Landscape Composition and Greater Prairie-chicken Lek Attendance: Implications for Management

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ABSTRACT -- I quantified landscape characteristics surrounding greater prairie-chicken (*Tympanuchus cupido*) leks to determine correlates of lek attendance in two Wisconsin populations with contrasting management histories. Populations in primary areas were associated with grassland reserves managed for greater prairie-chicken and populations in secondary areas were associated with large wetlands or areas of marginal agriculture with little or no management for greater prairie-chicken. Landscapes surrounding leks in primary areas were more conducive to greater prairie-chicken, with substantially more grassland, less forage crops and forest, fewer patches, and shorter distance to nearest-neighbor lek than in secondary areas. Landscape characteristics explained similar amounts (45% and 48%) of variation in models describing number of males attending leks, but models differed between landscapes. Number of males present at leks in primary areas was associated positively with amount of cropland and associated negatively with amount of forage crops and forest. Lek attendance in secondary areas was low relative to primary areas, with number of males positively associated with amount of grassland and negatively associated with forage crops and distance to nearest known lek. Differences in models are likely the result of different habitat availabilities as a consequence of land use and management. Results indicated that 1) conservation actions can have a substantial impact on landscapes and target populations; 2) prescriptions for conservation might not be universally applicable, even within a limited geographic area; and 3) secondary landscapes in Wisconsin will need substantial conservation effort, particularly establishment and

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conservation of grassland and enhanced connectivity among subpopulations, to maintain populations of greater prairie-chicken.

Key words: conservation planning, grassland bird, greater prairie-chicken, landscape ecology.

The greater prairie-chicken (*Tympanuchus cupido*) is the focus of extensive conservation efforts as its populations and range are reduced greatly from historic levels (Schroeder and Robb 1993). In some states, populations of greater prairie-chicken on private lands are less secure and are declining relative to those on public lands managed for greater prairie-chicken (Westemeier and Gough 1999), although even populations on managed lands can be susceptible to declines in number and fitness because of isolation (Bouzat et al. 1998, Westemeier et al. 1998). Consequently, wildlife management agencies are targeting habitat improvement efforts on private lands in an attempt to increase viability of these populations (Wisconsin DNR 1995, Mechlin et al. 1999).

The greater prairie-chicken was native to southern Wisconsin, but expanded its range throughout the state in the early 1900's as timber harvest and agriculture provided new habitat (Leopold 1931, Schorger 1943). Populations subsequently declined as southern croplands were cultivated more intensively and cutover forests in the north grew back, and by the 1950's the largest populations remaining in the state were in an open landscape containing the Buena Vista and Leola marshes (Hamerstrom et al. 1957). This area was selected as the highest priority for greater prairie-chicken conservation in Wisconsin, and scattered parcels of land in the Buena Vista and Leola landscape were acquired for grassland preservation and management (Hamerstrom and Hamerstrom 1973). The majority of greater prairie-chicken presently in Wisconsin are in the ~25,000 ha Buena Vista/Leola landscape, which contains ~6,000 ha of protected grasslands and wet meadows managed for greater prairie-chicken by the Wisconsin Department of Natural Resources (Keir 1999). These birds have been described as "probably the most intensively managed grouse in North America" (Bergerud 1988:722).

Additional populations of greater prairie-chicken associated with marginal agriculture or large wetlands are located in secondary landscapes northwest of the Buena Vista/Leola complex (Fig. 1; Niemuth 2000). Most lands in these areas are not protected and receive little or no management to maintain grassland habitat, even though some fall within boundaries of state wildlife areas. Of 20 leks known to be active in portions of Taylor, Clark, and Marathon counties in 1991 (Ken W. Jonas, Wisconsin Department of Natural Resources, personal communication), only four were known to be active in 2003 and two in 2005 (James R. Keir, Wisconsin Department of Natural Resources, personal communication, and Ken Luepke, Spencer, Wisconsin, personal communication).

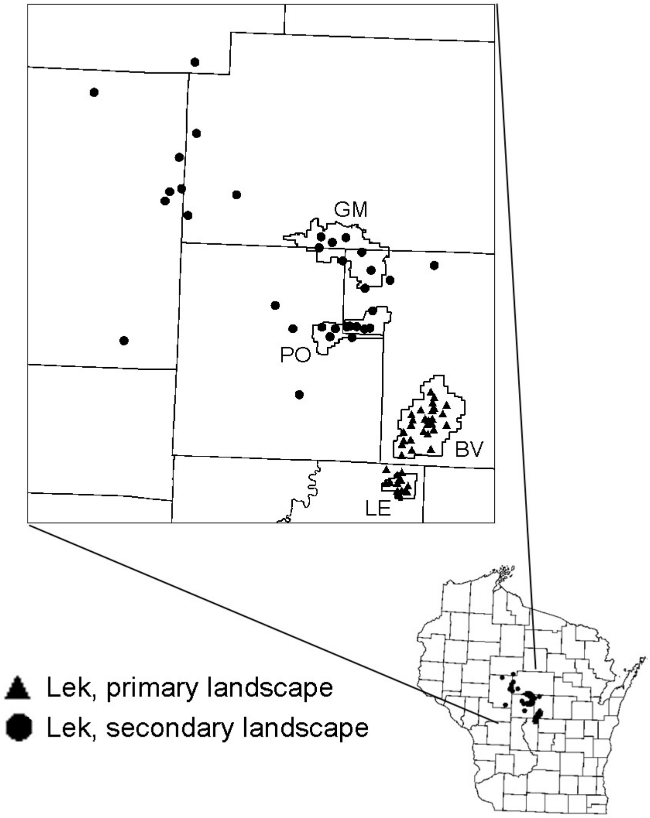

Figure 1. Location of greater prairie-chicken leks included in my analysis and the Buena Vista (BV), Leola (LE), Paul Olson (PO), and George Mead (GM) wildlife management areas in central Wisconsin.

I compared landscape characteristics that likely influenced habitat suitability for greater prairie-chicken in two areas in central Wisconsin. Because of intensive grassland management, large proportion of birds that they harbor, and their designation as the top priority areas for greater prairie-chicken in Wisconsin, I followed the terminology of Hamerstrom et al. (1957) and defined the Buena Vista and Leola landscapes as primary areas (Fig. 1). I defined all other landscapes, which have relatively little or no management for greater prairie-chicken, as secondary areas (Fig. 1). My objectives were to 1) determine if landscape characteristics and greater prairie-chicken response to landscape characteristics differed between primary and secondary areas, and 2) identify management needs and land treatments that would increase the quantity and quality of greater prairie-chicken habitat, particularly in secondary areas. Landscape-scale evaluation and treatment of habitat are appropriate as the presence and size of greater prairie-chicken populations are associated positively with the amount of grass in the landscape and associated negatively with forest cover and distance from other populations (Westemeier 1971, Merrill et al. 1999, Niemuth 2003). Landscape characteristics also can influence reproductive success of greater prairie-chicken (Ryan et al. 1998). Private lands management is a 10 year objective and high-priority strategy for management of greater prairie-chicken in Wisconsin, and evaluating greater prairie-chicken habitat is a high priority research need (Wisconsin Department of Natural Resources 1995).

METHODS

An annual spring census conducted throughout Wisconsin's greater prairie-chicken range identified most, if not all, greater prairie-chicken leks (Keir 1999). In April of 1997, previously active leks and potential habitat were visited during early morning display periods and number of males counted. Leks were visited at least two times, and the modal number of males was used in analysis. I marked lek locations on orthophotos or 1:50,000 land ownership maps and assigned them to corresponding cells in a geographic information system (GIS). In a few cases where leks were identified by legal descriptions, I assigned lek locations to the center of 16-ha parcels.

I used the Wisconsin Initiative for Statewide Cooperation on Landscape Analysis and Data (WISCLAND; Gurda 1994) for digital landcover information (available at http://www.dnr.state.wi.us/maps/gis/datalandcover.html). WISCLAND data are based on satellite imagery collected primarily in 1992 and follow a three-level hierarchical classification scheme. Because many of the landcover categories in WISCLAND were narrow classifications that I thought were not useful in evaluating greater prairie-chicken habitat (e.g., coniferous forested wetland vs. mixed deciduous-coniferous forested wetland), I combined categories to create eight biologically relevant landcover categories, five of which were included in analysis (Table 1). I excluded categories that were biologically meaningless or occurred infrequently, including areas obscured by clouds (0.01% of the state), urban areas (1.5%), barren ground (1.1%), and cranberry (*Vaccinium macrocarpon*) bogs (0.009%). I excluded open water (4.1%) from analysis as it does not directly provide habitat used by greater prairie-chicken, although open water can contribute to open space necessary around leks (Larry M. Mechlin, Missouri Department of Conservation, personal communication). The WISCLAND project divided the state into spectrally consistent units (SCCUs) for evaluation of classification success. Using multiple levels of data within the classification hierarchy makes it difficult to provide an exact accuracy assessment, but the two

Table 1. Variables used to characterize landscapes around leks in primary and secondary areas and to determine associations between landscape characteristics and attendance at greater prairie-chicken leks in central Wisconsin, spring 1997.

Landscape variable[a]	Description
Grassland (%)	Noncultivated herbaceous vegetation dominated by grasses, grass-like plants, or forbs. Includes cool and warm season grasses, restored prairie, timothy (*Phleum pratense*), rye (*Secale cereale*), pasture, idle farmland, and CRP fields.
Wetland (%)	Persistent and nonpersistent herbaceous plants associated with wet soils including grasses, sedges (*Carex* spp.), and cattails (*Typha* spp.). Does not include forested wetlands, areas of open water, or floating macrophytes.
Forage crops (%)	Cultivated forage crops including alfalfa (*Medicago sativa*), grass hay, and legume/hay mix.
Forest (%)	Woody vegetation greater than or equal to 2 m tall with definite crown, including upland and lowland hardwood, coniferous, and mixed forest.
Cropland (%)	Cultivated crops such as corn (*Zea mays*), potatoes (*Solanum jamesii*), soybeans (*Glycine max*), and small grains.
Distance (m)	Distance to nearest known greater prairie-chicken lek.
Patches (n)	Number of disjunct patches of all landcover categories in buffer zone. Patches could be as small a one GIS cell (0.4 ha); cells of the same habitat type were classified as belonging to the same patch only if they had at least one edge in common.

[a]Cover classes were combined from the WISCLAND database (Gurda 1994) and followed WISCLAND definitions.

SCCUs in which my study area was located reported accuracy of 82% and 80% at the finest thematic resolution. I used much of the data at a coarser level of thematic resolution, which had reported accuracy of 93% and 94%. I analyzed data in a raster format and used a nearest-neighbor operator to resample data to 60 m X 60 m resolution.

I used circular moving window analyses to calculate the number of patches and percentage of each landcover type (Table 1) within 1,560 m of every cell in the GIS data layers. Size of the sampling window was based on landscape-level habitat selection results of Merrill et al. (1999) and Niemuth (2000), the tendency of greater prairie-chicken to nest within 1.6 km of a lek (Hamerstrom 1939, Schroeder 1991), and high management priority of lands within 1.6 km of leks (Keir 1999). I used Idrisi® (version 2.0; Clark Labs, Worcester, Massachusetts) and ArcInfo GIS (version 8.2; Environmental Systems Research Institute, Redlands, California), to determine the proportion of the landscape in each cover class and calculate the number of patches surrounding each lek, respectively.

Number of males present, percent of the landscape in each cover class, number of patches, distance to nearest known lek, and associated standard errors were calculated for all leks in primary (n = 42) and secondary (n = 33) areas. Lek counts are considered an index of habitat quality (Hamerstrom and Hamerstrom 1973), so I used multiple linear regression to determine associations between number of males present and landscape characteristics in primary and secondary areas. Four leks in secondary areas where attendance was unknown were not included in the analysis. Distance to nearest lek was included as a candidate variable in all regression analyses because of its significance in greater prairie-chicken habitat colonization, metapopulation dynamics, and behavior, and also to model potential positive spatial autocorrelation inherent to clustered populations (see Augustin et al. 1996).

I used Akaike's Information Criterion corrected for small sample size (AICc) to select the model from a suite of candidate models that best explained variation in the data set (Burnham and Anderson 1998). I consider the analysis exploratory, although based on the general biology of greater prairie-chicken I assumed that lek attendance would be associated positively with grasslands, wet meadows, and proximity to other populations, and associated negatively with forests, agriculture, and landscape fragmentation. Residuals from linear regression were examined and tested to ensure that assumptions of normality and constant variance were met (Zar 1996). I used Number Cruncher Statistical System (NCSS, Kayesville, Utah) for statistical analyses.

RESULTS

Mean number of males attending leks was greater in primary areas than secondary areas (Fig. 2). Leks in primary areas were surrounded by more cover classified as grassland and wetland relative to secondary areas (Fig. 2), while landscapes surrounding leks in secondary areas had more forest and forage crops. The amount of cropland was similar in the two landscapes (Fig. 2). Leks in primary areas were substantially closer together than in secondary areas, and the number of patches in landscapes surrounding leks was greater in secondary areas than in primary areas (Fig. 2).

Number of males present was correlated strongly with landscape characteristics (Table 2), although models predicting number of males attending leks differed between the two landscapes. Number of males attending leks in secondary areas was associated positively with the amount of grassland in the landscape and associated negatively with forage crops and distance to nearest known lek (Table

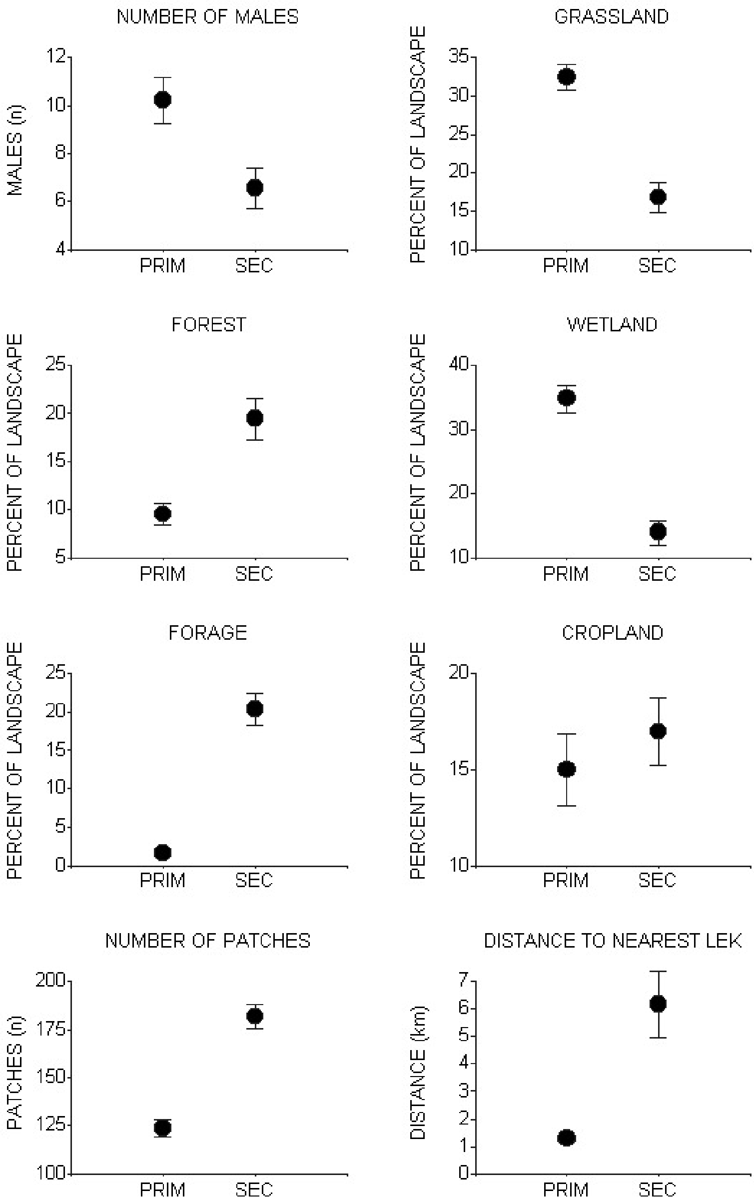

Figure 2. Mean values (± SE) for number of males, landscape characteristics, and distance to nearest lek for greater prairie-chicken leks in primary (PRIM; n = 42) and secondary (SEC; n = 33) areas in Wisconsin.

Table 2. Parameter estimates, SE, partial r^2, and model R^2 for regression models of landscape characteristics associated with number of males attending leks in primary and secondary areas in central Wisconsin.

Area	Leks (n)		Intercept	Grassland	Forage crops	Distance	Forest	Cropland	Model R^2
Secondary	29	Coefficient	7.4	0.27	-0.23	-0.00016			47.9
		SE	1.6	0.07	0.07	0.00009			
		Partial r^2		0.39	0.34	0.11			
Primary	42	Coefficient	11.9		-1.3	0.0016	-0.48	0.22	44.9
		SE	1.9		0.48	0.0016	0.11	0.07	
		Partial r^2			0.17	0.03	0.34	0.22	

2). Number of males attending leks in primary areas was associated negatively with amount of forest and forage crops and associated positively with amount of row crops, and showed a slight positive relationship with distance to nearest lek (Table 2). No other variables were included in models within two AIC units of the model best fitting the data. Assumptions of normality and constant variance were met for both regression models.

DISCUSSION

Landscapes surrounding leks on primary and secondary areas differed substantially, which affected models predicting number of males and has strong implications for the management and continued existence of greater prairie-chicken in central Wisconsin. Low amounts of grass, small numbers of males, and the correlation between male attendance and amount of grass in secondary areas indicated that greater prairie-chicken in these areas was affected strongly by grassland availability. Lack of a similar correlation in primary areas suggested that number of males was not limited by the amount of grassland in those areas. Small amounts of grassland in secondary areas demonstrated the critical need to conserve and increase the amount of grassland there, particularly grass with residual cover suitable for nesting. Ideally, blocks of grass should be large, which can reduce nest loss and increase conservation potential for greater prairie-chicken (Ryan et al. 1998).

The number of male greater prairie-chicken attending leks in primary areas was associated negatively with forest cover (Table 2), but lek attendance in secondary areas, where forest cover was greater (Fig. 2), was not correlated with forest area. This suggested that factors other than forest cover, such as grassland availability, more strongly influenced numbers of greater prairie-chicken in secondary areas. However, the negative effect of trees on greater prairie-chicken (Hamerstrom et al. 1957, Merrill et al. 1999, Niemuth 2000) cannot be ignored, and forest cover in landscapes surrounding leks should be reduced. Ideally, forest should be converted to grassland, but even without conversion to grass, the removal of forests, woodlots, and individual trees surrounding leks will remove perches and cover used by potential predators of nests, young, and adult greater prairie-chicken (Pedlar et al. 1997, Kuehl and Clark 2002), as well as increase the open aspect of the landscape and enhance movement.

The amount of forage crops surrounding leks was much higher in secondary areas than primary areas, which reflected higher levels of dairy farming in the secondary areas. Greater prairie-chicken will nest in forage crops (Ryan et al. 1998), and forage crops can contribute to open space required by greater prairie-chicken as well as provide lek sites, but the presence of forage crops can have a negative impact on populations. Haylands did not support greater prairie-chicken in North

Dakota (Kirsch et al. 1973), and hay harvest causes loss of greater prairie-chicken nests and young (Yeatter 1963, Ryan et al. 1998). Mean date for first cutting of hay has become progressively earlier in Wisconsin (Warner and Etter 1989), which increased the likelihood of nests in hayfields being destroyed before hatching. The effect of forage crops will likely differ among locations, depending on timing of harvest and regrowth of harvested vegetation. If possible, forage crops in landscapes surrounding leks should be converted to grassland with residual cover to provide nesting and brood-rearing habitat. Other options include converting forage crops to pasture, which is often used for leks and foraging by broods (Manske and Barker 1988), or providing incentives to landowners to harvest forage crops at a later date after eggs have hatched and chicks are better able to escape harvest equipment.

Agricultural crops can provide benefits (e.g., food, open space, loafing and lek sites) to greater prairie-chicken (summarized in Schroeder and Robb 1993), and row crops such as corn might be necessary for greater prairie-chicken to survive winters in northern areas (Hamerstrom et al. 1941). Number of males present was associated with row crops in primary areas, but the extent of this relationship likely is limited, as an excess of row crops will reduce available grassland habitat.

Distance to nearest known lek was much greater in secondary areas than primary areas (Fig. 2) and was associated negatively with number of males present in secondary areas (Table 2). Isolated leks might be less likely to have their numbers bolstered by dispersal from other populations, and proximity to other populations can influence demographic rescue (e.g., Martin et al. 2000), probability of lek presence (Niemuth 2003), and maintenance of genetic diversity (Bouzat et al. 1998, Westemeier et al. 1998, Johnson et al. 2003). Distance to nearest known lek also might reflect the propensity of greater prairie-chicken to seek out conspecifics and move among leks (see Hamerstrom and Hamerstrom 1973, Mechlin 1998, Mechlin et al. 1999, Moe 1999), or simply indicate proximity of additional habitat. The metapopulation structure of greater prairie-chicken in Wisconsin (Niemuth 2000) has strong conservation implications as peripheral populations of prairie grouse typically disappear before core populations (Westemeier et al. 1998, Morrow et al. 1996). The positive relationship between number of males and distance to nearest lek in primary areas accounted for little variation in male attendance and is likely a consequence of the high density of leks in primary areas. Landscapes around and between leks in secondary areas should be managed to enhance movement and provide habitat stepping stones between sub-populations.

The percentage of the landscape classified as wetland was higher on lands surrounding leks in primary areas than in secondary areas. The Buena Vista and Leola management areas, which comprised the primary areas, were formerly large wetlands that were drained in the early 1900's (Hamerstrom et al. 1957). These areas have extensive wet meadows and areas of peat soil that were classified as wetlands interspersed with grasslands even though they are saturated rarely.

Wetlands can be a key component of greater prairie-chicken habitat (Hamerstrom et al. 1957, Kobriger 1965, Westemeier 1971), but area of wetland was not associated with number of males present at leks in primary or secondary areas, and it was unlikely that wetland availability limited populations of greater prairie-chicken in central Wisconsin.

Number of patches in the landscape was much higher in secondary areas. Reproductive success of greater prairie-chicken nests might be lower in fragmented landscapes relative to landscapes comprised of large, contiguous patches of grass (Ryan et al. 1998), but number of patches was not associated with lek attendance in primary or secondary areas.

Previous analysis using 1997 landcover data identified area of grassland with residual cover as the only statistically significant variable ($P < 0.05$) associated with male attendance at secondary leks (Niemuth 2000), while the present analysis, using earlier landcover information, also identified negative associations with area of forage crops and distance to nearest lek and explained more variation in attendance. Male greater prairie-chicken show strong fidelity to leks, and increased explanation of male numbers by using WISCLAND data might be attributable to a lag in the response of populations to landscape characteristics (see Knick and Rotenberry 2000, Fuhlendorf et al. 2002). Other factors that also might contribute to differences in results include use of classified satellite imagery rather than manually digitized data, different class definitions, and improved model selection procedures. Landscape data were subject to errors in both analyses, but overall relationships were similar and biologically appropriate.

Of course, a variety of exogenous and endogenous factors also influence greater prairie-chicken populations, such as weather, parasites, microsite conditions, genetic variability, and predator communities (McKee et al. 1998, Westemeier et al. 1998, Schroeder and Baydack 2001, Peterson 2004). Fine-grained habitat characteristics such as presence of individual trees and structure and species composition of grasslands also must be considered, but coarse-grained spatial analysis allows identification of specific landscape conditions that might guide local management treatments intended to meet fine-grained habitat needs. My analysis was exploratory and based on a short time frame within a limited geographic extent, but demonstrated how landscape characteristics might differ between areas, and how these differences might affect bird-habitat relationships and management prescriptions. Consequently, caution should be used in applying management guidelines developed in one region to populations in another region. Habitat models will not be applicable universally, and local conditions and needs must be considered when developing management guidelines.

Conservation planning for greater prairie-chicken in Wisconsin would be enhanced by updating landcover information. The present range of greater prairie-chicken in Wisconsin is encompassed in one Thematic Mapper satellite scene, simplifying acquisition of current, accurate, and inexpensive landcover information. Current landcover information should be used to corroborate and update the patterns identified in my analysis and then verify conservation needs and target areas for treatment. Because some leks included in my analysis are no longer active and locations of others have shifted, some metrics such as distance to and location of nearest lek will be altered, with subsequent implications for local management. Updated landcover data should be used in conjunction with local studies to quantify the effects of landscape and local habitat characteristics on nesting success, movement, adult survival, and brood survival of greater prairie-chicken in the region and use resulting information to further guide management actions. Ideally, coarse-grained analyses such as this provide context for complementary fine-grained, local studies, which can provide information that helps interpret results of coarse-grained studies.

Poor landscape and habitat characteristics likely play a major role in the decline in the number of greater prairie-chicken individuals and leks in secondary areas, and secondary areas should be the focus of greater prairie-chicken conservation efforts in the state. However, conservation on private lands can be complicated by small tract size, presence of multiple landowners, conflicting goals for land use, and perceptions of rare species restricting use of private property. Mechanisms are needed to communicate the plight of greater prairie-chicken and other grassland birds in the region and engage private landowners and conservation partners to increase the amount and quality of grassland habitat in the study area.

Some of the patterns described in my analysis, such as high levels of grass in primary areas, are attributable directly to management for greater prairie-chicken. Other patterns, such as the amount of forage crops in the landscape, are influenced by local agricultural practices, which change over time (Hamerstrom and Hamerstrom 1973, National Agriculture Statistics Service 1999, James R. Keir, Wisconsin Department of Natural Resources, personal communication) and likely will continue to change. Private lands and their uses can be major components of greater prairie-chicken habitat in Wisconsin. But low lek attendance, poor habitat, and loss of leks in secondary areas indicated that relying on the vagaries of private land use was insufficient to maintain greater prairie-chicken populations over long time periods. Ultimately, directed management over broad landscapes will likely dictate the future of the greater prairie-chicken in Wisconsin, as well as other portions of its range.

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