Identifying landscapes for greater prairie chicken translocation using habitat models and GIS: a case study

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Abstract Declines in the number and range of prairie grouse (*Tympanuchus* spp.) in North America have prompted numerous translocation efforts to establish additional populations, but overall success of translocations has been low. Because success of a translocation is ultimately determined by the quantity and quality of habitat at the translocation site, evaluating habitat prior to translocation should be a critical consideration. I used landscape characteristics surrounding 75 greater prairie chicken (*T. cupido*) leks and 75 unused points to develop a habitat model identifying suitability of landscapes for greater prairie chickens in Wisconsin. Presence of leks was positively associated with amount of grassland and wetland in the landscape and negatively associated with forest cover and distance from nearest known lek. The model correctly identified 94% of sample leks and unused points. I applied the model to digital landcover data of the entire state of Wisconsin to create a spatially explicit map predicting suitability of unoccupied landscapes for translocation of greater prairie chickens. Sites identified as suitable for greater prairie chickens agreed with results of other prairie chicken habitat models and landscapes identified as having high priority for conservation of grassland birds in Wisconsin. The most suitable landscapes had substantial public ownership but would likely require fine-grained management to meet all habitat requirements of greater prairie chickens. Landscape-level habitat models combined with accurate digital data provide an efficient means of objectively assessing habitat for prairie chicken translocation.

Key words GIS, landscape ecology, prairie chicken, scale, sharp-tailed grouse, spatially explicit habitat model

Conversion of prairies and brushland to agriculture has caused dramatic declines in the range and number of prairie grouse (*Tympanuchus* spp.) in North America. For example, the 3 subspecies of the greater prairie chicken (*T. cupido*) collectively were once found in approximately 30 states and provinces (Johnsgard 1973). Of the 3 subspecies, the heath hen (*T. c. cupido*) is now extinct, the Attwater's prairie chicken (*T. c. attwateri*) is endangered and restricted to small portions of Texas, and the greater prairie chicken (*T. c. pinnatus*) is in danger of extirpation in 7 of the 11 states in which it occurs (Schroeder and Robb 1993, Westemeier and Gough 1999). Range and populations of lesser prairie chickens (*T. pallidicinctus*) and sharp-tailed grouse (*T. phasianellus*) follow similar patterns (Connelly et al. 1998, Giesen 1998), although the initial range of the lesser prairie chicken was much smaller. Remaining populations of prairie grouse are often small, isolated, and dependent on limited areas of suitable habitat, particularly at the fringes of their range (Giesen 1994, McDonald and Reese 1998, Westemeier and Gough 1999, Gregg and Niemuth 2000).

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Populations of the greater prairie chicken in Wisconsin followed a similar pattern. Prior to settlement by Europeans, greater prairie chickens were abundant in prairies and savannas in the southern third of Wisconsin, but their populations declined as these areas were developed for agriculture (Schorger 1943). At the same time, timber harvest, agriculture, and fire created suitable habitat in the previously forested northern part of the state, and during the early 1900s prairie chickens were found throughout Wisconsin (Leopold 1931, Schorger 1943). Presently, greater prairie chickens in Wisconsin are limited to portions of 6 counties in the central part of the state (Niemuth 2000); establishing additional populations would increase long-term viability of greater prairie chickens in Wisconsin, where they are listed as a threatened species (Sample and Mossman 1997).

Declining fortunes of prairie grouse have prompted numerous translocation efforts. Birds have been translocated to supplement existing populations (Silvy et al. 1999), establish additional populations to increase a species' security within a state (Hoffman et al. 1992), hasten the spread of prairie grouse into newly created habitat (Ammann 1957), populate unoccupied but seemingly suitable habitat within a species' former range (Mechlin et al. 1999), establish a species outside its natural range (Applegate 1997), and increase genetic diversity of a small, isolated population (Westemeier et al. 1998*a*). Some translocations have been successful (Ammann 1957, Hoffman et al. 1992), but overall success of translocations has been low (Ammann 1957, Toepfer et al. 1990, Giesen 1998, Snyder et al. 1999).

Translocation procedures can influence the initial establishment of translocated birds, and factors influencing translocation success have been much discussed (e.g., Griffith et al. 1989, Toepfer et al. 1990, Wolf et al. 1996, Snyder et al. 1999). Assuming that success of a translocation is defined as the establishment of a self-sustaining population (Griffith et al. 1989), translocation success ultimately will be determined by quantity and quality of habitat at the translocation site (Griffith et al. 1989, Toepfer et al. 1990). Therefore, evaluating habitat prior to translocation should be a critical component of a translocation effort. However, in a survey of wildlife translocation efforts, habitat quality in most cases was subjectively evaluated (Wolf et al. 1998), even though habitat quality was the factor most frequently cited as influencing translocation outcome (Wolf et al. 1996). Evaluation of prairie grouse habitat may be particularly problematic as prairie grouse populations require habitat on the scale of tens of km^2 (Grange 1948, Hamerstrom et al. 1957, Toepfer et al. 1990, Westemeier and Gough 1999, Niemuth 2000), requiring that large landscapes be evaluated.

A large number and variety of general prairie grouse habitat models have been developed that can aid in assessing habitat quality (e.g., Ammann 1957, Evans and Gilbert 1969, Prose 1985, Giesen and Connelly 1993). However, the evolution of Geographic Information Systems (GIS) and remote sensing technology make it possible to assess habitat in a spatially explicit manner using quantitative habitat models based on empirical relationships between grouse populations and landscape characteristics. Use of a landscape scale to identify greater prairie chicken habitat is appropriate for biological and management reasons. First, there is considerable evidence that greater prairie chickens require large blocks or aggregations of habitat and are influenced by the composition and configuration of that habitat (summarized in Niemuth 2000). Second, it is easier for managers to provide appropriate fine-grained habitat (e.g., manipulate vegetation structure using prescribed fire) within a suitable landscape than to alter a landscape surrounding a point with appropriate fine-grained habitat but unsuitable landscape characteristics.

Prairie grouse have long been known to respond to landscape characteristics (Grange 1948, Ammann 1957, Hamerstrom et al. 1957, Cannon et al. 1982), but many habitat models do not specifically incorporate a spatial or landscape context. I developed a spatially explicit habitat model to quantify prairie chicken habitat in central Wisconsin using a resource selection probability function (RSPF) based on logistic regression (Neter et al. 1989, Manly et al. 1993). RSPFs developed using logistic regression are useful in landscape modeling as they can quantify characteristics of habitats and habitat assemblages, rather than habitats as categories (Alldredge et al. 1998); this is particularly useful for species such as prairie grouse, the presence, density, and reproductive success of which are influenced by landscape composition and pattern (Cannon et al. 1982, Ryan et al. 1998, Merrill et al. 1999, Niemuth 2000, Woodward et al. 2001). I used the landscape around greater prairie chicken leks for sampling and analysis because leks are located in areas of nesting cover and high breeding potential (Schroeder and

White 1993) and are the focal point of prairie grouse habitat and behavior (Westemeier 1971, Hamerstrom and Hamerstrom 1973). Like other landscape-based models, this method takes a coarse-grained approach to conservation, assuming that necessary microhabitat features will be available or can be created within suitable landscapes.

Evaluating potential translocation sites is a 10-year objective and high-priority strategy for management of greater prairie chickens in Wisconsin (Wisconsin Department of Natural Resources 1995). The goals of my analysis were 2-fold: 1) to model relationships between landscape characteristics and presence of greater prairie chickens and 2) to use resultant models to create spatially explicit maps showing landscapes with similar characteristics that are potentially suitable for translocation of greater prairie chickens.

Methods

Lek locations

Active leks were located by visiting previously active leks and potential habitat throughout Wisconsin's prairie chicken range from 45 min prior to sunrise to 2.5 hr after sunrise in April of 1997. I used 33 leks found in landscapes that received little or no management for greater prairie chickens (Niemuth 2000) as well as 42 leks on the Buena Vista ($n=27$) and Leola management areas ($n=15$) in Portage and Adams counties. I included 2 leks located in large wetlands not managed for prairie chickens where birds were not observed displaying in 1997 but were present in previous and following years. Lek observations and landcover data were from slightly different time periods; however, locations of individual prairie chicken leks in the region are highly consistent from year to year (Westemeier 1971, Hamerstrom and Hamerstrom 1973). Location of some leks changed slightly from one year to the next, but even with changes, lek locations were strongly associated with specific areas of habitat that harbored prairie chickens (N. D. Niemuth, unpublished data). I marked lek locations on orthophotos or 1:50,000 land-ownership maps and assigned them to corresponding cells in the GIS. In some cases where leks were identified by legal descriptions, I assigned lek locations to the center of 16-ha parcels. Typically, a lek is considered to have ≥ 2 males. However, I included 3 leks where only 1 male was observed, because these were at traditional locations that had been used in previous years. I randomly selected unused points ($n=75$), constraining them to the same types of habitat (grassland, forage, row crop, wetland, barren, and shrub) in which leks were located and within 32 km of a known lek, the maximum distance observed between leks.

Landcover databases

I used the Wisconsin Initiative for Statewide Cooperation on Landscape Analysis and Data (WISCLAND) for digital landcover information (available at http://www.dnr.state.wi.us/org/at/et/geo/data/wlc.htm). WISCLAND was developed by a consortium of public and private partners to provide a comprehensive landcover database for the state of Wisconsin and is based on Landsat Thematic Mapper satellite data collected primarily in 1992 (Gurda 1994). WISCLAND follows a hierarchical classification scheme with 8 general landcover categories subdivided into 2 additional levels of classification with 37 landcover categories at the finest level of classification. Because many of the subdivided landcover categories were narrow classifications not useful in evaluating prairie grouse habitat (e.g., coniferous forested wetland vs. mixed deciduous-coniferous forested wetland), I combined categories from the WISCLAND database to create 8 biologically relevant landcover categories, 6 of which were included as candidate predictor variables in model selection (Table 1). Areas obscured by clouds and not classified (0.01% of the state) were excluded from model development, as were urban areas (1.5%), barren ground (1.1%), cranberry (*Vaccinium macrocarpon*) bogs (0.009%), and open water (4.1%), including areas of floating macrophytes. I analyzed data in a raster format with 60 × 60-m cells, because minimum size of classified upland habitat was 4 30 × 30-m cells. Producers of the WISCLAND database assessed classification accuracy from ground-truthed sites located in a stratified random sample of 1:24,000 quadrangle map boundaries. At the finest level of categorization, overall correct classification of uplands for the geographic area used to develop my model was 82%; at the middle level of categorization, overall correct classification was 93%. Producers of the WISCLAND database assessed classification accuracy of wetlands by comparing classifications from satellite imagery to data from the Wisconsin Wetlands Inventory; overall correct classification of wetlands was 85%. Correct classification of the landcover classes used in my analysis should

Table 1. Candidate variables used to determine associations between landscape characteristics and presence of 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, rye, pasture, idle farmland, and CRP fields.
Wetland (%)	Persistent and nonpersistent herbaceous plants associated with wet soils including grass, sedges (*Carex* spp.) and cattails (*Typha* spp.). Does not include forested wetlands, areas of open water, or floating macrophytes.
Forage (%)	Forage crops including alfalfa, hay, and hay mix.
Forest (%)	Woody vegetation ≥2 m tall with definite crown, including upland and lowland hardwood, coniferous, and mixed forest.
Shrub (%)	Woody vegetation <6 m tall with <10% tree cover. Includes lowland deciduous shrubs such as willow (*Salix* spp.) and upland shrubs such as scrub oak (*Quercus* spp.).
Cropland (%)	Corn, other row crops, field crops, and general agriculture.
Distance (m)	Distance to nearest known greater prairie chicken lek.
Patches (*n*)	Number of patches in each buffer.

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

exceed 82%, as combining specific cover classes into more general categories would reduce misclassification of similar classes that were previously more likely be confused than dissimilar classes that were not combined.

I used circular moving window analyses to calculate the number of patches and percentage of each landcover type (Tables 1 and 2) 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) and location of greater prairie chicken nests in relation to leks. In Wisconsin, 8 of 23 (35%) greater prairie chicken nests were found within 800 m of a lek; an additional 10 of 23 (43%) were found between 800 and 2,000 m of a lek (Hamerstrom 1939). In Colorado, 73 of 82 (89%) nests were found within 1,500 m of a lek (Schroeder 1991). Because reproductive success of greater prairie chickens can be impacted by landscape fragmentation (Ryan et al. 1998), I calculated the number of habitat patches within the 1,560-m-radius sampling window as an index of fragmentation. Patches were defined as disjunct clusters of landcover pixels with the same classification, linked by ≥1 common sides, but not diagonals. I then extracted characteristics of landscapes surrounding each lek and unused point from resulting GIS layers. I included distance to nearest known lek as a predictor variable to model spatial autocorrelation inherent to clustered populations (Augustin et al. 1996) and because of its potential importance in patch colonization and metapopulation dynamics (McDonald and Reese 1998, Niemuth 2000). I conducted all spatial analyses with Idrisi® (Clark Labs, Worcester, Mass.) and ArcInfo GIS (Environmental Systems Research Institute, Redlands, Calif.).

Model development and selection

I assumed that landscape characteristics, x_i, could predict the probability of use of a landscape unit according to the model

$$w^*(x) = \frac{\exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_k X_k)}{(1 + \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_k X_k))},$$

where $w^*(x)$ is a resource selection probability function (RSPF) and β_i are coefficients estimated with logistic regression (Neter et al. 1989, Manly et al. 1993). I treated the data as a census of used and a sample of unused sites (Manly et al. 1993) because an annual spring census conducted throughout Wisconsin's prairie chicken range identifies most, if not all, greater prairie chicken leks (Keir 1999).

I selected the model best describing presence of greater prairie chicken leks using Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson 1998). I developed candidate models using the knowledge that greater prairie chickens in Wisconsin are strongly associated with grasslands and wetlands (Grange 1948, Hamerstrom et al. 1957, Westemeier 1971) and are likely influenced by forests, shrubland, landscape fragmentation, and proximity to other populations of prairie chickens (Hamerstrom et al. 1957, Ryan et al. 1998, Merrill et al. 1999). I calculated Akaike weights (w_i) indicating the relative likelihood of each model given the data (Burnham and Anderson 1998). Success of the model at classifying leks and unused points in the data set used to develop the

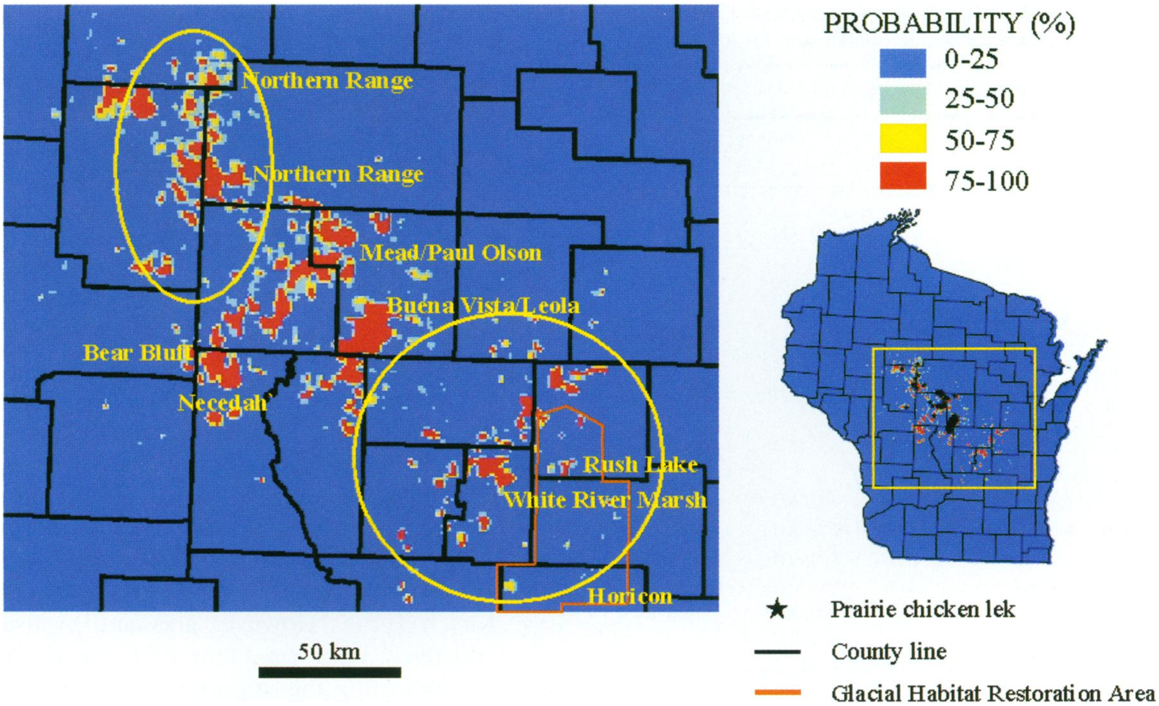

Figure 1. Suitability of Wisconsin landscapes for greater prairie chickens as predicted by probability model based on landscape characteristics. Circle indicates landscapes identified as most suitable for translocation of greater prairie chickens in Wisconsin. Ellipse indicates area of high number of greater prairie chicken leks in outlying areas during the early 1990s.

model was determined using a probability cutpoint of 0.5. Finally, I used Pearson's product-moment correlation to determine whether RSPF values for leks were correlated with lek attendance, which is considered an index of habitat quality (Hamerstrom and Hamerstrom 1973). All statistical analyses were conducted using Number Cruncher Statistical System (NCSS Kayesville, Ut.).

I then used the best model to create a habitat map showing probability of potential occupancy across the state by incorporating corresponding GIS layers created using the moving window analysis into the RSPF equation. Portions of the Buena Vista and Leola management areas, which contain the greatest number of prairie chickens in Wisconsin, had extensive wet meadows and areas of saturated soil that were classified as wetlands interspersed with grasslands. To prevent large areas of wetland without interspersed grassland in other portions of the state from unduly influencing predicted translocation suitability in the final habitat map (Figure 1), I capped maximum coverage by wetlands at 50%.

Table 2. Mean and standard deviation (SD) of landscape variables associated with 75 leks present in 1997 and 75 unused points used in development of landscape-level habitat model for greater prairie chickens in Wisconsin.

	Lek sites		Unused points	
Variable	Mean	SD	Mean	SD
Grassland (%)	25.5	13.5	13.7	9.5
Wetland (%)	25.6	16.4	3.6	4.5
Forage (%)	9.8	12.3	17.8	12.1
Forest (%)	13.9	11.2	35.1	18.7
Shrub (%)	3.9	6.5	3.9	6.2
Cropland (%)	15.8	11.4	19.7	15.4
Distance (m)	3,440	5,170	13,220	7,146
Patches (*n*)	149	43	155	40

Results

Landscapes surrounding greater prairie chicken leks differed considerably from landscapes surrounding unused points in that leks were closer together and were surrounded by more grassland and wetland and less forest and forage than unused points (Table 2). The logistic regression model best fitting the data showed a positive association with grassland and wetland cover types and a negative association with forest cover and distance to nearest neighbor lek (Tables 3 and 4). This model

Table 3. AIC differences (Δ_i), AIC weights (w_i), and concordance for competing models identifying 75 greater prairie chicken leks and 75 unused points in central Wisconsin, spring 1997. Parentheses indicate negative relationship.

Variables in model	Δ_i	w_i	Concordance (%)
Grassland, wetland, (forest), (distance)	0.0	0.921	94.0
Grassland, wetland, (forest)	5.7	0.053	92.7
Grassland, wetland, (forage), (distance)	7.2	0.025	92.7
Grassland, wetland, (forage)	14.5	<0.001	92.0
Grassland, wetland, (distance)	17.3	<0.001	89.0
Grassland, wetland, number of patches	32.5	<0.001	88.7
Grassland, wetland	32.6	<0.001	88.0
Wetland	48.8	<0.001	85.0
Grassland, (forest), (distance)	53.2	<0.001	85.0
Grassland	122.8	<0.001	73.0

correctly classified 94.6% of lek sites and 93.4% of unused sites used in model development, for overall concordance of 94% (Table 3). Area under the receiver operating characteristics (ROC) curve was 0.98, indicating high model accuracy (Swets 1988). Distance to nearest lek and wetland were strongly correlated ($r=-0.72$), and high correlation among predictor variables can cause the magnitude and sign of regression coefficient estimates to vary widely (Neter et al. 1989). However, estimated coefficients for distance to nearest lek and wetland in the final model (Table 4) did not differ from estimated coefficients in simpler models where distance and wetland were included singly. Both variables were included in the final model as it best fit the data and the variables were biologically appropriate.

Mean RSPF value for landscapes surrounding leks was 0.91 (SD=0.21), whereas the mean value for landscapes surrounding unused sample points was 0.09 (SD=0.18). At the 71 leks for which I had attendance data, number of males attending leks was positively correlated ($r=0.38$, $P=0.001$) with RSPF values. The probability map identified several areas, primarily south and east of present prairie chicken leks, as potentially suitable for greater prairie chickens (Figure 1).

Table 4. Coefficients and standard error (SE) for selected model predicting presence of greater prairie chicken leks as a function of landscape characteristics in Wisconsin, spring 1997.

Variable	Coefficient	SE
Intercept	–1.99	1.100
Grassland (%)	0.16	0.056
Wetland (%)	0.47	0.108
Forest (%)	–0.12	0.035
Distance (m)	–0.00017	0.000069

Discussion

Habitat model

Factors influencing location of greater prairie chicken leks strongly agreed with results of previous studies. For example, lek presence was influenced by the amount of grassland in the landscape, which is typically the limiting factor for prairie chickens (Hamerstrom et al. 1957, Westemeier 1971, Kirsch 1974). However, grassland by itself was a relatively poor predictor of lek presence (Table 3), indicating the importance of other factors in providing suitable habitat for greater prairie chickens. Lek locations were negatively associated with forest cover, as would be expected from a bird requiring large amounts of grassland and open space. Prairie chickens abandon leks as forest encroaches (Hamerstrom et al. 1957), and forest succession causes loss of the habitat and open space required by prairie chickens (Westemeier 1971).

Proximity to existing leks was an important predictor of lek presence. Prairie grouse typically do not disperse far, with most movements <10 km (Hamerstrom and Hamerstrom 1951, Hamerstrom and Hamerstrom 1973, Bowman and Robel 1977). Greater prairie chickens will make longer total movements, even moving among distant leks (Moe 1999), but intermediate habitat patches are critical for maintaining connectivity between populations and providing "stepping stones" for these movements (Hamerstrom and Hamerstrom 1973).

The strong selection for wetlands by greater prairie chickens in this analysis was likely exaggerated by 2 factors. First, greater prairie chickens in much of their Wisconsin range are found in areas of less intensive land use, often in proximity to wetlands (Niemuth 2000); many of these wetlands are temporary or seasonal, with no surface water present for most of the year. Second, the estimated regression coefficient for wetlands is high because the area of wetland surrounding unused points was extremely low, with the difference between used and unused points greater for wetlands than any other habitat type (Table 2). Nonetheless, wetlands can be an important component of prairie chicken habitat (Hamerstrom et al. 1957, Kobriger 1965, Toepfer and Eng 1988), and prairie chicken populations in the study region are "directly related to grassland and marshland acreage" (Westemeier 1971:ii).

The model was not directly validated by applying it to landcover and lek data from another region containing greater prairie chicken populations. Even though model results agreed qualitatively with findings of other studies of prairie chicken habitat selection, a quantitative validation could provide a more rigorous indication of the utility and generality of the model to greater prairie chicken habitat in other times and places.

Identification of habitat for translocation

In addition to areas presently harboring prairie chickens, the model identified 5 landscapes as potential prairie chicken habitat that also were identified by Sample and Mossman (1997) as first- or second-priority landscapes for grassland birds in Wisconsin, including the White River Marsh, Rush Lake Grasslands, Horicon Marsh Grasslands, Bear Bluff Wetlands, and Necedah Barrens landscapes (Figure 1). Portions of the Bear Bluff and Necedah landscapes presently harbor sharp-tailed grouse (Gregg and Niemuth 2000) and should be avoided for translocation to avoid possible congeneric competition (Ammann 1957, Sharp 1957, Griffith et al. 1989, Toepfer et al. 1990) and hybridization, which is relatively common between the 2 species (Ammann 1957). In addition, the Bear Bluff and Necedah landscapes are dominated by shrubby wetlands and have little upland grass available for nesting.

The area of unoccupied habitat identified by the model with the best landscape suitability and large blocks of habitat necessary for greater prairie chickens is southeast of existing populations (Figure 1). This region includes the White River Marsh, Rush Lake, and, to a lesser degree, the Horicon landscapes identified by Sample and Mossman (1997), as well as other sites potentially suitable for greater prairie chickens (Figure 1). Within this general region is part of the Glacial Habitat Restoration Area (GHRA, Figure 1), an area targeted by the Wisconsin Department of Natural Resources for restoration of 4,500 ha of wetlands and 15,000 ha of idle grasslands (Gatti et al. 1994). Suitability of landscapes for greater prairie chickens within the GHRA is likely higher than shown due to restoration of grasslands and wetlands since development of the WISCLAND data. However, suitability of the GHRA for greater prairie chickens might be compromised, as ring-necked pheasants (*Phasianus colchicus*) are a target species for habitat restoration and greater prairie chickens are not (Gatti et al. 1994). Ring-necked pheasants might negatively affect greater prairie chickens by disrupting lek displays and parasitizing nests (Vance and Westemeier 1979, Westemeier et al. 1998*b*).

Influence of landcover classification on success

Predicting habitat suitability is complicated by the often ephemeral nature of prairie grouse habitat. Succession of woody vegetation causes a site to become unsuitable for prairie grouse (Hamerstrom et al. 1957, Gregg and Niemuth 2000), and grassland can be converted to row-crop production. In contrast, new habitat can be created by changes in land use or disturbance. For example, agricultural programs such as the Conservation Reserve Program (CRP) can dramatically alter the amount of grassland habitat in an area (Reynolds et al. 1994) and its subsequent suitability for prairie grouse (Kirsch et al. 1973), as can fire and timber harvest (Gregg and Niemuth 2000). Because of potential changes and errors in identifying cover types, conditions at prospective translocation sites must be verified prior to releasing birds.

The visual impact of maps created from GIS layers can be strong, and results of GIS-based analyses can be compelling, but also misleading, as they can provide a false sense of certainty and precision. As with any model, output is dependent on input, and developing a model with one GIS data set and applying it using another data set with different availabilities or poor classification could produce misleading results. Customized classification focusing on pertinent landcover classes and using current imagery would increase accuracy of landcover assessment, model development, and identification of suitable habitat. In all cases, however, accuracy of landcover classification must be evaluated.

Developing and applying landscape-level habitat models for prairie grouse

A wide range of predictor variables can be incorporated into landscape-level habitat models, depending on the species and location of interest. For example, a landscape-level analysis of sage grouse (*Centrocercus urophasianus*) habitat might consider a suite of vegetation variables (Homer et al. 1993) as well as estimates of distance to surface water, distance to road or energy development, an index to predator density or community composition, and stocking rate in areas where cattle are grazed. Choosing the appropriate scale for modeling is critical, and will likely vary with species, habitat availability, and region. If biologically sound, models could incorporate variables sampled at multiple scales (e.g., a regional measure of habitat availability and a local measure of disturbance or development). For species or populations that move seasonally (Schroeder and Braun 1993), quality, proximity to, or availability of winter or summer range also could be incorporated into models (see also Homer et al. 1993). However, models developed in one region are likely not applicable to other areas for biological reasons (e.g., birds might have localized adaptations making them poorly suited to other locations) as well as statistical reasons (e.g., availabilities will differ among locations, influencing the true response relative to what is modeled). Consequently, it is essential to verify, prior to translocation, that landscapes identified as having high potential are indeed suitable. Ability to accurately identify landcover and identify habitat relationships will likely increase with the continuing evolution of remote sensing technology, which offers increasingly finer spatial and spectral resolution, and modeling techniques.

Management implications

Translocation can be used to establish populations at greater distances from existing populations, thereby overcoming the limited dispersal ability of prairie chickens. But quality and quantity of habitat at distant sites should be sufficient to establish populations large enough to prevent demographic stochasticity, loss of genetic variability (Lande and Barrowclough 1987), and decline in fitness (Bouzat et al. 1998, Westemeier et al. 1998*a*) sometimes associated with small, isolated populations. Proximity to other populations might be particularly important to prairie grouse as effective population size (N_e) is reduced because of strong sexual selection. Loss of fitness and subsequent population decline of greater prairie chickens in Illinois likely was caused by the disappearance of satellite populations in proximity to managed grasslands, following a pattern similar to that of the heath hen and Attwater's prairie chicken (Westemeier et al. 1998*a*). Proximity to multiple leks might also be important for behavioral reasons, as female prairie chickens frequently visit several leks prior to copulation and their home ranges typically encompass >1 lek (Schroeder 1991). Local populations of greater prairie chickens may be strongly interconnected (Hamerstrom and Hamerstrom 1973), and translocated birds have located existing leks 80 km from release sites (Moe 1999). The ability to persist in isolation might vary among species (Grange 1948), but spatial structure of landscapes should be considered when assessing potential prairie grouse habitat, as metapopulation dynamics and demographic rescue might be important to establishment and persistence of populations (see Hodder and Bullock 1997, Martin et al. 2000).

Proximity to other populations is likely important to greater prairie chickens, and habitat connectivity between existing populations and potential translocation sites might need to be improved to facilitate movement among populations. In cases where proximity to other populations is not important (e.g., large translocated population or strong dispersal ability), models can be developed or applied without the distance variable. However, the role of spatial autocorrelation in habitat modeling should not be ignored (see Augustin et al. 1996). Residuals from the final model including distance to nearest neighbor lek had slightly lower levels of positive spatial autocorrelation than a model containing only habitat variables, although positive spatial autocorrelation was nonsignificant for both models (N. D. Niemuth, unpublished data).

In addition to identifying potential areas for translocation, GIS-based models can be used to evaluate characteristics of landscapes presently occupied by prairie grouse and identify management prescriptions such as forest removal, creation of habitat stepping-stones to enhance movement among populations, or targeting of areas for CRP or Conservation Reserve Enhancement Program grasslands. However, fine-grained factors also must be considered, because not all features within a landscape will contribute to suitable habitat. Similarly, factors influencing greater prairie chicken demographics should be considered in management decisions. Intensive management used to maintain habitat on the Buena Vista and Leola management areas (e.g., prescribed burning, tree removal, and brush removal; Keir 1999) might be needed at potential translocation sites to ensure their suitability for prairie chickens.

The association of prairie chickens with upland grasses and wetlands indicates opportunities for combined management of prairie chickens and waterfowl. In fact, Grange (1948) felt that wetlands offered one of Wisconsin's greatest opportunities for prairie chicken management and were a component of ideal prairie chicken range. Similarly, greater prairie chickens used wetland meadows more often than expected by chance in Nebraska sandhills (Kobriger 1965). However, the role of wetlands in greater prairie chicken ecology needs to be better understood, as Wisconsin prairie chickens presently associated with wetlands are relict populations using remnant habitat. Wetlands could harbor predators that are absent from uplands, affecting survival and nesting success of prairie grouse in proximity to wetlands (Connolly 2001). The importance of wetlands might vary depending on location, for the range of greater prairie chickens (see Schroeder and Robb 1993) includes regions with few wetlands. But in Wisconsin, wetlands are an important component of landscapes that greater prairie chickens presently inhabit.

Translocation is not a substitute for management of existing populations (Mumme and Below 1999), and populations at risk should be identified and managed before translocation is necessary (Griffith et al. 1989). In Wisconsin several small, outlying populations of prairie chickens exist without the benefit of habitat protection or management in Taylor, Clark, and Marathon counties (Figure 1; Niemuth 2000). During the 1990s more than 30 leks were known in the area, and at least 20 were active in 1991; in 2001 only 8 were known to be active (J. Keir, Wisconsin Department of Natural Resources, personal communication). Landscapes surrounding leks in these outlying areas have less grassland than on the core Buena Vista and Leola areas (N. D. Niemuth, unpublished data); protection and management of habitat associated with outlying populations would help ensure long-term viability of greater prairie chickens in Wisconsin without the costs and risks associated with translocation.

Because of the importance of habitat to translocation success, it is essential that potential translocation sites be objectively evaluated to select sites that will maximize chances of success. Similarly, habitat quality should be considered in assessments of factors influencing translocation success, as some factors that appear to influence translocation success might be correlated with habitat quality. When used with accurate digital landcover databases, GIS and quantitative habitat models permit rapid and uniform coarse-grained assessment of prairie grouse habitat.

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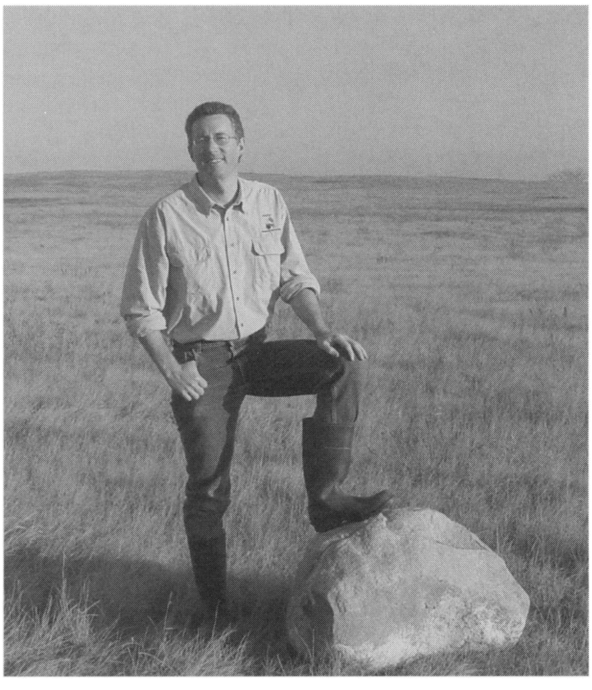

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