CHAPTER ONE

Spatially Explicit Habitat Models for Prairie Grouse

Neal D. Niemuth

Abstract. Loss, fragmentation, and isolation of grassland habitat have greatly reduced the range and numbers of prairie grouse (*Tympanuchus* spp.) across North America. Because prairie grouse are resident, area-sensitive species with relatively limited dispersal abilities, landscape characteristics such as the amount, types, and configuration of habitat influence the presence, abundance, and persistence of prairie grouse populations. Therefore, a landscape approach that uses spatially explicit models to guide prairie grouse conservation is both appropriate and necessary. To be effective for conservation, landscape models must incorporate prairie grouse biology, be developed at appropriate scales, and use accurate data with spatial and thematic resolution that are sufficiently fine to target sites for specific conservation actions. Uncertainties regarding the ecology of prairie grouse need to be addressed, including the form of relationships between the amount of habitat and the presence, density, and persistence of prairie grouse; and how landscape characteristics influence local movements, dispersal, and gene flow. Because many spatially explicit landscape models are developed using lek data, additional information is needed as to what lek counts represent to local prairie grouse populations. Adoption and implementation of a landscape approach to prairie grouse conservation will require that management perspectives be broadened to explicitly include landscapes and that development of landscape models shifts, at least in part, from the realm of research to that of management. Successful conservation of prairie grouse will require resolution of substantial socioeconomic and political obstacles, as well as an increased commitment from the conservation community to broad-scale habitat conservation.

Key Words: conservation, Greater Prairie-Chicken, landscape ecology, Lesser Prairie-Chicken, scale, Sharp-tailed Grouse, spatially explicit habitat model.

Niemuth, N. D. 2011. Spatially explicit habitat models for prairie grouse. Pp. 3–20 *in* B. K. Sandercock, K. Martin, and G. Segelbacher (editors). Ecology, conservation, and management of grouse. Studies in Avian Biology (no. 39), University of California Press, Berkeley, CA.

Sandercock_6480004_ch01.indd 3 7/18/11 11:11:59 AM

Loss and fragmentation of grassland and shrubland habitat in North America have dramatically reduced the numbers and range of North American prairie grouse (*Tympanuchus* spp.). For example, the Greater Prairie-Chicken (*T. cupido pinnatus*) was once found in portions of approximately 17 U.S. states and 4 Canadian provinces (Ross et al. 2006), but presently is in danger of extirpation in 7 of the 11 states in which it is found (Schroeder and Robb 1993). The Lesser Prairie-Chicken (*T. pallidicinctus*) is still found in all 5 of the states in which it originally occurred (Giesen 1998), but by 1980 its range had been reduced 92% from the 1800s (Taylor and Guthery 1980a). The Sharp-tailed Grouse (*T. phasianellus*) originally was found in 21 states and 8 provinces, but has since been extirpated from 8 states, and populations are small and isolated in much of the southern and eastern portions of its present range (reviewed in Connelly et al. 1998).

The primary cause of the declines for prairie grouse is broad-scale loss of grassland and brushland habitat. Concern about the effects of widespread habitat loss on bird populations has prompted recent bird conservation initiatives to adopt a landscape approach to conservation planning and implementation. The first of these was the North American Waterfowl Management Plan (NAWMP; U.S. Department of Interior and Environment Canada 1986), which, through the action of bird conservation joint ventures guided in part by landscape models, has positively influenced more than 5 million ha of breeding, migration, and wintering waterfowl habitat in North America (Abraham et al. 2007). Following the successes of the NAWMP, other efforts, including the Grassland Conservation Plan for Prairie Grouse (Vodehnal and Haufler 2007), have explicitly adopted a landscape approach to conservation planning.

An appreciation of the importance of landscapes to prairie grouse is not new: lacking radiotelemetry technology to track individuals, early researchers used lek counts, harvest monitoring, field surveys, and incidental observations to note the effects of patch size (Ammann 1957), isolation (Grange 1948), disturbance regimes (Grange 1948, Ammann 1957), and landscape composition and configuration (Grange 1948, Hamerstrom et al. 1957, Westemeier 1971) on the presence, size, and persistence of prairie grouse populations. However, the development of remotely sensed spatial data, geographic information systems (GIS), and statistical modeling techniques provides present-day researchers with unprecedented ability to identify and quantify relationships between landscape characteristics and prairie grouse (Kareiva and Wennergren 1995, Stauffer 2002, Wiens 2002). Increasingly isolated and declining populations of prairie grouse increase the impetus to explore relationships between landscape characteristics and grouse populations and identify the most appropriate locations for conservation.

The effects of habitat loss, fragmentation, and isolation may take place at a scale much broader in extent than the patches or habitat clusters occupied by local populations of prairie grouse, which is the scale at which prairie grouse are often studied and managed. Population dynamics of prairie grouse on managed reserves are often synchronous with adjacent populations off managed areas (Bergerud 1988a, Morrow et al. 1996), indicating that broad-scale as well as local factors influence prairie grouse populations. Because prairie grouse populations may be influenced by landscape factors out of the control or consideration of local efforts, conservation may fail if a landscape context is not considered, particularly if local populations are connected at landscape or regional scales by movements and if prairie grouse exhibit a metapopulation structure or source/sink dynamics. The need to consider landscape ecology and geospatial information in grouse conservation has previously been noted (Braun et al. 1994, Morrow et al. 1996, Samson et al. 2004), but specific relationships, hypotheses, and information needs have rarely been identified as they relate to prairie grouse.

Spatially explicit models provide a means of specifying relationships between landscape characteristics and species in a manner that is intuitive to use in conservation applications. The general class of models that includes species distribution models, spatially explicit population models, conservation design, or spatial planning tools provides a habitat-based context for conservation over broad spatial extents (Beissinger et al. 2006). These models differ from metapopulation models in that the entire landscape is considered in the context of multiple variables describing landscape characteristics rather than the presence or absence of populations in discrete habitat patches (Moilanen and Hanski 2001, Tischendorf and Fahrig 2001). Models are spatially explicit because

Sandercock_6480004_ch01.indd 4 7/18/11 11:11:59 AM

they use digital landcover data to consider the spatial configuration of habitat and objects and create maps showing modeled characteristics across the area of interest.

Recent improvements in spatial analysis software and availability of spatial data have led to increased interest in using spatially explicit models to direct conservation actions (Wiens 2002). However, although landscape approaches to bird conservation are popular, the development and application of spatially explicit models that result in improved conservation efficiency is a complex process that must consider many aspects of biology, statistics, data quality, scaling, and implementation (Shenk and Franklin 1991, Scott et al. 2002, Millspaugh and Thompson 2008). As is the case with any model, ignoring the complexities of model development can lead to landscape models that are inaccurate and misleading.

Spatially explicit landscape models offer several benefits for conservation. When landscape models are applied to appropriate GIS layers, the resulting maps can be used to guide prairie grouse conservation and management, including translocating prairie grouse or linking prairie grouse populations (McDonald and Reese 1998, Niemuth 2003). When suitable data are available, landscape models can be used to assess the effects of environmental perturbations such as energy development (i.e., wind, oil, and gas), conversion of grassland to cropland, or the benefits of programs such as the Conservation Reserve Program (CRP). Disturbance to prairie grouse can be minimal, as data collection for landscape models based on lek counts does not require trapping or handling of birds. There is considerable precedent for using lek-based landscape analyses to study the spatial ecology of prairie grouse (Westemeier 1971, Pepper 1972, Merrill et al. 1999, Niemuth 2000, Woodward et al. 2001), but there is also potential to apply this approach to conservation.

In this review, I summarize biological characteristics of prairie grouse that make them sensitive to landscape characteristics, review theories important to the landscape ecology of prairie grouse, and present ideas for landscape-scale research, conservation, and management of prairie grouse. My review focuses on analyses using lek location, attendance, and persistence as response variables in spatially explicit habitat models, acknowledging the desirability of incorporating information from more intensive, local studies into models and management. The primary premise of this approach is that conservation efforts should occur over broad areas, so landscape models may better inform conservation actions than detailed studies of local populations.

BIOLOGICAL TRAITS THAT PROMOTE LANDSCAPE SENSITIVITY

Several biological traits of prairie grouse make them sensitive to the amount and configuration of habitat as well as small population size, the effects of which are compounded by loss and fragmentation of habitat. Prairie grouse have fairly narrow habitat requirements and occur at low densities relative to many other gamebirds. In addition, prairie grouse are area sensitive, requiring large blocks or aggregations of habitat to be present (Ammann 1957, Niemuth 2000, Woodward et al. 2001). Area sensitivity is typically associated with increased probability of a species being present in an area, but prairie grouse also may be area sensitive in that reproductive success (Ryan et al. 1998, Manzer and Hannon 2005), density (Pepper 1972, Niemuth 2000), and persistence of leks or populations (Merrill et al. 1999, Woodward et al. 2001) also increase with amount of suitable habitat. Finally, prairie grouse are resident species, which are generally more susceptible to loss and fragmentation of habitat than latitudinal migrants (Bender et al. 1998).

As resident species, prairie grouse generally are not known to migrate or move long distances, even when juveniles disperse in fall. Mean dispersal distance for a brood of six transmitter-equipped juvenile Greater Prairie-Chickens in Kansas was 1.0 km, and maximum recorded dispersal for 24 juveniles was 10.8 km (Bowman and Robel 1977). Maximum recorded dispersal for a transmitter-equipped juvenile Lesser Prairie-Chicken in Texas was 12.8 km (Taylor and Guthery 1980b). Maximum recorded dispersal for a transmitter-equipped juvenile female Sharp-tailed Grouse in Wisconsin was 5.8 km (Gratson 1988), and 59% of banded juvenile Sharp-tailed Grouse reported by hunters in South Dakota were recovered <1 km from the site where they were trapped (Robel et al. 1972). Prairie grouse can make longer total movements (Moe 1999), but intermediate habitat patches are critical for maintaining connectivity between populations and providing "stepping stones" for these movements

Sandercock_6480004_ch01.indd 5 7/18/11 11:11:59 AM

(Hamerstrom and Hamerstrom 1973). Some populations of prairie grouse migrated in the past (Grange 1948, Ammann 1957), but the proportion of the population that migrated and distances that birds migrated are unknown. Partial migration, where a portion of the population moves between breeding and wintering areas, is evident in some populations of prairie grouse. In Colorado, female and male Greater Prairie-Chickens showed seasonal movements of 9.2 and 2.7 km, respectively, between breeding and wintering areas, with birds showing fidelity to leks, general nest sites, and wintering areas (Schroeder and Braun 1993). Greater Prairie-Chickens in the Sandhills of Nebraska also showed evidence of migration, apparently to winter in areas with grain for food (Kobriger 1965).

Limited movements by prairie grouse reduce interchange among subpopulations, with subsequent reductions in gene flow, both historically and following recent anthropogenic habitat loss (Johnson et al. 2003, Van den Bussche et al. 2003, Bouzat and Johnson 2004, Ross et al. 2006). Many populations of prairie grouse exhibit limited genetic diversity as a consequence of the lek mating system, low nest success, and historic population bottlenecks; these problems are exacerbated by the small size of many prairie grouse populations and reduced gene flow between populations that are increasingly isolated in the landscape (Bouzat et al. 1998, Westemeier et al. 1998a, Bouzat and Johnson 2004, Johnson et al. 2004). Limited movements among isolated populations reduce the potential for demographic rescue and maintenance of genetic diversity (Westemeier et al. 1998a, Reed 1999, Niemuth 2005). However, as important and problematic as loss of genetic diversity may be, it is largely a symptom of broad-scale habitat loss and isolation.

Many ecological processes that affect prairie grouse are influenced by landscape characteristics. Nesting success is considered the primary driver of grouse population dynamics (Bergerud 1988b, Peterson and Silvy 1996, Wisdom and Mills 1997), and the community composition and behavior of many nest predators are influenced by landscape characteristics (Pedlar et al. 1997, Sovada et al. 2000, Phillips et al. 2004, Manzer and Hannon 2005). Consequently, nesting success of prairie grouse can increase with the proportion of grassland in the surrounding landscape (Ryan et al. 1998, Manzer and Hannon 2005). Landscape characteristics of sites used by Ring-necked Pheasants (*Phasianus colchicus*) differed from those of sites used by Lesser Prairie-Chickens (Hagen et al. 2007a), suggesting that the potential for aggression and interspecific nest parasitism may vary across the landscape (see Vance and Westemeier 1979, Westemeier et al. 1998b). Large, newly created areas of habitat sometimes support high densities of grouse (reviewed in Bergerud 1988a). The mechanisms for this "big new space" phenomenon are unknown, but may include changes in vegetation structure, increased food availability, low predator densities, the creation of habitat patches that facilitate dispersal, or a lag in the establishment of predator populations (Bergerud 1988a, Niemuth and Boyce 2004). Anthropogenic processes associated with landscape composition can also influence reproductive success, as nests and young are often destroyed by farm equipment when prairie grouse nest in hay fields or stubble (Yeatter 1963, Pepper 1972, Ryan et al. 1998). Similarly, the distribution of fences and power lines, which can influence habitat use and cause substantial mortality of prairie grouse, is also associated with landscape composition and land use (Patten et al. 2005, Wolfe et al. 2007, Hagen et al., this volume, chapter 5). Population dynamics may be particularly sensitive to mortality if breeding females are more vulnerable than other sex–age classes, as is the case with loss of hens on nests (Hagen et al. 2007b).

DEVELOPMENT OF LANDSCAPE MODELS FOR CONSERVATION

Several key concepts underlie the development and application of spatially explicit habitat models for conservation. First, the approach assumes that habitat selection is a hierarchical process where birds first consider regional and landscape characteristics before selecting habitat at a finer scale, such as the home range, nest, or foraging site (Wiens 1973). Conservation planning therefore focuses on the landscape scale, and provides context for local management actions. If habitat is purchased or otherwise selected for management based on landscape characteristics, then local characteristics of the grassland, such as vegetation composition and structure, can be modified relatively easily. Conversely, it is more difficult to modify the landscape around a patch with suitable local characteristics in an unsuitable

Sandercock_6480004_ch01.indd 6 7/18/11 11:11:59 AM

landscape matrix. Local characteristics such as vegetation height, density, and composition will vary from year to year with precipitation, land use, grazing intensity, fire, and other edaphic factors; a landscape approach focuses on maintaining appropriate landscape conditions so that species can persist through time and flourish when local conditions are good.

Types of spatially explicit models vary, but generally cost of development and usefulness for conservation actions are positively related. Models using lek data to relate prairie grouse presence or lek attendance to landscape characteristics will not be as expensive or useful as models relating landscape characteristics and demographic parameters such as nesting success or adult survival, which require intensive study involving radio telemetry. Interestingly, because of the limited dispersal of prairie grouse, lek fidelity, and response to landscape characteristics, models relating long-term persistence of leks to landscape characteristics may provide an indication of demographic performance, although vital rates and specific mechanisms affecting long-term population persistence will be unknown. Methods for developing landscape models to guide conservation can range from simple conceptual models to complex statistical models that incorporate demographic processes and the spatial structure of prairie grouse populations, with the type of model depending on its intended purpose and available information and resources. The technical aspects of developing statistical models are relatively straightforward once a clear and explicitly stated purpose has been articulated and appropriate data collected. However, the quality and success of landscape models depend on several critical assumptions and details. Here, I will focus on specific factors related to the development of spatially explicit habitat models for prairie grouse. General discussions of modeling approaches, and landscape models in particular, can be found in Shenk and Franklin (2001), Scott et al. (2002), Beissinger et al. (2006), and Millspaugh and Thompson (2008).

The availability of digital data sets has increased greatly in recent years, but not all digital data sets are suitable for spatial planning. Therefore, the spatial and thematic accuracy of spatial data should be verified before use, as even coarse-scale range maps can suffer from large errors of omission and commission (Niemuth et al. 2009). Similarly, digital landcover data should reflect what is actually present on the ground at an acceptable level of spatial and thematic accuracy. Most digital landcover data that cover large spatial extents are based on satellite imagery that has been processed to separate digital signatures that can be associated with various landcover classes. However, classification of satellite imagery is subject to considerable error caused by variation in land use and vegetation, shading, atmospheric conditions, sensor variation, choice of landcover classes, timing, spatial error, and differences in phenology, soil types, and soil moisture (Lillesand and Kiefer 2000, Gallant 2009). Acceptable levels of error in any data set will be determined by the goals and intended use of the conservation assessment, but accuracy of landcover data should be reported for any spatially explicit habitat model.

Many prairie grouse habitat models are developed by characterizing landscapes around leks. Lek locations, however, may be poorly defined or may simply shift within or among years. Locations must be sufficiently accurate to link leks with the landscape the birds are using, but the objective of the model is usually to describe the landscape surrounding leks at broad scales (>1.6 km), rather than the actual lek locations. Positional errors of 100–200 m will have relatively little effect on parameter estimates, but accuracy of estimates will decline as positional error increases. Leks included in model development should be representative of the population of interest. Biases may be introduced if areas in which surveys were conducted were selected in a non-random manner, such as from roadside surveys (see Anderson 2001). For some small, isolated populations a complete census of leks may be possible, but this will be the exception. The timing of surveys can also introduce bias, as leks may be less likely to be detected and apparent lek attendance may be reduced in areas that are sampled late in the day or season.

The spatial scale at which models are created also must be considered, as it will affect the intended application of the model. Coarse-grained analyses that use watersheds, major land resource areas (MLRAs), EMAP hexagons, or county-level summaries are of little value for targeting specific acquisitions or treatments, as the proportion of the landscape occupied by prairie grouse may be small relative to the size of the reporting unit. Even if the proportion of a coarse-grained reporting unit occupied by prairie grouse is high,

Sandercock_6480004_ch01.indd 7 7/18/11 11:11:59 AM

coarse-grained occurrence records do not provide insights about biological relationships or allow precise targeting of conservation actions. Also, coarse-grained analyses can only provide crude measures of proximity or connectivity among subpopulations.

Spatially explicit models must have spatial resolution that is sufficiently fine to allow targeting of specific sites, but should also be developed at scales that accommodate the large expanses of habitat occupied by prairie grouse and environmental factors that operate at different spatial scales (Fuhlendorf et al. 2002, Mayor et al. 2009). One approach to determining the proper scale for spatial analysis is to consider previous research describing home range sizes, daily movements, brood ranges, and the distance from the lek within which most females nest (Merrill et al. 1999, Niemuth 2005). Another is to characterize the landscape within different buffer distances from leks and assess model fit for the various buffers (Hanowski et al. 2000, Niemuth 2000, Fuhlendorf et al. 2002). Selecting the proper scale for data analysis may be complicated if proximity to other populations, habitat selection, and amount of habitat are confounded. The issue of scaling is further complicated if landscape characteristics influence distance metrics used as measures of proximity or permeability (Moilanen and Nieminen 2002).

Often, the output of a spatially explicit model is used to determine optimal sites for the study species, and sites with sufficient habitat and proximity to other populations may then be targeted for preservation. However, sites can also be identified for other conservation treatments. Sites that are close to existing populations but have insufficient habitat would be suitable for habitat restoration, whereas sites with sufficient habitat that are far from other populations may benefit from efforts to link populations. Restoration and connection of sites with little habitat that are distant from other populations may be cost-prohibitive or receive little use by local prairie grouse populations.

TOPICS NEEDING ADDITIONAL RESEARCH

There are many information gaps and untested principles related to the ecology and conservation of grouse (Braun et al. 1994, Wisdom et al. 2002, Applegate et al. 2004); I review specific information needs and assumptions related to the spatial ecology of prairie grouse. Sensitivity analyses will be useful for determining the relative influence of these factors on prairie grouse and corresponding priorities for research and conservation (Wisdom and Mills 1997, Hagen et al. 2009).

Habitat Relationships

The relationship between habitat area and prairie grouse is almost certainly more complex than a simple, linear relationship between area of grassland or shrubland and the presence, density, reproductive success, or persistence of prairie grouse populations. The relationship may be non-linear, with a threshold below which local prairie grouse populations are not present or are destined for extirpation. Extinction thresholds are most likely to occur in species that are habitat specialists (Andrén 1994), occur in metapopulations (Kareiva and Wennergren 1995), or have limited dispersal capabilities (With and King 1999), all of which likely apply to prairie grouse. Spatial configuration of habitat may be problematic only when the amount of habitat drops below a threshold (Andrén 1994, Fahrig 1998), especially if the costs of dispersal vary among habitat types in the fragmented landscape. Consequently, identification of threshold levels, especially in relation to habitat fragmentation, is a critical information need, especially as landscapes presently harboring prairie grouse are increasingly subjected to conversion of native habitat to cropland and increased development of energy production facilities.

Non-linear relationships between area of grassland habitat and prairie grouse populations may differ among population metrics. Conversion of grassland habitat to crop fields has been the greatest factor contributing to the decline of prairie grouse populations, yet small amounts of cropland can have a positive effect on numbers of prairie chickens by providing additional food resources (Hamerstrom et al. 1957, Crawford and Bolen 1976, Christisen 1985). Consequently, numbers of prairie chickens at leks or long-term persistence of populations might be highest with some small amount of cropland in a grass-dominated landscape (Fig. 1.1A). However, nesting success of prairie grouse and other grassland nesting birds generally increases with the amount of grass in the landscape (Ryan et al. 1998, Herkert et al. 2003, Manzer and Hannon 2005; Fig. 1.1B). Therefore, the benefit afforded by providing additional grassland could vary depending on the

Sandercock_6480004_ch01.indd 8 7/18/11 11:11:59 AM

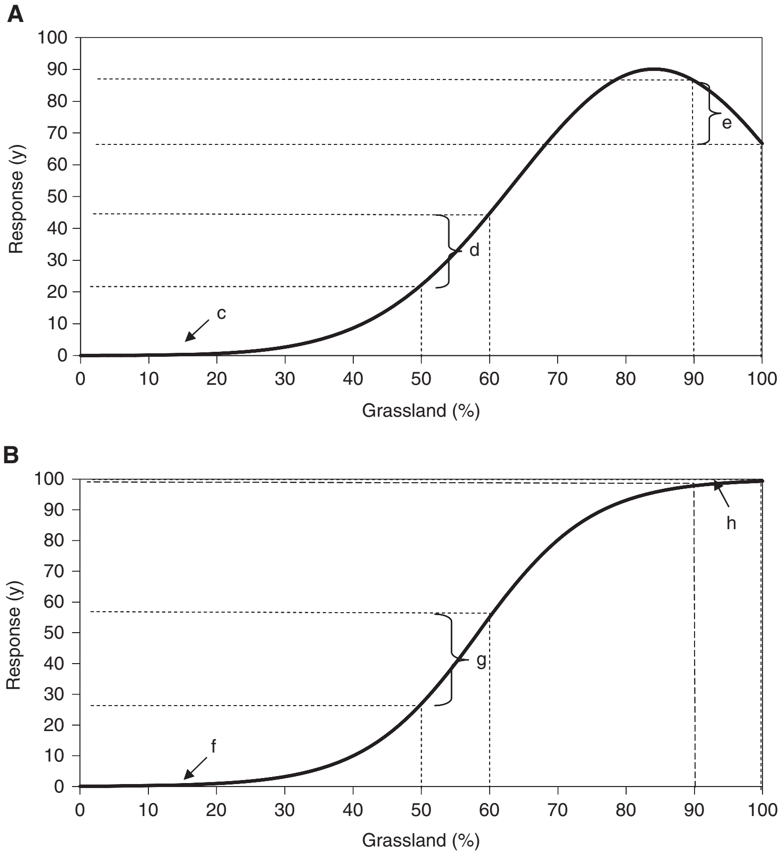

Figure 1.1. The type of relationship between landscape characteristics and prairie grouse can influence the degree and direction of response by prairie grouse to conservation efforts. In these hypothetical examples, an unspecified response by prairie grouse (y) such as density or probability of presence (heavy dark line) is scaled from 0 to 100 and varies quadratically (A) and asymptotically (B) with the amount of grass in the surrounding 800-ha landscape. (A) Prairie grouse response (y) increases by 0.5 when 80 ha of grass are added to a landscape comprised of 10% grass (c); increases by 22.5 when 80 ha of grass are added to a landscape comprised of 50% grass (d); and decreases by 19.8 when 80 ha of grass are added to a landscape comprised of 90% grass (e). (B) Prairie grouse response (y) increases by 0.7 when 80 ha of grass are added to a landscape comprised of 10% grass (f); increases by 28.1 when 80 ha of grass are added to a landscape comprised of 50% grass (g); and increases by 1.5 when 80 ha of grass are added to a landscape comprised of 90% grass (h). If the relationship is linear (not shown), prairie grouse response (y) is the same when 80 ha of grass are added regardless of the amount of habitat in the surrounding landscape. Size of the sampling window was based on landscape analyses (Merrill et al. 1999, Niemuth 2000) and distance of Greater Prairie-Chicken nests from leks (Schroeder 1991).

nature of the relationship (i.e., linear vs. curvilinear) and landscape context (Fig. 1.1). Because the degree and even direction of the response by prairie grouse to changes in the amount of habitat in the landscape varies, management treatments such as grassland restoration should explicitly consider landscape context as well as the population metrics the treatments are intended to address (Fig. 1.1). Responses to landscape characteristics can differ among populations as well as species, depending on the availability of different cover types in the landscape (Niemuth 2005). In all cases, the scale at which the landscape is assessed should be appropriate for the species, population metric, and conservation treatments being considered.

Similarly, the effects of habitat loss relative to habitat fragmentation are poorly understood. Problems include inconsistent definitions of fragmentation (Fahrig 2003), which are exacerbated

Sandercock_6480004_ch01.indd 9 7/18/11 11:11:59 AM

by the numerous fragmentation metrics available in GIS software packages. Quantitative models of prairie grouse response to landscape composition under a broad range of landscape characteristics should be developed; candidate models should consider biologically appropriate curvilinear relationships. Assessments of prairie grouse habitat should explicitly define metrics used to assess fragmentation, how the metrics differ from simple habitat loss, and how birds respond to habitat fragmentation versus habitat loss.

Many investigations have focused on minimum area requirements of prairie grouse (Samson 1980, Winter and Faaborg 1999). However, a landscape perspective is preferable because landscape characteristics can influence metapopulation dynamics and modify patterns of area sensitivity (Wiens 1997, Ribic et al. 2009). The Great Plains provides an opportunity to assess the role of landscape characteristics on prairie grouse at varying levels of habitat loss and fragmentation. Grasslands of the Great Plains follow a gradient of habitat loss, with tallgrass prairie in the east showing the greatest loss and short-grass prairie in the west showing the least loss, with intermediate loss in the mixed-grass region (Samson et al. 2004). Regional studies that span this gradient and incorporate varying levels of fragmentation will provide more information about the relative effects of habitat loss and fragmentation than localized studies where landscape characteristics show less variation. Of course, landscape characteristics may be confounded with other factors, as precipitation, grass height, grass density, and litter depth will also likely decrease from east to west. Therefore, potential confounding factors should be sampled and assessed in the framework of landscape models when possible.

Previous analyses of the spatial ecology of prairie grouse focused on populations at the periphery of the species' range (McDonald and Reese 1998, Merrill et al. 1999, Niemuth 2000). Focusing on peripheral populations is understandable, given the vulnerability of these populations and the high levels of management associated with them (Bergerud 1988a). Similar efforts are needed throughout the extant range of all prairie grouse. No populations of prairie grouse, even in the core of their range, are immune from the increasing pressures of agricultural conversion and energy development. In general, prairie grouse have been lost from places where other land uses were valued more highly than grazing, so remaining grouse populations may persist in marginal lands relative to sites where birds have been extirpated. Consequently, focusing conservation efforts on large, extensive populations where land values are relatively low will likely be more cost effective than trying to preserve small, isolated populations. Spatially explicit habitat models pertinent to core populations of prairie grouse should be developed, as the spatial ecology of large prairie grouse populations in extensive areas of habitat may differ from that of grouse in small, isolated populations (Braun et al. 1994, Fuhlendorf et al. 2002). However, small, isolated populations may be local management priorities or important to maintain connectivity among populations. Spatially explicit models can help determine cost and provide context when assessing habitat and populations for prioritization and conservation triage (Wisdom et al. 2005).

Prairie grouse habitat selection in the context of predation and nest parasitism also needs further investigation. For example, the distribution, nest site selection, and nesting success of Ring-necked Pheasants are influenced by landscape composition and configuration (Clark et al. 1999, Leif 2005). If the abundance of pheasants and, by extension, potential for interactions between prairie grouse and pheasants can be modeled (Hagen et al. 2007a), managers can better tailor treatments to benefit prairie grouse while minimizing or avoiding possible negative effects associated with Ring-necked Pheasants. Similar approaches could be used to guide conservation treatments with regard to predators that are influenced by landscape characteristics.

Movement

Connectivity among populations is an important component of prairie grouse ecology and conservation that will likely become even more important as grassland habitats continue to be converted to other uses and prairie grouse populations become more isolated. Because the population dynamics of prairie grouse often exhibit spatial structure, landscape models can benefit from inclusion of ideas derived from metapopulation theory and source–sink dynamics. Euclidean distance has been used as an index of connectivity and proximity to other populations, but more complex measures of movement distances may

Sandercock_6480004_ch01.indd 10 7/18/11 11:11:59 AM

be needed to better determine the influence of landscape composition and configuration on patterns of dispersal, colonization of new habitat, and, eventually, gene flow of prairie grouse (Moilanen and Nieminen 2002, Manel et al. 2003, Wang et al. 2008). Options include GIS-based friction or cost analyses of movements across landscapes with different compositions or configurations (Chetkiewicz et al. 2006, Kindlmann and Burel 2008). The response variable in models can be actual movement, assessed with radio-marked birds; observed colonization of new habitat; or evidence of movement, assessed with genetic analysis of samples from known locations (Manel et al. 2003). Information-theoretic methods can be used to evaluate competing models of movement cost (e.g., Burnham and Anderson 1998). Landscape models should incorporate measures of connectivity; information is needed on how landscape composition and configuration affect prairie grouse dispersal so movements can best be incorporated into models. Assessments of movement should consider changes in population size and amount of available habitat over time, as these can influence dispersal and connectivity. Important as connectivity may be to prairie grouse populations, though, minimum levels of habitat are the foundation of conservation efforts and must be preserved to attract dispersing birds and maintain local populations.

What Do Leks Represent?

Leks are often considered a focal point for prairie grouse ecology and management (Westemeier 1971, Hamerstrom and Hamerstrom 1973, Giesen and Connelly 1993), and the number of males attending leks can be used as an index of habitat quality (Hamerstrom and Hamerstrom 1973). Consequently, lek data are frequently used in the development of landscape models. However, lek-based landscape models—as well as non-spatial population models—make a variety of assumptions about what leks represent to prairie grouse populations. For example, the number of males attending a lek at any one time may represent only a portion of the males associated with that lek (Robel 1970, Rippin and Boag 1974, Clifton and Krementz 2006, but see Schroeder and Braun 1992). Incomplete attendance by all the males associated with a lek is not a problem *per se*, as the number of males present at a lek can be a useful index to the total number of males associated with a lek if the proportion of males attending a lek is constant. However, lek attendance varies with weather, daily and seasonal timing, changes in land use, lek age, and the presence of predators; the number of birds present that are detected can vary with observer ability, topography, vegetation, survey methodology, and time spent observing the lek (Robel 1970, Clifton and Krementz 2006, Haukos and Smith 1999, McNew et al., this volume, chapter 15). Maximum counts of birds observed at leks during multiple visits have the potential to reduce the influence of unusually low counts, for instance, where birds were disturbed by predators, but maximum counts will introduce bias if the number of visits varies among leks. Species-, time-, and region-specific estimates of the proportion of males attending leks and how this proportion varies are necessary to calibrate lek counts relative to the populations the leks represent.

Nesting success is considered the primary driver of grouse populations (Bergerud 1988b, Peterson and Silvy 1996, Wisdom and Mills 1997), but the relationship between counts of males at leks and the number of females associated with the lek, their survival, or their reproductive success is unknown or poorly understood. Several models of lek formation have been posed, but the balance of evidence indicates that males establish leks in areas where they can encounter many females (Schroeder and White 1993), which suggests that counts of males on leks may be correlated with number of females in the vicinity. Habitat quality is a function of density, survival, and reproduction vital rates (Van Horne 1983); landscape models predicting density provide an important component of that definition, but information on survival and reproductive success is necessary to ensure that sites with high densities are not population sinks (but see Bock and Jones 2004). Nevertheless, density models can help ensure that expenditure of limited conservation resources consider many, rather than few, birds and may be especially useful where conservation treatments enhance survival or reproductive success. Persistence of leks with many males over time suggests that survival and reproductive success of females in the vicinity are at or above maintenance levels, but this assumes a closed population. Male prairie grouse do not disperse as far as females and show strong fidelity to leks (Hamerstrom et al. 1957, Robel et al. 1972,

Sandercock_6480004_ch01.indd 11 7/18/11 11:12:00 AM

Nooker and Sandercock 2008), so the presence or number of males at a site might also reflect past conditions (Knick and Rotenberry 2000, Fuhlendorf et al. 2002). Similar landscape characteristics have been associated with lek presence, lek attendance, lek persistence, and nesting success (Ryan et al. 1998, Merrill et al. 1999, Fuhlendorf et al. 2002, Niemuth 2005, Aldridge et al. 2008, Gregory et al., this volume, chapter 2), which suggests some potential for lek-based analyses to identify areas that are attractive for nesting or have high nesting success. However, it has been shown with radio-marked Greater Sage-Grouse (*Centrocercus urophasianus*) that attractive nest sites may experience low nesting success (Aldridge and Boyce 2007). Relationships between numbers of males and females associated with leks must be identified to determine if lek counts are useful predictors of reproductive potential. Similarly, lek attendance and persistence should be related to hen survival and nesting success over time and across a broad range of landscape characteristics.

Lek counts do not consider the spatial distribution of leks or the effects of scale that are intertwined with the ecology of prairie grouse. For example, if lek size is considered an index of habitat quality, two leks in a given area, each with eight males, will be considered to indicate lower-quality habitat than one lek in the same area with 16 males. In a comparison using data from four long-term studies of prairie chickens, Cannon and Knopf (1981) found that the number of leks in an area was more strongly correlated with the density of displaying males than average lek size; therefore, number of leks may be a better index to populations than counts of males. However, because Cannon and Knopf's (1981) focus was population trends, their analysis treated all study sites as homogeneous units and did not consider differences in attendance among leks, which is the primary interest in a lek-based density model. Changes in numbers of birds and leks across years may reflect the presence or absence of temporary leks, which can have different timing, age structure, and attendance than permanent leks (Schroeder and Braun 1992, Haukos and Smith 1999). Lek dynamics can influence reproductive potential, as nesting success varies with age of females and nest initiation date (reviewed in Bergerud 1988b). The spatial distribution of leks, inter-lek distance, or lek density can be explicitly incorporated into landscape models, but the implications of lek attendance, lek type (temporary vs. stable), and lek density to the population ecology of prairie grouse need further research.

Finally, lek-based models assume that the landscapes (at some broad scale) surrounding leks are sufficient to meet the annual needs of prairie grouse. However, lek-based models will not include wintering habitat for those populations that move between breeding and wintering areas (Kobriger 1965, Schroeder and Braun 1993), particularly if prairie grouse move greater distances than has been documented. If wintering habitat is a limiting factor, research, modeling, and conservation efforts will have to be adjusted accordingly.

Broad-scale patterns of habitat use can provide information about underlying ecological relationships (Arthur et al. 1996), which can guide future, local studies of mechanisms responsible for observed patterns. For example, landscape-level analysis of Sharp-tailed Grouse leks in northern Wisconsin indicated that attendance was higher at leks in open landscapes created through clearcut harvest of insect-damaged timber relative to leks on landscapes managed for Sharp-tailed Grouse using prescribed fire (Niemuth and Boyce 2004). Additional research with radio-marked birds showed that Sharp-tailed Grouse nesting success and hen survival were also higher in clearcuts relative to landscapes managed with prescribed fire (Connolly 2001). Similar approaches could be used to assess broad-scale patterns and focus research regarding effects of other perturbations such as energy development on prairie grouse.

The reliability of information about grouse could be improved through monitoring and research that incorporates field experiments in an adaptive management framework (Holling 1978, Walters 1986). It is rarely possible to experimentally manipulate landscape characteristics in an active adaptive management context, but spatial information could be incorporated into sampling frameworks and study designs in a passive adaptive management context for both landscape-level and local research and monitoring (Aldridge et al. 2004, Powell et al., this volume, chapter 25). In addition to providing information about effects of management manipulations, monitoring programs also can provide baseline data useful for Before-After-Control-Impact (BACI; Green 1979, Stewart-Oaten et al. 1986) studies following perturbations or changes to portions of the landscape.

Sandercock_6480004_ch01.indd 12 7/18/11 11:12:00 AM

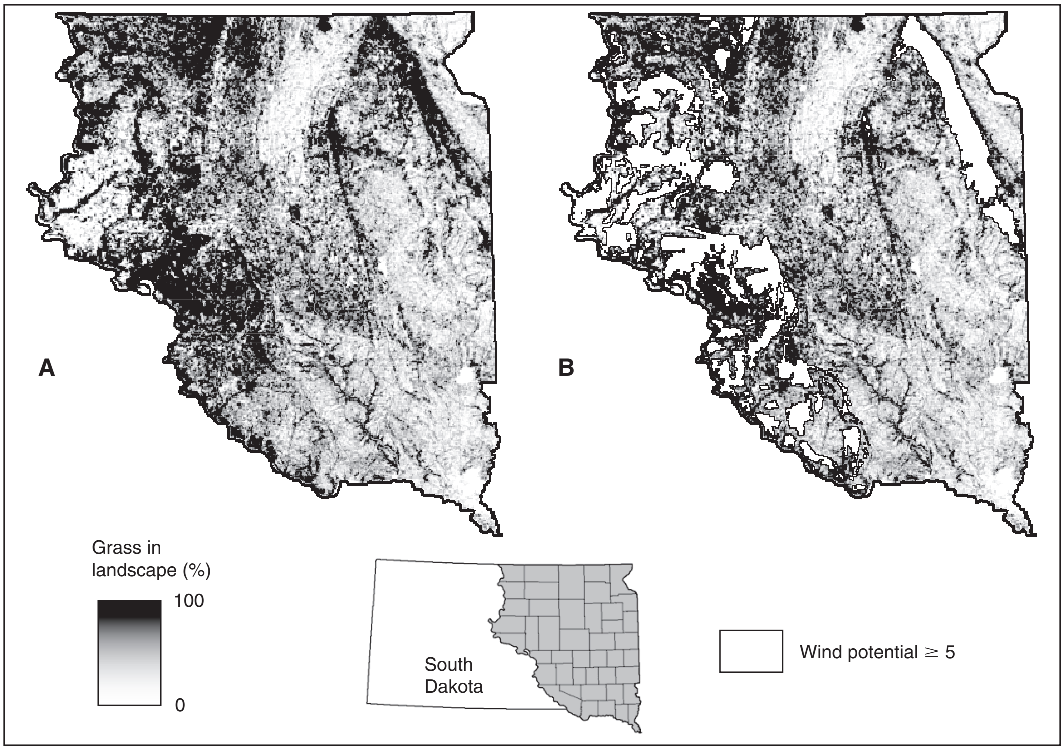

Figure 1.2. (A) Percent of landscape within 800 m comprised of grassland, hay, and Conservation Reserve Program grasslands in South Dakota east of the Missouri River. (B) Same region as (A) but overlain with areas of wind potential ≥ 4 where potential is rated on a scale of 1 (lowest) to 7 (highest). Landcover data described by Niemuth et al. (2008); wind data provided by the National Renewable Energy Laboratory (http://www.nrel.gov/gis/wind.html).

For example, areas in eastern South Dakota with high potential for wind development overlap substantially with remnant landscapes containing large amounts of grassland (Fig. 1.2); sampling Sharp-tailed Grouse and Greater Prairie-Chickens in these areas prior to and after installation of wind-generation towers would increase the strength of inferences about broad-scale effects of wind development on prairie grouse populations. Studies using a BACI approach to assess the effects of wind power development on Greater Prairie-Chickens in Kansas are in progress (B. K. Sandercock, pers. comm.).

MANAGEMENT RECOMMENDATIONS

Managers cannot change the biological traits that make prairie grouse sensitive to landscape characteristics, but managers can and should consider these characteristics when assessing and managing prairie grouse populations. A landscape perspective might require a paradigm shift from a local-management focus to management that incorporates local and landscape scales and that actively pursues reliable quantitative information (Braun et al. 1994, Applegate et al. 2004, Wisdom et al. 2005). Management does not take place in isolation; loss of satellite populations surrounding reserves managed for prairie chickens has likely contributed to declines in prairie chicken populations at core reserves (Morrow et al. 1996, Westemeier et al. 1998a). Concerns regarding the scale of Northern Bobwhite (*Colinus virginianus*) management were expressed by Williams et al. (2004:861), who stated that "traditional management principles currently are incompatible with the spatial scale necessary to address the nationwide decline in bobwhite abundance." Similarly, Wisdom et al. (2005) advocated a landscape approach to management of Greater Sage-Grouse habitat and populations, using landscape models to inventory resources, estimate costs, prioritize, and perform triage. Most prairie grouse conservation problems are land-use problems, and maps

Sandercock_6480004_ch01.indd 13 7/18/11 11:12:00 AM

resulting from spatially explicit habitat models can provide the context necessary for planners, politicians, and managers to better conserve prairie grouse.

Products from the North American Waterfowl Management Plan are a good example of how this can be accomplished. The "Thunderstorm Map" shows the breeding distribution and density of five species of dabbling ducks across several states in the U.S. Prairie Pothole Region (Reynolds et al. 2006). Copies of the Thunderstorm Map are found in resource agency offices throughout the northern prairies; these maps are used to prioritize and target landscapes for expenditures of approximately $13 million annually. These efforts have permanently protected >1.1 million ha of wetlands and grasslands in the U.S. Prairie Pothole Region, with tremendous benefits for other species in addition to waterfowl (Beyersbergen et al. 2004). The primary sources of funding for these efforts are the federal Migratory Bird Hunting Stamp Act ("Duck Stamp") and private groups such as Ducks Unlimited. Prairie grouse do not have comparable programs directly channeling millions of dollars into habitat, but similar spatial modeling techniques could be used to better identify and prioritize lands for conservation of prairie grouse and possibly garner additional support for conservation. For example, the science behind the Thunderstorm Map was sufficiently strong that the U. S. Department of Agriculture initiated a separate CRP practice that dedicated 40,000 ha of wetlands and grasslands to priority areas identified by the model.

The development of spatially explicit models will have to shift, at least in part, from the realm of research to management. A management focus would have several benefits, particularly in the continuity and long-term commitment provided by agencies charged with legal responsibility for a species as well as the synergy that arises when field biologists and modelers combine their expertise (Beissinger et al. 2006). Engagement of agency staff will help ensure the continuous feedback essential to adaptive management and the improvement of landscape models. Adopting a spatial approach to management and data collection will likely require changes in how prairie grouse are surveyed. Typically, prairie grouse are surveyed to assess population trends over time, often with little or no attention given to spatial balance of sampling to avoid geographic bias, stratification by land use and land cover, the range of land cover characteristics surrounding survey areas, or changes in land use over time. Spatial data should be used to identify and stratify areas for sampling (e.g., Fig. 1.2), similar to methodology in the recently developed national sampling framework for secretive marshbirds (Johnson et al. 2009). Precise locations and lek attendance will have to be recorded during surveys; the value of survey data will increase if common standards and methodology are adopted by multiple agencies (Connelly and Schroeder 2007). Repeated visits per season will enable estimation of probability of detection. Finally, many of the questions regarding what leks actually represent can be addressed through sentinel-lek surveys, where lek counts are adjusted using the results of additional monitoring and analysis conducted on a subset of the leks that are surveyed (Garton et al. 2007).

Developing landscape models that are useful across large regions will require cooperative, regional efforts, but the models can provide many benefits beyond identification of sites for preservation. For example, development of wind energy infrastructure already may be affecting prairie grouse and will continue to spread (Pruett et al. 2009a, 2009b; Brennan et al. 2009). Considerable uncertainty exists about the immediate and cumulative effects of stressors such as wind energy; management agencies could approach such issues proactively by stratifying the landscape by existing or potential land development, surveying leks, and evaluating the effects of stressors using landscape models and information-theoretic methods. Similar approaches have been used to evaluate the response of Sharp-tailed Grouse to ecological disturbances (Niemuth and Boyce 2004), as well as the response of Greater Sage-Grouse to energy development (Aldridge and Boyce 2007, Walker et al. 2007).

Incorporating spatially explicit habitat models into prairie grouse conservation efforts will not solve all prairie grouse problems. Spatial models are only tools to increase conservation efficiency and do not alter the root problem of human use and conversion of native habitats. Additional information, such as the risk of grassland conversion and the costs of conservation treatments will also have to be considered in conservation decisions. Environmental and ecological factors beyond human control also influence prairie

Sandercock_6480004_ch01.indd 14 7/18/11 11:12:00 AM

grouse populations, but spatially explicit models provide a scientifically and biologically sound means of assessing landscapes, identifying appropriate conservation actions, and demonstrating the benefits of those actions. However, landscape-level models and plans are of little value unless they are accompanied by a landscape-level commitment to on-the-ground action. Successful conservation of prairie grouse will require an increased commitment from society and the conservation community to broad-scale conservation of prairie grouse habitat.

ACKNOWLEDGMENTS

I thank the many colleagues who have discussed landscape-level conservation of prairie grouse with me over the years, particularly M. E. Estey, J. R. Keir, L. H. Niemuth, R. E. Reynolds, and J. A. Shaffer. This paper was greatly improved by comments from K. E. Church, J. S. Gleason, B. K. Sandercock, and two anonymous reviewers. The findings and conclusions in this article are those of the author and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

LITERATURE CITED

Abraham, K. F., M. G. Anderson, R. Clark, L. Colpitts, E. Reed, R. Bishop, J. Eadie, M. Petrie, F. Rohwer, M. Tome, and A. Rojo. 2007. Final report: North American Waterfowl Management Plan continental progress assessment. U.S. Fish and Wildlife Service, Arlington, VA. <http://www.fws.gov/birdhabitat/NAWMP/files/FinalAssessmentReport.pdf> (24 February 2009).

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–526.

Aldridge, C. L., M. S. Boyce, and R. K. Baydack. 2004. Adaptive management of prairie grouse: how do we get there? Wildlife Society Bulletin 32:92–103.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. Diversity and Distributions 14:983–994.

Ammann, G. A. 1957. The prairie grouse of Michigan. Technical Bulletin. Michigan Department of Conservation, Lansing, MI.

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294–1297.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366.

Applegate, R. D., C. K. Williams, and R. R. Manes. 2004. Assuring the future of prairie grouse: dogmas, demagogues, and getting outside the box. Wildlife Society Bulletin 32:104–111.

Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. Ecology 77:215–227.

Beissinger, S. R., J. R. Walters, D. G. Catanzaro, K. G. Smith, J. B. Dunning Jr., S. M. Haig, B. R. Noon, and B. M. Smith. 2006. Modeling approaches in avian conservation and the role of field biologists. Ornithological Monographs 59:1–56.

Bender, D. J., T. A. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79:517–533.

Bergerud, A. T. 1988a. Increasing the numbers of grouse. Pp. 686–731 *in* A. T. Bergerud and M. W. Gratson (editors), Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Saint Paul, MN.

Bergerud, A. T. 1988b. Population ecology of grouse. Pp. 578–685 *in* A. T. Bergerud and M. W. Gratson (editors), Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Saint Paul, MN.

Beyersbergen, G. W., N. D. Niemuth, and M. R. Norton. 2004. Northern Prairie and Parkland Waterbird Conservation Plan. Prairie Pothole Joint Venture, Denver, CO.

Bock, C. E., and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment 2:403–410.

Bouzat, J. L., H. H. Cheng, H. A. Lewin, R. L. Westemeier, J. D. Brawn, and K. N. Paige. 1998. Genetic evaluation of a demographic bottleneck in the Greater Prairie Chicken. Conservation Biology 12:836–843.

Bouzat, J. L. and K. Johnson. 2004. Genetic structure among closely spaced leks in a peripheral population of Lesser Prairie-Chickens. Molecular Ecology 13:499–505.

Bowman, T. J., and R. J. Robel. 1977. Brood break-up, dispersal, mobility, and mortality of juvenile prairie chickens. Journal of Wildlife Management 41:27–34.

Braun, C. E., K. Martin, T. E. Remington, and J. R. Young. 1994. North American grouse: issues and strategies for the 21st century. Transactions of the North American Wildlife and Natural Resources Conference 59:428–438.

Sandercock_6480004_ch01.indd 15 7/18/11 11:12:00 AM

Brennan, L. A., R. M. Perez, S. J. DeMaso, B. M. Ballard, and W. P. Kuvlesky, Jr. 2009. Potential impacts of wind farm energy development on upland game birds: questions and concerns. Pp. 179–183 *in* T. D. Rich, C. D. Thompson, D. Demarest, and C. Arizmendi, (editors), Tundra to tropics: Connecting birds, habitats, and people. Proceedings of the fourth international Partners in Flight conference, 13–16 February 2008, McAllen, TX.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, NY.

Cannon, R. W., and F. L. Knopf. 1981. Lek numbers as a trend index to prairie grouse populations. Journal of Wildlife Management 45:776–778.

Chetkiewicz, C. B., C. C. St. Clair, and M. S. Boyce. 2006. Corridors for conservation: integrating pattern and process. Annual Review of Ecology, Evolution, and Systematics 37:317–342.

Christisen, D. M. 1985. The Greater Prairie Chicken and Missouri's land-use patterns. Missouri Department of Conservation Terrestrial Series No. 15.

Clark, W. R., R. A. Schmitz, and T. R. Bogenschutz. 1999. Site selection and nest success of Ring-necked Pheasants as a function of location in Iowa landscapes. Journal of Wildlife Management 63:976–989.

Clifton, A. M., and D. G. Krementz. 2006. Estimating numbers of Greater Prairie-Chickens using mark-resight techniques. Journal of Wildlife Management 70:479–484.

Connelly, J. W., M. W. Gratson, and K. P. Reese, 1998. Sharp-tailed Grouse (*Tympanuchus phasianellus*). A. Poole and F. Gill (editors), The birds of North America No. 354. The Birds of North America, Inc., Philadelphia, PA.

Connelly, J. W., and M. A. Schroeder. 2007. Historical and current approaches to monitoring Greater Sage-Grouse. Pp. 3–9 *in* K. P. Reese and R. T. Bowyer (editors), Monitoring populations of sage-grouse. University of Idaho College of Natural Resources Experiment Station Bulletin 88, Moscow, ID.

Connolly, T. T. 2001. Reproductive ecology of Sharp-tailed Grouse in the pine barrens of northwestern Wisconsin. M.S. thesis, University of Wisconsin–Stevens Point, Wisconsin.

Crawford, J. A., and E. G. Bolen. 1976. Effects of land use on Lesser Prairie Chickens in Texas. Journal of Wildlife Management 40:96–104.

Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? Ecological Modelling 105:272–292.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology and Systematics 34:487–515.

Fuhlendorf, S. D., A. J. W. Woodward, D. M. Leslie, Jr., and J. S. Shackford. 2002. Multi-scale effects of habitat loss and fragmentation on Lesser Prairie Chicken populations of the US southern Great Plains. Landscape Ecology 17:617–628.

Gallant, A. L. 2009. What you should know about land-cover data. Journal of Wildlife Management 73:796–805.

Garton, E. O., D. D. Musil, K. P. Reese, J. W. Connelly, and C. L. Anderson. 2007. Sentinel lek-routes: an integrated sampling approach to estimate Greater Sage-Grouse population characteristics. Pp. 31–41 *in* K. P. Reese and R. T. Bowyer (editors), Monitoring populations of sage-grouse. University of Idaho College of Natural Resources Experiment Station Bulletin 88, Moscow, ID.

Giesen, K. M. 1998. Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*). A. Poole and F. Gill (editors), The birds of North America No. 364. The Academy of Natural Sciences, Philadelphia, PA, and the American Ornithologists' Union, Washington, DC.

Giesen, K. M., and J. W. Connelly. 1993. Guidelines for management of Columbian Sharp-tailed Grouse habitats. Wildlife Society Bulletin 21:325–333.

Grange, W. B. 1948. Wisconsin grouse problems. Wisconsin Conservation Department, Madison, WI.

Gratson, M. W. 1988. Spatial patterns, movements, and cover selection by Sharp-tailed Grouse. Pp. 158–192 *in* A. T. Bergerud and M. W. Gratson (editors), Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Saint Paul, MN.

Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. Wiley Interscience, Chichester, England.

Hagen, C. A., J. C. Pitman, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2007a. Niche partitioning by Lesser Prairie-Chicken *Tympanuchus pallidicinctus* and Ring-necked Pheasant *Phasianus colchicus* in southwestern Kansas. Wildlife Biology 13(Suppl. 1): 34–41.

Hagen, C. A., J. C. Pitman, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2007b. Age-specific survival and probable causes of mortality in female Lesser Prairie-Chickens. Journal of Wildlife Management 71:518–525.

Hagen, C. A., B. K. Sandercock, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2009. Spatial variation in Lesser Prairie-Chicken demography: a sensitivity analysis of population dynamics and management alternatives. Journal of Wildlife Management 73:1325–1332.

Hamerstrom, F. N., Jr., O. E. Mattson, and F. Hamerstrom. 1957. A guide to prairie chicken management. Wisconsin Conservation Department Technical Wildlife Bulletin 15, Madison, WI.

Sandercock_6480004_ch01.indd 16 7/18/11 11:12:00 AM

Hamerstrom, F. N., Jr., and F. Hamerstrom. 1973. The prairie chicken in Wisconsin: highlights of a 22-year study of counts, behavior, movements, turnover, and habitat. Wisconsin Department of Natural Resources Technical Bulletin 64, Madison, WI.

Hanowski, J. M., D. P. Christian, and G. J. Niemi. 2000. Landscape requirements of prairie Sharp-tailed Grouse *Tympanuchus phasianellus campestris* in Minnesota, USA. Wildlife Biology 6:257–263.

Haukos, D. A., and L. M. Smith. 1999. Effects of lek age on age structure and attendance of Lesser Prairie Chickens (*Tympanuchus pallidicinctus*). American Midland Naturalist 142:415–420.

Herkert, J. R., D. L. Reinking, D. A Wiedenfield, M. Winter, J. L. Zimmerman, W. E. Jensen, E. J. Finck, R. R. Koford, D. H. Wolfe, S. K. Sherrod, M. A. Jenkins, J. Faaborg, and S. K. Robinson. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. Conservation Biology 17:587–594.

Holling, C. S. 1978. Adaptive environmental assessment and management. John Wiley and Sons, New York, NY.

Johnson, D. H. Johnson, D. H., J. P. Gibbs, M. Herzog, S. Lor, N. D. Niemuth, C. A. Ribic, M. Seamans, T. L. Shaffer, G. Shriver, S. Stehman, and W. L. Thompson. 2009. A sampling design framework for monitoring secretive marshbirds. Waterbirds 32:203–215.

Johnson, J. A., M. R. Bellinger, J. E. Toepfer, and P. Dunn. 2004. Temporal changes in allele frequencies and low effective population size in Greater Prairie-Chickens. Molecular Ecology 13:2617–2630.

Johnson, J. A., J. E. Toepfer, and P. O. Dunn. 2003. Contrasting patterns of mitochondrial and microsatellite population structure in fragmented populations of Greater Prairie-Chickens. Molecular Ecology 12:3335–3347.

Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373:299–302.

Kindlmann, P., and F. Burel. 2008. Connectivity measures: a review. Landscape Ecology 23:879–890.

Knick, S. T., and J. T. Rotenberry. 2000. Ghosts of habitats past: contribution of landscape change to current habitats used by shrubland birds. Ecology 81:220–227.

Kobriger, G. D. 1965. Status, movements, habitats, and foods of prairie grouse on a Sandhills refuge. Journal of Wildlife Management 29:788–800.

Leif, A. P. 2005. Spatial ecology and habitat selection of breeding male pheasants. Wildlife Society Bulletin 33:130–141.

Lillesand, T. M., and R. W. Kiefer. 2000. Remote sensing and image interpretation. John Wiley & Sons, New York, NY.

Manel, S., M. K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: combining landscape ecology and population genetics. Trends in Ecology and Evolution 18:189–197.

Manzer, D. L., and S. J. Hannon. 2005. Relating grouse nest success and corvid density to habitat: a multi-scale approach. Journal of Wildlife Management 69:110–123.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. EcoScience 16:238–247.

McDonald, M. W., and K. P. Reese. 1998. Landscape changes within the historical distribution of Columbian Sharp-tailed Grouse in eastern Washington: is there hope? Northwest Science 72:34–41.

Merrill, M. D., K. A. Chapman, K. A Poiani, and B. Winter. 1999. Land-use patterns surrounding Greater Prairie-Chicken leks in northwestern Minnesota. Journal of Wildlife Management 63:189–198.

Millspaugh, J. J., and F. R. Thompson, III (editors). 2008. Models for planning wildlife conservation in large landscapes. Elsevier Science. Burlington, MA.

Moe, M. 1999. Status and management of the Greater Prairie Chicken in Iowa. Pp.123–127 *in* W. D. Svedarsky, R. H. Hier, and N. J. Silvy (editors). The Greater Prairie Chicken: a national look. University of Minnesota Agricultural Experiment Station Miscellaneous Publication 99-1999, Saint Paul, MN.

Moilanen, A., and I. Hanski. 2001. On the use of connectivity measures in spatial ecology. Oikos 95:147–151.

Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. Ecology 83:1131–1145.

Morrow, M. E., R. S. Adamcik, J. D. Friday, and L. B. McKinney. 1996. Factors affecting Attwater's Prairie-Chicken decline on the Attwater Prairie Chicken National Wildlife Refuge. Wildlife Society Bulletin 24:593–601.

Niemuth, N. D. 2000. Land use and vegetation associated with Greater Prairie Chickens in an agricultural landscape. Journal of Wildlife Management 64:278–286.

Niemuth, N. D. 2003. Identifying landscapes for Greater Prairie Chicken translocation using habitat models and GIS: a case study. Wildlife Society Bulletin 31:145–155.

Niemuth, N. D. 2005. Landscape composition and Greater Prairie-Chicken lek attendance: implications for management. Prairie Naturalist 37:127–142.

Niemuth, N. D., and M. S. Boyce. 2004. Influence of landscape composition on Sharp-tailed Grouse lek location and attendance in Wisconsin pine barrens. Ecoscience 11:209–217.

Sandercock_6480004_ch01.indd 17 7/18/11 11:12:00 AM

Niemuth, N. D., M. E. Estey, and R. E. Reynolds. 2009. Data for developing spatial models: Criteria for effective conservation. Pp. 396–411 *in* T. D. Rich, C. D. Thompson, D. Demarest, and C. Arizmendi, (editors), Tundra to tropics: connecting birds, habitats, and people. Proceedings of the fourth international Partners in Flight conference, 13–16 February 2008, McAllen, TX.

Niemuth, N. D., R. E. Reynolds, D. A. Granfors, R. R. Johnson, B. Wangler, and M. E. Estey. 2008. Landscape-level planning for conservation of wetland birds in the U.S. Prairie Pothole Region. Pp. 533–560 *in* J. J. Millspaugh and F. R. Thompson, III (editors), Models for planning wildlife conservation in large landscapes. Elsevier Science, Burlington, MA.

Nooker, J. K., and B. K. Sandercock. 2008. Phenotypic correlates and survival consequences of male mating success in lek-mating Greater Prairie-Chickens (*Tympanuchus cupido*). Behavioral Ecology and Sociobiology 62:1377–1388.

Patten, M. A., D. H. Wolfe, E. Shochat, and S. K. Sherrod. 2005. Habitat fragmentation, rapid evolution, and population persistence. 2005. Evolutionary Ecology Research 7:235–249.

Pedlar, J. H., L. Fahrig, and H. G. Merriam. 1997. Raccoon habitat use at two spatial scales. Journal of Wildlife Management 61:102–112.

Pepper, G. W. 1972. The ecology of Sharp-tailed Grouse during spring and summer in the aspen parklands of Saskatchewan. Saskatchewan Department of Natural Resources Wildlife Report Number 1, Regina, SK.

Peterson, M. J., and N. J. Silvy. 1996. Reproductive stages limiting productivity of the endangered Attwater's Prairie Chicken. Conservation Biology 10:1264–1276.

Phillips, M. L, W. R. Clark, S. M. Nusser, M. A. Sovada, and R. J. Greenwood. 2004. Analysis of predator movement in prairie landscapes with contrasting grassland composition. Journal of Mammalogy 85:187–195.

Pruett, C. L., M. A. Patten, and D. H. Wolfe. 2009a. It's not easy being green: wind energy and a declining grassland bird. BioScience 59:257–262.

Pruett, C. L., M. A. Patten, and D. H. Wolfe. 2009b. Avoidance behavior by prairie grouse: Implications for development of wind energy. Conservation Biology 23:1253–1259.

Reed, J. M. 1999. The role of behavior in recent avian extinctions and endangerments. Conservation Biology 13:232–241.

Reynolds, R. E., T. L. Shaffer, C. R. Loesch, and R. R. Cox, Jr. 2006. The farm bill and duck production in the Prairie Pothole Region: Increasing the benefits. Wildlife Society Bulletin 34:963–974.

Ribic, C. A., R. R. Koford, J. R. Herkert, D. H. Johnson, R. B. Renfrew, N. D. Niemuth, D. E. Naugle, and K. K. Bakker. 2009. Area sensitivity in North American grassland birds: patterns, processes, and research needs. Auk 126:233–244.

Rippin, A. B., and D. A. Boag. 1974. Recruitment to populations of male Sharp-tailed Grouse. Journal of Wildlife Management 38:616–621.

Robel, R. J. 1970. Possible role of behavior in regulating Greater Prairie Chicken populations. Journal of Wildlife Management 34:306–314.

Robel, R. J., F. R. Henderson, and W. Jackson. 1972. Some Sharp-tailed Grouse population statistics from South Dakota. Journal of Wildlife Management 36:87–98.

Ross, J. D., A. D. Arndt, R. F. C. Smith, J. A. Johnson, and J. L. Bouzat. 2006. Re-examination of the historical range of the Greater Prairie Chicken using provenance data and DNA analysis of museum collections. Conservation Genetics 7:735–750.

Ryan, M. R., L. W. Burger, Jr., D. P. Jones, and A. P. Wywialowski. 1998. Breeding ecology of Greater Prairie Chicken (*Tympanuchus cupido*) in relation to prairie landscape configuration. American Midland Naturalist 140:111–121.

Samson, F. B. 1980. Island biogeography and the conservation of nongame birds. Transactions of the North American Wildlife and Natural Resources Conference 45:245–251.

Samson, F. B., F. L. Knopf, and W. R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. Wildlife Society Bulletin 32:6–15.

Schroeder, M. A. 1991. Movement and lek visitation by female Greater Prairie-Chickens in relation to predictions of Bradbury's female preference hypothesis of lek evolution. Auk 108: 896–903.

Schroeder, M. A., and C. E. Braun. 1992. Greater Prairie-Chicken attendance at leks and stability of leks in Colorado. Wilson Bulletin 104:273–284.

Schroeder, M. A., and C. E. Braun. 1993. Partial migration in a population of Greater Prairie-Chickens in northeastern Colorado. Auk 110:21–28.

Schroeder, M. A., and L. A. Robb. 1993. Greater Prairie-Chicken (*Tympanuchus cupido*). A. Poole and F. Gill (editors), The birds of North America No. 36. The Birds of North America, Inc., Philadelphia, PA.

Schroeder, M. A., and G. C. White. 1993. Dispersion of Greater Prairie Chicken nests in relation to lek location: evaluation of the hot-spot hypothesis of lek evolution. Behavioral Ecology 4:266–270.

Scott, M. J., P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson. 2002. Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington, DC.

Sandercock_6480004_ch01.indd 18 7/18/11 11:12:00 AM

Shenk, T. M., and A. B. Franklin. 2001. Modeling in natural resource management: development, interpretation, and application. Island Press, Washington, DC.

Sovada, M. A., M. C. Zicus, R. J. Greenwood, D. P. Rave, W. E. Newton, R. O. Woodward, and J. A. Beiser. 2000. Relationships of habitat patch size to predator community and survival of duck nests. Journal of Wildlife Management 64:820–831.

Stauffer, D. F. 2002. Linking populations and habitats: Where have we been? Where are we going? Pp. 53–61 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson (editors), Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington, DC.

Stewart-Oaten, A. W., M. Murdoch, and K. R. Parker. 1986. Environmental impact assessment: "Pseudoreplication" in time? Ecology 67:929–940.

Taylor, M. A., and F. S. Guthery. 1980a. Status, ecology, and management of the Lesser Prairie-Chicken. USDA Forest Service General Technical Report RM-77. USDA Forest Service, Rocky Mountain Research Station, Ft. Collins, CO.

Taylor, M. A., and F. S. Guthery. 1980b. Fall-winter movements, ranges, and habitat use of Lesser Prairie Chickens. Journal of Wildlife Management 44:521–524.

Tischendorf, L., and L. Fahrig. 2001. On the use of connectivity measures in spatial ecology: a reply. Oikos 95:152–155.

U.S. Department of the Interior and Environment Canada. 1986. North American Waterfowl Management Plan. Washington, DC.

Vance, D. R., and R. L. Westemeier. 1979. Interactions of pheasants and prairie chickens in Illinois. Wildlife Society Bulletin 7:221–225.

Van Den Bussche, R. A., S. R. Hoofer, D. A. Wiedenfield, D. H. Wolfe, and S. K. Sherrod. 2003. Genetic variation within and among fragmented populations of Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*). Molecular Ecology 12:675–683.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Vodehnal, W. L., and J. B. Haufler. 2007. A grassland conservation plan for prairie grouse. North American Grouse Partnership, Fruita, CO.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater Sage-Grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

Walters, C. J. 1986. Adaptive management of renewable resources. McGraw Hill, New York, NY.

Wang, Y., K. Yang, C. L. Bridgman, and L. Lin. 2008. Habitat suitability modeling to correlate gene flow with landscape connectivity. Landscape Ecology 23:989–1000.

Westemeier, R. L. 1971. The history and ecology of prairie chickens in central Wisconsin. University of Wisconsin Research Bulletin 281, Madison, WI.

Westemeier, R. L, J. D. Brawn, S. A. Simpson, T. L. Esker, R. W. Jansen, J. W. Walk, E. L. Kershner, J. L. Bouzat, and K. N. Paige. 1998a. Tracking the long-term decline and recovery of an isolated population. Science 282:1695–1698.

Westemeier, R. L., J. E. Buhnerkempe, W. R. Edwards, J. D. Brawn, and S. A. Simpson. 1998b. Parasitism of Greater Prairie-Chicken nests by Ring-necked Pheasants. Journal of Wildlife Management 62:854–863.

Wiens, J. A. 1973. Pattern and process in grassland bird communities. Ecological Monographs 43:237–270.

Wiens, J. A. 1997. Metapopulation dynamics and landscape ecology. Pp. 43–62 *in* I. Hanski and M. Gilpin (editors), Metapopulation biology: ecology, genetics, and evolution. Academic Press, London, UK.

Wiens, J. A. 2002. Predicting species occurrences: Progress, problems, and prospects, Pp. 739–749 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson (editors), Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington, DC.

Williams, C. K., F. S. Guthery, R. D. Applegate, and M. J. Peterson. 2004. The Northern Bobwhite decline: scaling our management for the twenty-first century. Wildlife Society Bulletin 32:861–869.

Winter, M., and J. Faaborg. 1999. Patterns of area sensitivity in grassland-nesting birds. Conservation Biology 13:1424–1436.

Wisdom, M. J., and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. Journal of Wildlife Management 61:302–312.

Wisdom, M. J., M. M. Rowland, and R. J. Tausch. 2005. Effective management strategies for sage-grouse and sagebrush: a question of triage? Transactions of the North American Wildlife and Natural Resources Conference 70:206–227.

Wisdom, M. J., B. C. Wales, M. M. Rowland, M. G. Raphael, R. S. Holthausen, T. D. Rich, and V. A. Saab. 2002. Performance of Greater Sage-Grouse models for conservation assessment in the interior Columbia Basin, U.S.A. Conservation Biology 16:1232–1242.

With, K. A., and A. W. King. 1999. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. Landscape Ecology 14:73–82.
Wolfe, D. H., M. A. Patten, E. Shochat, D. L. Pruett, and S. K. Sherrod. 2007. Causes and patterns of mortality in Lesser Prairie-Chickens *Tympanuchus pallidicinctus* and implications for management. Wildlife Biology 13(Suppl. 1):95–104.
Woodward, A. J. W., S. D. Fuhlendorf, D. M. Leslie, Jr., and J. Shackford. 2001. Influences of landscape composition and change on Lesser Prairie-Chicken populations. American Midland Naturalist 145:261–274.
Yeatter, R. E. 1963. Population responses of prairie chickens to land-use changes in Illinois. Journal of Wildlife Management 27:739–757.

Sandercock_6480004_ch01.indd 20 7/18/11 11:12:00 AM