) and Texas (5) (counties containing study sites shaded) (adapted from Woodward et al. (2001)).

Study area and methods

Study region

This study was conducted on the US southern Great Plains in western Oklahoma and northern Texas (Figure 1). Five study sites were located in Harper, Ellis, and Texas counties of Oklahoma, and five in Hemp-hill, Wheeler, and Lipscomb counties in Texas (see Woodward et al. (2001) for more detailed site information). Lesser prairie-chickens currently occupy only a small part of their historical range (10%; Taylor and Guthery (1980a)). Before European settlement, their range comprised continuous prairies and shrublands, but currently landscapes contain a patchwork of rangeland, cropland, and pasture (Fuhlendorf et al. 2000). Native vegetation is dominated by grassland and shrubland communities, although specific compositions vary depending on historical manage-

ment and European settlement patterns of the landscape (Woodward et al. 2001).

Landscape structure and change

Landscapes were mapped from interpretation of black-and-white aerial photographs taken between 1959 and 1996 at a scale of 1:7,920. Dates for aerial photography across the region did not occur sequentially at regular time periods but corresponded to sampling times of lesser prairie-chicken populations (Table 1). Photo-interpreted landscape classifications were ground-truthed for each site. Landscapes were constructed with ARC/INFO software using topographic quadrangle maps (scale = 1:24,000) for georegistration (Environmental Systems Research Institute INC 1995). Landscapes were delineated into eight cover types (Table 2). Minimum resolution

Table 1. Summary of trend analysis for ten lesser prairie-chicken populations in southern Great Plains. Trends are regression slopes (log scale), units are expressed as natural logarithm of the lek count per year. Population trend (β) is the slope of the regression of the relationship between the transformed data and time. ‡ Indicates observed significance level ≤ 0.05 (adapted from Woodward et al. (2001)).

Lek Name	Years of Population Data	Years of Aerial Photography	Population Trend (β)	Change Per Decade (%)	Population Status
OKI	1980–1996	1983, 1995	-0.11‡	-92.1	declined
OK2	1965–1996	1965, 1973, 1981, 1990	-0.01	-30.9	sustained
OK3	1970–1996	1975, 1985, 1995	-0.14‡	-96.2	declined
OK4 ^a	1959–1996	1959, 1995			declined
OK5	1988–1996	1990, 1995	-0.20‡	-94.1	declined
TX1	1959–1996	1959, 1967, 1972, 1981, 1996	0.00	-12.7	sustained
TX2	1959–1996	1959, 1967, 1972, 1981, 1996	-0.03‡	-61.3	declined
TX3	1959–1996	1959, 1970, 1979, 1991	0.00	2.7	sustained
TX4	1959–1996	1959, 1970, 1979, 1991	0.01‡	32.9	sustained
TX5	1959–1996	1959, 1970, 1979, 1991	-0.03	-51.4	sustained

^a Current surveys indicate population not sustained.

Table 2. Descriptions of metrics (McGarigal and Marks 1995) used to quantify landscape structure and change for landscapes containing lesser prairie-chicken populations in the southern Great Plains of North America (1959 – 1996).

	Metric	Description	Units	
			Structure	Change
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 (% of landscape area).	% of Area	%/decade
ED	Edge Density	Mean amount of patch perimeter on a landscape (per ha).	m/ha	m/ha/decade
MSI	Mean Shape Index	Ratio of patch perimeter to area divided by a factor of 2	–	–
FD	Fractal Dimension	See McGarigal and Marks (1995)	–	–
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)	% Area	%/decade
	Nonhabitat	Open water, bare ground, and development	% Area	%/decade
	Tree	Tall, woody vegetation (riparian, windbreaks, <i>Juniperus</i> spp.)	% Area	%/decade
	Prairie	Native short-and midgrass prairie species	% Area	%/decade
	Pasture	Introduced or heavily manipulated pasture	% Area	%/decade
	Cropland	Cultivated fields	% Area	%/decade
	LD-Shrubland	Low-density (<15%) <i>Quercus hovordii</i> and other mixed shrubs	% Area	%/decade
	HD-Shrubland	High-density (>15%) <i>Quercus hovardii</i> and other mixed shrubs	% Area	%/decade
LCI	Landscape Change Index	Total landscape change in land use and vegetation (all cover types)	N/A	%/decade

(grain) and mapping unit (accuracy) corresponded to 2 m and 20 m actual distance, respectively.

Observations of telemetered 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 that represents a doubling of extent, corresponding to 452-,

905-, 1,810-, 3,619-, and 7,238-ha landscape extent, respectively. We were most concerned with relationships between observed landscape structure and population trends of lesser prairie-chickens, so 'scale' referred to the operational scale, or the spatial extent over which populations may respond to landscape structure and change (Jenerette and Wu 2000).

We quantified landscape composition, structure, and change in terms of eight cover types and eight landscape metrics (Table 2). All landscape metrics were computed using FRAGSTATS (McGarigal and Marks 1995; Hargis et al. 1998). We used results from a factor analysis performed by Ritters et al. (1995) to guide our selection of landscape metrics and minimize redundancy among variables. Formulas and algorithms used in all computations are listed in Appendix 3 of the FRAGSTATS manual except for the Landscape Change Index (LCI) (Woodward et al. 2001). LCI was calculated for each site as one-half of the sum of the absolute values of average changes of all cover types:

$$LCI = 1/2 \sum_i (\Delta A_i / t)$$

where ΔA_i was the absolute change in area (most recent composition minus initial historic composition) of each cover type and grouped category; t was the time (reported in decades) corresponding to photographic data. 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 (i.e., percentage of landscape area subject to change per decade; Woodward et al. (2001)). We used the metric because Woodward et al. (2001) found that population trends of lesser prairie-chickens were correlated inversely with landscape change as measured by the LCI. However, their analysis was only conducted at a single scale of 7,238-ha, which was the largest considered in the present study. Temporal change in landscape metrics (denoted by a "Δ" preceding the acronym) was calculated by subtracting the first sampling date from the last sampling date and standardizing to a per decade basis (change per decade) because the temporal extent of the data was not the same for all landscapes (Table 2).

Data analysis

Trends for 10 lesser prairie-chicken populations were calculated and presented in Woodward et al. (2001) using long-term data from repeated counts of established breeding display grounds (leks) obtained from the Oklahoma Department of Wildlife Conservation and Texas Parks and Wildlife (Table 1). The intent of the long-term counts was to describe the maximum birds using the breeding display grounds each year. The raw count data represented maximum number of birds on the lek based on multiple visits (at least 3 per year) during peak activity of each year. Status (declining and sustained) was assigned to each population and landscape corresponding to long-term population trends using simple established linear regression methods that have been used to estimate abundance and population trends of other avian species (Collins 1990; Moses and Rabinowitz 1990). To account for low and variable populations, spring lek counts were transformed by:

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

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). We chose a transformation constant by back-transforming data and comparing residual values ($\text{residual}_{ij} = \text{actual}_{ij} - \text{predicted}_{ij}$) (Collins 1990); residuals were minimized. For 9 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) (Table 1) (SAS Institute. 1985). Five populations were determined to be significantly *declining* ($P \leq 0.05$) and 5 populations were *sustained* (not significantly declining). Trend could not be calculated for one of the five landscapes with declining populations because of missing data but frequent surveys over the past 10 years indicate that the breeding ground is no longer used by prairie chickens (Woodward et al. 2001).

Effects of landscape configuration, composition, and change on lesser prairie-chicken populations were tested statistically using a repeated measures analysis of variance and correlation analysis. Each spatial scale in this study was considered a repeated measure because analyses at each spatial scale were not independent of the other scales. Metrics of landscape configuration, composition, and change were

tested for the significant interactions of status (declining and sustained) and scale (452-, 905-, 1,810-, 3,619-, and 7,238-ha landscape extent; $P \leq 0.10$). 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)). Multiple comparisons of means across scales were conducted using Fisher's Least Significant Difference test. Landscape metrics with significant interaction effects between status and scale were investigated for correlations (Pearson's) between population trend and landscape metrics across multiple scales but independent of declaration of status (SAS Institute. 1985). Landscape metrics that did not have a significant interaction were tested for main effects of status and scale. Multiple comparisons of means across scales were conducted using Fisher's Least Significant Difference test.

Results

Attributes of landscapes associated with lesser prairie-chicken populations were variable in space and time, and those patterns were dependent on spatial scale (Table 3). Percent Cropland ($F = 2.57$, $P = 0.0567$), Δ Tree ($F = 3.06$, $P = 0.0613$), Landscape Change Index (LCI, $F = 7.11$, $P = 0.0003$), and Δ Edge Density (Δ ED, $F = 2.08$, $P = 0.1069$) contained significant interactions between status and scale (Figure 2). Percent Cropland increased with scale on landscapes with declining populations (declining landscapes; $F = 8.13$, $P = 0.0001$) and was similar across scales on landscapes with sustained populations ($F = 0.48$, $P = 0.7523$), resulting in significantly more Cropland on declining landscapes than on sustained landscapes at the 7,238-ha scale ($F = 3.29$, $P = 0.0789$). Δ Tree increased with scale on declining landscapes ($F = 5.54$, $P = 0.0017$) and was similar across all scales on sustained landscapes ($F = 0.04$, $P = 0.9972$) with a significantly greater increase in Δ Tree on landscapes with declining populations at the 7,238-ha scale than on sustained landscapes at this scale ($F = 7.85$, $P = 0.0086$). LCI increased with scale on 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-ha ($F = 3.71$, $P = 0.0630$) and 7,238-ha ($F = 24.21$, $P < 0.0001$) scales between landscapes with declining and sustained populations. Differences in the LCI indicated that changes in com-

position were greater within declining landscapes and that effects of landscape change were most important at 3,619- and 7328-ha scales. Δ ED varied across scales but unlike the LCI, differences between landscapes with declining and sustained populations occurred only at 452-, 905-, and 1,810-ha scales ($F \geq 3.08$, $P \leq 0.10$). No other metrics contained significant interactions of status and scale, but main effects of status were significant for Δ Largest Patch Index (Δ LPI; $F = 15.83$, $P = 0.0043$). Reductions of Δ LPI were greater for declining landscapes (-6.0 % per decade ± 0.7) than sustained landscapes (-0.5 % per decade ± 0.4). Therefore, there were fewer large continuous patches on landscapes with declining populations of prairie-chickens than on those with sustaining populations.

Correlations between population trends and landscape metrics were independent of population status and supported results of the repeated-measures analyses. Correlations between population trends and Cropland, Δ Tree, and LCI were negative and increased in strength with increasing scale. At the 3,619-ha scale, Δ Tree ($r = -0.85$, $P = 0.0035$) and the LCI ($r = -0.62$, $P = 0.0739$) were correlated negatively with population trends (Figure 3). Those relationships were stronger at the 7,238-ha scale ($r = -0.84$, $P = 0.0043$; $r = 0.95$, $P = 0.0001$) and weaker at scales $< 3,619$ -ha. The correlation between Cropland and population trends was significant ($r = -0.76$, $P = 0.0185$) only at the 7,238-ha scale. Δ ED was significantly related to population trend at all spatial scales examined, and was the only metric related to status at the three finest scales (452-, 905-, 1,810 ha).

Although many landscape metrics did not contain an interaction of status and scale, there were significant main effects of scale, suggesting that most of those parameters were scale-dependent (Table 4). Variability of Patch Size (VAR-PS), Δ VAR-PS, LPI, Patch Richness (PR), Δ PR, Interspersion/Juxtaposition Index (IJI), Nonhabitat, Tree, and LD-Shrubland ($F \geq 2.25$, $P \leq 0.100$) all contained significant scaling effects. VAR-PS, PR, and IJI increased with scale indicating that landscape heterogeneity increased with increasing scale. However, Δ VAR-PS and Δ PR decreased as scale increased suggesting that VAR-PS and PR approached an asymptote 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), Δ MPS, Δ MSI, Δ FD, Δ IJI, Δ Lek, Δ Prairie,

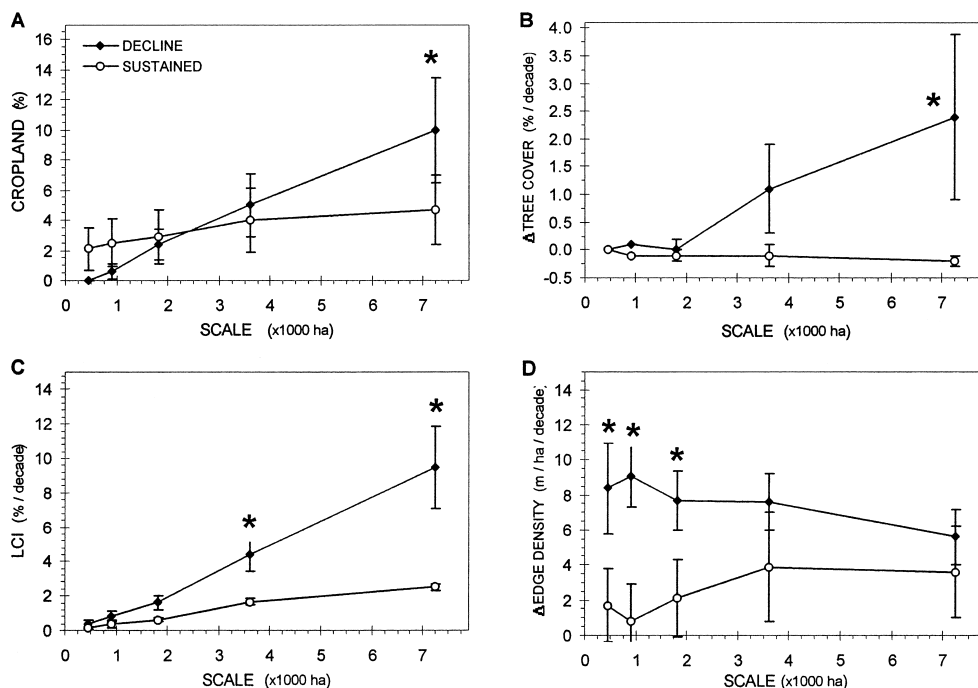


Figure 2. Mean percentage of cropland (a), mean change in tree cover (b), the landscape change index (LCI) (c), and changes in edge density (d) across five spatial scales for landscapes surrounding lesser prairie-chicken leks. * Indicates significant interactions between population status (Table 2) and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

Δ Pasture, and Δ HDShrubland were similar across scales (Table 3).

Discussion

Our analysis of landscapes with declining and sustained populations of lesser prairie-chickens indicates the importance of evaluating multiple scales (extents) when investigating relationships between landscapes and wildlife populations. Five of 32 measures that were evaluated had significant relationships with lesser prairie-chicken population trends and 4 of these 5 were scale-dependent. Percentage of cropland within the landscape, change in the cover of tree dominated landscape elements (Δ Tree), and the total amount of landscape change (LCI) differed at broad spatial scales and were higher on landscapes with declining populations than on landscapes with sustained populations. Change in edge density (Δ ED) was different at the 3 smallest extents and also highest on landscapes with declining populations. Mean changes in largest patch index (Δ LPI) were not scale-dependent, but were significantly more negative on land-

scapes with declining populations of lesser prairie-chickens than landscapes with sustained populations.

Landscape changes through time are rarely analyzed with population changes over the same period (Swetnam et al. 1999; Knick and Rotenberry 2000), but in our study, 4 of the 5 landscape factors that were significantly related to lesser prairie-chicken populations measured such change in time. Most studies attempt to relate wildlife population trends with current habitat structure, which assumes 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 or populations do not efficiently disperse after such changes, then the current state of the habitat and a population may appear to be unrelated. Such situations require an analysis of historical change in land use and landscape structure. Species, such as the lesser prairie-chicken, that exhibit high site fidelity may be associated with lag times longer than species that do not exhibit site fidelity (Knick and Rotenberry 2000). Changes in landscape structure over the past several decades had stronger relationships with dynamics of lesser prairie-chicken populations than current landscape structure.

Table 3. Summary statistics for metrics of landscape structure and change for landscapes surrounding lesser prairie-chicken leks in the southern Great Plains of North America. Significant effects are listed next to means ($\alpha=0.10$). Effect of each metric was identified as a significant main effect of scale (Scale) and status (Status) or a significant interaction between scale and status (Interact). A dash in the Effect column represents no significant differences.

Metric	Structure					Change (Δ)				
	Effect	Mean	SE	Min	Max	Effect	Mean	SE	Min	Max
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

The importance of landscape change to lesser prairie-chicken populations was thought to be limited to the reduction of native rangelands through cultivation that mostly occurred before the start of this study (Jackson and DeArment 1963; Crawford and Bolen 1976; Taylor and Guthery 1980a; Cannon and Knopf 1981; Woodward et al. 2001). Similarly, our data indicated that cultivation patterns are indeed important to the current status of lesser prairie-chicken populations (average percentage of cropland was 2.5 times greater on declining landscapes than on sustained), but they also suggested that reductions in cultivated land alone might not reverse population declines. Overall, changes in the amount of cropland were not significant and cropland actually decreased during the years evaluated in our study. Much of the marginal cropland within the region was converted to pasture as part of the Conservation Reserve Program (CRP) offered by the United States Department of Agriculture to control soil erosion and reduce commodity surplus (Fuhlendorf et al. 2000). The only influence of the CRP program that we could detect was the contribution of cropland decline and pasture increase to overall landscape change, which was negatively

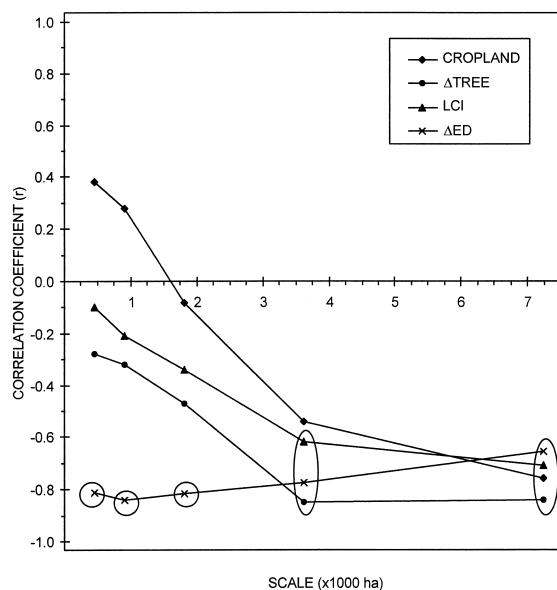


Figure 3. Correlation coefficients for the relationship between each landscape metric and lesser prairie-chicken population trends (Table 1) across the 5 spatial scales. Relationships are presented for the variables that had a significant interaction between scale and status (Cropland, Δ Tree, LCI, and AED). Circles around points indicate significant correlations ($\alpha = 0.10$).

Table 4. Means and standard errors of landscape metrics containing significant scaling effects for landscapes surrounding lesser prairie-chicken leks ($n = 10$) at five spatial scales in the southern Great Plains of North America. Capital letters in the same row represent multiple comparison of means across scales ($\alpha = 0.10$). VAR-PS = variability of patch size; Δ VAR-PS = change in variability of patch size; LPI = largest patch index; PR = patch richness; Δ PR = change in patch richness; IJI = interspersion/juxtaposition index (Table 2).

Metric	Scale (ha)									
	452		905		1810		3619		7238	
	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
Δ VAR-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
Δ PR	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

associated with population trends. Conversion of cropland to pasture could have contributed to declines in prairie chickens because in many cases cropland was replaced with introduced grass monocultures that could serve as sink habitats but this relationship is inconclusive.

Overall landscape changes that were most associated with changes in lesser prairie-chicken populations occurred most often at the broad spatial scales of this study. The importance of broad-scale landscape dynamics to lesser prairie-chicken populations was demonstrated by the interactive effect of status and scale on LCI, where the greatest differences occurred at the 2 largest spatial scales. Similar patterns were evident in the change in tree-dominated cover types, with declining landscapes having a larger increase in tree cover over the study duration than landscapes with sustained populations. The increase in trees on these grasslands and shrublands is associated primarily with the encroachment by *J. virginiana* and intentional planting of *J. virginiana* and other trees as windbreaks. The introduction or encroachment of trees into open habitats is a type of fragmentation that can be detrimental to grassland specific wildlife (Coppedge et al. 2001) and is occurring at exponential rates throughout the southern Great Plains of North America (Archer 1994; Fuhlendorf et al. 1996).

The importance of these changes at broad scales and not small scales suggests that changes over the past 50 years are leading to the isolation of local populations that may have historically been a part of larger meta-populations (Pulliam 1988; Pulliam et al.

1992). 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 effects of regional landscape fragmentation and local change within a home range. Local extinction rates and patch occupancy have been linked directly to patch size and isolation for some species (Ritchie 1997). A study of spruce grouse (*Falcipectnis Canadensis*) in the northeastern United States demonstrated a direct relationship between patch occupancy and interpatch distance suggesting that distance could be a barrier to dispersal and limit local populations (Fritz 1979). As these landscapes become more fragmented, changes within the landscape become more important because recolonization of unoccupied patches is less likely when local populations are separated by large distances of unsuitable habitat. These patterns suggest that more research is needed to evaluate movement within meta-populations and determine the effect of landscape pattern on factors that effect local population dynamics, such as density dependence, competition, predation and genetics (Ritchie 1997).

Changes in the spatial arrangement of cover types are related to changes in land use and may be important to many wildlife populations (McGarigal and McComb 1995; Burke and Goulet 1998; Ryan et al. 1998; Saab 1999; Bergin et al. 2000; Niemuth 2000). Changes in landscape configuration and pattern in our study are further indications that a critical element

contributing to the decline in lesser prairie-chicken populations is fragmentation of continuous grassland and shrubland habitats resulting in local populations that are isolated. Our data indicated that changes in largest patch index (ΔLPI) and edge density (ΔED) were greater on landscapes with declining populations over the past 10–35 years. Declines in largest patch index were 12 times greater on declining landscapes than on sustained landscapes, indicating a reduction of patch size and fragmentation of continuous habitat on these landscapes. Changes in edge density were greatest on declining landscapes at the three smallest scales, which indicates fragmentation of landscapes in relative close proximity to breeding grounds. Traditionally, edge has been thought to benefit many wildlife species (Leopold 1933) by creating heterogeneity at local levels (Forman and Godron 1986) and providing a variety of habitats in close proximity (1–100 m). However, at broad spatial scales (such as all scales in this study), an increase in edge may represent fragmentation of critical cover types, such as the edges created by the cultivation of rangeland or encroachment of trees. This type of fragmentation can have major effects on wildlife population dynamics by altering factors such as predation and extinction rates (Andren 1994; Cutler 1991; Tschamtkke 1992; Leimgruber et al. 1994; Farina 2000).

Conclusions

Differences between these landscapes with declining populations and sustained populations of lesser prairie-chickens are highly scale-dependent and support previous statements of the importance of multi-scale analyses (Wiens 1989; Levin 1992; Schneider 1994; Bissonette 1997). Any of the individual spatial scales that were evaluated would not have given completely accurate results of the influences of landscape structure and change on lesser prairie-chicken populations. The smallest spatial scales would have predicted that changes in edge density and largest patch size were the only important variables, while broad-scale analysis would have suggested that the amount of cropland, increase in trees (*J. virginiana*) and general landscape changes were most important. The multi-scale relationship between these populations and landscape dynamics suggests that these local populations may be viewed appropriately from a meta-population perspective.

Evaluation of these populations across all scales demonstrated that lesser prairie-chicken populations are particularly vulnerable to fragmentation of native prairies and shrublands. Isolated populations on fragmented landscapes may require more stable landscapes than populations that are not isolated. Landscape dynamics where populations are less isolated may have less effect on population trends because of more active emigration and immigration between local populations than on fragmented landscapes. Future research on this imperiled species in fragmented landscapes should evaluate factors that are critical to local and meta-populations such as effects of fragmentation on dispersal, colonization and extinction patterns.

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