SAGE-GROUSE AND ENERGY DEVELOPMENT: INTEGRATING SCIENCE WITH CONSERVATION PLANNING TO REDUCE IMPACTS

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SAGE-GROUSE AND ENERGY DEVELOPMENT:
INTEGRATING SCIENCE WITH CONSERVATION PLANNING
TO REDUCE IMPACTS

By

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Dissertation

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Effective conservation planning in the face of rapid land use change requires knowledge of which habitats are selected at landscape scales, where those habitats are located, and how species ultimately respond to anthropogenic disturbance. I assessed sage-grouse (*Centrocercus urophasianus*) large scale habitat ecology and response to energy development in the winter and nesting seasons using radio-marked individuals in the Powder River Basin, Montana and Wyoming, USA. Landscape scale percent sagebrush (*Artemisia spp.*) cover at 4-km² was the strongest predictor of use by sage-grouse in winter. After controlling for vegetation and topography, the addition the density of coal-bed natural gas wells within 4 km² improved model fit (AIC -6.66, $w_i = 0.965$) and indicated that sage-grouse avoided energy development. Nesting analyses showed that landscape context must be considered in addition to local scale habitat features ($w_i = 0.96$). Findings provide managers a hierarchical filter in which to manage breeding habitats. Twice the amount of nesting habitat at 3, 5 and 10-km scales surrounded active leks versus random locations. Spatially explicit nesting and wintering models predicted independent sage-grouse locations (validation $R^2 \geq 0.98$). I incorporated knowledge of energy impacts into a study design that tested for threshold responses at regional scales analyzing 1,344 leks in Wyoming from 1997-2007. Potential impacts were indiscernible at 1-12 wells within 32.2 km² of a lek (~1 well / 640 ac). At higher wells densities a time-lag showed higher rates of lek inactivity and steeper declines in bird abundance 4 years after than immediately following development. I spatially prioritized core areas for breeding sage-grouse across Wyoming, Montana, Colorado, Utah and the Dakotas and assessed risk of future energy development. Findings showed that bird abundance varies by state, core areas contain a disproportionately large segment of the breeding population and that risk of development within core areas varies regionally. My analyses document behavioral and demographic responses to energy development, offer new insights into large scale ecology of greater sage-grouse and provide resource managers with practical tools to guide conservation.
DEDICATION
This work would not have been possible without the support and unconditional love of my wife Melissa. She shared all the inevitable ups and downs that occur when pursuing a graduate degree. When I hit the lows she helped me through. When I hit my highs, I had a best friend to laugh and share the moments. I want to thank my parents Chad and Joan Doherty who taught me through honesty and hard work you can accomplish anything in this world you set your mind to. I would also like to thank my brother Keith who taught me to never give up and has made me a much stronger person than I would have been without him. I want to thank my in-laws Charlie and Kathy Kuckler for welcoming me into their family and showing Melissa at an early age that it is OK for boys to disappear during the fall. I also want to dedicate this to my new son Aiden Bryant Doherty, whose early arrival postponed the completion of this product, but added a new joy and fulfillment to my life that words cannot describe. Through his laughs, smiles, and wide open curious eyes, I am reassured and reminded of why I choose the life of conservation of our natural world.
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SAGE-GROUSE AND ENERGY DEVELOPMENT: INTEGRATING SCIENCE WITH CONSERVATION PLANNING TO REDUCE IMPACTS

CHAPTER 1: INTRODUCTION

Over the past century, human activities have caused heavy sagebrush loss and fragmentation such that sagebrush ecosystems are among the most threatened habitats in North America (Mac et al. 1998, Knick et al. 2003). The impacts of agriculture, livestock grazing, fire, urbanization, and juniper encroachment are all major causes of past and current degradation (Noss et al. 1995, Saab and Rich 1997, Paige and Ritter 1999). Changes in land use practices which have been primarily considered a local scale environmental issue are emerging as a force of global importance (Foley et al. 2005). The spatial extent of environmental change is unprecedented relative to pre-industrial times and is expected to increase in rate and extent over the next several decades (Noon and Dale 2002). Energy development is driving a new source of land use change. Global demand for energy increased by >50% in the last half-century, and a similar increase is projected between now and 2030 (National Petroleum Council [NPC] 2007). Fossil fuels will likely remain the largest source of energy, with oil, natural gas, and coal accounting for 83-87% of total world demand (NPC 2007). The land base required to support increased demand and its ultimate impacts on ecosystems is largely unknown.

Increasing energy demand of an expanding human population poses a challenge to conservation of wildlife populations in North America (Sawyer et al. 2006, Walker et al. 2007). Land use managers must balance trade-offs between immediate human consumption of energy and maintenance of long-term ecosystem function including viable wildlife populations (Foley et al. 2005). Energy development is known to impact wildlife directly by altering habitat use (Doherty et al. 2008) and population dynamics (Sorensen et al. 2008), and indirectly by facilitating the spread of invasive plants (Bergquist et al. 2007) and exotic diseases (Zou et al. 2006, Doherty 2007). Unrestricted or poorly planned development can result in cumulative impacts that overwhelm natural systems and leave wildlife managers unable to maintain small populations.

Loss and degradation of native habitats has impacted much of the sagebrush (Artemisia spp.) ecosystem and its associated wildlife (Knick et al. 2003, Connelly et al.)
Sage-grouse are a gallinaceous species native only to western semiarid sagebrush landscapes (Schroeder et al. 1999). Previously widespread, sage-grouse have been extirpated from nearly half of their original range in western North America (Schroeder et al. 2004), with a range-wide population decline of 45-80\% and local declines of 17-92\% (Connelly and Braun 1997, Braun 1998, Connelly et al. 2004). Energy development has emerged as a range-wide issue in conservation for three reasons: First, research shows that oil and gas development negatively affects sage-grouse (Chapters 2 and 4). Secondly, landscapes being developed contain some of the highest abundance estimates for sage-grouse in North America (Naugle et al. *in press*, Chapter 5). Thirdly, 7 million ha of the federal mineral estate has already been authorized for exploration and development within the species eastern range (Naugle et al. *in press*). Recent scientific evidence has documented impacts of energy development to sage-grouse populations. There are 7 peer reviewed studies that all reported direct negative impacts of energy development on sage-grouse (Lyon and Anderson 2003, Holloran 2005, Kaiser 2006, Aldridge and Boyce 2007, Holloran et al. 2007, Walker et al. 2007, Doherty et al. 2008). No study reported any positive influence of development on populations or habitats. Findings suggested that development in excess of 1 pad / 2.6 km\(^2\) resulted in impacts to breeding populations (Holloran 2005), and that impacts at conventional well densities (e.g., 8 pads / 2.6 km\(^2\)) exceeded the species’ threshold of tolerance (Holloran 2005, Walker et al. 2007, Doherty et al. 2008). Negative impacts are known for three different sage-grouse populations in different types of development including shallow coal-bed natural gas in the Powder River Basin of northeast Wyoming and extreme southeast Montana (Walker et al. 2007, Doherty et al. 2008), deep gas in the Pinedale Anticline Project Area in southwest Wyoming (Lyon and Anderson 2003, Holloran 2005, Kaiser 2006, Holloran et al. 2007), and oil extraction in the Manyberries Oil Field in southeast Alberta (Aldridge and Boyce 2007).

Negative responses of sage-grouse to energy development were consistent among studies regardless of whether they examined lek dynamics or demographic rates of specific cohorts within populations. Recent research showed that sage-grouse populations decline when cumulative impacts of development negatively affect reproduction or survival (Aldridge and Boyce 2007), when birds behaviorally avoid infrastructure in one
or more seasons (Doherty et al. 2008), or both (Lyon and Anderson 2003, Holloran 2005, Kaiser 2006, Holloran et al. 2007). Avoidance of energy development reduces the distribution of sage-grouse and may result in population declines if density-dependence or habitat suitability lowers survival or reproduction among displaced birds (Holloran and Anderson 2005, Aldridge and Boyce 2007).

I split my dissertation into two main themes. I first address gaps in our scientific understanding of sage-grouse in Chapters 2 and 3, and secondly I integrate science into conservation planning for sage-grouse in Chapters 4 and 5. In Chapters 2 and 3, I address major unanswered questions about impacts of energy development and large scale ecology to sage-grouse populations. Chapter 2 is the first study to quantify how abundance of sagebrush at a landscape scale influences sage-grouse winter habitat selection and was the first to document behavioral avoidance of sage-grouse to CBNG development during the winter. Statistical and model selection approaches in Chapter 2 that were published in the Journal of Wildlife Management (Doherty et al. 2008) form the basis of my nesting study in Chapter 3. Chapter 3 documents the importance of hierarchy in habitat selection to nesting sage-grouse, previously a missing link in the sage-grouse literature. This chapter is unique in that it specifically tests the importance of large scale ecology versus local scale vegetation. My analysis clearly demonstrates that landscape context must be considered along with local scale habitat features and provides managers a hierarchical filter in which to view and manage sage-grouse nesting habitats.

The second theme of this dissertation is the integration of scientific understanding into conservation planning for sage-grouse. Policies and strategies to reduce impacts are lacking despite our increased understanding of the biological response of sage-grouse to energy development. Chapter 4 incorporated our enhanced understanding of impacts at local scales into a study design that tested for threshold responses to development at regional scales. I used prior hypotheses to generate and test if specific predictions from local scale studies were validated across all energy developments in Wyoming. I identified thresholds of development compatible with conservation of sage-grouse populations, quantified the severity of impacts to populations at thresholds that are incompatible with conservation and created a tool for use in future regional risk assessments. In Chapter 5, I spatially prioritized sage-grouse breeding conservation areas
across Wyoming, Montana, Colorado, Utah and the Dakotas to enable decision-makers to make conservation policy decisions, while I simultaneously assessed risk to these conservation areas using readily available GIS layers. My analyses provided a framework that clearly illustrates tradeoffs between sage-grouse conservation and energy development.

All of my chapters indicate the need to manage landscapes for sage-grouse at much larger scales than currently documented in the literature and support prior suggestions that abundance of sagebrush at the landscape scale is required for the persistence of sage-grouse (Schroeder et al. 1999, Connelly et al. 2000, Connelly et al. 2004, Crawford et al. 2004). Severity of impacts of energy development within this dissertation and in the scientific literature coupled with continued leasing of the public mineral estate dictate the need to shift from local to landscape conservation. The scientific basis of this shift should transcend state and other political boundaries to develop and implement a plan for conservation of sage-grouse populations across the western U.S and Canada. Ultimately, multiple stressors—not just energy development—must be managed collectively to maintain populations over time in priority landscapes. Integrated analyses should consider how additional stressors such as habitat loss (Knick et al. 2003), restoration (Wisdom et al. 2002), range management (Crawford et al. 2004), disease (Naugle et al. 2004), invasive weeds (Bergquist et al. 2007) and others will cumulatively affect sage-grouse populations over time. Results of this dissertation highlight the need to integrate a quantitatively based landscape research and management paradigm with our extensive knowledge of local-scale vegetation if we are to effectively conserve sage-grouse populations.

From “I” to “We”

This dissertation was written in the traditional format using “I”, however parts of all chapters were conducted collaboratively and all resulting publications are or will be co-authored publications. My PhD advisor D. Naugle was involved with all aspects of this research and is a co-author on every chapter herein. In chapters 2 and 3, B. Walker helped collect field data and provided editorial comments. Jon Graham wrote statistical code for the statistical bootstrap analyses in Chapter 2 that helped place research results
into context. Chapter 5 included 3 other co-authors, J. Kiesecker, H. Copeland, and A. Pocewicz who assisted in risk assessment conceptualization and writing of these results.

**Literature Cited**


CHAPTER 2: GREATER SAGE-GROUSE WINTER HABITAT SELECTION AND ENERGY DEVELOPMENT

Abstract: Recent energy development has resulted in rapid and large-scale changes to western shrub-steppe ecosystems without a complete understanding of its potential impacts on wildlife populations. I modeled winter habitat use by female greater sage-grouse (*Centrocercus urophasianus*) in the Powder River Basin (PRB) of Wyoming and Montana to: 1) identify landscape features that influenced sage-grouse habitat selection, 2) assess the scale at which selection occurred, 3) spatially depict winter habitat quality in a Geographic Information System, and 4) assess the effect of coal-bed natural gas (CBNG) development on winter habitat selection. I developed a model of winter habitat selection based on 435 aerial relocations of 200 radio-marked female sage-grouse obtained during the winters of 2005 and 2006. Percent sagebrush (*Artemisia* spp.) cover on the landscape was an important predictor of use by sage-grouse in winter. The strength of habitat selection between sage-grouse and sagebrush was strongest at a 4-km² scale. Sage-grouse avoided coniferous habitats at a 0.65-km² scale and riparian areas at a 4-km² scale. A roughness index showed that sage-grouse selected gentle topography in winter. After controlling for vegetation and topography, the addition of a variable that quantified the density of CBNG wells within 4 km² improved model fit by 6.66 Akaike’s Information Criterion (AIC) points (Akaike wt = 0.965). The odds ratio for each additional well in a 4-km² area (0.877; 95% CI = 0.834-0.923) indicated that sage-grouse avoid CBNG development in otherwise suitable winter habitat. Sage-grouse were 1.3 times more likely to occupy sagebrush habitats that lacked CBNG wells within a 4-km² area, compared to those that had the maximum density of 12.3 wells/4 km² allowed on federal lands. I validated the model with 74 locations from 74 radio-marked individuals obtained during the winters of 2004 and 2007. This spatially explicit winter habitat model based on vegetation, topography, and CBNG avoidance was highly predictive (validation $R^2 = 0.984$). My spatially explicit model can be used to identify areas that provide the best remaining habitat for wintering sage-grouse in the PRB to mitigate impacts of energy development.
Understanding landscape-scale habitat selection during critical life stages is essential for developing conservation plans for sensitive species. Studies of habitat selection at small scales further our ecological understanding of species-habitat relationships but do not convey spatially-explicit information about habitat quality at a scale useful for prioritizing landscapes for conservation. Recent advances in modeling habitat selection from high-resolution satellite imagery using resource selection functions (RSF) offers the ability to rank specific areas by their relative probability of use (Manly et al. 2002). Resulting probability layers can then be mapped in a Geographic Information System (GIS) to identify regions where high quality habitat is available. Further, these models allow cross-validation and testing against independent datasets to ensure that inferences regarding habitat selection are robust (Boyce et al. 2002, Johnson et al. 2006). The relative influence of variables thought to be important in habitat selection can also be assessed in a competing-model framework (Burnham and Andersen 2002).

Previously widespread, greater sage-grouse (Centrocercus urophasianus) have been extirpated from approximately 50% of their original range in western North America (Schroeder et al. 2004), with an estimated range-wide population decline of 45-80% and local declines of 17-92% (Connelly and Braun 1997, Braun 1998, Connelly et al. 2000, Aldridge and Brigham 2003). Despite increased concern for their populations, little effort has gone into measuring landscape-scale winter habitat selection by greater sage-grouse (hereafter sage-grouse). Previous winter habitat studies have focused on the importance of micro-site vegetation features such as height, canopy cover, or crude protein levels of sagebrush (e.g., Eng and Schladweiler 1972, Beck 1977, Connelly et al. 2000, Crawford et al. 2004, Sauls 2006). In winter, sage-grouse inhabit areas with moderate to dense sagebrush (Eng and Schladweiler 1972, Homer et al. 1993, Connelly et al. 2000) and typically prefer areas with gentle (<10%), south or west facing slopes (Beck 1977, Hupp and Braun 1989). Previous demographic studies have documented high rates...
of winter survival (reviewed in Connelly et al. 2004). However, Moynahan et al. (2006) demonstrated that severe winters can have substantial population-level impacts. Birds also must often move long distances to find suitable winter habitat (Patterson 1952 in Connelly et al. 2004; Connelly et al. 1988; Robertson 1991). Impacts to wintering habitat may have disproportionate effects on regional population size and persistence. For example, Beck (1977) found that 80% of use sites occurred in <7% of the area of sagebrush available in northern Colorado, suggesting that winter habitat may be limited. The relationship between sagebrush and sage-grouse is arguably the closest during winter when birds switch from a diet of insects, forbs, and sagebrush to one composed of >96% sagebrush (Remington and Braun 1985, Welch et al. 1991, Connelly et al. 2000, Crawford et al. 2004). Heavy snowfall may even further reduce the amount of suitable habitat by limiting the abundance of sagebrush above the snow (Hupp and Braun 1989, Connelly et al. 2000, Connelly et al. 2004).

Coal bed natural gas (CBNG) development in the PRB has caused rapid, large-scale changes to sagebrush habitats in Montana and Wyoming. The sage-grouse sub-population in the Powder River Basin (PRB) is a critical component of the larger Wyoming Basin population, which represents 25% of sage-grouse in the species’ range (Connelly et al. 2004). The population in the PRB has a high density of active leks and serves as a link to populations in eastern Wyoming and western South Dakota and between the Wyoming Basin and central Montana (Connelly et al. 2004). The CBNG field in the PRB is one of the largest developed energy fields in North America. In this region, approximately 29,000 CBNG wells have been drilled on public and private lands, and another approximately 37,000 wells are expected within a 2.4-million ha area, roughly the size of the state of New Hampshire (Bureau of Land Management [BLM] 2003a, b). Drilling is typically authorized at a maximum density of 1 well/32 ha on lands where federally owned gas reserves are extracted, however there are no well density restrictions placed on private or state owned gas reserves. Wells, power lines, roads, vehicle traffic, pipelines, compressor stations, and water storage ponds within a gas field this size contribute to fragmentation of sagebrush habitats and may impact sagebrush obligates (Knick et al. 2003).
I investigated sage-grouse winter habitat use in the PRB as part of a larger study of the potential impacts of CBNG development on sage-grouse populations. My objectives were to: 1) create a robust habitat selection model for sage-grouse in winter, 2) evaluate the appropriate scale at which females select winter habitat, 3) spatially depict habitat suitability in a GIS to identify areas with a high probability of use, and 4) assess the influence of CBNG development on winter habitat selection.

**Study Area**

My study area in the PRB covered portions of Johnson, Sheridan, and Campbell counties in Wyoming, and Bighorn, Rosebud, and Powder River counties in Montana. Shrub-steppe habitat in the PRB was dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) with an understory of native and non-native grasses such as bluebunch wheatgrass (*Pseudoroegneria spicata*), western wheatgrass (*Agropyron smithii*), prairie junegrass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*), Japanese brome (*Bromus japonicus*), cheatgrass (*Bromus tectorum*), and crested wheatgrass (*Agropyron cristatum*). Plains silver sagebrush (*Artemisia cana cana*) was also present in drainages but at much lower abundance. Rocky mountain juniper (*Juniperus scopulorum*) and ponderosa pine (*Pinus ponderosa*) were located in wooded draws and formed forests across the extreme northern extent of the study area. Conifers were largely absent from the southern half of the study area. Land use was dominated by cattle ranching; only 4% of the landscape consisted of dry land or irrigated agriculture. The PRB typically was cold and dry in January with average temperatures of -6.0°C and 16.3 cm of snowfall. Winter weather conditions in 2004 and 2005 were almost identical to historical averages. The winter of 2006 was mild; in January, temperatures were 6.5°C above normal and snowfall was 15 cm below average. The January 2007 average temperature of -5.5°C was near historical norms; however snowfall was 60% above normal.
Methods

Marking and Monitoring Protocols

I captured sage-grouse by rocket-netting (Giesen et al. 1982) and spotlighting (Wakkinen et al. 1992) on and around leks in 3 study areas: 1) Bighorn County, Montana, 2) Campbell County, Wyoming, and 3) Johnson County, Wyoming during March-April and August of 2003-2006. I aged and sexed grouse and fitted females with a 21.6-g necklace style radio collar with a 4-hour mortality switch (model A4060 Advanced Telemetry Systems Isanti, MN). Sage-grouse in the Bighorn and Campbell county study areas were non-migratory. In contrast, many birds in the Johnson Country study area were migratory, with distinct breeding, summer, and winter ranges. In all study sites, I obtained winter locations after birds in my migratory population had moved to wintering areas but before they had moved back to the breeding grounds. I monitored sage-grouse via aerial radiotracking during the winters of 2005-2007. I used a fixed-wing airplane with aerial telemetry antennas mounted on both wings struts and connected to a switch box. I used a Global Positioning System (GPS) receiver to record locations of used sites as I circled sage-grouse at approximately 100-200-m elevation above the ground. I radiotracked sage-grouse on foot during the winter of 2004, and recorded their positions with a GPS receiver when I obtained visual sightings of radiomarked birds. I estimated the 95% error ellipse of aerial locations by relocating a transmitter placed in rolling sagebrush cover 40 times from the air in a blind trial. I then calculated a bivariate normal home range estimator (Jennrich and Turner 1969) using these relocations to quantify my maximum resolution to estimate the location of an unknown collar (78.2-m radius). The ability of the plane to tightly circle sage-grouse was not constrained by rugged areas nor conifer dominated landscapes in the PRB because birds were not located in these habitat features; thus my test was representative of the maximum precision of the aerial telemetry locations in rolling sagebrush habitats. I did not quantify error for ground based locations, but I assumed error estimates were smaller than aerial based methods. Since I treated my aerial telemetry error test as a maximum precision estimate, I conducted all analyses at scales ≥100 m to ensure that my inference was not confounded by location error.
Designation of Used and Available Sites

I employed a used-available design to evaluate sage-grouse habitat relationships in winter (Boyce 2002, Manly 2002, Johnson et al. 2006). I defined used points as the sites where I located radiomarked sage-grouse during radiotracking. I split sage-grouse used locations into those I analyzed to build a statistical model to quantify large scale habitat relationships and those I analyzed to test the predictive ability of my spatially explicit winter habitat model. I located birds I used to build the model during 3 flights from 2-25 January 2005 (n = 292 locations on 106 individuals) and on 3 flights from 24 December 2005 - 1 February 2006 (n = 241 locations on 94 individuals). To test the model, I used 87 locations collected on the ground from 15-18 January 2004 (n = 30 locations on 28 individuals) and on 2 flights on 18 and 26 January 2007 (n = 57 locations on 57 individuals). Of the 85 individuals used to test the model, 57 were not included among birds marked during 2005 or 2006. I found some radiomarked birds together in flocks. To avoid the possibility of dependency in my data, I retained only one used location per flock. The final data set contained 435 used locations for building the model and 74 used locations for testing the model.

I selected available points within circles that had a radius to the farthest winter used point and were centered on either the lek of capture or on the lek closest to where birds were captured via spotlighting. I merged circles that overlapped within each study area to create 3 non-overlapping polygons that corresponded with my 3 study areas. I randomly selected available points from a spatial Poisson distribution (Beyer 2004) proportional to twice the number of used points within a polygon and year to ensure a representative sample of available habitats.

GIS Habitat Classification

I acquired SPOT-5 satellite imagery (Terra Image USA, Santa Barbara, California) for the northern portion of the study area in August 2003 and for the southern portion in August 2004 when the project expanded to encompass a larger geographic area. I ortho-rectified SPOT-5 imagery to existing digital ortho-quads of the study area. The SPOT-5 panchromatic and multi-spectral images were combined into a single panchromatic, multi-spectral file. I then used the panchromatic 25-m²-pixel image to perform pan-sharpening to reduce the multi-spectral image pixel size from 100 m² to 25
m², greatly increasing the resolution of my analysis. I used eCognition™ 4.0 software (Definiens Imaging, Germany) to cluster the pixels into regions representing spectrally similar ground features. I exported clusters into ArcGIS 9.2 software (Environmental Systems Research Institute, Redlands, California) to create a polygon database. I collected field training points (n = 7,092) that were stratified by space and landowner access to classify 5 habitat cover classes as sagebrush, conifer, grassland, riparian, and barren. Classification accuracy assessed by withholding subsamples of data (i.e., k-fold cross validation with 10 folds; Boyce et al. 2002) was 83% for sagebrush, 77% for conifer, 76% for grassland, 70% for riparian, and 80% for barren with an overall accuracy of 78%. I removed urban areas and strip mines from analyses.

**Vegetation, Topography, and Energy Development Variables**

I quantified characteristics of vegetation, topography (e.g., Beck 1977, Remington and Braun 1985, Hupp and Braun 1989, Sauls 2006) and energy development around used and available points using a GIS to evaluate landscape predictors of sage-grouse winter habitat selection. I used used and available points to select individual 5 × 5-m raster pixels which I then buffered by 100 m, 400 m, and 1,000 m. I quantified variables within a square centered on each used and available pixel at 3 spatial scales: 205 × 205-m (0.04-km²), 805 × 805-m (0.65-km²), and 2,005 × 2,005-m (4-km²). I calculated the percent of total area covered by each of the 5 vegetation cover classes to quantify vegetation. To quantify topography, I processed a 900-m² resolution digital elevation model (DEM) using Spatial Analyst in ArcGIS 9.2 and used it to estimate slope and solar radiation for each pixel in the landscape. Solar radiation calculates how much sun a particular pixel receives dependent on slope and aspect. I estimated solar radiation using the hillshade command in Spatial Analyst using the angle and aspect of the sun during 15 January 2007 at 1300 hours (U.S. Navy 2007). I used the standard deviation of the DEM elevations within each buffer size to calculate an index to describe the roughness of the landscape. Elevation was not included as a predictor variable for GIS habitat modeling because elevational migration of sage-grouse does not occur in the PRB, and minor differences in elevation at used and available locations were biologically irrelevant. In the northern PRB, mean elevation was 1,210 m (3.8 SE) for available locations and 1,248 m (3.9 SE) for used locations. In the southern PRB, mean elevation was 1,363 m (4.1
SE) for available locations and 1,378 m (3.4 SE) for used locations. I used the density of CBNG wells as a measure of the extent of energy development. Wells are the only segment of the energy footprint accurately mapped and publicly available for the entire PRB from the Wyoming Oil and Gas Conservation Commission and Montana Board of Oil and Gas Conservation, and well density within a buffer is strongly correlated with other features of CBNG development such as roads, ponds, and power lines (D. E. Naugle, University of Montana, unpublished data).

**Statistical Analyses**

I employed logistic regression with used and available points for model selection and RSF model parameter estimates (Boyce 2002, Manly 2002, Johnson et al. 2006). I pooled used locations of individual animals and made inferences at the population level (Design I; Erickson et al. 2001, Manly et al. 2002).

I first assigned variables into one of 3 model categories: vegetation, topography, or energy development. Because no published landscape scale studies existed upon which to base a priori models (Burnham and Anderson 2002), I tested all variables individually and removed variables with odds ratios overlapping one. I tested all buffer distances for each variable and identified the scale that best represented sage-grouse habitat selection for each variable using log-likelihood values. I then allowed the best scale for each variable to compete with all possible combinations of other variables within the same category to identify the most parsimonious model. I used information-theoretic methods (Burnham and Andersen 2002) to choose between competing models by converting log-likelihood values computed in logistic regression to Akaike’s Information Criterion (AIC) values. I brought models within 2 AIC points to the next hierarchy of model selection. After identifying the top model(s) within vegetation, topography, and energy development, I allowed models to compete across categories to see if the additional information increased model fit.

I did not allow correlated predictors ($r \geq |0.7|$) in the same model at any level of model selection. If variables were correlated ($r \geq |0.7|$), I chose the variable I felt had the greatest biological meaning according to known characteristics of winter sage-grouse habitat from published studies. When variables were moderately correlated (i.e., $|0.3| \leq r < |0.7|$), I checked for stability and consistency of regression coefficient estimates as I
added predictor variables to models. If a regression coefficient switched signs or
standard errors increased substantially when correlated variables were in the same model,
I removed one variable from analysis if the other was an important predictor.

I evaluated whether sage-grouse avoided energy development in winter by using
AIC values to determine if the addition of CBNG wells/km² to the top habitat model
explained more information than habitat alone. I then examined the resulting
corresponding model coefficient for CBNG wells to determine if sage-grouse avoided or
were attracted to energy development and to what degree. I performed a bootstrap
analysis to quantify the change in odds of use with the introduction of CBNG wells in the
form of 95% confidence intervals around the odds ratios for differences in the number of
wells. Because the best approximating model had a high AIC weight (\(w_i = 0.965\)), I used
beta coefficients from the best approximating model for all computations (see Results;
Burnham and Anderson 2002). For each bootstrap data set \((n = 5,000)\) I calculated and
stored model coefficients and the mean value for all used locations for each variable. I
then repeated this bootstrap analysis, varying the number of CBNG wells in a 4-km² area
from 0-22 wells, the full range of well density I observed in my original data set. For
each of the 5,000 simulations I computed the odds of use with the logistic equation. I
then ordered these ratios and used a rankit adjustment (Chambers et al. 1983) to compute
2.5% and 97.5% percentiles for the upper and lower 95% confidence interval bounds.

I then used the same bootstrap technique to quantify how the amount of sagebrush
within a 4-km² area affected the odds of use in winter with and without CBNG
development (12.3 wells/4 km² and 0.0 wells/4 km², respectively). I used the logistic
equation to generate odds of use for each bootstrap dataset \((n = 5,000)\) by applying stored
model coefficients to mean values of parameters at used locations while systematically
varying percent sagebrush within 4 km² from 0-100% at 0.0 and 12.3 wells/4 km². To
test if the odds of use were significantly different with the addition of CBNG I computed
the difference in odds generated from each bootstrap data set with and without CBNG.
Again, I ordered odds ratios with and without CBNG and their differences and used a
rankit adjustment (Chambers et al. 1983) to compute 2.5% and 97.5% percentiles for the
upper and lower 95% confidence interval bounds.
To turn my statistical model into a spatially explicit GIS habitat model, I employed a RSF model that had the form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k),$$

where $w(x)$ is the raw RSF value for each pixel in the landscape, and $x_1, x_2, \ldots x_k$ represent values for vegetation, topography, and energy development generated from a moving-window analysis for each pixel, and $\beta_1, \ldots, \beta_k$ are the model parameters estimated with logistic regression (Boyce 2002, Manly 2002, Johnson et al. 2006). I applied $\beta$-coefficients from equation 1 to GIS layers in ArcView Spatial Analyst. The output was a new GIS layer that represents the RSF values generated from equation 1 for each individual 25-m$^2$ pixel for the entire landscape. I created each component GIS layer by moving-window analyses for key vegetation, topographic, and energy development variables identified in model selection. These analyses resulted in summary statistics for each pixel in the GIS layer at the desired scale. I re-sampled sagebrush to a 900-m$^2$ pixel size because the time required to process a 4-km$^2$ buffer area for 625 million pixels exceeded my computational capacity. Sagebrush resampled well and little information was lost when evaluating the 900-m$^2$ resampled sagebrush layer versus the original 25-m$^2$ resolution sagebrush layer ($r = 0.934$). Conifer resampled poorly ($r = 0.793$) so I kept this variable at the original pixel size.

I categorized RSF values into 5 ordinal 20% quantile bins representing progressively selected habitats. I validated my spatial model with the test data set of sage-grouse locations collected during the winters of 2004 and 2007. I regressed the observed proportion of the test data set in each RSF bin against the expected proportion of use from the original RSF model to evaluate model fit (Johnson et al. 2006). A good model fit should have a high validation R$^2$ value, a slope not different from 1.0, and an intercept not different from zero (Johnson et al. 2006).

**Results**

Sagebrush at the 4-km$^2$ scale was the dominant variable in univariate space (Table 1). Sagebrush and grassland accounted for $>95\%$ of the total vegetation cover at used locations, which explains their strong negative correlation ($r = -0.78$). Within a 4-km$^2$ area, used sites contained $>75\%$ sagebrush cover intermixed with grassland. There was
14.5% more sagebrush at used (76.0%, SE = 0.55) than at available sites (61.5%, SE = 0.61). Sage-grouse used sites that averaged 19.1% (SE = 0.53) grassland cover within a 4-km² area.

The best model for sage-grouse vegetation use consisted of sagebrush and riparian (4-km² scale), as well as conifer and barren (0.65-km² scale; Table 2). The roughness index at a 0.65-km² scale and slope were both important topographic predictors of sage-grouse use (Table 2). The number of CBNG wells within a 4-km² area was the best model to represent energy development (Table 1).

Model fit increased when the best approximating models from vegetation, topography, and energy development were combined (Table 3). I removed barren ground from the final vegetation model because it lacked stability and consistency due to its correlation with roughness (r = 0.32). When roughness and barren ground were in the same model, the coefficient for barren ground switched from a negative to a positive effect and its standard error increased, causing the odds ratio interval to overlap one (odds 0.96- 1.06). Roughness was a more stable predictor and was unaffected by the inclusion of barren ground. The final combined model was 1.96 AIC points better when barren ground was removed.

Sage-grouse selected large expanses of sagebrush with gentle topography and avoided conifer, riparian, and energy development (Table 4). The addition of the average number of wells per 4-km² improved model fit by 6.66 AIC points (Table 3). An Akaike weight (w₁ = 0.965) indicated that the model with both habitat and energy variables had overwhelming support (Table 3). The resulting model coefficients from the habitat and energy model indicate that after adjusting for sage-grouse habitat preference, birds avoid CBNG development in otherwise suitable habitat (Table 4).

My bootstrap analysis demonstrated that current legal maximum well density on federal lands (approx. 12.3 wells/4 km², or 32-ha spacing) decreased the odds of sage-grouse use by 0.30 compared to the average landscape selected by my radio-marked sage-grouse (odds 0.57 vs. 0.87; Figure 1). Sage-grouse were 1.3 times more likely to use winter habitat if CBNG development was not present. The odds of sage-grouse winter habitat use increased with greater percentage sagebrush cover within 4 km² (Figure 2a). The difference in odds of use with and without CBNG development was statistically
significant at all levels of sagebrush ($P < 0.05$); however these differences were more pronounced in high quality winter habitats dominated by sagebrush cover (Figure 2b). Avoidance of CBNG was not relevant to winter habitat selection at low levels of sagebrush cover because sage-grouse showed strong avoidance of those areas prior to development (Figure 2a).

The best approximating model including vegetation, topography, and energy variables accurately predicted an independent data set of 74 winter locations (validation $R^2 = 0.98$, Figure 3). Using 6-, 7-, or 8-bin ordinal RSF models with quantile breaks did not change the strength or pattern of model validation. The slope of observed versus expected values did not differ from 1.0 (slope = 1.14, 95% CI = 0.87 - 1.41) and the intercept did not differ from zero (-2.85, 95% CI = -1.06 - 4.9). The top 2 RSF classes accounted for 86.6% of the 435 locations used to build the RSF model and 90.5% of the 74 locations used to test the winter habitat model (Figure 3).

**Discussion**

My study is the first to show that abundance of sagebrush at a landscape scale influences sage-grouse habitat selection in winter. Recent advances in RSF modeling and habitat mapping using satellite imagery enabled us to document what all major reviews on sage-grouse habitat requirements have suggested (Schroeder et al. 1999, Connelly et al. 2000, Connelly et al. 2004, Crawford et al. 2004). At the largest scale evaluated (4 km$^2$), sage-grouse selected for sagebrush and grassland landscapes (>95% area) that were dominated by sagebrush (>75%) with little tolerance for other cover types. Conversion of sagebrush negatively influences sage-grouse populations (Leonard et al. 2000, Smith et al. 2005). Sage-grouse avoided riparian areas at the 4-km$^2$ scale and conifer habitats and rugged landscapes at a 0.65-km$^2$ scale, relationships that would have been less discernible at broader spatial scales. My roughness index was a much stronger predictor than the rest of my suite of topographic variables, but slope further increased model fit. Roughness is readily calculated from available DEMs and may be applicable to other life stages for sage-grouse. In the only other sage-grouse landscape study that has evaluated habitat selection at multiple scales, birds selected large expanses (>1 km$^2$) of sagebrush and avoided anthropogenic edge during the breeding season (Aldridge and Boyce 2007). My
findings from winter in conjunction with those of Aldridge and Boyce (2007) highlight the need for landscape scale research to gain further insight into sage-grouse ecology.

My habitat model was highly predictive. I built my model using sage-grouse locations collected during mild to average winter conditions and validated it in years with average temperatures or above-average snowfall. I do not know whether I defined winter habitat broadly enough to include refugia necessary for birds to survive a 50- or 100-year winter storm event (Moynahan et al. 2006), but I believe the model is useful to identify habitat available in most winters. Extreme events may move birds into rugged landscapes as they search for exposed sagebrush, thermal cover, and protection from high winds (Beck 1977, Hupp and Braun 1989, Robertson 1991, Connelly et al. 2004).

A multi-scale approach is needed to understand the relative importance of local and landscape factors influencing sage-grouse habitat selection. Local vegetation measures have been the primary focus of sage-grouse habitat research to date (Eng and Schladweiler 1972, Beck 1977, Connelly et al. 2000, Crawford et al. 2004, Sauls 2006). Ideally, local variables should compete against landscape factors in an AIC framework to predict sage-grouse habitat use. Examination of ecological processes at the landscape scale does not eliminate the need to understand habitat relationships at local scales; rather, it will likely require a combination of scales to completely understand how sage-grouse respond to their environment.

My spatially explicit habitat model provides resource managers with a practical tool to guide conservation planning. Effective planning requires that I know which habitats are selected at landscape scales, where those habitats are located, and how species respond to disturbances. Recent advances in wildlife ecology enable biologists to develop RSF models that link resource use with changes in habitat quality and potential stressors (Boyce and McDonald 1999, Manly et al. 2002, Johnson et al. 2004). Moreover, RSFs estimate the strength of selection and enable predictive equations to be linked in a GIS to depict spatial relationships across a planning region (Manly et al. 2002, Johnson et al. 2004). Spatially-explicit planning tools should be used to prioritize landscapes with the highest probability of supporting populations. Once identified, local biologists provide on-site recommendations for how to best deliver on-the-ground conservation.
After adjusting for sage-grouse habitat preference, sage-grouse avoided energy development in otherwise suitable habitats in winter. Previous research has shown that breeding sage-grouse in oil and gas fields avoid development, experience higher rates of mortality, or both (Holloran 2005, Kaiser 2006, Aldridge and Boyce 2007). Accumulating evidence of the impacts of energy development in sagebrush-steppe ecosystems extends beyond that of sage-grouse. Mule deer (*Odocoileus hemionus*) avoided otherwise suitable habitats within 2.7-3.7 km of gas wells (Sawyer et al. 2006) and densities of Brewer’s sparrow (*Spizella breweri*) and sage sparrow (*Amphispiza belli*) declined 36-57% within 100-m of dirt roads in gas fields (Ingelfinger and Anderson 2004). Some suitable winter habitat remains undeveloped for sage-grouse in the PRB (RSF bins 4 and 5; Figure 3), but the anticipated addition of another 37,000 CBNG wells at 32-ha spacing has the potential to affect >1.18 million ha of land. As remaining winter habitats are developed, and sage-grouse can no longer avoid CBNG, it is unclear whether birds will be able to adapt to a disturbance of this magnitude.

**Management implications**

Sage-grouse avoidance of energy development in winter shows that a comprehensive strategy is needed to maintain suitable habitats in all seasons. Identifying and setting aside areas of undeveloped, high-quality habitat within the project area should be top priority. Currently, only 0.5-km² (1/4 mile buffer) of land surrounding a lek is excluded from development, an area that is 8 times smaller than the scale at which individual sage-grouse selected winter habitats (i.e., 4 km²). Timing stipulations that restrict CBNG development within 3.2 km of a lek during the breeding season (15 Mar – 15 Jun) are insufficient because they do not prevent infrastructure from displacing sage-grouse in winter. An additional stipulation in Montana that restricts new drilling activities within crucial winter range (1 Dec - 31 Mar) only protects sage-grouse habitat during the winter in which the drilling is scheduled. Current stipulations leave only a small fraction of the land undeveloped, place no restrictions on the location of wells in winter habitat, and allow human access to all areas throughout the life of the producing gas field. My spatially explicit winter habitat model can be used to identify areas in the PRB that provide the best remaining habitat for sage-grouse in winter.
Acknowledgments
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Literature Cited


Table 1. Vegetation, topographic, and energy development variables that were evaluated as potential landscape predictors of sage-grouse winter habitat selection, Powder River basin, Montana and Wyoming, 2005 and 2006. Log-likelihoods were used to identify the best scale at which selection occurred for individual variables and to select variables (in bold) that competed in model selection.

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<th>Model Category</th>
<th>Variable</th>
<th>Buffer area</th>
<th>Log Likelihood</th>
<th>Odds ratio</th>
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<td>-898.349</td>
<td>0.960</td>
<td>0.987</td>
<td>0.934</td>
</tr>
<tr>
<td>Topography</td>
<td>Roughness</td>
<td>0.65-km²</td>
<td>-838.257</td>
<td>0.888</td>
<td>0.909</td>
<td>0.868</td>
</tr>
<tr>
<td>--------------</td>
<td>-----------</td>
<td>----------</td>
<td>----------</td>
<td>-------</td>
<td>-------</td>
<td>-------</td>
</tr>
<tr>
<td>Roughness</td>
<td>0.04-km²</td>
<td>-844.885</td>
<td>0.815</td>
<td>0.850</td>
<td>0.782</td>
<td></td>
</tr>
<tr>
<td>Roughness</td>
<td>4-km²</td>
<td>-848.668</td>
<td>0.921</td>
<td>0.936</td>
<td>0.905</td>
<td></td>
</tr>
<tr>
<td>Solar radiation</td>
<td>0.0009-km²</td>
<td>-902.677</td>
<td>0.997</td>
<td>1.002</td>
<td>0.992</td>
<td></td>
</tr>
</tbody>
</table>

| Slope        | 0.0009-km² | -863.384 | 0.879    | 0.907 | 0.852 |

<table>
<thead>
<tr>
<th>Energy Development</th>
<th>Distance to nearest well</th>
<th>-</th>
<th>-865.638</th>
<th>1.000</th>
<th>1.002</th>
<th>0.997</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number wells</td>
<td>4-km²</td>
<td>-857.717</td>
<td>0.961</td>
<td>0.985</td>
<td>0.939</td>
<td></td>
</tr>
<tr>
<td>Number wells</td>
<td>0.65-km²</td>
<td>-859.699</td>
<td>0.833</td>
<td>0.943</td>
<td>0.736</td>
<td></td>
</tr>
<tr>
<td>Number wells</td>
<td>0.04-km²</td>
<td>-863.083</td>
<td>0.434</td>
<td>1.102</td>
<td>0.171</td>
<td></td>
</tr>
</tbody>
</table>

---

4 Grass was excluded from further habitat models because of its correlation with sagebrush (r = -0.78)

5 Roughness = Index calculated using the standard deviation of a digital elevation model.
Table 2. Log-likelihood (LL), number of parameters (K), Akaike value (AIC), change in AIC value from the top model (ΔAIC) and Akaike weight (w_i) results of sage-grouse winter habitat selection for vegetation and topography models, Powder River Basin, Montana and Wyoming, winters of 2005 and 2006.

<table>
<thead>
<tr>
<th>Model</th>
<th>LL</th>
<th>K</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>w_i</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Vegetation Models</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sagebrusha + Conifer + Riparian + Barren</td>
<td>-716.337</td>
<td>5</td>
<td>1442.674</td>
<td>0.000</td>
<td>0.998</td>
</tr>
<tr>
<td>Sagebrush + Conifer + Riparian</td>
<td>-723.772</td>
<td>4</td>
<td>1455.544</td>
<td>12.870</td>
<td>0.002</td>
</tr>
<tr>
<td>Sagebrush + Conifer + Barren</td>
<td>-744.539</td>
<td>4</td>
<td>1497.078</td>
<td>54.404</td>
<td>0.000</td>
</tr>
<tr>
<td>Sagebrush + Conifer</td>
<td>-749.355</td>
<td>3</td>
<td>1504.710</td>
<td>62.036</td>
<td>0.000</td>
</tr>
<tr>
<td>Sagebrush + Riparian + Barren</td>
<td>-780.350</td>
<td>4</td>
<td>1568.700</td>
<td>126.026</td>
<td>0.000</td>
</tr>
<tr>
<td>Sagebrush + Riparian</td>
<td>-787.762</td>
<td>3</td>
<td>1581.524</td>
<td>138.850</td>
<td>0.000</td>
</tr>
<tr>
<td>Sagebrush + Barren</td>
<td>-799.877</td>
<td>3</td>
<td>1605.754</td>
<td>163.080</td>
<td>0.000</td>
</tr>
<tr>
<td><strong>Topography Models</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Roughnessb + Slopec</td>
<td>-835.881</td>
<td>3</td>
<td>1677.762</td>
<td>0.000</td>
<td>0.798</td>
</tr>
<tr>
<td>Roughness</td>
<td>-838.257</td>
<td>2</td>
<td>1680.514</td>
<td>2.752</td>
<td>0.202</td>
</tr>
<tr>
<td>Slope</td>
<td>-863.384</td>
<td>2</td>
<td>1730.768</td>
<td>53.006</td>
<td>0.000</td>
</tr>
</tbody>
</table>

a Vegetation variables = percent cover of each GIS vegetation category within a selected buffer distance chosen by LL values in Table 1.

b Roughness = Index calculated using the standard deviation of a digital elevation model.
Slope = slope of pixel calculated using a DEM
Table 3. Log-likelihood (LL), number of parameters (K), Akaike value (AIC), change in AIC value from the top model (ΔAIC) and Akaike weight ($w_i$) results of sage-grouse winter habitat model selection, Powder River Basin, Montana and Wyoming, winters of 2005 and 2006.

<table>
<thead>
<tr>
<th>Model$^a$</th>
<th>LL</th>
<th>K</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation$^b$ + Topography$^c$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>+ CBNG$^d$</td>
<td>-683.644</td>
<td>7</td>
<td>1381.288</td>
<td>0.000</td>
<td>0.965</td>
</tr>
<tr>
<td>Vegetation + Topography</td>
<td>-687.974</td>
<td>6</td>
<td>1387.948</td>
<td>6.660</td>
<td>0.035</td>
</tr>
<tr>
<td>Vegetation + CBNG</td>
<td>-718.083</td>
<td>5</td>
<td>1446.166</td>
<td>64.878</td>
<td>0.000</td>
</tr>
<tr>
<td>Vegetation</td>
<td>-723.772</td>
<td>4</td>
<td>1455.544</td>
<td>74.256</td>
<td>0.000</td>
</tr>
<tr>
<td>Topography + CBNG</td>
<td>-826.657</td>
<td>3</td>
<td>1659.314</td>
<td>278.026</td>
<td>0.000</td>
</tr>
<tr>
<td>Topography</td>
<td>-835.881</td>
<td>3</td>
<td>1677.762</td>
<td>296.474</td>
<td>0.000</td>
</tr>
<tr>
<td>CBNG</td>
<td>-857.717</td>
<td>2</td>
<td>1719.434</td>
<td>338.146</td>
<td>0.000</td>
</tr>
</tbody>
</table>

$^a$ Models represent the AIC best combination of variables within each model category

$^b$ Vegetation = % sagebrush and riparian within 4-km$^2$ and % conifer within 0.65-km$^2$

$^c$ Topography = roughness of land within 0.65-km$^2$ and slope

$^d$ CBNG = number of wells/4-km$^2$
Table 4. Logistic regression $\beta$-coefficients (SE) and odds ratios from the best model ($w_i = 0.965$) describing winter habitat selection and energy avoidance for sage-grouse, Powder River Basin, Montana and Wyoming, 2005 and 2006.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Estimate</th>
<th>SE</th>
<th>Odds Ratio</th>
<th>95% upper</th>
<th>95% lower</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-1.106</td>
<td>0.369</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Roughness$^a$</td>
<td>-0.039</td>
<td>0.017</td>
<td>0.962</td>
<td>0.994</td>
<td>0.931</td>
</tr>
<tr>
<td>Slope$^b$</td>
<td>-0.102</td>
<td>0.022</td>
<td>0.903</td>
<td>0.943</td>
<td>0.865</td>
</tr>
<tr>
<td>Conifer$^c$</td>
<td>-0.203</td>
<td>0.033</td>
<td>0.966</td>
<td>0.992</td>
<td>0.940</td>
</tr>
<tr>
<td>Sagebrush$^d$</td>
<td>0.028</td>
<td>0.004</td>
<td>0.816</td>
<td>0.871</td>
<td>0.765</td>
</tr>
<tr>
<td>Riparian$^e$</td>
<td>-0.131</td>
<td>0.026</td>
<td>1.028</td>
<td>1.037</td>
<td>1.020</td>
</tr>
<tr>
<td>CBNG wells$^f$</td>
<td>-0.035</td>
<td>0.014</td>
<td>0.877</td>
<td>0.923</td>
<td>0.834</td>
</tr>
</tbody>
</table>

$^a$Roughness = topographic index calculated as the SD of a DEM within 0.65-km$^2$.
$^b$Slope = slope of pixel calculated from DEM.
$^c$Conifer = % conifer cover within 0.65-km$^2$.
$^d$Sagebrush = % sagebrush cover within 4-km$^2$.
$^e$Riparian = % Riparian cover within 4-km$^2$.
$^f$CBNG = number of CBNG wells within 4-km$^2$. 
Figure 1. Reduction in the odds (solid line) and 95% confidence intervals (dashed line) of sage-grouse winter habitat use versus available habitat with increasing coal-bed natural gas (CBNG) well density, Powder River Basin, Montana and Wyoming, 2005-2006. Odds and 95% confidence intervals are based on 5,000 bootstrap samples with densities varying between 0-22 wells/4 km², the range of CBNG development we observed in my sample of used and available points.
Figure 2. Odds of sage-grouse winter habitat use in relation to % sagebrush cover/4 km², Powder River Basin, Montana and Wyoming, 2005-2006. Odds and 95% confidence intervals are based on 5,000 bootstrap samples with sagebrush varying from 0-100%, with and without coal-bed natural gas (CBNG) development. a) The grey line represents CBNG development (12.3 wells/4 km², 95% CI small dashed line) and the black line represents no CBNG development (0.0 wells/4 km², 95% CI large dashed line). b) The difference of means for odds of use with and without CBNG (black line minus grey line from part [a] above) is plotted against varying amounts of sagebrush cover/4 km² (95% CI dashed line).
Difference in odds ratios

% sagebrush cover/4 km²
Figure 3. Percent of sage-grouse use locations in each of 5 ordinal resource selection function bins (RSF category) we used to build (black bars, $n = 436$ locations from 2005-2006) and test (grey bars, $n = 74$ locations from 2004 and 2007) the winter habitat model, Powder River Basin, Montana and Wyoming.

\[ R^2 = 0.98 \]
CHAPTER 3: HIERARCHY OF HABITAT SELECTION BY NESTING SAGE-GROUSE

Abstract: Identifying the scales that influence habitat selection in sensitive or declining species is critical to successfully implementing conservation actions. I analyzed habitat selection by nesting female greater sage-grouse (*Centrocercus urophasianus*) at multiple scales in the Powder River Basin, Montana and Wyoming, USA. I used resource selection functions (RSF) to identify important predictors of selection at each scale, to map locations of important habitats in a GIS and to quantify the spatial extent at which landscapes should be managed for populations. Findings demonstrated that selection is best viewed hierarchically because individual patches of habitat coalesced to form landscapes capable of supporting populations. My model predicted an independent nest dataset ($R^2 = 0.99$) and twice the amount of nesting habitat (RSF bins 4 and 5) at 3, 5 and 10 km scales predicted the locations of active leks. Patch and local scale measures were the best predictors of selection but topographic and landscape predictors in the multi-scale model ($w_i = 0.96$) indicated that selection is dependent on factors that extend beyond the nest site. Sage-grouse selected for less rugged patches of high-density sagebrush with little tolerance for conifer, grassland and riparian habitats. Odds of nesting were greatest when 75% of a patch was in high-density sagebrush and when sagebrush canopy cover at the nest was 17-32%; selection for both attributes was inversely related to their availability. I caution managers to limit habitat treatments that modify or remove sagebrush because attempts to enhance one seasonal habitat may be detrimental to another. Increased emphasis on large-scale habitat management would improve current efforts directed at sage-grouse conservation.

Key words: *Centrocercus urophasianus*, greater sage-grouse, habitat, nesting, resource selection function, sagebrush, scale.

Conservation strategies for sensitive or declining species must encompass all habitat requirements within and between seasons to be successful. Studies of habitat selection using resource selection functions have been widely used to identify critical
habitat needs and map those habitats at appropriate scales for a wide range of species such as grizzly bears (*Ursus arctos*, McLoughlin et al. 2002), elk (*Cervus* Boyce et al. 2003), woodland caribou (*Rangifer tarandus*, Johnson et al. 2004); and greater sage-grouse (*Centrocercus urophasianus*, hereafter ‘‘sage-grouse’’, Aldridge and Boyce 2007, Doherty et al. 2008). However species vary in the extent or scale at which habitat influences selection such that habitat selection usually occurs at multiple scales and the absence of suitable large-scale habitat conditions may negate the value of otherwise suitable conditions at much smaller scales. For example, the absence of large-scale habitat characteristics minimizing wolf (*Canis lupus*) predation for woodland caribou cause areas with otherwise suitable small scale forage to be avoided (Rettie and Messier 2000). Understanding the combinations of habitat features at different scales that determine which habitats are most suitable and where those habitats are located is crucial for identifying appropriate conservation strategies.

The critical concept of scale in conservation research is now recognized by nearly all ecologists (Turner et al. 2001, Turner 2005, Urban 2005). Hierarchy theory suggests landscape scale context or constraints may influence species habitat selection as well as the interpretation of results of research conducted at finer scales (Bissonette 2003, Turner et al. 2001). Current research illustrates the importance of landscape context in interpretation of results of studies with small spatial extents such as duck nest success (Stephens et al. 2003), forest fragmentation affects (Andren 1995, Donovan et al. 1997, Hartley and Hunter 1998) or Capercaillie survival in Europe (Kurki and Linden 1995, Kurki et al. 2000). The relative importance of landscape-scale versus local scale habitat selection is also essential to fully understand life history characteristics and context of past literature.

Sage-grouse are a gallinaceous species native only to western semiarid sagebrush habitats (Schroeder et al. 1999). Previously widespread, loss and degradation of sagebrush habitat has resulted in extirpation of the species from almost half of its original range (Schroeder et al. 2004). All major reviews of sage-grouse suggest that the abundance of sagebrush at the landscape scale is required for the persistence of sage-grouse (Schroeder et al. 1999, Connelly et al. 2000a, Connelly et al. 2004, Crawford et al.
2004). However, only recently have studies quantified scale in habitat selection using GIS techniques (e.g., Aldridge and Boyce 2007, Doherty et al. 2008), and none have empirically evaluated the relative importance of landscape context to local scale habitat selection. Studies of sage-grouse nesting selection at small scales have dramatically increased our ecological understanding of habitat relationships (e.g., 24 peer reviewed sage-grouse nesting studies were recently reviewed in Hagen et al. 2007), but they do not convey spatially-explicit information about habitat quality at a scale useful for prioritizing landscapes for conservation, nor do they address landscape context or constraints in habitat selection. Ultimately the relative influence of local versus landscape variables should also be assessed in a competing-model framework when comprehensive data sets are available (Burnham and Andersen 2002, Boyce 2006). A multi-scale approach is needed to synthesize the vast local scale habitat research with the relative importance of landscape context to fully realize landscape conservation objectives for sage-grouse.

I investigated habitat selection of nesting sage-grouse in the Powder River Basin as part of a larger study testing the response of sage-grouse populations and individuals to energy development. Objectives of this component of the study were to: (1) create a robust habitat selection model for nesting sage-grouse, (2) evaluate the relative importance of local- versus landscape-scale factors influencing habitat selection, (3) assess the influence of coal-bed natural gas development (CBNG) on habitat selection, (4) validate the best approximating habitat model with independent datasets, and (5) use the model to identify specific portions of the landscape with a high probability of use by nesting females.

Study Area

My study area in the Powder River Basin covered portions of Johnson, Sheridan and Campbell counties in northeast Wyoming, and Bighorn, Rosebud, and Powder River Counties in southeast Montana. Shrub-steppe habitat was dominated by Wyoming big sagebrush (Artemisia tridentata wyomingensis) with an understory of native and non-native grasses such as bluebunch wheatgrass (Pseudoroegneria spicata), western
wheatgrass (*Agropyron smithii*), prairie junegrass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*), Japanese brome (*Bromus japonicus*), cheatgrass (*Bromus tectorum*), and crested wheatgrass (*Agropyron cristatum*). Plains silver sagebrush (*Artemisia cana*) was also present in drainages. Rocky mountain juniper (*Juniperus scopulorum*) and ponderosa pine (*Pinus ponderosa*) occurred in wooded draws and formed forests across the extreme northern extent of the study area. Conifers were largely absent from the southern half of the study area. Land use was dominated by cattle ranching, and only 4% of the landscape consisted of dry land or irrigated agriculture.

The Powder River Basin contains one of the largest energy fields in North America with >35,000 producing CBNG wells, and another 31,000 wells expected within a 2.4-million ha area (Naugle et al. *in press*). Impacts of CBNG to lek persistence in the Powder River Basin were severe (Walker et al. 2007) such that too few females remained within gas fields to evaluate habitat selection in areas with full development. Few leks within the extent of my imagery experienced full development (~100 wells/3.2-km radius around lek) and had ≥10 males. To capture meaningful numbers of females I largely captured sage-grouse at leks on the edge of CBNG fields and in newly developing areas.

**Methods**

**Marking and Monitoring Protocols**

I captured sage-grouse by rocket-netting (Giesen et al. 1982) and spotlighting (Wakkinen et al. 1992) on and around leks from March-April and July-October in 2003-2007 in 3 study areas: (1) Bighorn County, Montana, (2) Johnson County, Wyoming, and (3) Campbell County, Wyoming. In Campbell County in 2003 I monitored for 4 months 12 radio-marked females from 5 small leks (2-8 displaying males/lek) inside a gas field that contained ~100 wells within 3.2-km of leks (32 ha spacing) until a severe outbreak of West Nile virus resulted in the extirpation of this local population (Walker et al. 2004). I continued to trap and monitor sage-grouse at the edge and outside of development in 2004-2007 because only 1 lek inside of development within my study area had ≥10 displaying males (PPL lek in 2005; *n* = 13 males).
I aged and sexed grouse and fitted females with a 21.6-g necklace style radio collar with a 4-hour mortality switch (model A4060 Advanced Telemetry Systems Isanti, MN). I located sage-grouse nests by ground based radio tracking during the breeding seasons of 2003-2007. I used Global Positioning System (GPS) receivers (Garmin eTrex Legend) to record exact locations of nests after they hatched or failed. All GPS locations were collected when error estimates were < 7 m. I conducted GIS analyses at scales ≥100 m to ensure that inference was not confounded by GPS location error.

**Designation of Used and Available Sites**

I employed a used-available design to evaluate nesting habitat selection (Boyce et. al 2002, Manly et. al 2002, Johnson et al. 2006). I defined used points as nest locations of radio-marked females during 2003-2007. I separated nest locations used to build the model from those used as a test dataset for model validation. I used 381 nests from 2004-2006 to build the model and 146 nest locations from 2003 and 2007 to test the model. I also grouped test locations into those independent by year (n = 146) and independent by year and individual (n = 88) to avoid possible pseudo replication due to site fidelity of individuals to nesting areas (Holloran et al. 2005). Available nesting locations were randomly selected from a spatial Poisson distribution (Beyer 2004) proportional to the number of nests within a study area and year. I constrained available nest locations to a 5-km circle centered on either the lek of capture or the lek closest to where birds were captured via spotlighting (Holloran and Anderson 2005).

**GIS Habitat Classification**

I acquired SPOT-5 satellite imagery (Terra Image USA, Santa Barbara, CA) for the northern portion of the study area in August 2003 and for the southern part in August 2004 when the project expanded to encompass a larger geographic area. I rectified imagery using digital ortho-photographs from the National Agricultural Inventory Program (NAIP). I increased resolution of analyses from 100 m$^2$ to 25 m$^2$ by using the 25- m$^2$-pixel panchromatic image to perform pan-sharpening. I used eCognition™ 4.06 software (Definiens Imaging, Munich, Germany) to cluster pixels into regions representing spectrally similar ground features. I created a polygon database by exporting clusters into ArcGIS 9.2 software (Environmental Systems Research Institute,
Redlands, CA). I manually digitized agriculture, urban, water, and strip mines visually discernible on 1-m NAIP photos and pan-sharpened SPOT-5 imagery. I also collected field training points ($n = 7,092$) stratified by area and land ownership to classify 6 habitat cover classes: sagebrush, sagebrush/grassland mix, grassland, conifer, riparian and sparse vegetation. I also used training points to identify a cut off value for classifying sparse vegetation. Sparse vegetation was classified as those areas $>1.5$ SD below the mean spectral values for SPOT bands 1-4, Normalized Difference Vegetation Index, and the first principal component of the SPOT-5 imagery.

Final classification was a two-stage process. After manually digitized polygons for agriculture, water, mine, and urban areas were removed, I classified the landscape into three cover classes including prairie, riparian and conifer. Stage 1 cross validation accuracies using k-fold validation with 10 folds (Boyce et al. 2002) were 93.6% for prairie, 87.8% for riparian and 73.3% for conifer. I used photographs collected from an additional 716 training points to further sub-divide the prairie class into grassland, sagebrush/grassland mix (<10% sagebrush canopy cover) and moderate to high-density sagebrush (>10% sagebrush canopy cover). I identified cut off values for these new classes using descriptive statistics from the 716 stage 2 training points that characterized the multi-spectral information from raw satellite imagery within each polygon segment. Stage 2 accuracies within the prairie class were 97.0% for sagebrush, 71.6% for grassland, and 72.3% for sagebrush/grassland mix. Misclassification rates within the prairie class between sagebrush and grassland were $< 3%$.

**Habitat Variables at Multiple Scales**

I quantified characteristics of vegetation, topography and energy development around used and available locations in a GIS to evaluate habitat selection at 2 landscape scales (3- and 1.5-km radii), 2 patch scales (0.35- and 0.10-km radii) and 1 local scale $\leq 15$ m of the nest. The 2 landscape scales (3 and 1.5 km) were selected to capture natural or anthropogenic processes thought to influence habitat selection, such as topography (Doherty et al. 2008) or modifications to land use that result in loss of sagebrush (Knick et al. 2003). I selected the two patch scales (0.35 and 0.10 km) as potential surrogates for mechanisms that affect habitat selection at extents intermediate to those at larger scales. I
used established protocols (Connelly et al. 2003) to quantify local vegetative features known to influence habitat selection within 15 m of nest and available points (e.g., Connelly et al. 2000a, Hagen et al. 2007). I considered most variables at all landscape and patch scales because little a priori information was available to predict the scale at which variables most strongly influenced habitat selection (Burnham and Anderson 2002).

I calculated abundance of dominant habitat types as percent of area of each of the 6 cover classes at each of 4 landscape and patch scales. I calculated percent area at patch scales by summing the number of 25-m² pixels in classified imagery. I also summed pixels at landscape scales after re-sampling imagery from 25-m² to 625-m² because processing small pixels at large spatial extents exceeded my computational capacity. I included a quadratic term for percent high-density sagebrush to further evaluate if sage-grouse select for intermediate densities of sagebrush (Aldridge and Boyce 2007). I used topography to calculate roughness of the landscape as the standard deviation of a digital elevation model (900-m² resolution; Doherty et al. 2008). I used density of CBNG wells to quantify the extent of energy development. Wells were digitally mapped and publicly available from the Wyoming Oil and Gas Conservation Commission and Montana Board of Oil and Gas Conservation. I quantified length of roads and power lines within each scale and estimated the distance to the nearest CBNG well, road and power line.

Locations of power lines were obtained digitally from Powder River Energy from 2004-2007. Time stamps on locations of wells and power lines enabled us to depict annual additions to human infrastructure. I mapped new roads each spring using hand-held GPS units because extensive CBNG development occurred following acquisition of imagery.

Local-scale vegetative variables immediate to the nest or available points included shrub canopy cover, shrub density, shrub height, nest shrub height, visual obstruction and grass height (e.g., Connelly et al. 2000a, Hagen et al. 2007). These measures at used locations were centered on the nest bowl. I collected shrub canopy cover using the line-intercept method (Canfield 1941, Connelly et al. 2003) along two perpendicular 30-m line transects centered on the nest bowl at used locations. Transects at available locations were centered on the shrub nearest to the random point and >35 cm in height. I included
a quadratic term for shrub canopy cover to evaluate if sage-grouse select for intermediate canopy cover (Aldridge and Boyce 2007). Density of shrubs >15 cm in height were counted within 1 m on either side of line transect (total number of shrubs / 120 m²). I also measured the average of recorded heights of the nearest shrub within 1 m at 3-m intervals along the transect line. I estimated visual obstruction by collecting height-density readings (5-cm segments) at 0, 1, 3 and 5 m from the nest or random nest shrub in each cardinal direction 4 m from the pole at a height of 1 m horizontal to the pole (Robel et al. 1970). I collected vegetative droop height of nearest and tallest grass within Daubenmire plots (Daubenmire 1959).

**Statistical Analyses**

I employed logistic regression with used and available points for model selection and RSF model parameter estimates (Boyce 2002, Manly 2002, Johnson et al. 2006). I identified resource use for each nesting individual and defined availability at the population level (Design II; Erickson et al. 2001, Manly et al. 2002).

I first assigned variables into one of 4 model categories: topography and vegetation variables at landscape, patch or local scales. I tested each variable individually and removed those with odds ratios that overlapped 1.0. I then tested scale for each variable and selected the scale that best represented habitat selection for each category. I then allowed each variable to compete with all other possible combinations of variables within the same model category to identify the most parsimonious model. I used information-theoretic methods (Burnham and Andersen 2002) to choose between competing models based on Akaike’s Information Criterion values adjusted for small sample size (AICc). I brought models within 2 AICc units to the next hierarchy of model selection. After identifying the top model(s) within vegetation (landscape, patch and local) and topography, I allowed models to compete across categories to see if the additional information increased model fit. After selecting the AICc best approximating habitat model, I repeated the process of variable screening and hierarchical selection using energy variables, and added the AICc best supported CBNG model to the AICc best approximating habitat model. I examined the resulting AICc value and coefficient for CBNG development to evaluate sage-grouse response to energy development.
I validated the final statistical model on 2003 and 2007 data and tested if parameter estimates were stable across years and whether AIC$_c$ model selection supported the top habitat model and inclusion of anthropogenic variables. I calculated AIC$_c$ because the ratio of nests ($n = 166$ nests in 2003; $n = 292$ in 2003 and 2007) to $K$ was < 40 (Burnham and Andersen 2002). I quantified distances from nests to CBNG wells and roads separately for yearlings and adults to assess whether an age-specific analysis was justified because recent findings suggest that yearling females avoid energy development within natal areas whereas adults may not due to nest-site fidelity (Holloran et al. 2007). I validated the AIC$_c$ best approximating habitat and energy model using nests from 2007 because CBNG roads were not mapped in 2003.

I did not allow highly correlated variables ($r \geq 0.7$) in the same model at any level of model selection. If variables were correlated ($r \geq 0.7$), I chose the variable I felt had the greatest biological meaning according to known characteristics of habitat selection from published studies. When variables in the same model were moderately correlated (i.e., $0.3 \leq r < 0.7$), I checked for stability and consistency of regression coefficients. I removed the least relevant variable from analysis if a coefficient switched signs or standard errors substantially increased.

I turned my statistical model into a spatially explicit model that could be linked to a GIS by employing the RSF model:

\[ w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k), \]  

where $w(x)$ is the raw RSF value for each pixel in the landscape; $x_1, x_2, \ldots, x_k$ represent values for vegetation, topography, and CBNG variables generated from a moving-window analysis for each pixel; and $\beta_1, \ldots, \beta_k$ are the model parameters estimated from logistic regression (Boyce 2002, Manly 2002, Johnson et al. 2006). I applied $\beta$-coefficients from equation 1 to GIS layers identified in model selection in ArcView 9.2 Spatial Analyst. The output was a new GIS layer that represented RSF values for each individual pixel over the entire landscape.

I performed a bootstrap analysis to depict relationships between key predictor variables and odds of habitat use by nesting females. I used beta coefficients from the AIC$_c$ best approximating model that received overwhelming support ($w_i = 0.960$). I used
the logistic equation to generate odds of use for each bootstrap dataset \((n = 5,000)\) by applying model coefficients to mean values of parameters at nest locations while systematically varying predictor variables over the observed range of values. I computed odds of habitat use with the logistic equation for each simulation. I then ordered the odds ratios and used a rankit adjustment (Chambers et al. 1983) to compute 2.5% and 97.5% percentiles for upper and lower 95% CIs. I evaluated availability of selected habitat by comparing odds of use with the graphical distribution of the key predictor at available locations throughout the study area.

I validated my spatial model with an independent set of nest locations collected in 2003 and 2007. I categorized RSF values for individual pixels into 5 ordinal 20% quantile bins representing progressively selected habitats. I then ran a regression of the observed proportion of the test data set in each RSF bin against the expected proportion of use from the original RSF model to evaluate model fit (Johnson et al. 2006). A model with good fit should show similar patterns between build and test data sets, have a high validation \(R^2\) value, a slope not different from 1.0, and an intercept not different from zero (Johnson et al. 2006).

I also validated my model against known lek locations. Hotspot theory of lek evolution suggests that leks become established in landscapes where males are most likely to encounter receptive, pre-nesting females (Schroeder and White 1993, Gibson 1996) and leks typically occur centrally within suitable nesting habitat (Holloran and Anderson 2005). Thus, I reasoned that a robust nest model should predict greater nesting habitat around leks than available locations because leks are not located randomly. I tested this prediction by quantifying in a GIS the amount of area that my model classified as nesting habitat (RSF bins 4 and 5 see results) within 3-, 5- and 10-km of active leks and available locations. I obtained locations and counts of displaying males at known leks data bases maintained by Wyoming Game and Fish Department and Montana Fish, Wildlife and Parks. I used 88 leks that had \(\geq 5\) males counted in 2005, the mid-point of my 5-yr study, reasoning that leks with at least 5 males are likely to support breeding populations. I randomly selected for comparison 88 available locations from a spatial Poisson distribution (Beyer 2004).
Results

Landscape scales (3 and 1.5 km).—Amount of high-density sagebrush, riparian area and tillage agriculture were predictors of habitat selection at the 1.5 km landscape scale (Table 1). Selection was positively related to area of high-density sagebrush (44.6% [SE = 0.8] of area around nests vs 40.7% [SE 0.7] of area around available points; \(P = 0.020\)) and negatively associated with area of riparian habitat (0.4% [SE 0.1] vs 1.2% [SE 0.7]; \(P < 0.001\)) and tillage agriculture (0.1% [SE 0.1] vs 0.8% [SE 0.26]; \(P = 0.040\)).

Patch scales (0.35 and 0.10 km).—Amounts of riparian area at 0.35 km and high-density sagebrush, grassland and conifer at 0.10 km were predictors of habitat selection at patch scales (Table 2). Females selected areas with less riparian vegetation (0.3% [SE 0.1] around nests vs 1.4% [SE 0.2] around available points; \(P < 0.001\)), less grassland (4.6% [SE 0.5] vs 11.1% [SE 0.9]; \(P = 0.002\)) and less conifer (0.4% [SE 0.1] vs 1.2% [SE 0.7]; \(P = 0.022\)). Sparse vegetation at 0.10 km was the only patch scale variable that did not increase model fit (+1.99 AICc units; Table 2). I removed sparse vegetation from further modeling because its inclusion destabilized coefficients, inflated SEs and decreased model fit. Females selected less rough terrain for nesting at 0.10 km (-3.8 AICc points; Table 2). A quadratic term modeling the amount of high-density sagebrush at 0.10 km was moderately supported (\(w_i = 0.60\); Table 2). Nesting sage-grouse selected for patches containing high-density sagebrush (52.3% [SE = 1.3] of area around nests vs 41.6% [SE 1.5] available points; \(P = 0.001\)). Odds of use were highest when 75% of area within 0.10 km of a nest was in high-density sagebrush cover (odds = 1.58 [95% CIs = 1.36-1.91]; Figure 1). Average odds of use remained above 1.00 at 100% sagebrush cover but dropped below 1.00 when < 25% of area around the nest was high-density sagebrush (Figure 1). Selection for high-density sagebrush was inversely related to its abundance; only 14.6% of patches contained \(\geq 75\%\) high-density sagebrush (Figure 1).

Local scale.—Predictors of habitat selection at the local scale included visual obstruction as estimated by the Robel index and sagebrush canopy cover (Table 1). Selection was positively related to increasing estimates of visual obstruction near the nest (15.6 cm [SE 0.4] at nests vs. 11.7 cm [SE 0.4] at available points). Sagebrush canopy
cover averaged 19.1% (SE 0.5) at nests compared to 11.6 % (SE 0.5) at available locations. The AICc best approximating model included the quadratic term for sagebrush canopy cover and visual obstruction (\(w_1 = 0.69\); Table 1). Sage-grouse nested in sagebrush when canopy cover was 9-41% but odds of use were highest at 25% sagebrush canopy cover; birds were twice as likely to nest in stands of sagebrush when canopy cover was 17-32% than when values were lower or higher (Figure 2). Sagebrush canopy cover exceeded 40% at 2.7% of nest locations.

Combining models across scales.—Local scale variables were stronger predictors of nesting selection independently, but a combined model including habitat variables from all scales investigated had overwhelming statistical support (-41.6 AIC units; Table 4). Sage-grouse selected for patches of high-density sagebrush (Figure 1) and flat topography at 0.10 km, for sagebrush canopy cover at the local scale (Figure 2), and against conifer and grassland at 0.10 km and riparian cover at 0.35 km (Table 5) in the AICc best approximating habitat model. I removed from the combined landscape and patch scale model 2 variables at the 1.5 km scale because they were correlated with the same attributes at patch scales (\(r = 0.61\) for sagebrush at 0.10 km and \(r = 0.63\) for riparian at 0.35 km). Model fit improved 2.02 AICc units after their removal. I opted to remove landscape variables because patch level attributes remained stable when models were combined but standard errors of landscape coefficients became inflated and their odds overlapped 1.0. I also removed from the combined patch and local scale model the high-density sagebrush quadratic term (0.10 km) because it explained the same source of variation as the sagebrush canopy cover quadratic term. I removed the patch scale variable because when model classes were combined the coefficient of high-density sagebrush switched signs. Model fit improved by another 2.44 AICc units.

Energy development.—Study areas in which I monitored nesting females on the edge of CBNG experienced low development that averaged one-third (< 35 wells within 28.27 km² of available points; 81 ha spacing) of conventional well densities (32 ha spacing). In 2007 the Johnson County study area averaged half of conventional well density (61 ha spacing). The only study site that approached full field development (41 ha spacing) was Campbell County in 2003. Within low density CBNG development the
best predictors of selection were lengths of roads at 1.5 and 0.35 km and distances to roads and CBNG wells; all other variables had odds ratios that overlapped 1.0. Lengths of roads at 1.5 and 0.35 km could not be used in the same model because they were highly correlated ($r = 0.72$). Distances to roads and distance to CBNG wells were also moderately correlated ($r = 0.45$); distance to road was the better predictor (-11.54 AIC$_c$ units). Distance to road was also the best overall predictor (-0.71 AIC$_c$ units) when models were combined across categories with lengths of roads at 1.5 or 0.35 km. When distance to road was in the same model as length of roads at 1.5 or 0.35 km the coefficient for distance to road remained stable but SEs for lengths of roads at both scales became inflated and resulting odds ratios overlapped 1.0. The addition of distance to road to my AIC$_c$ best approximating habitat model increased model fit (-16.72 AIC$_c$ units). The coefficient for distance to road ($\beta_{\text{distroad}} = 0.0002$) suggested that nesting sage-grouse may avoid CBNG roads.

*Model Validation.*—Model validation showed uncertainty in the effects of anthropogenic disturbance but not habitat variables. Model validation using an independent set of nest locations in 2007 did not support inclusion of distance to road with the AIC$_c$ best approximating habitat model. When tested, distance to road did not improve model fit ($\Delta$AIC$_c$ increased 0.91), the coefficient switched signs, SEs increased and the odds ratio overlapped 1.0. Age-specific models were not tested because average distances to roads and CBNG wells were similar for yearlings and adults ($P > 0.05$) and 95% CIs of distances overlapped for each study site in each year. Model validation using an independent set of nest locations in 2003 and 2007 did not support inclusion of the amount agriculture at 1.5 km to the best approximating habitat model. When tested, AIC$_c$ model selection showed slightly increased model fit (AIC$_c$ - 1.28), however the coefficient switched signs, SEs increased and the odds ratio overlapped 1.0. Road and agriculture variables were removed from the final model that I turned into a spatially explicit nest occurrence model (Table 5).

My AIC$_c$ best approximating model (Table 5) predicted sets of nests independent by year and individual from those used to build the model ($R^2 = 0.99$; Figure 3). Approximately 70% of nests used to build and test my model fell within just 20% of the
landscape (RSF bin 5). Likewise >90% of nest locations fell within 40% of the landscape (RSF bins 4 and 5; Figure 3).

The model I linked to GIS also predicted locations of active leks because individual pixels as identified by patch scale variables at 0.35 and 0.10 km coalesced into landscapes capable of supporting nesting populations (Figure 4 and 5). Landscapes with active leks contained twice the amount of nesting habitat (RSF bins 4 and 5) as available locations at each of the 3 scales evaluated (Figure 4 and 5).

**Discussion**

My analyses clearly demonstrate landscape context must be considered in addition to local scale habitat features and give managers a hierarchical filter in which to view and manage sage-grouse nesting habitats. Past research has shown that multiple spatial scales often define species habitat relationships (e.g., Johnson 1980). This is the case for sage-grouse and modeling habitat hierarchies allowed unique insight into this multi-scale relationship. First, linking patch scale nesting habitat selection with a GIS elucidated higher order selection by documenting coalescence of nesting patches into large nesting landscapes capable of supporting populations (Figure 5). Both patch and local scale measures were the best predictors of nest site selection (Tables 4 and 5) but twice the amount of nesting habitat (RSF bins 4 and 5) at 3, 5 and 10 km scales predicted the locations of active leks (Figure 4 and 5). Leks can be used as an indicator of population level selection because leks that hens breed on are a strong predictor of final nesting locations (64% within 5-km, Holloran et al. 2005; 95% within 10-km this study). Further, hotpot theory of lek placement states that leks form in environs, such as high quality nesting areas, to increase encounter rates of breeding females (Schroeder and White 1993, Gibson 1996). The magnitude of differences in amounts of predicted nesting habitat between leks and available landscapes coupled with stability of this result out to very large extents (i.e. 5 and 10 km; Figure 4) shows at landscape scales selection is not random. Second, within the patch scale, the strength and diversity of GIS predictors clearly shows that nesting decisions are not solely based on amount of sagebrush within a patch or the traditional vegetation plot (Figures 3 and 4, Tables 2 and 5). Both patch and
landscape predictors substantially improved model fit and a combined local, patch, and landscape model had overwhelming statistical support ($w_i = 0.96$, Table 4). Finally, below the patch scale, simultaneous quantification of local scale selection validate the importance of the extensive local scale literature (e.g., Connelly et al. 2000a, Hagen et al. 2007) and provides managers with on-the-ground vegetation goals for local areas once priority landscapes are identified.

Seasonal habitats of sage-grouse that vary strongly by life stage reiterate the vast size and diversity of landscapes necessary to support populations. Habitat relationships showed that sage-grouse select for less rugged patches of high-density sagebrush (Figure 1) with little tolerance for conifer, grassland and riparian habitats (Table 5). However, riparian habitats that sage-grouse avoid during nesting may provide forbs and insects for broods in late-summer (Crawford et al. 2004, Dahlgren et al. 2006), and extremely dense sagebrush canopy (>40%) under which birds were unlikely to nest (Figure 2) may be a reliable food supply in deep snow in winter (Beck 1977, Hupp and Braun 1989). My results indicate habitat treatments in the PRB should avoid removing areas with high-density sagebrush. Sage-grouse selected for nest sites with high sagebrush canopy cover at the local scale (peak 25%, range 9-41%) even though areas with canopy cover >15% are uncommon (Figure 2). Many papers indicate that sagebrush removal can adversely impact sage-grouse (e.g., Klebenow 1970, Connelly et al. 2000 a, b, Leonard et al. 2000, Smith et al. 2005, Walker et al. 2007), but there appears to be no peer-reviewed research showing that burning, spraying, or mechanically removing sagebrush has substantial positive impacts to grouse. My results corroborate recommendations of Woodward (2006), who stated that management for herbaceous cover may positively influence sage-grouse but management should not come at the expense of sagebrush canopy. The range of canopy cover selection (Figure 2) agrees with the published sage-grouse habitat guidelines of Connelly et al. (2000a) and the recent meta-analysis of sage-grouse nest-site selection (Hagen et al. 2007).

Impacts of energy development to sage-grouse populations are well documented (Naugle et al. in press) but nesting response to full development could not be thoroughly investigated here because severity of CBNG development to leks in the PRB (Walker et
al. 2007) left too few birds to monitor inside gas fields. The best energy development predictor for birds that nested on the edge or within low levels of CBNG development increased model fit (-16.72 units) of my AIC best habitat model (Table 4). This finding is equivocal because an independent test of this model did not support inclusion of distance to road to the AIC best habitat model. My inability to validate findings or capture large samples of sage-grouse in fully developed fields is not surprising because Holloran et al. (2007) reported high female nest site fidelity, but lower survival of nesting adult sage-grouse in gas fields combined with avoidance of infrastructure by yearlings resulted in a time lag of 3-4 years between the onset of development activities and lek loss (Holloran 2005). The time lag observed by Holloran (2005) in the Pinedale Anticline in southwest Wyoming matched that for leks that became inactive 3-4 years following CBNG development in the PRB (Walker et al. 2007). The extent and pace of energy development requires landscape planning to reduce impacts (Chapter 5), and spatial analyses that integrate multiple life stages can identify landscapes capable of supporting populations (Naidoo et al. 2006, Margules and Sarkar 2007).

Validation with independent leks and nest data sets confirmed that failing to manage at larger scales is likely to negate habitat values for nesting sage-grouse at smaller scales. Selection for large and intact sagebrush landscapes is an emerging theme in the sage-grouse literature that applies to multiple life stages. Individual wintering sage-grouse in northeast Wyoming selected for sagebrush-dominated landscapes (4 km²) with little tolerance for other habitat types or anthropogenic disturbance (Doherty et al. 2008). An endangered population of sage-grouse in Alberta, Canada, selected for sagebrush-dominated landscapes and avoided anthropogenic disturbances during nesting and brood-rearing seasons at the largest scale evaluated (1 km²; Aldridge and Boyce 2007). Two additional lines of evidence suggest that conservation actions may need to extend as far as 10 km from leks to maintain populations. Nesting females reduced predation risk by dispersing widely such that > 90% of nests were within 10 km of a lek in this study (54, 79 and 97% of nests within 3, 5 and 10 km of lek) and throughout central and southwest Wyoming (45, 64 and 91%; Holloran and Anderson 2005). More importantly, females that spaced their nests more closely to one another had lower nest
success (Holloran and Anderson 2005), a vital rate that explains 31% of population growth (Walker and Naugle in press). In Alberta, Canada, nest and brood source habitats were within 6 km of active leks, but a curvilinear relationship suggested a threshold at 10 km of leks, within which 90% of all predicted source habitat occurred (Aldridge and Boyce 2007).

**Management implications**

Focusing conservation efforts for sage-grouse at the local scales without considering landscape context may negate the effectiveness of conservation actions. When developing conservation plans careful thought needs to be given to both landscape context and local scale habitat requirements. Even if local scale habitat conditions are met (Figures 4 and 5) areas will likely be avoided if they are not embedded in suitable landscape scale habitat allowing nesting hens to disperse (Holloran et al 2005). Spatially explicit models provide resource managers with a practical tool to incorporate landscape context to guide conservation (Figure 5). Further, mapping and quantifying spatially explicit models in a GIS empirically support prior suggestions (Schroeder et al. 1999, Connelly et al. 2000a, 2004, Crawford et al. 2004) that maintenance of sagebrush-dominated landscapes is fundamental to persistence of populations. A sagebrush-dominated landscape 314 km² in size (3.4 townships) is a biologically defensible estimate of the area necessary to maintain nest success for a group of females that distribute their nests within 10 km of a single lek (this study, Holloran and Anderson 2005). The average distance to leks across all of management zones I and II was 4.8-km (Chapter 5), thus a 10-km buffer will likely envelope neighboring leks, but size of a landscape capable of supporting the nesting area of a number of lek-complexes could easily exceed 1,000 km² (> 10 townships). Additional habitat area necessary to maintain a population depends largely upon its migratory status and juxtaposition of other seasonal habitats (Connelly et al. 2000a). I encourage managers to implement actions that conserve sagebrush-dominated landscapes but caution them to carefully consider habitat treatments that modify or remove sagebrush because attempts to enhance one seasonal habitat may be detrimental to another. Scarcity of dense sagebrush at patch and local scales suggests
that its removal is not warranted in most landscapes that support nesting sage-grouse in the Powder River Basin.

**Acknowledgments**

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Table 1. Model selection at landscape scales for nesting sage-grouse ($n = 381$) in the Powder River Basin, Montana and Wyoming, 2004-2006.

<table>
<thead>
<tr>
<th>Model$^a$</th>
<th>LL</th>
<th>K</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta\text{AIC}_c$</th>
<th>$w_i$</th>
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$^a$Log-likelihood (LL), number of parameters (K), Akaike Information Criterion value ($\text{AIC}_c$), change in AIC value from the top model ($\Delta\text{AIC}_c$), and Akaike weight ($w_i$)

$^b$Rip = % riparian area within 1.5 km of nests and available locations

$^c$Sage = % high-density sagebrush at 1.5 km

$^d$Ag = % tillage agriculture at 1.5 km

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<tr>
<th>Model (^a)</th>
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<tr>
<td>-----------------------------------</td>
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<td>------</td>
</tr>
<tr>
<td>Rip&lt;sup&gt;b&lt;/sup&gt;+Grass&lt;sup&gt;c&lt;/sup&gt;+Sage&lt;sup&gt;d&lt;/sup&gt;+Conif&lt;sup&gt;e&lt;/sup&gt;</td>
<td>-523.89</td>
<td>2</td>
<td>1051.79</td>
<td>81.45</td>
<td>0.00</td>
</tr>
<tr>
<td>Vegetation and topography</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Patch&lt;sup&gt;g&lt;/sup&gt;+Roughness&lt;sup&gt;h&lt;/sup&gt;</td>
<td>-477.25</td>
<td>6</td>
<td>966.49</td>
<td>0.00</td>
<td>0.87</td>
</tr>
<tr>
<td>Patch</td>
<td>-480.17</td>
<td>5</td>
<td>970.33</td>
<td>3.84</td>
<td>0.13</td>
</tr>
<tr>
<td>Sagebrush quadratic test</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sage&lt;sup&gt;i&lt;/sup&gt; + Roughness</td>
<td>-475.84</td>
<td>7</td>
<td>965.68</td>
<td>0.60</td>
<td></td>
</tr>
<tr>
<td>Patch + Roughness</td>
<td>-477.25</td>
<td>6</td>
<td>966.49</td>
<td>0.40</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>Log-likelihood (LL), number of parameters (K), Akaike Information Criterion value (AIC<sub>c</sub>), change in AIC<sub>c</sub> value from the top model (ΔAIC<sub>c</sub>), and Akaike weight (wij)

<sup>b</sup>Rip = % riparian area at 0.35 km

<sup>c</sup>Grass = % grassland at 0.10 km

<sup>d</sup>Sage = % high-density sagebrush at 0.10 km

<sup>e</sup>Conif = % conifer at 0.10 km

<sup>f</sup>Spar = % sparse vegetation at 0.10 km

<sup>g</sup>Patch = AIC<sub>c</sub> best approximating set of patch-scale predictors

<sup>h</sup>Roughness = topographic index calculated as SD of a digital elevation model at 0.10 km

<sup>i</sup>Sage<sup>2</sup> = Quadratic term to evaluate if birds select for intermediate densities of sagebrush
Table 3. Local-scale model selection for nesting sage-grouse in the Powder River Basin ($n = 381$), Montana and Wyoming, 2004-2006.

<table>
<thead>
<tr>
<th>Model(^a)</th>
<th>LL</th>
<th>K</th>
<th>AIC(_c)</th>
<th>∆AIC(_c)</th>
<th>(w_i)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sage(^2) + Robel(^c)</td>
<td>-436.39</td>
<td>4</td>
<td>880.78</td>
<td>0.00</td>
<td>0.69</td>
</tr>
<tr>
<td>Sage(^2) + Robel + Silver(^d)</td>
<td>-436.21</td>
<td>5</td>
<td>882.41</td>
<td>1.64</td>
<td>0.31</td>
</tr>
<tr>
<td>Sage(^2)</td>
<td>-446.84</td>
<td>3</td>
<td>899.68</td>
<td>18.90</td>
<td>0.00</td>
</tr>
<tr>
<td>Sage(^e) + Robel</td>
<td>-456.77</td>
<td>3</td>
<td>919.55</td>
<td>38.77</td>
<td>0.00</td>
</tr>
<tr>
<td>Sage + Robel + Silver</td>
<td>-456.40</td>
<td>4</td>
<td>920.80</td>
<td>40.03</td>
<td>0.00</td>
</tr>
<tr>
<td>Sage</td>
<td>-464.16</td>
<td>2</td>
<td>932.32</td>
<td>51.55</td>
<td>0.00</td>
</tr>
<tr>
<td>Sage + Silver</td>
<td>-464.09</td>
<td>3</td>
<td>934.18</td>
<td>53.40</td>
<td>0.00</td>
</tr>
<tr>
<td>Robel</td>
<td>-484.92</td>
<td>2</td>
<td>973.84</td>
<td>93.06</td>
<td>0.00</td>
</tr>
<tr>
<td>Shrub Height(^f)</td>
<td>-488.87</td>
<td>2</td>
<td>981.74</td>
<td>100.97</td>
<td>0.00</td>
</tr>
<tr>
<td>Silver</td>
<td>-516.79</td>
<td>2</td>
<td>1037.57</td>
<td>156.80</td>
<td>0.00</td>
</tr>
</tbody>
</table>

\(^a\)Log-likelihood (LL), number of parameters (K), Akaike Information Criterion value (AIC\(_c\)), change in AIC\(_c\) value from the top model (ΔAIC\(_c\)), and Akaike weight (\(w_i\))

\(^b\)Sage\(^2\) = Quadratic term to evaluate if birds select for intermediate canopy coverage of Wyoming big sagebrush
Robel = Estimated height-density readings within 4 m of the nest
Silver = Silver sagebrush canopy cover
Sage = Wyoming big sagebrush canopy cover
Shrub height = Average height of shrubs within 30 m of the nest
Table 4. Multi-scale model selection for nesting sage-grouse \((n = 381)\) in the Powder River Basin, Montana and Wyoming, 2004-2006\(^a\).

<table>
<thead>
<tr>
<th>Model(^a)</th>
<th>LL</th>
<th>K</th>
<th>AIC(_c)</th>
<th>(\Delta)AIC(_c)</th>
<th>(w_i)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Landscape(^b) + Patch(^c) + Local</td>
<td>-410.57</td>
<td>9</td>
<td>839.13</td>
<td>0.00</td>
<td>0.96</td>
</tr>
<tr>
<td>Patch + Local</td>
<td>-414.74</td>
<td>8</td>
<td>845.48</td>
<td>6.35</td>
<td>0.04</td>
</tr>
<tr>
<td>Landscape + Local</td>
<td>-426.23</td>
<td>7</td>
<td>866.45</td>
<td>27.32</td>
<td>0.00</td>
</tr>
<tr>
<td>Local(^d)</td>
<td>-436.39</td>
<td>4</td>
<td>880.78</td>
<td>41.64</td>
<td>0.00</td>
</tr>
<tr>
<td>Landscape + Patch</td>
<td>-470.56</td>
<td>8</td>
<td>957.11</td>
<td>117.98</td>
<td>0.00</td>
</tr>
<tr>
<td>Patch(^e)</td>
<td>-475.84</td>
<td>7</td>
<td>965.68</td>
<td>126.55</td>
<td>0.00</td>
</tr>
<tr>
<td>Landscape(^f)</td>
<td>-509.01</td>
<td>4</td>
<td>1026.03</td>
<td>186.90</td>
<td>0.00</td>
</tr>
</tbody>
</table>

\(^a\)Log-likelihood (LL), number of parameters (K), Akaike Information Criterion value (AIC\(_c\)), change in AIC\(_c\) value from the top model (\(\Delta\)AIC\(_c\)), and Akaike weight (\(w_i\))

\(^b\)% sagebrush and riparian area at 1.5 km were removed because the same variables at patch scales explained similar variation

\(^c\)Quadratic term for sagebrush canopy cover at 0.10 km was removed because the same local-scale variable explained similar variation

\(^d\)Local = Quadratic sagebrush canopy cover and Robel index

\(^e\)Patch = % riparian area at 0.35 km and % grassland, conifer, quadratic high-density sagebrush, and roughness index at 0.10 km

\(^f\)Landscape = % riparian, sagebrush, and tillage agriculture at 1.5 km

<table>
<thead>
<tr>
<th>Parameter(^a)</th>
<th>Estimate</th>
<th>SE</th>
<th>Odds ratio</th>
<th>Lower CI</th>
<th>Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>0.069</td>
<td>0.295</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conifer(^b)</td>
<td>-0.070</td>
<td>0.029</td>
<td>0.932</td>
<td>0.880</td>
<td>0.988</td>
</tr>
<tr>
<td>Grassland(^c)</td>
<td>-0.022</td>
<td>0.007</td>
<td>0.979</td>
<td>0.965</td>
<td>0.992</td>
</tr>
<tr>
<td>Riparian(^d)</td>
<td>-0.289</td>
<td>0.067</td>
<td>0.749</td>
<td>0.657</td>
<td>0.853</td>
</tr>
<tr>
<td>Sagebrush(^e)</td>
<td>0.026</td>
<td>0.010</td>
<td>1.026</td>
<td>1.006</td>
<td>1.047</td>
</tr>
<tr>
<td>Sage(^2)</td>
<td>-2.0E-04</td>
<td>0.0001</td>
<td>0.999</td>
<td>1.001</td>
<td>0.999</td>
</tr>
<tr>
<td>Roughness(^g)</td>
<td>-0.064</td>
<td>0.026</td>
<td>0.938</td>
<td>0.890</td>
<td>0.988</td>
</tr>
</tbody>
</table>

\(^a\)\(\beta\)-coefficients, SEs, odds ratios and 95% upper and lower CIs for the \(\text{AIC}_c\)

\(^b\)Conifer = % conifer area at 0.10 km

\(^c\)Grassland = % grassland area at 0.10 km

\(^d\)Riparian = % riparian area at 0.35 km

\(^e\)Sagebrush = % high-density sagebrush at 0.10 km

\(^f\)Sage\(^2\) = Quadratic term to evaluate if birds select for intermediate canopy coverage of Wyoming big sagebrush

\(^g\)Roughness = topographic index calculated as the SD of a digital elevation model at 0.10 km
Figure 1. Odds of sage-grouse nesting habitat use versus available habitat with increasing amounts of high density sagebrush within a 100-m buffer, Powder River Basin, Montana and Wyoming 2004-2006. Odds (solid line) and 95% confidence intervals (dashed line) are based on 5,000 bootstrap samples with percent high density sagebrush within a 100-m buffer varying between 0 - 100%. Grey bars represent the percent of available nests locations within each sagebrush canopy cover category ($n = 381$).
Figure 2. Odds of sage-grouse nesting habitat use versus available habitat with increasing sagebrush canopy cover, Powder River Basin, Montana and Wyoming 2004-2006. Odds (solid line) and 95% confidence intervals (dashed line) are based on 5,000 bootstrap samples with sagebrush canopy cover varying between 0 - 50%. Grey bars represent the percent of available nests locations within each sagebrush canopy cover category ($n = 381$).
Figure 3. Percent sage-grouse nest locations in each of the 5 ordinal resource selection function categories I used to build ($n = 381$ nests from 2004-2006) and test ($n = 146$ nests from 2003 and 2007) the nest occurrence model, Powder River Basin, Montana and Wyoming, USA. Test populations consisted of nests independent by year (Test $n = 146$) and those independent by year and individual (Test Ind $n = 88$). Each resource selection function category accounts for 20% of my study area.

Validation $R^2 = 0.99$
Figure 4. Percent of total landscape classified as predicted sage-grouse nesting habitat (resource selection function bins 4 and 5) within -3, -5 and -10 km buffers of leks with ≥ 5 male sage-grouse in 2005 (n = 88) and random lek locations (n = 88), Powder River Basin, Montana and Wyoming. Error bars = 95% CI’s of means.
Figure 5. Patch scale model linked in a GIS predicted locations of active leks because individual pixels (RSF bins 4 and 5) as identified by patch scale variables at 0.35- and 0.10-km radii coalesced into landscapes capable of supporting nesting populations Powder River Basin Montana and Wyoming.
CHAPTER 4: THRESHOLDS OF ENERGY DEVELOPMENT AND PRESISTENCE OF SAGE-GROUSE POPULATIONS

Abstract: Impacts from energy development to greater sage-grouse populations (Centrocercus urophasianus) are forecasted to increase as the U.S. ramps up domestic production to reduce our dependence on foreign energy. Here I use counts of male sage-grouse at leks (n = 1,190) and number of oil and gas wells within 32.2 km² (2-mi radius) of a lek to identify thresholds of development compatible with conservation of populations in Wyoming. Findings demonstrate that impacts from oil and gas development across the state are consistent with those documented in southwest (Holloran 2005) and northeast (Walker et al. 2007) Wyoming. A time-lag showed higher rates of lek inactivity and steeper declines in bird abundance 4 years after than immediately following development. Potential impacts were indiscernible at 1-12 wells within 32.2 km² of a lek (~1 well / 1 mi²), a threshold of development compatible with conservation. Above this threshold land managers can expect to see rate of lek inactivity double at 13-39 wells and jump to > 5 times (40-100 wells) that outside of widespread development in northeast Wyoming. Additional impacts should also be anticipated in south central and southwest Wyoming where rate of inactivity more than doubled and bird abundance at affected leks declined by 55-59% at intensities of development that are at (40-100 wells) or below (13-39 wells) those typically permitted on public lands. Post-hoc analyses of 17 leks showed that clustering wells to provide open areas for nesting may increase opportunities for restoration by keeping a few small but active leks inside intensely developed landscapes.

Key words: Centrocercus urophasianus, energy development, leks, populations, sage-grouse, thresholds, Wyoming

Land use change is the most significant contemporary agent of habitat degradation in terrestrial ecosystems (Forman 1995, Sanderson et al. 2002). Previously considered a local environmental concern, land use change has emerged as a major issue of global importance (Foley et al 2005). The spatial extent of change is unprecedented
relative to pre-industrial times and is expected to increase in rate and extent in the next few decades (Noon and Dale 2002, Hoekstra et al. 2005). Energy development represents a new type of land use that rapidly modifies landscapes with extensive networks of new roads, power lines, pipelines and related infrastructure. The future extent of additional change is expectantly large because for the next 20 years fossil fuels will remain the largest source of energy worldwide, accounting for 83-87% of total global demand (National Petroleum Council 2007). As the U.S. increases domestic production to reduce its dependence on foreign energy, the land base required to support this increase demand and its ultimate impacts on ecosystems is largely unknown.

Wildlife populations decline when cumulative impacts from unrestricted or poorly planned developments overwhelm the ability of natural systems to adapt to change (Gutzwiller 2002). The key to conservation is identification of thresholds of change that are compatible with maintenance of wildlife populations and ecosystem function. Increasing energy demand poses a challenge to conservation because it is known to impact wildlife directly by altering habitat use (Sawyer et al. 2006, Doherty et al. 2008) and population dynamics (Sorensen et al. 2008), and indirectly by facilitating the spread of invasive plants (Bergquist et al. 2007) and exotic diseases (Zou et al. 2006). In the last century, anthropogenic change has resulted in loss and fragmentation of native sagebrush ecosystems in western North America (Noss et al. 1995, Saab and Rich 1997, Paige and Ritter 1999, Knick et al. 2003). Greater sage-grouse (Centrocercus urophasianus; hereafter “sage-grouse”) is a gallinaceous bird native only to western semiarid sagebrush landscapes (Schroeder et al. 1999) that has been extirpated from half of its original range (Schroeder et al. 2004). Energy development has emerged as a major issue in the sagebrush ecosystem (Knick et al. 2003) because sage-grouse populations decline in response to development and because 7 million ha of public lands have been authorized for drilling within the species range (Naugle et al. in press).

The goal of this study is to incorporate knowledge of impacts at local scales into a study design that tests for threshold responses to development at regional scales. Objectives are to identify thresholds of development compatible with conservation of sage-grouse populations, quantify the severity of impacts to populations at thresholds that
are incompatible with conservation and to create a tool for use in regional risk assessments. I evaluated four predictions by testing whether 1) risk of lek loss was higher inside than outside of energy development, 2) bird abundance was lower at leks that remained active inside than outside of development, 3) rates of lek inactivity and bird abundance were related to thresholds of development as measured by number of oil and gas wells in the landscape, and if 4) time-lags influenced lek inactivity or bird abundance inside versus outside of development. I tested for threshold responses to development and incorporate a time-lag into analyses because impacts to sage-grouse can be severe (Naugle et al. *in press*). If thresholds can be identified, decision-makers and land managers can use this information to design and implement policies that permit responsible development while safeguarding other natural resource values.

**Study Area**

I conducted this study in Wyoming where energy development has increased exponentially since the 1980s (Naugle et al. *in press*). The extent and pace of oil and gas development in Wyoming provided the range of variation necessary to test for threshold responses to disturbance (Figure 1, Appendix I). Wyoming is central to sage-grouse conservation, representing >25% of the range-wide population (Connelly et al. 2004) and 64% of the known population in the eastern range of the species (Chapter 5). I analyzed all leks throughout Wyoming so that findings apply to the types and intensities of energy development common to sagebrush ecosystems in the West.

**Methods**

**Lek count data**

I used lek count data to test for differences in rates of lek inactivity and changes in bird abundance at five intensities of energy development. Lek count data is a reliable index to relative abundance that is used by agencies to monitor trends in sage-grouse numbers (e.g., Reese and Bowyer 2007). Each spring state, federal and contract employees count the number of displaying males at each known lek throughout Wyoming. Leks are typically counted in early morning ≥ 3 times in spring. Detailed
protocol for counting leks is available in the Wyoming Greater Sage-Grouse Conservation Plan (Wyoming Game and Fish 2003). I obtained lek count data from Wyoming Game and Fish, the state agency that maintains this public database.

I used maximum counts of males during 1997-2007 at active \((n = 1,190)\) and inactive \((n = 154)\) leks to test if risk of inactivity was higher or if bird abundance was lower inside than outside of development. I classified a lek as active when 3 criteria were met: \(\geq 5\) males counted at least once in 11 years, \(\geq 2\) males counted in 2 different years, and \(\geq 2\) males counted in one of the last 3 years (Connelly et al. 2003). The third criteria helped to maintain sample sizes because each lek is not counted every year but most are counted at least once every 3 years. If a lek was active in 2005 but was not surveyed again in 2006 or 2007 I presumed it remained active. I classified a lek as inactive if it met the first 2 criteria but had zero males counted in the last year surveyed and was located > 2.5-km from an active lek. The last criterion reduced bias in rates of inactivity by excluding from analyses the status of satellite leks whose formation and fate is typically tied to that of a larger nearby lek (Connelly et al. 2004). I used maximum number of males counted in 2007 at active leks \((n = 1,035)\) to test if bird abundance was lower inside than outside of development. Number of active leks is reduced in this analysis because all known leks were not counted in 2007.

**Intensity of development**

I used number of wells within 32.2 km\(^2\) (3.2-km radius) of a lek to classify each lek into 1 of 5 categories of energy development. A radius of 3.2 km is a conservative estimate of the distance at which leks are impacted by oil and gas activities (Holloran 2005, Walker et al. 2007). Category 1 represents control leks with no wells within 32.2 km\(^2\). Categories 2-5 represent increasing intensities of development that are either known to impact populations (Holloran 2005, Walker et al. 2007) or are commonly permitted on state and federal lands. Category 2 tested for impacts at 1-12 wells within 32.2 km\(^2\) (i.e., 1 well per section of land in English units), an intensity compatible with sage-grouse conservation in southwest Wyoming (Holloran 2005) but well below what is permitted on public lands. Category 3 tested for impacts at 13-39 wells, an intensity higher than that recommended by Holloran (2005), but lower than levels which resulted in severe impacts
in northeast Wyoming (Walker et al. 2007) and still below what is commonly permitted. Category 4 tested for impacts at 40-100 wells, an intensity that is known to severely impact populations (Walker et al. 2007) and is commonly permitted on state and federal lands (80-32 ha well spacing). Category 5 tested for impacts at 101-199 wells, an intensity that is permitted on some federal lands outside the Powder River Basin in Wyoming. I excluded from analyses 1 lek with >199 wells within 32.2 km². Locations (n = 54,369) obtained from the Wyoming Oil and Gas Conservation Commission 15 February 2008 represents wells that were in the ground by 1 March 2007. I excluded from analyses approved permits for wells that had not yet been drilled, plugged and abandoned wells that I assumed were reclaimed and 121 well locations that lacked a status code.

Spatial and temporal framework for analyses

I adopted as a spatial framework for analyses the Western Association of Fish and Wildlife Agencies’ Sage-Grouse Management Zones (Stiver et al. 2006). I stratified analyses by Management Zones I and II that divide Wyoming (Figure 1) because average lek size is larger in Zone II than I (Connelly et al. 2004) and intensity of development is greater in Zone I than II (Naugle et al. in press). I also incorporated a temporal component into analyses because research has shown that it takes time for cumulative impacts from development to manifest into population declines. High site fidelity but low survival of adult sage-grouse combined with lek avoidance by yearlings (Holloran et al. 2007) resulted in a time-lag of 3-4 years between the onset of energy development and lek loss (Holloran 2005). The time-lag observed by Holloran (2005) in conventional gas fields in southwest Wyoming matched that for leks that became inactive 3-4 years following coal-bed natural gas development in northeast Wyoming (Walker et al. 2007). I hypothesized that observed impacts would become more severe in time than immediately following development. I simulated a 4-year lag by reclassifying leks into 1 of 5 categories of development based on number of wells within 32.2 km² in 2003. I also controlled for time by analyzing a subset of leks whose category of development remained the same between 2003 and 2007 (Appendix I). I included wells (n = 33,275) that were in the ground by 1 March 2003. I included in analyses wells had not been
plugged and abandoned by 1 March 2003 because these well sites were not reclaimed by the start of 2003 lek counts.

**Statistical tests**

I used $\chi^2$ (Moore and McCabe 1999) to test for differences in rates of lek inactivity between category 1 (Control) and the other 4 categories of development. I first used the rate of lek inactivity in category 1 to determine the expected proportion of inactive leks that was not attributable to development. I calculated expected numbers of inactive leks for each category by multiplying the expected proportion of inactive leks by the total numbers of active and inactive leks within categories 2-5. I calculated $\chi^2$ statistics using expected and observed counts of inactive leks for each of 4 categories of development. I calculated the proportional change in rates of lek inactivity in relation to 4 levels of development by dividing the proportion of inactive leks in each category by the proportion of inactive leks in the control population. I put proportional increases in lek inactivity into context by also calculating actual change in rate of lek inactivity by subtracting the observed rate within category 1 from rates within categories 2-5 (Appendix II).

I used a 2-sample t-test (Moore and McCabe 1999) to test for differences in bird abundance between category 1 (Control) and the other 4 categories of development. I used separate variances to account for unequal variation between categories of development (Quinn and Keough 2002). I calculated the ratio of standard deviations within category 1 (i.e., control with no development) to that within other categories. Ratios were approximately equal between categories 1 and 2 and were < 2 between all other categories except category 5. I present estimates without $p$-values for category 5 because ratios were ≥ 2 in Sage-Grouse Management Zones I (ratio = 2.1) and II (5.3) and ratio of sample sizes between control and High development was 1 to 23.5 and 1 to 139 (Quinn and Keough 2002). Tests involving categories 1-4 conservatively run the risk of claiming no effect of development when one exists (Type II error) because treatment categories all had smaller sample sizes and variances.

I conducted a post-hoc analysis after findings indicated that inactivity rates increased and bird abundance decreased with increasing intensities of energy
development (see Results). I mapped and inspected visually the spatial arrangement of wells for the 17 leks counted in 2007 that remained active despite having ≥ 40 wells within 32.2 km² for ≥ 4 years (Appendix I-b). I did so in hope of finding a pattern that might explain a way in which sage-grouse and energy development may co-exist in the future.

**Results**

I identified the first of two thresholds at 1-12 wells per 32.2 km² (< 1 well per section of land) as an intensity of development within which impacts to leks were indiscernible (Tables 1 and 2). Above this threshold (13-39 wells) the rate of lek inactivity doubled (Table 1) and 31-55% fewer birds remained at affected leks (Table 2). Declines in birds at affected leks were steeper in Management Zone II than I (Table 2). I identified a second threshold within Management Zone I at > 40 wells within 32.2 km² (Table 1). When development in Management Zone I increased to 40-100 wells, an intensity of development that is typically permitted for public lands, rate of inactivity increased from 2 to 5 times that outside of development (Table 1) with 18% fewer birds at affected leks (Table 2). At this intensity of development (40-100 wells) in Management Zone II, the increased rate of lek inactivity was 3 times that outside of development (Table 1) and bird abundance at remaining leks inside development dropped by 59% (Table 2). Differences between zones may be related to initial size of leks (size of control leks in zones I [\(\bar{x} = 27.2, \ SE = 2.6\]) and II [\(\bar{x} = 47.8, \ SE = 1.9\)]) and overall extent of development within zones (Figure 1). Background rates of lek inactivity outside development were 12% in Management Zone I and 9% in Zone II.

A time-lag response showed higher rates of inactivity and steeper declines in abundance 4 years after than immediately following development (Tables 1 and 2). Time lag effects in bird abundance were most apparent at lower intensities of development (13-39 wells) whereas rate of inactivity was most effected at greater intensities of development (40-100 wells) (Tables 1 and 2). The largest time-lag effect on inactivity was in Management Zone I (Figure 1) where rate of lek loss initially doubled and after 4 years was 5 times that outside of development (Table 1). This rate corresponded to a 47-55% increase in lek inactivity when development was > 40 wells within 32.2 km².
The greatest time-lag effect on bird abundance was in Management Zone II (Figure 1) where male counts on affected leks declined by 55.5% (Table 2).

In Wyoming 15.1% of active leks ($n = 156$ of 1,035) had > 12 wells within 32.2 km² in 2007, of which 17 (10.9%) remained active with > 40 wells within 32.2 km² for ≥ 4 years (Appendix I). Bird abundance was 55% lower than the state-wide average at these 17 leks that remained active despite high development. A post-hoc visual inspection showed that wells were clustered in a pattern that maintained open areas within 32.2 km² for 64.7% (11 of 17) of these leks (Figure 2). Further evaluation of Oil City 1 lek (Figure 2) showed that it was 1 of 4 leks that remained active within Management Zone I despite high development (40 -100 wells for ≥ 4 years; Appendix I). A maximum count of 40 males at Oil City 1 lek in 2007 was 1.47 times higher compared to leks outside of development in Management Zone I. If Oil City 1 was removed from analyses declines in abundance for leks with 40 -100 wells for ≥ 4 years doubled (from -18.2 to -32.6% ($p = 0.125$) and -23.2 to -46.5% ($p = 0.030$; Table 2).

**Discussion**

Findings here demonstrate that impacts from oil and gas development across Wyoming are consistent with those documented previously in southwest (Holloran 2005) and northeast (Walker et al. 2007) parts of the state. Predictions from these studies were validated on an increased spatial and temporal scale as evidenced by: higher risk of lek loss and lower bird abundance inside development, a threshold level of development at which effects were evident, and a strong influence of the amount of time in development.

I found that potential impacts were indiscernible at 1-12 wells within 32.2 km² (< 1 well per 640 ac of land area), a threshold of development that is compatible with sage-grouse conservation (Holloran 2005; Tables 1 and 2). However, I detected impacts at lower levels of development (13-39 wells) than those investigated in Walker et al. (2007). Above 1-12 wells within 32.2 km² land managers can expect to see impacts similar to those in Management Zone I where rate of lek inactivity doubled at 13-39 wells and then jumped to > 5 times (40-100 wells) that outside of widespread development (Figure 1). Additional impacts are also anticipated in Management Zone II (Figure 1) where rate of
inactivity more than doubled (Table 1) and bird abundance at affected leks declined sharply (-55 to -59%; Table 2) at intensities of development that are at (40-100 wells) or below (13-39 wells) those commonly permitted on public lands (Bureau of Land Management 2003 a,b). Declines in Management Zone II where drilling is now underway in earnest are especially disconcerting because affected leks are some of the largest anywhere in the remaining range of the species (Connelly et al. 2004).

I analyzed all leks in Wyoming so that findings apply to the type and intensity of energy development common to sagebrush ecosystems in the West. I replicated by management zone to identify regional thresholds and provided valid estimates of impacts by comparing affected leks to those outside of development (i.e., control populations). Resulting impacts at low levels of development (i.e. 13-39 wells) highlight the need for control populations completely outside the influence of development because analyses will underestimate impacts even if control populations have relatively few wells surrounding leks. Increased rates of inactivity and steeper declines in abundance 4 years after development (Tables 1 and 2) reiterate the importance of incorporating time-lags into analyses (Holloran 2005, Walker et al. 2007). The importance of accounting for the effects of time-lags shown here for oil and gas development are comparable to those in a recent meta-analysis of the consequences of wind energy to bird abundance within wind farms (Stewart et al. 2007). Land managers using monitoring data to evaluate impacts should adjust protocols to account for lag effects that over time increase the severity of impacts from energy development to populations.

The extent and intensity of oil and gas development anticipated throughout the West will require conservation planning and implementation to reduce impacts to sage-grouse populations. Estimates of impacts presented here can be used with maps of leks to quantify anticipated consequences for different development scenarios. A plausible scenario is to restrict drilling in the best remaining areas, to stipulate a reduced intensity of development where sage-grouse and energy values overlap and to allow more intense development where conflict is low (Chapter 5). My post-hoc analyses showed that clustering wells to provide open areas for nesting may maintain a few small but active leks inside intensely developed landscapes (Figure 2). This technique may increase our
ability to restore populations following development because strong site fidelity (e.g., Berry and Eng 1985, Dunn and Braun 1985) makes natural re-colonization slow and past precedence has documented that anthropogenic translocations into areas with no resident populations are highly unlikely to succeed (Reese and Connelly 1997, Baxter et al. 2008).

Acknowledgements
I thank state and federal wildlife managers in Sage-Grouse Management Zones I and II for helping us envision this project. I thank Wyoming Game and Fish (WGF) for providing lek count data. I also thank T. Christiansen and N. Whitford of WGF for their assistance in answering questions about lek databases. J. Kiesecker, H. Copeland and A. Pocewicz with the Nature Conservancy in Lander, Wyoming, provided thought provoking conversation throughout the analysis. Funding was provided by the state offices of the U.S. Bureau of Land Management in Montana and Wyoming, Wolf Creek Charitable Foundation, Hewlett Foundation, Liz Claiborne & Art Ortenberg Foundation and the University of Montana.

Literature Cited


Table 1. Proportional increase in lek inactivity and resulting $\chi^2$ test of divergence from expected means between control leks (0 wells / 32.2 km$^2$) and those inside of 4 categories of increasing intensity of energy development, Wyoming 1997-2007.

a) Sage-Grouse Management Zones I and II combined $^a$

<table>
<thead>
<tr>
<th>Number of wells $^b$</th>
<th>No time-lag</th>
<th>4-yr time-lag $^c$</th>
<th>4-yr time-lag $^d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-12</td>
<td>0.90 ($p &gt; 0.250$)</td>
<td>1.17 ($p &lt; 0.250$)</td>
<td>0.94 ($p &gt; 0.250$)</td>
</tr>
<tr>
<td>13-39</td>
<td>1.79 ($p &lt; 0.010$)</td>
<td>2.37 ($p &lt; 0.001$)</td>
<td>2.33 ($p &lt; 0.001$)</td>
</tr>
<tr>
<td>40-100</td>
<td>3.00 ($p &lt; 0.001$)</td>
<td>4.80 ($p &lt; 0.001$)</td>
<td>4.74 ($p &lt; 0.001$)</td>
</tr>
<tr>
<td>101-199</td>
<td>5.01 ($p &lt; 0.001$)</td>
<td>3.06 (NA $^c$)</td>
<td>3.47 (NA $^c$)</td>
</tr>
</tbody>
</table>

b) Management Zone I only $^a$

<table>
<thead>
<tr>
<th>Number of wells $^b$</th>
<th>No time-lag</th>
<th>4-yr time-lag $^c$</th>
<th>4-yr time-lag $^d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-12</td>
<td>0.71 ($p &gt; 0.250$)</td>
<td>1.06 ($p &gt; 0.250$)</td>
<td>0.70 ($p &gt; 0.250$)</td>
</tr>
<tr>
<td>13-39</td>
<td>1.07 ($p &gt; 0.250$)</td>
<td>2.00 ($p &lt; 0.020$)</td>
<td>1.61 ($p &lt; 0.200$)</td>
</tr>
<tr>
<td>40-100</td>
<td>2.64 ($p &lt; 0.001$)</td>
<td>5.07 ($p &lt; 0.001$)</td>
<td>5.00 ($p &lt; 0.001$)</td>
</tr>
<tr>
<td>101-199</td>
<td>4.88 ($p &lt; 0.001$)</td>
<td>5.74 (NA $^c$)</td>
<td>7.87 (NA $^c$)</td>
</tr>
</tbody>
</table>

c) Management Zone II only $^a$

<table>
<thead>
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<th>Number of wells $^b$</th>
<th>No time-lag</th>
<th>4-yr time-lag $^c$</th>
<th>4-yr time-lag $^d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-12</td>
<td>0.93 ($p &gt; 0.250$)</td>
<td>1.14 ($p &lt; 0.050$)</td>
<td>1.00 ($p &gt; 0.250$)</td>
</tr>
<tr>
<td>13-39</td>
<td>2.40 ($p &lt; 0.001$)</td>
<td>2.36 ($p &lt; 0.010$)</td>
<td>2.67 ($p &lt; 0.005$)</td>
</tr>
<tr>
<td>40-100</td>
<td>2.03 ($p &lt; 0.150$)</td>
<td>2.82 ($p &lt; 0.100$)</td>
<td>3.00 ($p &lt; 0.050$)</td>
</tr>
<tr>
<td>101-199</td>
<td>1.86 (NA $^c$)</td>
<td>NA (NA $^c$)</td>
<td>NA (NA $^c$)</td>
</tr>
</tbody>
</table>

$^a$ I stratified analyses by Sage-Grouse Management Zones I and II to reflect differences in average lek size and intensity of development (Connelly et al. 2004).

$^b$ I quantified intensity of development as number of energy wells within 32.2 km$^2$ of a lek (Walker et al. 2007).
c I incorporated a time-lag into analyses because it takes 4-yrs for cumulative impacts from development to manifest into population declines (Holloran 2005, Walker et al. 2007).

d I removed leks that switched categories between 2003 and 2007 to control for confounding effect of increasing intensity of development.

e $\chi^2$ tests were not performed where sample sizes were < 5 inactive leks inside of development (Appendix I).
Table 2. Proportional decrease in peak male count numbers between control leks (0 wells / 32.2 km$^2$) and those inside of 4 categories of increasing intensity of energy development, Wyoming 2007. Resulting p-values are from 2 sample t-test with separate variances. The 4-year lag effect is estimated by using March 2003 well data with March 2007 lek count data.

<table>
<thead>
<tr>
<th>Sage-grouse Management Zones$^a$</th>
<th>No time-lag</th>
<th>4-yr time-lag$^c$</th>
<th>4-yr time-lag$^d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-12 wells / 32.2 km$^2$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zone I</td>
<td>-2.5%</td>
<td>-2.1%</td>
<td>6.9%</td>
</tr>
<tr>
<td>(p = 0.430)</td>
<td>(p = 0.432)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zone II</td>
<td>-8.0%</td>
<td>0.1%</td>
<td>-2.9%</td>
</tr>
<tr>
<td>(p = 0.133)</td>
<td>(p = 0.502)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>13-39 wells / 32.2 km$^2$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zone I</td>
<td>-17.0%</td>
<td>-31.4%</td>
<td>-29.2%</td>
</tr>
<tr>
<td>(p = 0.093)</td>
<td>(p = 0.004)</td>
<td>(p = 0.023)</td>
<td></td>
</tr>
<tr>
<td>Zone II</td>
<td>-35.9%</td>
<td>-55.5%</td>
<td>-58.8%</td>
</tr>
<tr>
<td>(p = 0.002)</td>
<td>(p &lt; 0.001)</td>
<td>(p &lt; 0.001)</td>
<td></td>
</tr>
<tr>
<td>40-100 wells / 32.2 km$^2$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zone I</td>
<td>-41.4%</td>
<td>-18.2%</td>
<td>-23.2%</td>
</tr>
<tr>
<td>(p = 0.001)</td>
<td>(p = 0.211)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zone II</td>
<td>-55.1%</td>
<td>-59.0%</td>
<td>-58.6%</td>
</tr>
<tr>
<td>(p = 0.001)</td>
<td>(p &lt; 0.001)</td>
<td>(p &lt; 0.001)</td>
<td></td>
</tr>
<tr>
<td>101-199 wells / 32.2 km$^2$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zone I</td>
<td>-34.4%</td>
<td>-77.3%</td>
<td>-78.3</td>
</tr>
<tr>
<td>(NA $^f$)</td>
<td>(NA $^f$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zone II</td>
<td>-68.5%</td>
<td>-69.5%</td>
<td>-69.4%</td>
</tr>
<tr>
<td>(NA $^f$)</td>
<td>(NA $^f$)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a$I stratified analyses by Sage-Grouse Management Zones I and II to reflect differences in average lek size and intensity of development (Connelly et al. 2004).
b I quantified intensity of development as number of energy wells within 32.2 km² of a lek (Walker et al. 2007).

c I incorporated a time-lag into analyses because it takes 4-yrs for cumulative impacts from development to manifest into population declines (Holloran 2005, Walker et al. 2007).

d I removed leks that switched categories between 2003 and 2007 to control for confounding effect of increasing intensity of development.

e T-tests were not performed because of inadequate sample sizes in both treatment and control categories coupled with the ratio of SD between control and treatments was > 2 (Appendix I).
Appendix I. Sample sizes of leks within each treatment categories for a) lek inactivity and b) lek abundance.

a) Lek activity in Wyoming 1997-2007\(^a\)

<table>
<thead>
<tr>
<th>Number of wells (^b)</th>
<th>Active 2007</th>
<th>Inactive 2007</th>
<th>4-yr time-lag (^c)</th>
<th>Inactive 2007</th>
<th>Active 2007</th>
<th>4-yr time-lag (^d)</th>
<th>Inactive 2007</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 = Control</td>
<td>766</td>
<td>80</td>
<td>835</td>
<td>86</td>
<td>744</td>
<td>79</td>
<td></td>
</tr>
<tr>
<td>1-12</td>
<td>257</td>
<td>24</td>
<td>260</td>
<td>32</td>
<td>181</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td>13-39</td>
<td>108</td>
<td>22</td>
<td>74</td>
<td>21</td>
<td>52</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>40-100</td>
<td>48</td>
<td>19</td>
<td>16</td>
<td>13</td>
<td>12</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>101-199</td>
<td>10</td>
<td>9</td>
<td>5</td>
<td>2</td>
<td>4</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1189</td>
<td>154</td>
<td>1190</td>
<td>154</td>
<td>1002</td>
<td>125</td>
<td></td>
</tr>
</tbody>
</table>

Sage-grouse Management Zone I\(^1\)

<table>
<thead>
<tr>
<th>Number of wells (^b)</th>
<th>Active 2007</th>
<th>Inactive 2007</th>
<th>4-yr time-lag (^c)</th>
<th>Inactive 2007</th>
<th>Active 2007</th>
<th>4-yr time-lag (^d)</th>
<th>Inactive 2007</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 = Control</td>
<td>104</td>
<td>15</td>
<td>137</td>
<td>18</td>
<td>103</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>1-12</td>
<td>81</td>
<td>8</td>
<td>100</td>
<td>14</td>
<td>61</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>13-39</td>
<td>64</td>
<td>10</td>
<td>40</td>
<td>12</td>
<td>27</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>40-100</td>
<td>30</td>
<td>15</td>
<td>7</td>
<td>10</td>
<td>4</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>101-199</td>
<td>8</td>
<td>8</td>
<td>1</td>
<td>2</td>
<td>na</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>284</td>
<td>56</td>
<td>285</td>
<td>56</td>
<td>1002</td>
<td>125</td>
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</tbody>
</table>
Appendix 1 a) continued

Sage-grouse Management Zone II)

<table>
<thead>
<tr>
<th>Number of wells b</th>
<th>Active 2007</th>
<th>Inactive 2007</th>
<th>4-yr time-lag c</th>
<th>Inactive 2007</th>
<th>Active 2007</th>
<th>Inactive 2007</th>
<th>4-yr time-lag d</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 =</td>
<td>662</td>
<td>65</td>
<td>698</td>
<td>68</td>
<td>641</td>
<td>64</td>
<td>64</td>
</tr>
<tr>
<td>Control</td>
<td>176</td>
<td>16</td>
<td>160</td>
<td>18</td>
<td>120</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>1-12</td>
<td>44</td>
<td>12</td>
<td>34</td>
<td>9</td>
<td>25</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>13-39</td>
<td>18</td>
<td>4</td>
<td>9</td>
<td>3</td>
<td>8</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>40-100</td>
<td>5</td>
<td>1</td>
<td>4</td>
<td>na</td>
<td>4</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td>101-199</td>
<td>Total</td>
<td>905</td>
<td>98</td>
<td>905</td>
<td>98</td>
<td>1002</td>
<td>125</td>
</tr>
</tbody>
</table>

a I stratified analyses by Sage-grouse Management Zones I and II to reflect differences in average lek size and intensity of development (Connelly et al. 2004).

b I quantified intensity of development as number of energy wells within 32.2 km² of a lek (Walker et al. 2007).

c I incorporated a time-lag into analyses because it takes 4-yrs for cumulative impacts from development to manifest into population declines (Holloran 2005, Walker et al. 2007).

d I removed leks that switched categories between 2003 and 2007 to control for confounding effect of increasing intensity of development.

e 1 lek with greater than 199 wells was removed from the analyses.
b) Leks surveyed in Wyoming during 2007 with ≥ 2 male sage-grouse \((n = 1035)\) used for abundance tests blocked by Sage-grouse Management Zones I and II.

<table>
<thead>
<tr>
<th>Number of wells (^b)</th>
<th>Sage-grouse Management Zone I (^a)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Active 2007</td>
<td>4-yr time-lag (^c)</td>
<td>4-yr time-lag (^d)</td>
</tr>
<tr>
<td>0 = Control</td>
<td>94</td>
<td>129</td>
<td>93</td>
</tr>
<tr>
<td>1-12</td>
<td>74</td>
<td>91</td>
<td>55</td>
</tr>
<tr>
<td>13-39</td>
<td>63</td>
<td>39</td>
<td>27</td>
</tr>
<tr>
<td>40-100</td>
<td>29</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>101-199</td>
<td>4</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>264</td>
<td>265</td>
<td>180</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Number of wells (^b)</th>
<th>Sage-grouse Management Zone II (^a)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Active 2007</td>
<td>4-yr time-lag (^c)</td>
<td>4-yr time-lag (^d)</td>
</tr>
<tr>
<td>0 = Control</td>
<td>556</td>
<td>618</td>
<td>538</td>
</tr>
<tr>
<td>1-12</td>
<td>155</td>
<td>112</td>
<td>102</td>
</tr>
<tr>
<td>13-39</td>
<td>39</td>
<td>31</td>
<td>22</td>
</tr>
<tr>
<td>40-100</td>
<td>16</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>101-199</td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Total</td>
<td>770</td>
<td>770</td>
<td>671</td>
</tr>
</tbody>
</table>

\(^a\) I stratified analyses by Sage-grouse Management Zones I and II to reflect differences in average lek size and intensity of development (Connelly et al. 2004).

\(^b\) I quantified intensity of development as number of energy wells within 32.2 km\(^2\) of a lek (Walker et al. 2007).

\(^c\) I incorporated a time-lag into analyses because it takes 4-yrs for cumulative impacts from development to manifest into population declines (Holloran 2005, Walker et al. 2007).

\(^d\) I removed leks that switched categories between 2003 and 2007 to control for confounding effect of increasing intensity of development.

\(^e\) 1 lek with greater than 199 wells was removed from the analyses.
Appendix II. Percent increase in leks inactivity within treatment classes after removing background lek inactivity rates (control leks) and resulting $\chi^2$ test of divergence from expected means between control leks (0 wells / 32.2 km$^2$) and those inside of 4 categories of increasing intensity of energy development, Wyoming 1997-2007.

a) Sage-Grouse Management Zones I and II combined $^a$

<table>
<thead>
<tr>
<th>Number of wells $^b$</th>
<th>No time-lag</th>
<th>4-yr time-lag $^c$</th>
<th>4-yr time-lag $^d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-12</td>
<td>-0.92 ($p &gt; 0.250$)</td>
<td>1.62 ($p &lt; 0.250$)</td>
<td>0.55 ($p &gt; 0.250$)</td>
</tr>
<tr>
<td>13-39</td>
<td>7.47 ($p &lt; 0.010$)</td>
<td>12.77 ($p &lt; 0.001$)</td>
<td>12.79 ($p &lt; 0.001$)</td>
</tr>
<tr>
<td>40-100</td>
<td>18.90 ($p &lt; 0.001$)</td>
<td>35.49 ($p &lt; 0.001$)</td>
<td>35.86 ($p &lt; 0.001$)</td>
</tr>
<tr>
<td>101-199</td>
<td>37.91 ($p &lt; 0.001$)</td>
<td>19.23 (NA $^e$)</td>
<td>23.73 (NA $^e$)</td>
</tr>
</tbody>
</table>

b) Management Zone I only $^a$

<table>
<thead>
<tr>
<th>Number of wells $^b$</th>
<th>No time-lag</th>
<th>4-yr time-lag $^c$</th>
<th>4-yr time-lag $^d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-12</td>
<td>-3.62 ($p &gt; 0.250$)</td>
<td>0.67 ($p &gt; 0.250$)</td>
<td>-3.76 ($p &gt; 0.250$)</td>
</tr>
<tr>
<td>13-39</td>
<td>0.91 ($p &gt; 0.250$)</td>
<td>11.46 ($p &lt; 0.020$)</td>
<td>7.88 ($p &lt; 0.200$)</td>
</tr>
<tr>
<td>40-100</td>
<td>20.73 ($p &lt; 0.001$)</td>
<td>47.21 ($p &lt; 0.001$)</td>
<td>50.92 ($p &lt; 0.001$)</td>
</tr>
<tr>
<td>101-199</td>
<td>48.93 ($p &lt; 0.001$)</td>
<td>55.05 (NA $^e$)</td>
<td>87.29 (NA $^e$)</td>
</tr>
</tbody>
</table>

c) Management Zone II only $^a$

<table>
<thead>
<tr>
<th>Number of wells $^b$</th>
<th>No time-lag</th>
<th>4-yr time-lag $^c$</th>
<th>4-yr time-lag $^d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-12</td>
<td>-0.61 ($p &gt; 0.250$)</td>
<td>1.24 ($p &lt;0.05$)</td>
<td>0.01 ($p &gt; 0.250$)</td>
</tr>
<tr>
<td>13-39</td>
<td>12.49 ($p &lt; 0.001$)</td>
<td>12.05 ($p &lt; 0.010$)</td>
<td>15.12 ($p &lt; 0.005$)</td>
</tr>
<tr>
<td>40-100</td>
<td>9.24 ($p &lt; 0.150$)</td>
<td>16.12 ($p &lt; 0.100$)</td>
<td>18.19 ($p &lt; 0.050$)</td>
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<tr>
<td>101-199</td>
<td>7.73 (NA $^e$)</td>
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<td>NA (NA $^e$)</td>
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</tbody>
</table>

$^a$ I stratified analyses by Sage-grouse Management Zones I and II to reflect differences in average lek size and intensity of development (Connelly et al. 2004).

$^b$ I quantified intensity of development as number of energy wells within 32.2 km$^2$ of a lek (Walker et al. 2007).
c I incorporated a time-lag into analyses because it takes 4-yrs for cumulative impacts from development to manifest into population declines (Holloran 2005, Walker et al. 2007).
d I removed leks that switched categories between 2003 and 2007 to control for confounding effect of increasing intensity of development.

$\chi^2$ tests were not performed where sample sizes were < 5 inactive leks inside of development (Appendix I).
Figure 1. Location of active (2005-2007) and inactive (1999-2007) sage-grouse leks in relation to oil and gas development in Wyoming.
Figure 2. Spatial arrangement of oil and gas wells at 11 leks in Wyoming. These leks remained active despite having >40 wells within a 3.2-km radii of the lek for ≥ 4 years. Number of males counted in spring 2007 is shown for at each lek.
CHAPTER 5: ENERGY DEVELOPMENT AND CONSERVATION TRADEOFFS: SYSTEMATIC PLANNING FOR SAGE-GROUSE IN THEIR EASTERN RANGE

Abstract. The Rocky Mountain West is poised for a dramatic increase in energy development. Correspondingly we need a dramatic change in how we plan for associated impacts. Here I develop a framework for conservation planning to evaluate options for reducing development impacts. I focus on greater sage-grouse (Centrocercus urophasianus) in the portion of their range in Wyoming, Montana, Colorado, Utah and North and South Dakota that contains some of the largest populations and highest risk of energy development. Using lek count data (N = 2,336 leks) in a GIS, I delineated high abundance population centers which I termed core areas, that when grouped together contained 25, 50, 75, and 100% of the known breeding population. I then assessed vulnerability of these areas by examining risk of future land transforming uses from energy development. Findings showed that bird abundance varies by state, core areas contain a disproportionately large segment of the breeding population and that cores vary dramatically by risk of future energy development. Wyoming contains 64% of the known sage-grouse population and more active leks than the other states combined within my study area, but conservation success here will depend on leasing and permitting policy decisions because this state has the highest risk of development. Montana contains fewer birds (24%) than Wyoming, but actions that reduce sagebrush tillage by incentivizing private landowners to maintain sagebrush-dominated landscapes would provide lasting benefits because core areas here are at comparatively low development risk. Habitat restoration in areas with low risk of development but containing fewer birds fit into an overall conservation strategy by targeting populations that promote connectivity of core areas. This vulnerability assessment illustrates the tradeoffs between conservation and energy development and provides a framework for maintaining populations across the species’ eastern range.

Key Words: Centrocercus urophasianus, conservation planning, core areas, energy development, lek counts, prioritization, risk assessment, sage-grouse, Wyoming
World demand for energy is predicted to increase by ≥50% in the next 20 years (International Energy Agency 2007, National Petroleum Council 2007). The Rocky Mountain West will be one of the most heavily affected landscapes in the continental United States as it has 7% of proven onshore oil reserves and 26% of natural gas reserves (U.S. Department of the Interior et al. 2006). Meeting 20% of US energy demand with wind could impact 50,000 km², a significant portion of which would be in the Rocky Mountain West (U.S. Department of Energy 2008). Increasing energy demand of an expanding human population poses a challenge to conservation of wildlife populations in North America (Sawyer et al. 2006, Walker et al. 2007). Energy development is known to impact wildlife directly by altering habitat use (Doherty et al. 2008) and population dynamics (Sorensen et al. 2008), and indirectly by facilitating the spread of non-native invasive plants (Bergquist et al. 2007) and new diseases such as West Nile Virus (Naugle et al. 2004, Zou et al. 2006). The ability to identify areas of high biological value and assess the potential for adverse habitat alteration is a component of a proactive rather than a reactive approach to conservation (Groves et al. 2002). Not all wildlife areas are created equal and mapping high abundance population centers for a priority species can help frame regional plans. Realization of conservation goals requires that plans be constructed at broad spatial scales to provide for effective management (Soule and Terborgh 1999, Margules and Pressey 2000). Given the scale of anticipated energy development in the western U.S., plans that explicitly examine tradeoffs between wildlife conservation and energy development will need to be equally broad in scale to be effective.

Loss and degradation of native vegetation has impacted much of the sagebrush (Artemisia spp.) ecosystem and its associated wildlife (Knick et al. 2003, Connelly et al. 2004). Greater sage-grouse (Centrocercus urophasianus; hereafter “sage-grouse”) is a gallinaceous species native only to western semiarid sagebrush landscapes (Schroeder et al. 1999). Previously widespread, sage-grouse have been extirpated from nearly half of their original range in western North America (Schroeder et al. 2004), with a range-wide population decline of 45-80% and local declines of 17-92% (Connelly and Braun 1997, Braun 1998, Connelly et al. 2004). Energy development has emerged as a key issue in
sage-grouse conservation for three reasons: (1) sage-grouse populations decline with oil and gas development (Holloran 2005, Aldridge and Boyce 2007, Walker et al. 2007), (2) landscapes being developed contain some of the highest abundance estimates for sage-grouse in North America, and (3) 44% of the lands that the federal government has authority to control for oil and gas development in the eastern range of sage-grouse (7 of 16 million ha) have already been authorized for exploration and development (Naugle et al. in press).

Given sage-grouse sensitivity to oil and gas development, and the projected rate of increased development, it is urgent that I identify areas of high biological value and areas of potential future development to evaluate options for reducing impacts (Abbitt et al. 2000, Balmford et al. 2001 Wilson et al. 2005). To illustrate the process of risk assessment and to contrast opposing conservation strategies, I focused on identifying core areas of sage-grouse abundance. Lek count data provided an opportunity to spatially identify the distribution and abundance of core areas of habitat that support breeding populations. My goal was to develop a conservation planning framework (e.g., Pressey and Bottrill 2008) to address the following questions using readily available spatial data: (1) Where are landscapes of highest biological value for sage-grouse? (2) How do these landscapes differ with respect to risk from future energy development? and (3) How does variation and juxtaposition in risk and biological values of areas affect the potential to develop a successful conservation strategy for sage-grouse?

**Study Area**

My study area included landscapes within the eastern distribution of sage-grouse (Schroeder et al. 2004) including portions of Colorado, Montana, North and South Dakota, Utah and Wyoming (Figure 1). Schroeder et al. (2004) used a combination of lek survey data, GIS habitat layers to exclude barren areas, alpine areas, and forest habitats, along with radio-collared sage-grouse locations to delineate the current occupied distribution for sage-grouse in all of North America. I modified this boundary to include 27 additional known lek locations in Montana, South Dakota, Wyoming and Colorado outside the boundaries suggested by Schroeder et al. (2004). I adopted a spatial
organizational framework based on Western Association of Fish and Wildlife Agencies Management Zones (Connelly et al 2004, Stiver et al. 2006) which are delineated by floristic provinces and used to group sage-grouse populations together for management actions. I restricted analyses to areas within the eastern distribution that fell within the sage-grouse Management Zones I and II (Figure 1; Connelly et al. 2004, Stiver et al. 2006) because these populations are experiencing the highest risk of energy development. All analyses presented herein evaluate the relative importance of an individual breeding area to all other breeding areas within of Management Zones I and II (Figure 1).

Methods

Sage-grouse Abundance Data

Knowledge of high abundance population centers for priority species represent a starting point to frame regional conservation initiatives and can direct management actions to landscapes where they will have the largest benefit to regional populations (Groves et al. 2002, Sanderson et al. 2002). Techniques such as resource selection functions in the absence of large scale survey data have been widely used to identify critical habitat needs and to map those habitats at appropriate scales for a wide range of species such as grizzly bear (*Ursus arctos*; McLoughlin et al. 2002), elk (*Cervus elaphus*; Boyce et al. 2003), woodland caribou (*Rangifer tarandus*; Johnson et al. 2006); and sage-grouse (Aldridge and Boyce 2007, Doherty et al. 2008). No seamless habitat coverage is available for sage-grouse to build seasonal models that could form the comparison of the relative biological value of different landscapes. Fortunately, sage-grouse are one of the few species in which there exist extensive data sets on the distribution and relative abundance across their entire breeding distribution making an analyses of this scale possible (e.g., Schroeder et al. 2004, Connelly et al. 2004). The concept of using high abundance centers to define the size, shape, connectivity, replication and spacing of conservation areas is well documented in other systems (e.g., Myers et al. 2000, Groves et al. 2002, Sanderson et al. 2002).

Lek data has been widely used by agencies to monitor sage-grouse population trends and is considered a reasonable index to relative abundance (e.g., Walsh et al. 2004,
Reese and Bowyer 2007). Each spring the numbers of displaying males are counted within each state on sage-grouse breeding grounds at leks in a large coordinated effort by state, federal, and contract employees across their entire distribution. Typically, leks are visually surveyed at least 3 times from the air or ground and the number of displaying males are counted during the early morning. Protocols for counting males at leks were almost identical between states following the recommendations of Connelly et al. (2003), which allowed for comparisons between state populations.

We used the maximum count of sage-grouse to identify high abundance areas in this analysis. Each state game and fish agency assembled and provided us a maximum lek count for each year the lek was surveyed over the past 11 years along with spatial coordinates of the lek locations. This maximum count database provided us the ability to map relative abundance of sage-grouse breeding areas. I analyzed 2,336 active leks to delineate breeding core areas. I defined active leks as those in which \( \geq 2 \) males were counted in the last year the lek was surveyed. Because not all leks are counted each year but most leks are counted within a 3-yr interval I used the highest count during the 2005-2007 period. However, 249 leks in Montana primarily in Rosebud, Custer, and Garfield counties were not counted during this interval so I used the most recent survey within the 11-yr interval to assign abundance values to these leks. I also included the last count of 5 leks in Colorado after consultation with regional biologist indicated that “zeros” recorded in 2007 were likely a result of no survey effort.

**Mapping Core Sage-grouse Breeding Areas**

Kernel density functions have been commonly used in ecology to delineate home ranges of individual animals and to map concentrated areas of use by populations (e.g., Silverman 1986, Worton 1989). A kernel is a mathematical density function that groups cells of concentrated use by attributing a grid placed over top of a study site with animal use or count data (Silverman 1986, Worton 1989). I populated a 1-km\(^2\) grid of cells with counts of sage-grouse males at leks across the eastern range of sage-grouse. I used this grid to select individual leks for conservation priority groupings. However, I modified the kernel function because choice of smoothing bandwidth is well known to drastically affect area estimates and outer-boundaries of home-ranges and concentrated areas of use.
by populations (Seaman et al. 1999, Kernohan et al. 2001, Horne and Garton 2006). I therefore circumvented the bandwidth choice problem and used known distributions of nesting females around leks to delineate the outer boundaries of core areas (Holloran and Anderson 2005, Table B-1; Colorado Division of Wildlife 2008).

The value of each grid cell is a function of the number and proximity of leks in the surrounding landscape. I attributed each cell with counts of males at leks within a radius of 6.4 km (4.0 mi). I chose this distance because nesting females distribute their nests spatially in relation to lek location with 79% of nests located within a 6.4 km (4.0 mi) radius from lek-of-capture (Table B-1; Colorado Division of Wildlife 2008). I ordered leks by their abundance value and placed them into four groups that each contained 25, 50, 75 and 100% of the known breeding population and buffered these leks by 6.4 km to delineate nesting areas. I extended the radius from 6.4 to 8.5 km (5.3 mi; Holloran and Anderson 2005) for leks in 75 and 100% core areas because a post-hoc analysis showed that 6.4 km was too small an area to contain simulated nest densities in lower density areas and fragmented habitats where a few leks were located far apart (e.g., North and South Dakota; Table 1). Increasing the radius in 75 and 100% core areas provided more realistic estimates of the area needed to support breeding populations in low abundance or fragmented landscapes. My model output is a grouping of leks shaded by four colors that represent the smallest area necessary to contain 25, 50, 75, and 100% of the nesting sage-grouse population. Area estimates are inclusive, meaning that 25% core areas are included within the boundaries 50% core areas.

**Mapping Energy Potential**

We used readily available spatial data to rapidly assess the potential for energy development in sage-grouse core areas. My risk assessment included indictors for two major forms of energy development in the eastern range: oil and gas and more recently wind. I acquired information on oil and gas development by compiling the locations of authorized oil and gas leases within Montana, North and South Dakota, Wyoming, Colorado and Utah from BLM State offices. Leases were authorized for exploration and development on or before 1 June 2007 for all states except Utah (1 May 2007). I obtained geo-referenced data layers depicting locations of producing oil and gas wells as of 1
September 2007 on public and private lands in Montana, North and South Dakota, Wyoming, Colorado and Utah from IHS Incorporated. I used data from the National Renewable Energy Laboratory (NREL) to represent the potential for commercial wind potential (National Renewable Energy Laboratory 2008). Wind classes are grouped from 1 – 7 with all wind classes ≥4 having potential for commercial energy production.

**Conservation Planning Analyses**

Systematic conservation planning requires identification of areas to achieve specific goals (Pressey et al. 2007). My core-areas analyses delineate specific landscapes that differ markedly in their biological value and thus offer a means to rank their relative importance. However, conservation planning also requires that areas identified with high value have the ability to persist over time (Groves et al. 2002). I conducted a series of GIS overlays of biological values of sage-grouse with the potential for energy development to frame the opportunities and challenges facing sage-grouse in relation to energy development. The intersection of high biological value with high energy potential frames the risk of development to sage-grouse populations. I first quantified the proportion 25, 50, 75, and 100% core areas that are at risk from oil and gas, wind, or both. I quantified the risk of oil and gas and wind development to 75% core areas by state and quantified the proportion of land within federal management to document how risk varies by state. I then mapped the location of current oil and gas wells in relation to core areas to highlight the importance of core areas next to development to promote resilience of areas disturbed by energy development (Groves et al. 2002, Lindenmeyer et al. 2008). Lastly, I used a factorial analysis to categorically define biological value and energy potential into four categories which show opportunities for both conservation and energy development across the landscape based on all possible combinations of biological value (low or high) and energy potential (low or high). I defined an area as having high biological value if it was in the top 3 classes of breeding densities; 25, 50 and 75% core areas, as these classes contained 75% of the regional breeding population in only 30% of the total eastern sage-grouse distribution (see results). I included 100% core areas as high biological value in North and South Dakota because these fringe populations experienced the highest risk of extirpation (Aldridge et al. 2008). I defined
my 100% core area class as low biological value elsewhere. If an area did not have a lek within 8.5 km (Holloran and Andersen 2005), it was not assigned a biological value because I did not have information on other seasonal habitats. I considered an area to have high potential for energy development if it had either an authorized oil or gas lease from the federal government or showed potential for commercial wind production. Areas excluded from the high potential category were classified as having low potential for energy development. Resulting output was four categorical and spatially explicit classes (Figure 3) that I mapped in a geographic information system (GIS).

**Results**

Sage-grouse abundance regionally exhibited a clumped distribution, making it possible to identify core areas that contained a large proportion of the breeding population within a small proportion of the species eastern range (Figure 1). Core areas contained 25, 50, 75, and 100% of the breeding population within 5, 12, 30 and 60% of the eastern sage-grouse range. Bird abundance varied within core areas. Among the six states, Wyoming contained the highest proportion of high-density areas (Figure 1), largest number of leks, highest male sage-grouse abundance at leks, and the broadest species distribution within my study area (Table 1). Wyoming provides habitat for nearly two-thirds of all known birds in my study area, while Montana, having the second largest and most expansive bird population, provides habitat for an additional quarter of the birds (Table 1). A small area of northwest Colorado also supports an especially high abundance of breeding birds per unit area, relative to the entire eastern range of sage-grouse (Figure 1).

Risk of energy development to core areas increased as the relative biological value of sage-grouse core areas increased across the entire eastern range (Table 2). Half (51%) of 25% core areas are at risk from either wind or oil and gas development whereas 39% of the 100% core areas are at risk. This is a function of the locations of oil and gas leases. Over one-third of the 25% core areas have been leased for oil and gas development whereas, one-fifth of the eastern distribution is leased (Table 2). Potential for wind energy development is also widespread across the eastern range, however core
areas did not exhibit increasing risks as biological value increased (19-21% risk, Table 2). Development risk is highly non-complimentary with <5% spatial overlap occurring between potential oil/gas and wind development, which increased the total land area at risk (Table 2, Figure 2).

Energy development risks differed by state (Table 3, Figure 2) and are highest in Wyoming, intermediate in Colorado, and lowest in Montana, the 3 states with 95% of the birds (Table 3). Wyoming has the highest percent of 75% core areas at risk from both oil and gas and wind development of these populations (Table 3). In Colorado and Utah oil and gas development is the primary threat, while wind development poses a greater risk to sage-grouse core areas in Montana and the Dakotas (Table 3). Overall, threats from energy development to 75% core areas ranged from 9-73% of breeding areas (Table 3).

Factorial analysis documented large landscapes within each category of risk (Figure 3). Analyses classified 84,896 km² of land as low biological value with high potential for energy development (25% of range; Figure 3) and 64,641 km² as low potential for energy development (19% of range, Figure 3). The inclusion of 100% core areas in North and South Dakota brought the total area classified as high biological value to 31%. Analyses classified 46,419 km² of land as high biological value for sage-grouse with high potential for energy development (14% of range; Figure 3) and 59,237 km² as low energy potential (17%; Figure 3). The proportion of areas with high biological value and low energy potential varied greatly by state as did federal surface and mineral ownership (Table 3). Montana had 72% of its high value core areas with low potential for development and had 31% federal surface ownership and 45% federal subsurface ownership (Figure 3, Table 3). Wyoming had 49% of areas with high biological value and low energy potential but was 57% federally owned on the surface and 69% controlled by federal sub-surface ownership. Large scale development has already occurred next to core areas especially in Wyoming (Figure 1).

Discussion

The western US is currently undergoing unprecedented development of both renewable and non-renewable energy resources, stemming from increased demand, interest in
energy security, and recognition of potential impacts from climate change. The Rocky Mountain West has 7% of proven onshore oil reserves and 26% of natural gas reserves (United States Department of Interior et al. 2006). Meeting 20% of US energy demand with wind could impact 50,000 km², a significant portion of which would be in the Rocky Mountain West (United States Department of Energy 2008). Landscape planning to balance wildlife conservation with those of resource development must be analogous in scale to be effective given the spatial extent of anticipated impacts. Furthermore, for planning to be successful it must embrace the social and political realities of the region (Lindenmeyer et al. 2008). The analysis presented is both broad enough in scale to allow a relevant examination of the necessary tradeoffs and by assessing the potential impacts of energy development I bring recognition of the political reality of energy development in the West. The framework presented here provides the necessary structure to clearly illustrate the tradeoffs between sage-grouse conservation and energy development. The next generation of analyses to direct conservation action should identify spatially which landscapes meet the seasonal habitat needs of sage-grouse by linking existing bird information with new land cover and all relevant stressors.

Resources available to implement landscape conservation invariably are in short supply relative to need. Accordingly, setting priorities for conservation action is a necessary and major task for agencies and organizations concerned with the conservation of species and ecosystems (Groves et al. 2002, Newborn et al. 2005). Core areas enable decision-makers to spatially prioritize their targets for sage-grouse conservation. My results suggest that given the nature of sage-grouse distribution, a large portion of the breeding population can be conserved within core areas. For example, 75% of the breeding population can be captured within only 30% of the area. However, the distribution of the core areas and their value vary across the study area. Wyoming contains 64% of the known breeding population in this study and more active leks than all the other states combined. In concordance with variation in value of core areas, risks to core areas vary dramatically as well. Wyoming has the greatest combined risk from both wind and oil and gas development, but also has the greatest potential for conservation in terms of the value of the core areas. The intersection of the value of the
core areas and the risks to which they are exposed (Figs. 2 and 3), suggests a series of strategies needed to ensure long-term persistence of sage-grouse: (1) in areas of high biological value, policy changes are needed to manage leasing and permitting of oil and gas development on federal lands and to proactively site future wind developments; (2) rapid implementation of conservation and enhancement of high-value biological areas without energy resources; and (3) restoration of fringe habitats and low density areas with limited risk. In the discussion that follows I explore each of these strategies in detail.

Landscapes with high biological value and high risk for development represent the greatest challenge facing land use managers in regards to sage-grouse. This is a concern because 44% of areas with high biological value are at risk for energy development (red areas, Figure 3). The rapid pace and scale of oil and gas drilling has emerged as a major issue because areas being developed (i.e., southwest Wyoming and northwest Colorado) include some of the largest remaining sagebrush landscapes with the highest densities of sage-grouse in North America (Figure 1; Connelly et al. 2004). The future of sage-grouse conservation is in question in the eastern range in part because 44% of the lands that the federal government has authority to control for oil and gas development (7 of 16 million ha) has been authorized for exploration and development (Naugle et al. in press). Lease sales continue despite concerns because no policy is in place that would permit an environmental assessment of risk at the scale at which impacts occur. Severity of impacts (Holloran 2005, Aldridge and Boyce 2007, Walker et al. 2007) and the unprecedented leasing of the public mineral estate dictate the need for a shift from piecemeal to landscape-scale conservation. Analyses presented here will enable policy makers to consider a portfolio of set-aside areas, priority conservation areas, lease consolidations and more stringent spatially-based best management practices as creative solutions to balance energy development with sage-grouse conservation.

Wind power is an emerging issue contributing to the overall risk of energy development to sage-grouse populations in the West (Figure 2 and 3). There is an urgent need for policies that promote landscape-scale considerations when siting wind facilities as well as replicated research to quantify potential impacts (Stewart et al. 2007). The low overlap between wind potential and oil and gas leasing highlight the need to incorporate
multiple stressors in planning efforts because unconsidered stressors could negate conservation actions. Lands with federal surface ownership are being leased at increasing rates for wind development, and a similar portfolio of tools as above could be considered to reduce impacts on these lands. However, much of the future wind energy development is anticipated to occur on private lands where there is little or no regulatory oversight. The lack of a landscape planning paradigm is especially a concern for populations in Montana and the Dakotas where the primary risk is unplanned large-scale wind development on private lands. Private lands with high value sage-grouse habitat might be considered for purchased conservation easement agreements with landowners that limit surface development. Yet the high purchase cost of easements and even higher profitability of wind development for private landowners require broader strategies to minimize wind development footprints. Ultimately, policy decisions on the placement of new energy transmission corridors built to carry electricity from new wind developments will be a major driver of wind development and may be used to further refine risk assessment.

High biological value and low energy potential identify low conflict areas to focus conservation actions immediately. Currently, 17% of the eastern sage-grouse range has high biological value and low risk from energy development (orange areas Figure 3). Maintaining these quality sage-grouse habitats, especially in areas adjacent to development (Figure 1) or where development is anticipated (Figure 2 and 3), will be critical to ensure genetic connectivity (Oyler-McCance et al. 2005a,b) and natural recolonization after oil and gas development activities have ceased (Gonzalez et al. 1998, Baxter et al. 2008). In these high value and low energy potential areas, strategies should further focus on reducing risks from other stressors to sagebrush habitats (e.g., Klebenow 1970; Connelly et al. 2000 a, b; Leonard et al. 2000, Smith et al. 2005, Walker et al. 2007), such as tillage (Farrell et al. 2006; United States Government Accounting Office 2007), residential development (Theobald 2003, Theobald 2005) and invasive plants such as cheat grass (Bromus tectorum; Bergquist et al. 2007). Rural areas with desirable natural amenities and recreational opportunities throughout the United States have experienced a surge in rural development since the 1970s (Brown et al. 2005), with
growth in the Inter-mountain West during the 1990s occurring faster than in any other region of the country (Hansen et al. 2002). Conservation easements are one tool to reduce residential development and agricultural conversion on private lands (e.g., Kiesecker et al. 2007). Opportunities also exist to target existing federal and state incentive programs to these areas focusing on compatible grazing practices and habitat enhancement activities. A preponderance of private surface ownership in Montana and Utah coupled with low risks of development make core areas in many parts of these states ideal places to develop incentives to ranching and rural lifestyles through long-term easement programs such as the Conservation Reserve Program that reduces habitats lost by conversion to agriculture. Opportunities for easements and management programs are available in Wyoming because of the sheer size of this population, but long-term viability is more of a public policy decision.

Areas of low biological value and low energy potential (19% of eastern range, light-blue areas Figure 3) represent low conflict opportunities for sage-grouse. My analyses document the importance of these areas in maintaining connectivity to the high value core areas in Montana (Figure 3). Core areas with low biological value and low energy potential will be important in this regard, with restoration being one of the key strategies. Recent experience has shown the difficulty of maintaining Gunnison Sage-Grouse (Centrocercus minimus; Oyler-McCance et al. 2005a) and Lesser Prairie-Chicken (Tympanuchus pallidicinctus; Hagen et al. 2004) when only small and fragmented populations remain. Sage-grouse have already been lost from half of their former range (Schroeder et al. 2004), and many of the low value and low potential areas identified in this analysis are the same areas where continued range contraction is expected to be most severe (Aldridge et al. 2008). Fringe populations in the Dakotas, Montana and Canada need to pursue aggressive habitat restoration programs if they hope to maintain their biological value. Programs should focus on restoring adjacent lands in tillage agriculture to sagebrush-dominated grasslands in addition to enhancing existing native habitats.

Explicitly combining information about the vulnerability of landscapes to anthropogenic risk enables conservation planners to consider aspects of urgency as well the probability for success of a given conservation strategy (Wilson et al. 2005, Copeland
et al. 2007, Pressey and Bottrill 2008). Core areas and assessment of the potential future impacts they may experience represents a starting point to initiate conservation in landscapes where results will have the largest benefit to populations. The need to support implementation of core areas with studies that document seasonal habitat use and migration patterns of radio-marked sage-grouse (e.g., Aldridge and Boyce 2007, Doherty et al. 2008) ensure priority landscapes meet all life history needs. Prioritization of landscapes is simply an admission that threats are large, resources are limited, and that conservation action targeting every remaining population is improbable. Core areas represent a proactive attempt to identify a set of conservation targets to maintain a viable and connected set of populations before the opportunity to do so is lost.

Strategies must be integrated among all states involved for landscape-scale conservation to be successful. Each state will need to do their part to maintain sage-grouse distribution and abundance. Successful implementation in one state, such as Montana, will not be enough to compensate for losses in important places like Wyoming. Conservation concerns related to sage-grouse and other declining species will remain at the forefront until collaborative landscape planning and conservation are demonstrated. Analyses reported here provide a framework for planning across state boundaries and a currency for measuring the success of its implementation.

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Table 1. Characteristics of Greater sage-grouse leks used to delineate core areas.

<table>
<thead>
<tr>
<th></th>
<th>Number of leks</th>
<th>Average maximum male count (SD)</th>
<th>Percent relative abundance</th>
<th>Average distance (km) to nearest lek (SD)</th>
<th>Median distance (km) to nearest lek</th>
<th>Current distribution (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>200</td>
<td>33.4 (32.4)</td>
<td>8%</td>
<td>4.6 (4.2)</td>
<td>3.5</td>
<td>17,061 b</td>
</tr>
<tr>
<td>Coloradoa</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Montana</td>
<td>869</td>
<td>23.6 (20.5)</td>
<td>24%</td>
<td>4.6 (4.2)</td>
<td>3.5</td>
<td>127,242</td>
</tr>
<tr>
<td>North Dakota</td>
<td>14</td>
<td>15.4 (14.5)</td>
<td>&lt;1%</td>
<td>8.6 (2.6)</td>
<td>8.3</td>
<td>2,829</td>
</tr>
<tr>
<td>South Dakota</td>
<td>21</td>
<td>28.2 (13.0)</td>
<td>1%</td>
<td>10.4 (5.2)</td>
<td>9.8</td>
<td>10,074</td>
</tr>
<tr>
<td>Utahc</td>
<td>71</td>
<td>37.3 (34.6)</td>
<td>3%</td>
<td>4.4 (4.6)</td>
<td>2.7</td>
<td>7,046</td>
</tr>
<tr>
<td>Wyoming</td>
<td>1190</td>
<td>47.3 (45.2)</td>
<td>64%</td>
<td>5.0 (3.6)</td>
<td>4.3</td>
<td>176,424</td>
</tr>
<tr>
<td>Sage-Grouse Management Zones I and II d</td>
<td>2336</td>
<td>37.2 (40.0)</td>
<td>100%</td>
<td>4.8 (3.7)</td>
<td>4.1</td>
<td>338,789 e</td>
</tr>
</tbody>
</table>

a Total included 29 leks located in sage-grouse Management Zone VII
b Area estimate included portions of sage-grouse Management Zone VII
c Included leks in sage-grouse Management Zone II
d Leks do not sum because Colorado includes 29 leks from Management Zone VII
Area estimate excludes Idaho, Canada and sage-grouse Management Zone VII in Colorado.
Table 2. Summary of Greater Sage-Grouse core areas at risk of wind and/or oil and gas development in Wyoming, Montana, Colorado, Utah, South Dakota and North Dakota (through September 2007).

<table>
<thead>
<tr>
<th>Percent of Core Areas At Risk From Energy Development</th>
<th>High Wind Potential a</th>
<th>Authorized Oil and Gas Leases b</th>
<th>Both</th>
<th>Either</th>
</tr>
</thead>
<tbody>
<tr>
<td>25% Cores</td>
<td>20.2</td>
<td>34.3</td>
<td>3.7</td>
<td>50.8</td>
</tr>
<tr>
<td>50% Cores</td>
<td>19.4</td>
<td>31.5</td>
<td>4.1</td>
<td>46.9</td>
</tr>
<tr>
<td>75% Cores</td>
<td>19.0</td>
<td>28.0</td>
<td>3.9</td>
<td>43.1</td>
</tr>
<tr>
<td>100% Cores</td>
<td>18.7</td>
<td>23.4</td>
<td>3.2</td>
<td>38.8</td>
</tr>
<tr>
<td>Eastern Distribution</td>
<td>21.4</td>
<td>20.8</td>
<td>3.3</td>
<td>38.8</td>
</tr>
</tbody>
</table>

a I defined high wind potential as a wind class rating \(\geq 4\) (NREL 2008)

b Authorized leases include federal oil and gas leases authorized for exploration and development on or before 1 June 2007 for each state except Utah (1 May 2007)
Table 3. Summary of Greater Sage-Grouse 75% core areas at risk of wind and/or oil and gas development by state (through September 2007).

<table>
<thead>
<tr>
<th>State</th>
<th>Relative Abundance</th>
<th>High Wind Potential&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Authorized Oil &amp; Gas Leases&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Both</th>
<th>Either</th>
<th>Federal Surface Ownership</th>
<th>Federal Subsurface Ownership</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wyoming</td>
<td>64%</td>
<td>21.2</td>
<td>35.7</td>
<td>5.7</td>
<td>51.2</td>
<td>57.1</td>
<td>68.5</td>
</tr>
<tr>
<td>Montana</td>
<td>24%</td>
<td>19.8</td>
<td>8.5</td>
<td>0.6</td>
<td>27.7</td>
<td>31.4</td>
<td>44.9</td>
</tr>
<tr>
<td>Colorado</td>
<td>8%</td>
<td>0.3</td>
<td>33.7</td>
<td>0.1</td>
<td>33.8</td>
<td>43.3</td>
<td>60.0</td>
</tr>
<tr>
<td>Utah</td>
<td>3%</td>
<td>0.4</td>
<td>8.6</td>
<td>0.0</td>
<td>9.1</td>
<td>46.5</td>
<td>55.2</td>
</tr>
<tr>
<td>S. Dakota</td>
<td>1%</td>
<td>72.3</td>
<td>3.7</td>
<td>3.2</td>
<td>72.9</td>
<td>11.5</td>
<td>38.5</td>
</tr>
<tr>
<td>N. Dakota</td>
<td>&lt;1%</td>
<td>28.9</td>
<td>10.0</td>
<td>2.2</td>
<td>36.6</td>
<td>56.8</td>
<td>28.2</td>
</tr>
</tbody>
</table>

<sup>a</sup> I defined high wind potential as a wind class rating ≥4 (NREL 2008)

<sup>b</sup> Authorized leases include federal oil and gas leases authorized for exploration and development on or before 1 June 2007 for each state except Utah (1 May 2007)
Figure 1. Core areas that contain 25, 50, 75, and 100% of the known breeding population of Greater Sage-Grouse in their eastern range (Sage-grouse Management Zones I and II; Connelly et al. 2004). Inset depicts locations of producing oil and gas wells (black triangles) as of September 2007.
Figure 2. Potential for oil and gas and wind development in the eastern range of Greater Sage-Grouse (Management Zones I and II; Connelly et al. 2004). Wind potential is defined as the potential for commercial development where wind class ratings $\geq 4$ from the NREL (2008). Oil and gas potential is defined by locations where leases have been authorized for exploration and development by the federal government on or before 1 June 2007 for each state except Utah (1 May 2007). A swath of authorized leases across southern Wyoming following the interstate between Laramie and Rock Springs appears lighter in color because of the checker board pattern of mineral ownership.
Figure 3. Overlay of biological value with energy potential to assess risk of development to Greater Sage-Grouse core areas. Landscapes of high biological value were defined by 25, 50, and 75% Sage-grouse core areas (100% cores in North and South Dakota). High potential for energy development was defined by a wind class rating $\geq 4$ (NREL 2008) or an oil and gas lease that was authorized for exploration and production by the federal government on or before 1 June 2007 for each state except Utah (1 May 2007).