Wildlife Monographs 190:1–39; 2014; DOI: 10.1002/wmon.1014

Habitat Prioritization Across Large Landscapes, Multiple Seasons, and Novel Areas: An Example Using Greater Sage-Grouse in Wyoming

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ABSTRACT Animal habitat selection is an important and expansive area of research in ecology. In particular, the study of habitat selection is critical in habitat prioritization efforts for species of conservation concern. Landscape planning for species is happening at ever-increasing extents because of the appreciation for the role of landscape-scale patterns in species persistence coupled to improved datasets for species and habitats, and the expanding and intensifying footprint of human land uses on the landscape. We present a large-scale collaborative effort to develop habitat selection models across large landscapes and multiple seasons for prioritizing habitat for a species of conservation concern. Greater sage-grouse (*Centrocercus urophasianus*, hereafter sage-grouse) occur in western semi-arid landscapes in North America. Range-wide population declines of this species have been documented, and it is currently considered as "warranted but precluded" from listing under the United States Endangered Species Act. Wyoming is predicted to remain a stronghold for sage-grouse populations and contains approximately 37% of remaining birds. We compiled location data from 14 unique radiotelemetry studies (data collected 1994–2010) and habitat data from high-quality, biologically relevant, geographic information system (GIS) layers across Wyoming. We developed habitat selection models for greater sage-grouse across Wyoming for 3 distinct life stages: 1) nesting, 2) summer, and 3) winter. We developed patch and landscape models across 4 extents, producing statewide and regional (southwest, central, northeast) models for Wyoming. Habitat selection varied among regions and seasons, yet preferred habitat attributes generally matched the extensive literature on sage-grouse seasonal habitat requirements. Across seasons and regions, birds preferred areas with greater percentage sagebrush cover and avoided paved roads, agriculture, and forested areas. Birds consistently preferred areas with higher precipitation in the summer and avoided rugged terrain in the winter. Selection for sagebrush cover varied regionally with stronger selection in the Northeast region, likely because of limited availability, whereas avoidance of paved roads was fairly consistent across regions. We chose resource selection function (RSF) thresholds for each model set (seasonal × regional combination) that delineated important seasonal habitats for sage-grouse. Each model set showed good validation and discriminatory capabilities within study-site boundaries. We applied the nesting-season models to a novel area not included in model

Received: 24 July 2012; Accepted: 24 March 2014

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development. The percentage of independent nest locations that fell directly within identified important habitat was not overly impressive in the novel area (49%); however, including a 500-m buffer around important habitat captured 98% of independent nest locations within the novel area. We also used leks and associated peak male counts as a proxy for nesting habitat outside of the study sites used to develop the models. A 1.5-km buffer around the important nesting habitat boundaries included 77% of males counted at leks in Wyoming outside of the study sites. Data were not available to quantitatively test the performance of the summer and winter models outside our study sites. The collection of models presented here represents large-scale resource-management planning tools that are a significant advancement to previous tools in terms of spatial and temporal resolution. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS brood, *Centrocercus urophasianus*, core regions, extent, functional response, greater sage-grouse, logistic regression, nesting, radiotelemetry, resource selection function, sagebrush, seasonal variation, winter.

Priorización del Hábitat a través de Paisajes Extensos, Estaciones Múltiples, y Áreas Nuevas: Un Ejemplo Usando al Urogallo Mayor en Wyoming

RESUMEN La selección de hábitat es un área de investigación importante y en expansión en el campo de la ecología animal. En particular, el estudio de la selección de hábitat es crítico en los esfuerzos de priorización para especies sensibles o amenazadas. La planeación a nivel de paisajes para especies de interés está ocurriendo a escalas cada vez más extensas debido a una creciente apreciación del papel que juegan los patrones a gran escala en la persistencia de las especies, al mejoramiento de las bases de datos existentes para especies y hábitats, y a la expansión e intensificación de los efectos antropogénicos en el uso del paisaje. En este estudio, presentamos un esfuerzo de colaboración a gran escala para desarrollar modelos de selección de hábitat a través de paisajes extensos y múltiples estaciones, con el fin de priorizar el hábitat para una especie amenazada. El urogallo mayor (*Centrocercus urophasianus*) habita los paisajes semiáridos del oeste de Norte América. Declives a gran escala en el rango de hogar del urogallo han sido documentados y actualmente se considera una como una especie "justificada pero excluida" de ser enlistada en el Acta de Especies en Peligro de Los Estados Unidos. Es de predecir que el Estado de Wyoming, en los Estados Unidos, que cuenta con el 37% de los individuos actuales, siga representando una plaza fuerte para las poblaciones de urogallo. Compilamos datos de ubicación de 14 estudios de radio-telemetría (datos colectados entre 1994–2010) e información de hábitat a partir de capas de Sistemas de Información Geográfica (SIG) de alta calidad y biológicamente relevantes. Desarrollamos modelos de selección de hábitat para el urogallo en el estado de Wyoming durante tres etapas distintivas en el ciclo de vida: 1) anidación, 2) verano, e 3) invierno. Desarrollamos modelos a nivel de parche y del paisaje a través de 4 extensiones, produciendo modelos estatales y regionales (suroeste, central, noreste) para el estado de Wyoming. La selección del hábitat por parte del urogallo varió entre regiones y estaciones sin embargo, los atributos de los hábitats preferidos coincidieron generalmente con los requerimientos estacionales de hábitat reportados en la literatura. A través de las estaciones y las regiones, las aves prefirieron áreas con un alto porcentaje de cobertura de artemisia y evitaron caminos pavimentados, áreas agrícolas y bosques. Las aves prefirieron de manera consistente áreas con alta precipitación en el verano y evitaron terreno escarpado in el invierno. La selección por cobertura de artemisia varió regionalmente con una preferencia más fuerte en la región Noreste, mayormente debido a la disponibilidad limitada, mientras que la evasión de caminos pavimentados fue bastante consistente a través de regiones. Para cada grupo de modelos (combinación estación x región) elegimos umbrales de funciones de selección de recursos (RSF por sus siglas en inglés) que delinearan hábitat estacionalmente importante para el urogallo. Cada grupo de modelos presentó capacidades de validación y discriminación satisfactorias, dentro de los límites del sitio de estudio. Aplicamos los modelos de la estación de anidación a un área nueva no incluida en el desarrollo de los modelos. El porcentaje de ubicaciones independientes de nidos localizados directamente dentro de hábitat identificado como importante no fue muy impresionante en el área nueva (49%); sin embargo, al incluir una zona de amortiguación de 500 m alrededor de hábitat importante, logramos capturar el 98% de las ubicaciones independientes de los nidos incluidos en el área nueva. Adicionalmente, usamos los harems y los picos de conteo de machos asociados a estas zonas de exhibición, como una representación del hábitat de anidación por fuera de los sitios de estudio utilizados para desarrollar los modelos. Una zona de amortiguación de 1.5 km alrededor de los hábitats importantes para la anidación incluyó el 77% de los machos contados en las zonas de exhibición por fuera de los sitios de estudio en Wyoming. No contamos con los datos necesarios para examinar de manera cuantitativa el desempeño de los modelos de invierno y verano por fuera de los sitios de estudio. Los modelos aquí presentados constituyen una herramienta de planeación del manejo de recursos a gran escala, representando un avance significativo con respecto a herramientas previamente existentes en términos de su resolución espacial y temporal.

Habitat Priorités au sein de Vastes Paysages, Plusieurs Saisons, et les Aires de Nouveaux: Un Exemple d’utilisation du Tétras des Armoises dans le Wyoming

RÉSUMÉ Sélection de l’habitat abstrait animal est un domaine important et vaste de la recherche en écologie. En particulier, l’étude de la sélection de l’habitat est essentiel dans l’habitat efforts de priorisation pour les espèces préoccupantes de conservation. L’aménagement du paysage pour species qui se passe à des degrés toujours plus en raison de l’appréciation du rôle de modèles échelle du paysage dans la persistance de l’espèce couplé à l’amélioration des ensembles de données pour les espèces et les habitats, et l’empreinte s’étend et s’intensifie de l homme et utilise le paysage. Nous présentons un effort de collaboration à grande échelle pour développer des modèles de sélection de l’habitat à travers de vastes paysages et de multiples saisons pour priorité l’habitat d’une espèce préoccupante de conservation. Tétras des armoises (*Centrocercus urophasianus*, ci-après tétras des armoises) se produire dans des paysages semi-arides de l’ouest en Amérique du Nord. déclin de la population Gamme échelle de cette espèce ont été documentés, et il est actuellement considéré comme «justifiée mais empêché” de l’inscription en vertu dela Loi sur les espèces en voie de disparition aux États-Unis. Wyoming devrait demeurer un bastion pour les populations de Tétras des armoises et contient environ 37% des oiseaux restants. Nous avons compilé les données de localisation à partir de 14 études de télémesure uniques (données recueillies 1994–2010) et les données de l’habitat de haute qualité du système, de l’information géographique d’intérêt biologique (SIG) couches dans le Wyoming. Nous avons développé des modèles de sélection de l’habitat pour les tétras des armoises dans le Wyoming pour trois étapes de la vie distincts: 1) la nidification, 2) été, et 3) l’hiver. Nous avons développé des modèles de patch et du paysage à travers 4 degrés, la production de tout l’État et régionale (sud-ouest, nord-est, centrales) des modèles pour le Wyoming. Sélection de l’habitat varie selon les régions et les saisons, encore attri de l’habitat préféré tes généralement identifié la vaste littérature sur Tétras des armoises besoins en habitat de saison. Les saisons et les régions, les oiseaux préfèrent les zones avec une plus grande couverture de pourcentage de l’armoise et de routes pavées évitées, l’agriculture et les zones boisées. Oiseaux zones toujours privilégiées avec des précipitations plus abondantes en été et le terrain accidenté éviter en hiver. Sélection pour la couverture d’armoise varier régional avec forte sélection dans la région Nord-Est, probablement en raison de la disponibilité limitée, tandis que l’évitement des routes revêtues est assez cohérente dans toutes les régions. Nous avons choisi la fonction de sélection des ressources (RSF) seuils pour chaque ensemble de modèles (saisonnière combinaison régional) qui cernait les habitats saisonniers importants pour tétras des armoises. Chaque model ensemble a montré une bonne validation et capacités discriminatoires dans les limites étude de site. Nous avons appliqué les modèles de nidification saison à un nouveau domaine non inclus dans l’élaboration du modèle. Le pourcentage de sites de nidification indépendants qui tombait directement avec dans un habitat important identifié n’était pas trop impressionnant dans la zone roman (49%); cependant, y compris un 500-m tampon autour des habitats importants capturé 98% des sites de nidification indépendants dans la zone roman. Nous avons également utilisé les arènes et le pic mâle associé compte comme un proxy pour un habitat de nidification à l’extérieur des sites d’étude utilisées pour élaborer des modèles. A 1.5 km tampon autour des importantes limites de l’habitat de nidification inclus 77% des hommes recensés au leks dans le Wyoming en dehors des sites d’étude. Les données n’étaient pas disponibles pour quantitatively tester les performances des modèles d’été et d’hiver en dehors de nos sites d’étude. La collection de modèles présentés ici représente des outils de planification des ressources de gestion à grande échelle qui sont une avancée significative à outils précédents en teefficace de la résolution spatiale et temporelle.

Contents

INTRODUCTION

Habitat prioritization, particularly for species of conservation concern, is an important and urgent management concern. Efforts to manage habitats are increasingly implemented across larger geographic regions and the importance of regional and systematic prioritization is paramount. Large, landscape-scale patterns can influence population dynamics and conservation, and our capacity to address questions at large scales has been enabled by technical advances in telemetry and mapping systems (Atamian et al. 2010, Moss et al. 2010). In general, conservation biology is moving from a focus on extrapolated inferences from single study sites, to sampled inferences across larger spatial extents and multiple study sites. In parallel, small-scale conservation and land-use planning are being combined with, and strengthened by, regional landscape-level approaches to habitat prioritization and management.

Animals select resources at multiple scales (Johnson 1980, Boyce et al. 2003, Boyce 2006) and scale is defined by the grain (i.e., smallest unit measured) and extent (i.e., the size of the area; Turner et al. 2001). Conservation and management strategies for species should match the scales and extents important to the species relative to annual movements, seasonal habitats, and selected landscape and local components. The availability of quality species-occurrence data across large extents is a major obstacle to landscape-level planning. Collaborations of many individuals and organizations are necessary to adequately sample variation in wildlife habitat selection across large and diverse habitat gradients that may be beneficial for wide-ranging species.

Habitat characterization represents a trade-off between extent and resolution, falling into 2 general categories of large extent with coarse spatial resolution and small extent with fine spatial resolution. For example, many species distribution models cover large spatial extents (e.g., species range) but are limited in their resolution because of limited species data, and inputs from coarse-scale geographic information systems (GISs) data. Alternatively, many examples exist of accurate, fine-scale habitat selection models that are developed using marked individuals and local habitat data. However, these models are typically limited to the extent of the study site, with little effort to apply results outside of specific study areas (Miller et al. 2004, Aldridge et al. 2012). Both approaches have merit and inform habitat conservation and ecological understanding.

An ideal approach for development of habitat prioritization models would incorporate strengths of both approaches by covering large extents with fine-resolution data on species presence and habitat. Until recently, this type of study was impractical because of a lack of data and computer-processing limitations. However, our capacity to execute large-scale habitat characterization is growing with increasing numbers of individual studies and marked individuals, and increasing accuracy, resolution, and availability of remotely sensed GIS data. The coupling of increased availability of spatially explicit data (for both species and habitats) with collaborative efforts to increase sample size and variation in habitat sampled could result in powerful tools for species management and unprecedented capabilities to address important large-scale ecological questions.

Seasonal variation in habitat use is an important consideration when developing models to predict the probability of resources being selected. Pooling data across seasons can mask intra-annual variation in habitat selection and lead to misleading inferences (Schooley 1994) or low predictive capabilities (Aarts et al. 2008). Seasonal variation in habitat use has been explicitly addressed for multiple species, particularly for migratory ungulates (Rettie and Messier 2000, Leblond et al. 2011, Polfus et al. 2011), deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*; Ager et al. 2003), and fish (Blanchfield et al. 2009). Regional variation in habitat availability also can confound habitat selection models if not considered explicitly (Aarts et al. 2008), and is of particular concern when applying habitat selection models to novel areas (Aldridge et al. 2012). For example, changing the proportion of available habitat within areas (or study sites) can influence relative use in trade-off situations, referred to as the functional response in habitat use (Mysterud and Ims 1998). The strength of habitat selection (i.e., steepness of the functional response) increases with the amount of unused habitat sampled. Alternatively, in some species, selection for particular habitat components can remain constant across landscapes despite variation in availability if alternative habitat components can provide animals with similar resources (Morellet et al. 2011).

The application of habitat selection models to novel areas should be done with caution because of the many concerns associated with this type of extrapolation (Miller et al. 2004, Coe et al. 2011). However, models can perform well in novel areas when covariates associated with probability of animal use are consistent with species' biology (Coe et al. 2011) and have a similar range and relationship in the novel environment as in the training environment. Identification of consistent biological drivers of habitat selection is thus crucial to the performance of models in novel areas. The spatial interpolation and extrapolation of habitat selection models are most accurate when the availability of habitats is approximately the same in the novel areas (Mladenoff et al. 1999, Aarts et al. 2008) because of the functional response in habitat use (Mysterud and Ims 1998). For example, Coe et al. (2011) found that elk models performed best in novel areas for seasons in which forage was likely limited (i.e., when selection for forage would likely be strongest).

Additionally, good model performance in novel areas suggests similar composition of resources, or sufficient generality in model form. Models developed in a given site may need to capture the specifics of that site to perform well, and therefore, may be too site-specific to perform well in novel areas. Therefore, when habitat availabilities are different in the extrapolated area, models estimated from other sites may fail to capture the response in the novel area (Mysterud and Ims 1998) unless the models are sufficiently general to be more broadly applied.

Loss and degradation of native vegetation have affected much of the sagebrush (*Artemisia* spp.) ecosystem in western North America, and this ecosystem has become increasingly fragmented because of conifer encroachment, exotic annual grass invasion, and anthropogenic development (Knick et al. 2003, Connelly et al. 2004, Davies et al. 2011). Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a species of conservation concern that occurs throughout the sagebrush ecosystem (Schroeder et al. 1999; Fig. 1). Range-wide declines in sage-grouse populations also have been documented and are predicted to continue in many populations (Garton et al. 2011) and the species has been extirpated from nearly half of its original range (Schroeder et al. 2004). Currently sage-grouse are considered "warranted, but precluded" for listing under the United States Endangered Species Act of 1973 (U.S. Fish and Wildlife Service [USFWS] 2010), Endangered under the Canadian Species at Risk Act, and "Near Threatened" on the International Union for Conservation of Nature (IUCN) Red List. The USFWS concluded that the lack of regulatory mechanisms and habitat and population fragmentation represented significant threats to the species (USFWS 2010). Thus, habitat prioritization is an important need and a challenge for many land and wildlife management agencies.

Informed habitat prioritization in Wyoming is likely fundamental to the long-term persistence of sage-grouse. Wyoming contains approximately 37% of sage-grouse range wide and 64% of sage-grouse in the eastern range of the species (Doherty et al. 2010*b*; Fig. 1), and Wyoming is predicted to remain a stronghold for sage-grouse populations (Knick et al. 2003). Sage-grouse demonstrate fairly consistent habitat preferences across their range (Aldridge and Boyce 2007, Hagen et al. 2007, Doherty et al. 2008, Atamian et al. 2010, Connelly et al. 2011) and are therefore well-suited for large-extent, habitat prioritization efforts. Furthermore, sage-grouse are a resident species with limited migration in Wyoming (Fedy et al. 2012) making assessment of seasonal habitat requirements less complicated than for species with more extensive migratory behavior.

Sage-grouse use distinct seasonal habitats throughout their annual cycle for breeding, brood rearing, and wintering. Seasonal habitats for sage-grouse are generally considered across 3 life

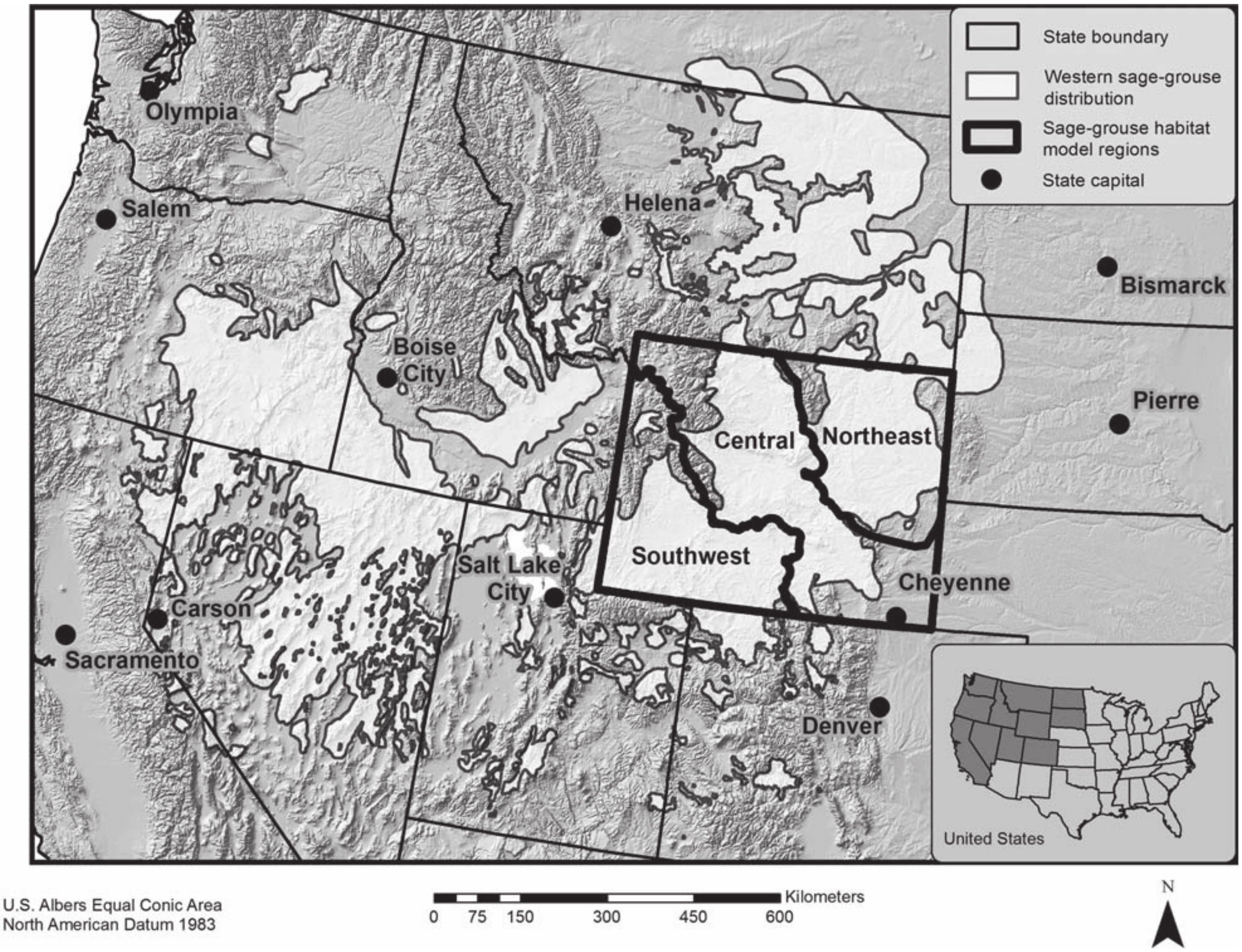

Figure 1. Greater sage-grouse distribution in the United States. Wyoming contains approximately 37% of the remaining birds range-wide (Doherty et al. 2010*b*). Regional boundaries for this modeling effort are indicated with black lines inside Wyoming. Inset shows the western states containing sage-grouse.

stages: 1) breeding habitat (including lekking, nesting, and early brood-rearing); 2) summer (i.e., late brood-rearing habitat); and 3) winter habitat (Connelly et al. 2011, Fedy et al. 2012). Habitat requirements during these life stages differ in several ways. Nesting and early brood-rearing habitat typically fall within a specific range of values for sagebrush, forb, and grass cover and height (Hagen et al. 2007, Kirol et al. 2012). Broods move to summer ranges a few weeks post-hatch (Connelly et al. 1988). Hagen et al. (2007) defined the late brood-rearing period as >6 weeks post-hatch and suggested that selection for mesic plant communities with greater herbaceous cover during late brood-rearing reflects a preference for areas with abundant invertebrates and forbs (Johnson and Boyce 1990, Drut et al. 1994*b*). Summer habitats are typically used from July to September, depending on weather conditions (Peterson 1970, Wallestad 1971, Gregg et al. 1993, Drut et al. 1994*a*). During this time, hens generally move toward more moist sites (in some cases moving up in elevation) where herbaceous plants are most plentiful (Connelly et al. 1988). However, during particularly wet summers, hens and broods will remain in sagebrush communities where herbaceous plants are available throughout the summer (Holloran 2005). In addition, late-brood-rearing habitat of sage-grouse in xeric big sagebrush (*Artemisia tridentata*) communities may be characterized by grass and sagebrush cover and height similar to levels that sage-grouse use for nesting and early brood rearing (Kirol et al. 2012). During winter, sage-grouse rely on sagebrush protruding above the snow for food and shelter (Schroeder et al. 1999). Therefore, snow depth and shrub height are influential components of sage-grouse distributions in winter (Remington and Braun 1985, Homer et al. 1993, Schroeder et al. 1999, Connelly et al. 2000, Crawford et al. 2004). Selection of particular sagebrush species in winter can also be influenced by variation in the phytochemistry of different shrubs (Frye et al. 2013). Sage-grouse also avoid conifers at the landscape scale and avoid riparian areas, conifers, and rugged landscapes at finer scales in winter (Doherty et al. 2008, Carpenter et al. 2010).

Current efforts in large-scale habitat prioritization are ongoing in the form of the core-regions concept, which was developed by the Governor of Wyoming's Sage-grouse Implementation Task Force (Kiesecker et al. 2011). The core regions are intended to delineate important breeding habitat for sage-grouse in Wyoming. Core regions were developed based on breeding biology focused on lek sites and refined by models of breeding density across the state (Doherty et al. 2011). The core areas used for management in Wyoming represent an adapted version of biological core areas as presented in Doherty et al. (2011), modified to reflect multiple land-use decisions. These core areas strongly influence land-use decisions, with more stringent stipulations required for development on federal and state lands within the core areas than compared to outside the core areas. Core regions tend to capture a greater number of nesting locations than late summer or winter locations (Fedy et al. 2012). Therefore, Doherty et al. (2011) noted that future work should consider all seasonal habitats.

Our overall goal was to develop habitat selection models for sage-grouse in Wyoming for 3 seasons: nesting, summer (i.e., late brood rearing), and winter. Specifically, we intended to use GIS data in conjunction with numerous telemetry studies across the state to develop statewide models of habitat requirements for sage-grouse in Wyoming. We separated seasons because habitat needs for sage-grouse vary across seasons (Connelly et al. 2011). Wyoming also exhibits considerable variation in habitat characteristics across ecoregions, ranging from low-elevation, mixed big sagebrush-silver sagebrush (*Artemisia cana*)-prairie transitions in the northeast to high-elevation, big sagebrush basins in the southwest. Therefore, to address regional variation, we developed models independently for 3 regions across Wyoming in addition to our statewide models. Furthermore, because habitat selection occurs at multiple scales (Boyce et al. 2003, Boyce 2006, Doherty et al. 2010*a*, Aldridge et al. 2012), we generated models at both the patch (0.006–1 km^2) and landscape (7–139 km^2) scales. Thus, we developed 24 independent habitat selection models in Wyoming (4 regions [including statewide] × 3 seasons × 2 scales). We included different potential covariates (predictor variables) in each model among seasons to reflect the unique seasonal requirements of sage-grouse (Connelly et al. 2000). Fedy et al. (2012) presented a brief summary of seasonal habitat characteristics, and we attempted to capture as many of those habitat components as possible in this research.

We developed a series of general predictions about model performance. During the breeding season, sage-grouse are central-place foragers. Individuals are either fixed to a lek, lek complex, or for females, to a nest site. Thus, movements during the nesting season are expected to be more restricted than during other seasons. Because of the limited movement and strong selection for specific features around nest locations (Fischer et al. 1993, Hagen et al. 2007, Doherty et al. 2010*a*, Aldridge et al. 2012), we predicted nesting models would perform better than either summer or winter models. Sage-grouse habitat use in the winter is strongly related to availability of sagebrush above snow (Remington and Braun 1985, Homer et al. 1993, Schroeder et al. 1999, Connelly et al. 2000, Crawford et al. 2004). Local patterns of snow cover, accumulation, and redistribution of snow as a result of wind are difficult to predict through GIS models. Winter habitat selection models have been developed successfully for sage-grouse (Doherty et al. 2008, Carpenter et al. 2010) but at much smaller extents than the state of Wyoming. Therefore, we predicted that our winter season models would be the least accurate of all our seasonal models. We expected that regional models would better characterize availability than statewide models because habitat selection models can be strongly influenced by the definition and distribution of available habitat components (Jones 2001, Coe et al. 2011). Thus, we predicted that our regional models would perform better in terms of discrimination and validation than our statewide habitat selection models. Similarly, we predicted that models developed in areas with similar habitat-availability metrics would perform best in novel areas.

Our efforts to develop habitat selection models for sage-grouse throughout their annual cycle and across Wyoming allowed us to address fundamental questions in habitat selection modeling and habitat prioritization. We further examined how selection changes across space (different regions) and time (different seasons). We investigated tradeoffs between using a single model for conservation planning resulting in averaged habitat selection over the state, and using 3 regional models that focused on smaller areas to capture variation in availability and selection patterns.

STUDY AREA

Wyoming, USA is 253,000 km^2 and contains one of the largest intact sagebrush ecosystems in the world (Connelly et al. 2004). Approximately 70% of the state is occupied by sage-grouse (Fig. 1). We compiled location data for sage-grouse for 11 study sites from 1994 to 2010 across Wyoming (Figs. 2–4; contributors of study-site data are outlined in the Acknowledgments). Data compilation methods were the same as those detailed in Fedy et al. (2012). These data were collected using standard capture and monitoring techniques by several government agencies and other organizations. All study sites were dominated by sagebrush habitats (Table 1) and details for some study sites can be found in site-specific publications (Holloran et al. 2005; Doherty et al. 2008, 2010*b*; Dzialak et al. 2011; Kaczor et al. 2011; Kirol et al. 2012).

The current distribution of sage-grouse in Wyoming covers 174,580 km^2, and available habitats have substantial variation in configuration and percent canopy cover of sagebrush across the landscape (Table 1). Therefore, to address our regional model objective, we divided Wyoming into 3 regions (southwest, central, and northeast) based on a combination of level 2 (i.e., subregion) hydrologic units, Wyoming Game and Fish sage-grouse management unit boundaries, data availability for training models, and expert input on sage-grouse and sagebrush habitats in Wyoming (Figs. 2–4). Most of the southwest region was contained in a single hydrologic unit and included Jackson, Kemmerer, Pinedale, Farson, Hiawatha, Atlantic Rim, and Stewart Creek study sites. Because the Jackson and Kemmerer study sites were near the edge of this unit, we included them in the southwest region. We used sage-grouse management unit boundaries to divide the remainder of the state into 2 regions: central (study sites included Simpson Ridge, Lander, Moneta, and Casper) and northeast (study sites included Powder River Basin, Thunder Basin, and Hulett study). When a study site straddled the regional boundaries, we assigned all locations to the region containing the majority of the locations.

METHODS

Data Collection

Sage-grouse were captured at each study site following established capture and handling approaches (e.g., spotlighting, Giesen et al. 1982, Wakkinen et al. 1992). Birds were fitted with a very-high-frequency (VHF) necklace-style radio transmitter in most (8) studies (Table 2), and with global-positioning-system (GPS) markers using a rump-mounted figure 8 harness (Rappole and Tipton 1991, Bedrosian and Craighead 2007) in 3 studies (1 of 2 studies in the Moneta study area, 1 of 2 studies in the Powder River Basin study area, and the Jackson study site; Table 2). The GPS markers were typically heavier (e.g., 30 g) than VHF markers (e.g., 14 g) and the additional weight could have affected the movement behavior of birds. However, Fedy

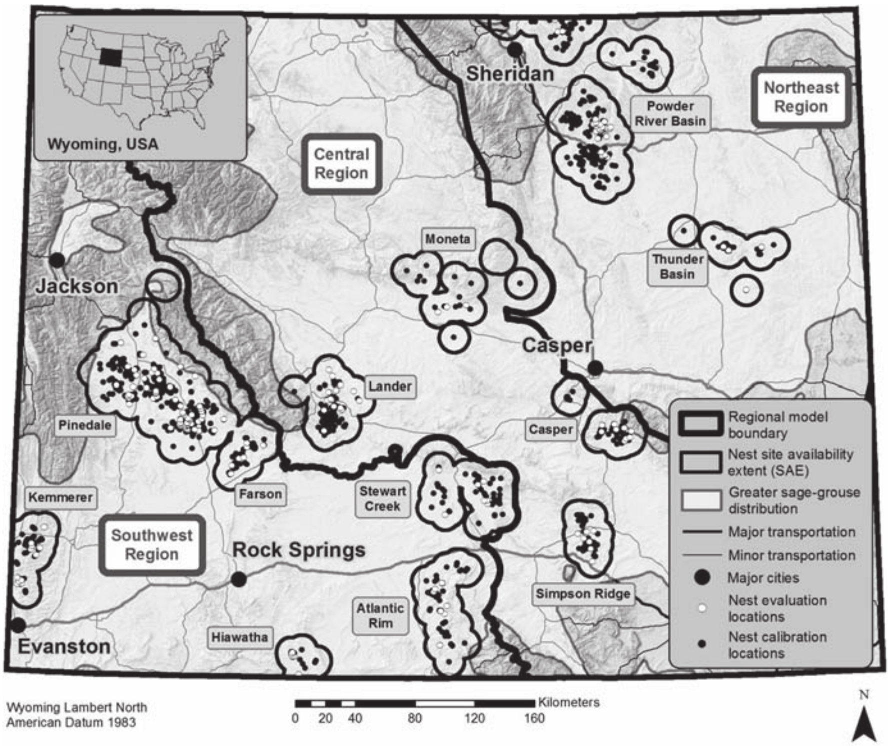

Figure 2. Study locations of greater sage-grouse for the nesting season, 1994–2009. The study sites included for the nesting season are labeled. Small black circles represent the telemetry locations used for model calibration and white circles represent locations used for model evaluation. The study-site-availability extents (SAE) used to define availability for each study site are represented by the black lines encompassing each set of study site locations. Regional boundaries are indicated by the thick black lines and were delineated based primarily on hydrologic units and sage-grouse management zones.

Table 1. Habitat summaries for each greater sage-grouse study site in Wyoming across regions (southwest, central, and northeast). Values presented are summarized across large spatial areas using geographic information system data. The canopy cover estimates are not directly comparable to local on-the-ground measured canopy cover estimates. See Homer et al. (2012) for more discussion. We summarized relevant variables across the available (i.e., not used) habitat locations within each study site.

	Elevation (m)		Total annual precipitation, average (mm)	Sagebrush percent canopy cover[a]		Herbaceous percent canopy cover[a]	
Study site	**Min.**	**Max.**		**Average**	**SD**	**Average**	**SD**
Southwest							
Atlantic Rim	1,924	2,405	37	12	5	11	8
Farson	2,031	2,465	27	13	4	15	6
Hiawatha	2,040	2,379	30	6	4	9	4
Kemmerer	1,889	2,381	34	13	6	18	10
Pinedale	2,039	2,786	30	12	7	20	14
Stewart Creek	1,877	2,371	29	9	4	8	5
Central							
Casper	1,573	2,376	40	11	8	21	11
Lander	1,534	2,373	33	13	6	15	8
Moneta	1,587	2,390	31	9	5	18	10
Simpson Ridge	1,949	2,371	31	9	4	10	6
Northeast							
Hulette	954	1,061	38	10	5	30	16
Powder River Basin	1,049	1,501	36	9	4	36	15
Thunder Basin	1,238	1,612	33	8	3	25	7
Novel							
Bighorn Basin	1,138	2,379	33	5	3	22	15

[a] Canopy cover estimated as mean percent canopy cover within a pixel as defined by Homer et al. (2012).

et al. (2012) reported that GPS radiocollars did not affect interseasonal movement distances within the 2 study sites that were assessed. Studies led by members of the University of Wyoming were approved by the University of Wyoming Animal Care and Use Committee.

Location data for GPS collars were typically remotely recorded; however, GPS units in some cases were also configured with beacons for ground tracking. Triangulation and ground tracking were the primary sources of location data for all VHF studies during the nesting and summer seasons. Because of the large number of GPS locations, we resampled these data to ensure similar contributions relative to the VHF datasets following methods outlined in Fedy et al. (2012). Resampled and full GPS datasets produced similar estimates of interseasonal movement distances of sage-grouse in the 2 study sites where we could test this (Fedy et al. 2012). Animal capture and handling protocols for

Table 2. Sample-size distribution for greater sage-grouse in Wyoming across regions (southwest, central, and northeast), study sites, and seasons. Columns labeled *n* presents the total number of unique individuals included in both the calibration and evaluation datasets. We present the number of locations used in the calibration datasets as n_c and the number of locations in the evaluation datasets as n_e. Years represent when data were collected (1994–2010). Total represents the total number of locations used in both the calibration and evaluation datasets. Blank cells indicate that no data were available.

	Nest					Summer					Winter				
Study site	**Years**	***n***	**n_c**	**n_e**	**Total**	**Years**	***n***	**n_c**	**n_e**	**Total**	**Years**	***n***	**n_c**	**n_e**	**Total**
Southwest															
Atlantic Rim	2008	49	46	11	57	2008	63	228	59	287	2007–2010	121	406	23	429
Farson	1994–1996	67	66	9	75										
Hiawatha	2008	19	20	8	28	2008	34	46	3	49	2007–2009	103	474	69	543
Jackson						2007–2009	45	474	61	535					
Kemmerer	2000–2002	79	86	11	97	2000–2002	18	17	2	19					
Pinedale	1998–2009	422	532	73	605	1998–2007, 2009	328	559	29	588	2006–2008	145	251	15	266
Stewart Creek	1996–1997, 2008	54	48	7	55	2008	21	90	31	121	2008–2010	47	152	10	162
Total		690	798	119	917		509	1,414	185	1,599		416	1,283	117	1,400
Central															
Casper	1997–1999	70	68	9	77										
Lander	2000–2005	114	124	15	139	2000–2005	113	197	7	204					
Moneta	2008–2009	18	16	3	19	2008–2009	146	480	76	556	2008–2009	91	337	66	403
Simpson Ridge	2009	48	50	8	58	2009	60	310	92	402					
Total		250	258	35	293		319	987	175	1,162		91	337	66	403
Northeast															
Hulette	2006	1	2	0	2	2006	9	60	23	83					
PRB[a]	2003–2008	238	290	36	326	2003–2008	253	2,873	510	3,383	2005, 2006, 2008	112	360	59	419
Thunder Basin	2001–2007	33	40	6	46	2001–2007, 2009	44	243	8	251	2001–2006	24	112	4	116
Total		272	332	42	374		306	3,176	541	3,717		136	472	63	535

[a] Powder River Basin.

each individual study were approved by the Wyoming Game and Fish Department.

GIS data were processed using ArcGIS Desktop v.9.3.1–v.10.0, SP3 (http://www.esri.com/), ERDAS 2009–2010 (http://www.erdas.com), Python v2.5.4–v.2.6.2 (http://python.org/), Geospatial Data Abstract Library (GDAL 2010), and Geospatial Modeling Environment (http://www.spatialecology.com/gme/). All GIS data products were converted to U.S. Albers Conical Equal Area (datum WGS 1984) and raster data were resampled to 30-m resolution when necessary. We resampled the PRISM precipitation and Moderate Resolution Imaging Spectroradiometer (MODIS) Normalized Difference Vegetation Index (NDVI) from a moderate resolution (less than 400-m spatial resolution) to a fine spatial resolution (30 m) so we could create resource selection function (RSF) surfaces (GIS requires agreement of pixel sizes between data that are jointly analyzed). Alternatively, we could have resampled all data to the moderate resolution (400 m), but most of our GIS data were better represented at larger spatial scales than what would have been indicated at that resolution. For example, the sagebrush products with a spatial resolution of 30 m would have been significantly degraded and these products were used in modeling sage-grouse habitat. We did not apply moving windows to the precipitation or NDVI products at the patch scale because this would have been inappropriate use of the data's inherent scale. We did not increase the resolution of the inputs, such as the MODIS data; all 30-m pixels within the 400-m area effectively contained the same value.

Scales, Hierarchy, and Seasons

Sage-grouse select habitats across multiple spatial scales (Aldridge and Boyce 2007; Doherty et al. 2008, 2010*b*; Aldridge et al. 2012). We therefore included characteristics such as vegetation, topography, anthropogenic, and hydrological variables measured at 5 spatial extents. Neighborhood statistics (hereafter referred to as moving windows) provide summary statistics of an area larger than a single raster cell in a GIS context (e.g., a square 3 × 3, or circular 564-m-radius kernel, is passed over a dataset and a summary statistic is derived for each cell based on neighboring cells within the kernel). Therefore, this analysis provides a method to capture landscape characteristics at different scales, which are biologically relevant to a species. We grouped the 5 moving windows (extents) into patch and landscape scales. The patch scale included the 2 smallest circular window sizes that summarized predictor variables using radii of 0.045 km ($0.006\ \mathrm{km}^2$) and 0.564 km ($1\ \mathrm{km}^2$). The landscape scale included the 3 largest moving windows that summarized predictor variables at the following radii: 1.5 km ($7.07\ \mathrm{km}^2$), 3.2 km ($32.17\ \mathrm{km}^2$), and 6.44 km ($138.67\ \mathrm{km}^2$). We based these spatial extents on previously published extents and areas of influence known to affect sage-grouse habitat selection (Aldridge and Boyce 2007, Carpenter et al. 2010, Doherty et al. 2010*a*), movements (Holloran and Anderson 2005*b*, Fedy et al. 2012), or fitness and population dynamics (Aldridge and Boyce 2007, Walker et al. 2007, Holloran et al. 2010). We replicated all methods in variable and model selection described below independently at both the patch and landscape scales to derive final models of sage-grouse seasonal habitat selection to capture the hierarchical relationships in habitat selection. This design resulted in separate patch and landscape models of selection for each season and each region. We combined our final patch and landscape models to create spatial predictions from our models of selection.

We based the nesting models on nest locations rather than all bird locations during the nesting seasons, which are defined in Schroeder et al. (1999). Following Fedy et al. (2012), we defined the summer season for birds as 15 June–31 August to capture summer movements because habitats become drier in the summer (Patterson 1952, Dunn and Braun 1986). We chose 15 June as the beginning of the summer season because chicks from many initial nesting attempts should be volant, and able to make relatively long-distance movements by this date (Schroeder et al. 1999). We chose 31 August as the end of the summer season to ensure clear distinction between summer and winter and because of the coincident decrease in telemetry locations after the end of August. The winter season included all observations during 1 November–28 February. Most winter location data were obtained through aerial telemetry, which can have accuracy errors of up to 100 m (Doherty et al. 2008). Therefore, we did not include our smallest moving window size (45-m radius) in the winter habitat models.

Spatial Predictor Variables

We developed spatial variables that were considered potentially important predictors of sage-grouse habitat selection during the 3 primary life stages, based on the extensive literature on habitat use by sage-grouse. Our goal was to develop spatial predictions across the majority of sage-grouse range in Wyoming. Therefore, any spatial data included in our development of RSF models had to be available across the entire range of sage-grouse in Wyoming. Furthermore, the level of detail and coverage for each of the potential spatial predictors had to be similar across the Wyoming sage-grouse range. If spatial predictors did not meet these criteria, we could not consider the predictors in candidate models. For example, some spatial datasets were considered biologically relevant (e.g., National Hydrologic Data [NHD] as a surrogate to riparian habitat) and available throughout sage-grouse range in Wyoming. However, assessment of the layer revealed that detail and accuracy varied widely across the state and therefore we did not use the NHD. We also assessed selection in relation to proximity of several variables of interest (outlined below).

We calculated Euclidean distances, as well as exponential decays as a function of Euclidean distance (Nielsen et al. 2009, Fedy and Martin 2011) to assess non-linearity for all measures of the distance to a landscape feature. We developed decay variables corresponding to each scale using the form $e^{(-d/\alpha)}$ where d was the distance in meters from the center of each pixel to a landscape feature, and α was set to correspond with each window-size radius (e.g., 0.045 km, 0.564 km). This transformation scaled each variable between 0 and 1, with the highest values close to the feature of interest and 0 at farther distances. Thus, the influence of a variable decreased much faster using distance decays and also had thresholds of influence at which distance effects approach 0. Therefore, coefficients associated with decays are interpreted opposite of coefficients associated with Euclidean distance. For example, positive association with Euclidean distance to a feature suggests avoidance of that feature (i.e., higher probability of selection with increasing Euclidean distance), whereas a positive association with a decay distance would suggest selection for closer proximity to a feature, although the effect is non-linear. We considered distance metrics in both landscape and patch models; however, we did not consider Euclidean distances at the patch scale because the influential distances were typically much greater than the radius of the patch-extent metrics.

We measured multiple vegetation variables. Sage-grouse show strong selection for sagebrush cover and associated vegetation across life stages (for reviews see Schroeder et al. 1999; Connelly et al. 2000, 2011; Hagen et al. 2007). Our vegetation cover components included estimated percent canopy cover of shrubs (all species), sagebrush (all *Artemisia* species combined), and Wyoming big sagebrush (*A. tridentata wyomingensis*; Homer et al. 2012; Table 3). We used a moving window to calculate the mean and standard deviation of all neighboring cell values that were located within a radius of the target pixel and then assigned the resulting summary statistic to each target cell. For example, if the pixels within the originating data set represent an estimated percent canopy cover of sagebrush, each target pixel within the derived data set denotes the mean percent canopy cover of all pixel values within that neighborhood. We used standard deviation to capture habitat heterogeneity (Aldridge and Boyce 2007, Aldridge et al. 2012). In addition to canopy-cover estimates for shrubs, we also assessed spatial predictions capturing estimates of percent cover for herbaceous vegetation, litter, and bare ground, as well as shrub height (Homer et al. 2012; Table 3). The GIS products of Homer et al. (2012) are a continuous cover estimated within a cell that is similar to a ground cover estimate in field techniques in terms of what they are trying to estimate. This estimate differs from landscape cover, which is defined as the number of categorical cells in a landscape containing a certain, categorical habitat type.

We derived landscape cover of forest and conifer habitats by calculating the proportion of pixels classified as present (forest or conifer) within each moving window scale. Conifer encroachment into sagebrush habitats has been occurring at an increasing rate since European settlement, and has accelerated in some areas since approximately 1950 (Miller et al. 2011). Conifer encroachment can have negative impacts on sage-grouse habitat quality, particularly at higher elevations (Connelly et al. 2000), either through direct loss of sagebrush habitats and increased fragmentation (Crawford et al. 2004, Miller et al. 2011), or indirectly, by increasing exposure to avian predators that perch or nest in conifers (Coates et al. 2008, Coates and Delehanty 2010). Greater sage-grouse in the Powder River Basin of Wyoming avoid conifers during the winter, with the strongest effect at a moderate spatial scale (0.65 km^2; Doherty et al. 2008). Similarly, Gunnison sage-grouse (*Centrocercus minimus*) avoided nesting in habitats in proximity to conifer-juniper forests (Aldridge et al. 2012), with nesting habitat quality decreasing within 350 m of forested habitat. Therefore, we also calculated mean percent cover and distance to forests and conifers using the Regional-National Gap Analysis Program (ReGAP) within each scale. The Northwest ReGAP data provided landcover classifications (presence–absence) as opposed to percent canopy cover. We derived distances to forests and conifers from the binary classification.

We summarized 2 topographic variables at each window size. Greater sage-grouse avoid rugged terrain in the winter (Doherty et al. 2008, Carpenter et al. 2010). We estimated a Terrain Ruggedness Index (TRI) based on the Vector of Ruggedness Measure (Sappington et al. 2007). Low ruggedness values indicated flatter areas (low slope), moderate values reflected steep but even terrain (high slope, low ruggedness), and high ruggedness values identified areas that were steep and uneven (high slope).

During brooding, rearing sage-grouse can show preference for mesic sites as identified by a terrain-derived index called the Compound Topographic Index (CTI; Aldridge and Boyce 2007). We calculated the mean for both TRI and CTI across each moving window size. However, computational complexities prevented generation of TRI at the largest window size.

The CTI is an indicator of soil moisture derived from a digital elevation model (see Evans 2002), and is correlated with soil moisture and nutrients in many cases (Gessler et al. 1995). The CTI was an accurate predictor of sage-grouse habitat use in previous studies (Aldridge and Boyce 2007) and influenced habitat selection within our study sites in our analyses (B. C. Fedy, University of Waterloo, unpublished data). However, when we generated the CTI across the sage-grouse range in Wyoming, we noted a low-elevation area of high CTI values in the southwest region of the state. High CTI values should indicate higher levels of soil moisture and nutrients. The area noted in the southwest region was the Red Desert, which is known for poor soil nutrients and low moisture (annual cumulative precipitation of approx. 20 cm). This concern was originally noted by Evans (2002) who observed that CTI accumulation numbers in flat areas will be large and suggested that, in those cases, CTI will not correctly assess soil moisture nutrients. Thus, despite CTI's good predictive performance within our study sites, application of this variable to novel areas produced incorrect results because the biological meaning of the index changed in the novel areas. We did not include CTI in the final models in the interest of producing models with better predictive capabilities when applied to novel areas.

Sage-grouse habitat use can be influenced by multiple anthropogenic features on the landscape (Aldridge and Boyce 2007, Carpenter et al. 2010, Doherty et al. 2010*a*). Sage-grouse tend to avoid areas with high agricultural footprint (Aldridge and Boyce 2007, Walker et al. 2007, Aldridge et al. 2008, Tack 2009) but can use alfalfa (*Medicago sativa*) fields adjacent to sagebrush habitats during the late summer (Patterson 1952, Wallestad 1971). We calculated distance metrics and percent landcover for all irrigated, non-irrigated, and a combination of both non-irrigated and irrigated agriculture (i.e., all irrigated and altered vegetation [tilled] lands). Hereafter, non-irrigated and irrigated lands are referred as agricultural lands, which may include any type of tilled or non-tilled land (e.g., land used for crop cultivation, or haying purposes and distinguished as irrigated and/or non-irrigated land). We interpreted data from National High Altitude Program (NHAP) color infrared aerial photography or collected with GPS units. Wyoming Water Resources

Table 3. Variables considered in the development of resource selection function models for greater sage-grouse across Wyoming from 1994 to 2010. Range is presented for statewide models including use and available locations across all seasons in which the variable was present. We did not assess extent a (0.045-km radius) for winter models.

Variable	Scales[a]	Season[b]	Definition	Range[c]
Vegetation				
Herb	*a*, *b*, *c*, *d*, *e*	n, s	Mean estimated percentage cover of herbaceous vegetation cover for a given scale	1–96%
Herb_SD	*a*, *b*, *c*, *d*, *e*	n, s	Standard deviation of the mean estimated percentage cover of herbaceous vegetation cover for a given scale	0–28
Sage	*a*, *b*, *c*, *d*, *e*	n, s, w	Mean estimated percentage canopy cover of all sagebrush (Inter-Mountain Basins Big Sagebrush Shrubland, Inter-Mountain Basins Big Sagebrush Steppe, Inter-Mounatin Basins Montane Sagebrush Steppe, *Artemisia tridentata* spp. Vaseyana Shrubland Alliance, Colorado Plateau Mixed Low Sagebrush Shrubland, Wyoming Basins Dwarf Sagebrush Shrubland and Steppe, Great Basin Xeric Mixed Sagebrush Shrubland, Columbia Plateau Low Sagebrush Steppe) cover for a given scale	0–40%
Sage_SD	*a*, *b*, *c*, *d*, *e*	n, s, w	Standard deviation of the mean estimated percentage canopy cover of all sagebrush cover for a given scale	0–16
Shrub_height	*a*, *b*, *c*, *d*, *e*	n, s, w	Mean estimated shrub height of all shrubs for a given scale	0–196 cm
Shrub_height_SD	*a*, *b*, *c*, *d*, *e*	n, s, w	Standard deviation of the mean estimated shrub height of all shrubs for a given scale	0–50
NDVI_2004	Pixel	n, s	16-day Maximum Normalized Difference Vegetation Index Composite. Values calculated from −1 to 1 indicating live green vegetation. Values <0 indicated non-vegetation. Estimated for data from 2004 (Julian date of 193)	32–9,169
NDVI_2007	Pixel	n, s	16-day Maximum Normalized Difference Vegetation Index Composite. Values calculated from −1 to 1 indicating live green vegetation. Values <0 indicated non-vegetation. Estimated for data from 2007 (Julian date of 193)	180–9,451
Forest_dist	Decays *a*, *b*, *c*, *d*, *e*, and Euclidean	n, s, w	WYReGap—distance to forested area with decays corresponding to each scale and Euclidean distance included at the landscape extent	0–1
Forest	*a*, *b*, *c*, *d*, *e*	n, s, w	WYReGap—mean percent cover of forested areas within a given scale	0–1
Roads				
Paved_road_dist	Decays *a*, *b*, *c*, *d*, *e*, and Euclidean	n, s, w	Distance to road classes 1 (primary highway paved) and 2 (secondary highway paved)	0–1
Paved_road_ dens	*a*, *b*, *c*, *d*, *e*	n, s, w	Line density of road classes 1 and 2 within each scale (length/area)	0–0.02
Unpaved_road_dist	Decays *a*, *b*, *c*, *d*, *e*, and Euclidean	s	Distance to road classes 4 (primitive road, sedan clearance, not regularly maintained) and 5 (primitive road, high clearance, not regularly maintained)	0–1 decay
Unpaved_road_dens	*a*, *b*, *c*, *d*, *e*	s	Line density of road classes 4 and 5 within each scale (length/area)	0–0.04
Wells				
Well	*a*, *b*, *c*, *d*, *e*		Time-stamped (1998–2008) density of active wells within a moving window (n/m^2)	0–0.0009
Agriculture				
Irrigated_dist	Decays *a*, *b*, *c*, *d*, *e*, and Euclidean		Distance to irrigated land	0–1 decay
Irrigated	*a*, *b*, *c*, *d*, *e*		Mean percent cover for irrigated land within a given scale	0–1
Non_irrigated_dist	Decays *a*, *b*, *c*, *d*, *e*, and Euclidean		Distance to non-irrigated land	0–1 decay
Non_irrigated	*a*, *b*, *c*, *d*, *e*		Mean percent cover for non-irrigated land within a given scale	0–1
Agr_dist	Decays *a*, *b*, *c*, *d*, *e*, and Euclidean		Distance to irrigated and non-irrigated land	0–1 decay
Agr	*a*, *b*, *c*, *d*, *e*		Mean percent cover for irrigated and non-irrigated land within a given scale	0–1
Topography				
TRI	*a*, *b*, *c*, *d*	n, s, w	A vector ruggedness index that distinguishes between steep and even terrain (high slope and low ruggedness) versus steep uneven terrain (high slope and high ruggedness)	0–1
Climate				
Precip	*b*, *c*, *d*, *e*	s	Mean of 30-year (1971–2000) monthly averaged daily precipitation totals (mm)	16–153 mm
Precip_SD	*b*, *c*, *d*, *e*	s	Standard deviation of 30-year (1971–2000) monthly averaged daily precipitation totals	0–1

[a] The extents for each variable estimate are presented and correspond to the 5 different moving window radii. Patch scale: $a = 0.045$ km and $b = 0.564$ km; landscape scale: $c = 1.5$ km, $d = 3.2$ km, and $e = 6.44$ km.

[b] The seasonal models for which the variable was considered: n, nesting; s, summer; w, winter.

[c] The largest range of standard deviation estimates occurred at the smallest scales.

Division provided data on irrigated lands that we used in conjunction with an earlier data source provided by the Wyoming Geographic Information Science Center (WYGISC, http://www.uwyo.edu/wygisc/) of non-irrigated land and University of Montana irrigated land layers. We combined the University of Montana irrigated land data with the WYGISC data to correct some known inaccuracies in the Powder River Basin study site.

Greater sage-grouse avoid non-natural edge habitats during nesting (Aldridge and Boyce 2007) and winter (Carpenter et al. 2010), and show strong avoidance of all urban development when rearing young (Aldridge and Boyce 2007). The urban areas layer (U.S. Census Bureau TIGER http://www.census.gov/geo/www/tiger) we explored was inaccurate and over-estimated the size of most urban areas outside of our study sites. Therefore, we excluded the urban areas layer from final modeling efforts because of under-prediction of available habitat.

Road development in sagebrush habitat results in direct loss and fragmentation of habitat (Schroeder et al. 1999, Connelly et al. 2004) and has been associated with local extirpations of sage-grouse (Wisdom et al. 2011). Behavioral avoidance of habitats in close proximity to roads also has been suggested (Lyon and Anderson 2003), and therefore road development is considered functional habitat loss. Increased road traffic has been associated with a suite of potentially negative impacts on sage-grouse including reduced nest initiation rates, larger lek-to-nest movements by females (Lyon and Anderson 2003), declines in male lek attendance (Holloran 2005), and possibly lek abandonment (Braun et al. 2002). We developed road density (linear km/km^2) estimates across all moving windows, and generated all distance metrics including Euclidean distance and decays (Table 3). We used an interim transportation dataset developed jointly by the Bureau of Land Management (BLM) Cheyenne State office, and the U.S. Geological Survey (USGS) Fort Collins Science Center. We hand digitized vector data from 1-m National Agricultural Imagery Program (NAIP) data (i.e., aerial photography). We attributed these data using USGS digital line graph (DLG) standards (USGS, http://nationalmap.gov/standards/dlgstds.html), which we then categorized into 5 classes (class 1: 1700402, 1700201, 1700203; class 2: 1700205; class 3: 1700209; class 4: 1700210; class 5: 1700211; reclassification based on TIGER Census major categories [A1–A5], http://www.census.gov/geo/www/tiger/tgrshp2011/TGRSHP2011_TechDoc.pdf). Roads classed 1 and 2 represented primary and secondary paved highways. Aldridge and Boyce (2007) found brood occurrence increased slightly with increasing density of primitive, unpaved roads (trails), which they suggested could be related to the increased abundance of succulent invasive species (e.g., dandelions, *Taraxacum* sp.) that, can serve as food sources. Therefore, we also examined the influence of unpaved roads classed 4 and 5 for the summer models. We defined class 4 roads as sedan clearance, not regularly maintained; and class 5 roads as 4-wheel drive or high clearance, not regularly maintained.

Oil and natural gas wells and associated development can affect sage-grouse habitat use (Aldridge and Boyce 2007, Doherty et al. 2008, Carpenter et al. 2010, Holloran et al. 2010). We used data on location and development dates of oil and gas wells provided by the USGS Energy Program and the Wyoming Oil and Gas Conservation Commission (http://wogcc.state.wy.us/). Our telemetry data were collected between 1994 and 2010. Oil and gas development in Wyoming was extensive throughout that time, with an increase in active wells from 57,094 active wells in 1994 to approximately 101,475 by 2010. We generated well location data layers for each year from 1998 to 2008. We used time-stamped well data when calculating well density for each window size. We included a well location after it was drilled (spud date), and in all subsequent years in which the well was active. We removed wells that eventually became inactive (permanently abandoned) during the years of interest from the dataset at that time and we did not consider them in related estimates associated with well locations. Thus, the well information was accurate to the year a bird was sampled. For example, we used well densities in 2002 for each bird located in 2002. When a study site had observations over multiple years, we generated the well data for each of those years. To assign annual well densities to available locations (for comparison in our use vs. available design), we first calculated the proportional distribution of used locations within each study site. We then randomly assigned available locations to a given year based on the proportion of used locations within that year. We summarized our well metrics for available locations for the assigned year. For example, if a 2-year study recorded 40% of use locations in 2001 and 60% in 2002, we randomly assigned 40% of the available locations to 2001 and 60% to 2002, and estimated the well metrics based on those assigned years. If telemetry data existed outside of our time-stamped range (e.g., pre-1998), well densities assigned were for the closest year.

Sage-grouse use mesic habitats associated with permanent and ephemeral water sources likely because wet habitats provide enhanced forb and insect abundance, particularly during brood rearing (Crawford et al. 2004). We used hydrologic flowlines and water body features from the NHD and calculated variables representing ephemeral and permanent water sources. We also developed a combined variable that included both ephemeral and permanent water sources. We treated these data as a seamless dataset within Wyoming, but they were mapped with variable accuracy and precision. Typically, the accuracy and precision of the hydrological variables were consistent within each study site, and thus, statistical models could be optimized to the localized variation and produced reasonable relationships within a study site. However, when considered across the range of sage-grouse in Wyoming, differences in resolution and detail resulted in inaccurate predictions. Therefore, we excluded these metrics from final model development. In addition to examining hydrologic features, we also assessed annual precipitation normals (averaged) between 1971 and 2000 (downscaled 400-m resolution developed by http://www.climatesource.com/) to quantify spatial variation of mesic habitats.

Sage-grouse habitat use in the winter can be influenced by snow depth and the amount of sagebrush available above snow (Remington and Braun 1985, Homer et al. 1993, Schroeder et al. 1999, Connelly et al. 2000, Crawford et al. 2004). These variables are difficult to capture and assess across large landscapes, and have yet to be directly evaluated. However, we acquired daily snow deposition from the National Oceanic and Atmospheric Administration (NOAA) SNOw Data Assimilation System

(SNODAS) 1-km gridded data (National Operational Hydrologic Remote Sensing Center 2004), resampled the data to 30-m cell resolution to match the other GIS input data, and then summarized the data from 2004 to 2011 (all available dates) to develop a normalized snow deposition measurement. We restricted snow-depth measurements between November and February for sage-grouse winter habitats. We first calculated maximum and median snow depth within each winter and then averaged maximum and median snow depths among all years (2004–2011). We then applied moving windows to estimate shrub height (Homer et al. 2012) above the average maximum and median snow depth.

In addition to the vegetation variables detailed above, we also developed brightness, greenness, wetness, and NDVI indices using a tasseled cap transformation that provided the mean value of the index for each scale (Table 3). These indices have been successfully used for sage-grouse habitat modeling across life stages as they are used to represent fine-scale variations in vegetation cover (Aldridge and Boyce 2007, Carpenter et al. 2010, Aldridge et al. 2012). We used MODIS data from the (cumulatively) driest (2004) and wettest (2007) years based on available MODIS dates (2000–2010). The MODIS (Terra) 16-day composite (product MOD13A2, version 5, 193 Julian date, 250 m) provided the NDVI, and the tasseled cap was derived from the MODIS surface reflectance 8-day composite product (MOD09A1, version 5, 193 Julian date, 500 m) and published tasseled cap coefficients (Lobser and Cohen 2007). We were unable to include several of these variables in the final models.

Defining Availability

The determination of biologically meaningful areas that are available for selection by individuals is a key first step to developing habitat selection models (Jones 2001). The availability of habitats should be carefully considered and based on the biology of the species (Johnson 1980). Availability is often influenced by how far the animal moves, and thus what portions of the landscape could conceivably be accessible to them during a given life stage. The distances moved by sage-grouse differ among seasons (Fedy et al. 2012) and therefore, we defined availability differently for the 3 seasons. Several studies have assessed movement distances from lek to nesting sites during the breeding season (Holloran and Anderson 2005*b*, Doherty et al. 2010*a*) and we defined availability for the nesting season as a 10-km radius from nest sites (Fig. 2). Nesting activities occur in proximity to leks, with approximately 95% of nest sites occurring within 10 km from the lek where the female was captured for 2 studies in Wyoming (Holloran and Anderson 2005*b*, Doherty et al. 2010*a*). Fedy et al. (2012) quantified interseasonal movement distances for Wyoming greater sage-grouse from nesting to summer locations, and from summer to winter locations. We defined availability for our summer models based on nest to summer movement distances (18-km radius; Fig. 3) and availability for our winter models based on summer to winter movement distance (20-km radius; Fig. 4). After defining the movement distances for each season, we buffered the seasonal location data using the appropriate distance, which defined habitat availability for each study site for a given season (hereafter referred to as the study-site-availability extent

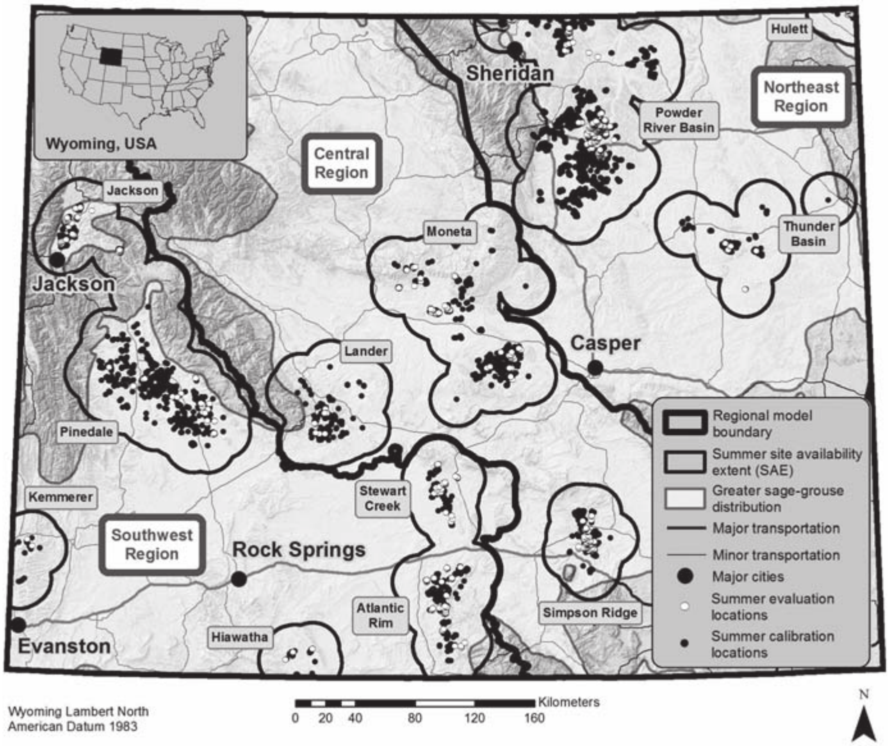

Figure 3. Study locations of greater sage-grouse for the summer season, 1998–2009. The study sites included for the summer season are labeled. Small black circles represent the telemetry locations used for model calibration and white circles represent locations used for model evaluation. The study-site-availability extents (SAE) we used to define availability for each study site are represented by the black lines encompassing each set of study site locations. Regional boundaries are indicated by the thick black line and were delineated based primarily on hydrologic units and sage-grouse management zones.

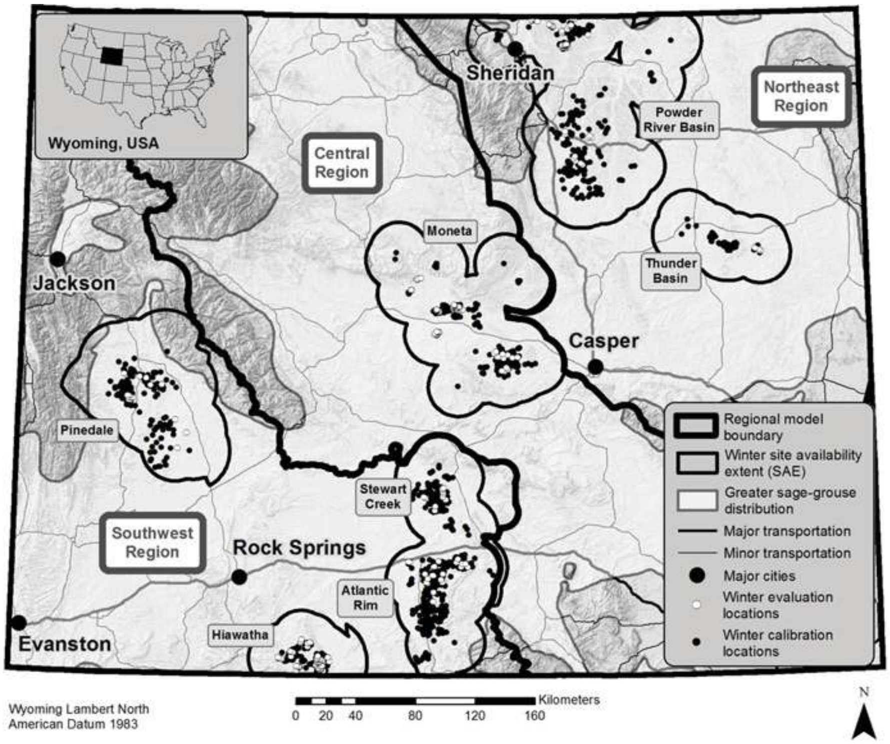

Figure 4. Study locations of greater sage-grouse for the winter season, 2001–2010. The study sites included for the winter season are labeled. Small black circles represent the telemetry locations used for model calibration and white circles represent locations used for model evaluation. The study-site-availability extents (SAE) used to define availability for each study site are represented by the black lines encompassing each set of study site locations. Regional boundaries are indicated by the thick black line and were delineated based primarily on hydrologic units and sage-grouse management zones.

[SAE]). We added a small proportion of winter use locations after we had established the SAE. All of these locations fell within the SAE; however, a small subset of these data were buffered by <20 km in all directions (e.g., evident in the Pinedale, Atlantic Rim, and Stewart Creek SAEs; Fig. 4). We randomly generated available locations within each SAE using a density of 1 per km^2 and a minimum distance of 30 m between available locations (nest = 27,603; summer = 53,227; winter = 44,646) to sample variation in habitat availability. Available locations were limited to areas within the SAEs that were not masked within the data layers (areas masked included open water bodies, forested canopy percentages >35%, elevations >2,377 m, and areas contaminated with cloud and cloud shadows). Additionally, we restricted available locations for nesting habitats from occurring within 60 m of oil and gas well locations, as this area generally represented a hard surface well pad not suitable for nesting.

Model Development and Selection

Compilation of telemetry data across study sites was described by Fedy et al. (2012). Once we compiled all data, we divided the datasets within each study site into calibration and evaluation datasets. We used the calibration data for model development. We used the evaluation data for assessment of model performance and did not included these data in the calibration datasets. To divide the datasets, we first randomly identified 10% of the number of use locations within each site and season to set aside as evaluation datasets. Some individual sage-grouse were monitored in multiple years and contributed multiple locations. Therefore, individuals could be included in both the calibration and evaluation datasets after this initial step. However, to ensure independence of locations and individual birds in our evaluation dataset, we prevented individuals from occurring in both datasets. We added all locations associated with an individual that was initially drawn for the evaluation dataset to the evaluation dataset. Thus, the evaluation datasets represented ≥10% (range 10–16%) of the number of use locations for any given site and season combination. Annual variation in availability could potentially be a concern (Schooley 1994, Coe et al. 2011), and therefore, we randomly selected evaluation data across years of each study.

We developed RSF (Manly et al. 2002) models using logistic regression (Hosmer and Lemeshow 2000) to characterize habitat selection for sage-grouse in Wyoming for 3 distinct life stages. Because models could be heavily biased toward the larger sample of available resource units, we used an importance weight that gave full weighting to the radiotelemetry (used) samples and down-weighted the available samples proportional to the ratio of sampled points to available points (STATACORP 2007; see Hirzel et al. 2006), resulting in presence to available ratios of 1:1. We calculated weights separately for each seasonal and regional model combination. This step effectively valued the number of observations for each model subset to 2× the number of use locations, ensuring variance estimates (SE and CI) were not artificially decreased because of the large number of available locations and preventing model likelihoods from being inflated.

We selected models using a Bayesian Information Criterion (BIC) approach. Akaike's Information Criterion (AIC) and

BIC metrics are similar and use the same base equation of $-2 \times \ln(\text{likelihood})$ to assess model fit (Burnham and Anderson 2002, STATACORP 2007). However, AIC and BIC penalty terms differ in that AIC adds $2 \times k$ to the results of the base equation above and BIC adds $\ln[N] \times k$, where k equals the number of parameters and N equals the number of observations (Burnham and Anderson 2002, STATACORP 2007). In practice, these differences in penalty terms result in AIC favoring relatively large model structures because of the lower penalty for inclusion with large sample sizes and BIC selecting more parsimonious models. We used BIC because we used large data sets and a large set of candidate predictor variables, with a desire to identify the simplest solutions from these candidates. BIC has increased emphasis on reducing complexity in model results because of the more conservative penalty term (Burnham and Anderson 2002). We selected top models from all possible variable combinations using BIC. We eliminated uninformative variables that switched signs between positive and negative within the candidate model set and did not consider them in the top model sets (Arnold 2010).

We assessed all predictor variables for correlation (Pearson's $r \geq |0.65|$) before estimating models to avoid multicollinearity issues. When variables were correlated, we chose the most predictive variable (lowest BIC value in univariate model comparisons) or the variable with the most intuitive biological interpretation and support based on previous habitat-selection research. For example, 2 variables from our original list of variables for inclusion in the modeling efforts included bare ground and litter variables; however, we dropped these before modeling because they were highly correlated at all scales and within each region with herbaceous cover. Numerous publications have shown that herbaceous cover influences sage-grouse habitat selection or quality, and therefore, we included herbaceous cover for its biological relevance. We assessed correlation among variables separately for each season and regional combination.

We initially assessed variables considered for inclusion in models predicting occurrence within each scale (patch and landscape). We identified the most predictive window size and form (e.g., distance or density) of each variable type with single variable models compared across window sizes and carried the top window size forward in our development of the complete candidate set of models for each scale, region, and season. Furthermore, the comparison of window sizes always included an intercept-only (null) model. If the variable was not more predictive (based on BIC) than the null model, we excluded the variable from all subsequent analyses. Generally, better model results can be obtained for a generalized linear model when the variables are integrated at the scale at which they make the highest contribution to the explained variance in univariate models (Graf et al. 2005).

Instability in coefficients across model runs can result from nonlinear responses. We also explored quadratic relationships when variables displayed instability. For a variable to be retained with its quadratic term, the variable had to meet certain criteria. First, we calculated selection ratios as the observed count/expected count across 10 quantiles and plotted these ratios across the range of the variable. Inspection of the selection-ratio graph had to suggest a quadratic relationship. Second, the addition of the quadratic term had to improve model performance in terms of BIC. When these criteria were met, we carried forward the quadratic form of the variable for building combined model sets.

We ranked candidate models based on the difference in BIC values (ΔBIC) and we used BIC weights (w_i) to assess the strength of evidence that a particular model was the best in a candidate set, given the data. We generated model weights across the entire model set for each season and region. We then selected all top models composed of 90% of the summed model weights. We generated new model weights based on the top 90% subset and calculated model-averaged coefficients and standard errors based on the relative weight of each model within the top 90% set (Burnham and Anderson 2002). We conducted all analyses in STATA 10.1 (STATACORP 2007).

Variance decomposition is a mechanism to examine contribution of components across multiple scales, and involves fitting a single full model and multiple subsets of models to partition out variation explained by different models (Borcard et al. 1992, Lawler and Edwards 2006). We defined our full model for variance decomposition analyses as the total set of variables that composed our final patch and landscape models. We defined 2 subsets of models as groups of variables that composed either patch or landscape models separately. Top models contained all variables included in any of the top 90% of summed BIC weights. We used variance decomposition to isolate variation explained between scales into pure and shared components (Cushman and McGarigal 2002, Lawler and Edwards 2006). Shared variation is jointly explained by different models. Pure variation equates to variation that is independently explained by a single subset model (patch or landscape, in our case). We subtracted different components of variation using statistical deviance to isolate 1 shared and 2 pure components of variation. We isolated patch-scale variation by subtracting the deviance explained ($-2 \times \log$ likelihood) by the landscape model from the full multiscale model ($-2 \times$ [log likelihood of the null model $-$ log likelihood of the full model]). We isolated the pure landscape-scale variation by subtracting the deviance explained by the patch model from the full multiscale model. We isolated the shared component by subtracting the deviance explained by both the patch and landscape scales. We calculated relative contribution to total explained variance for the patch scale by dividing the patch deviance by total deviance explained by the full multiscale model. We calculated percent deviance explained by landscape and shared components following the same methods.

Model Evaluation

We used RSF models to generate continuous surface maps that represent the predicted relative probability of selection for any given pixel. We scaled all RSF predictions between 0 and 1 with β_0 included, following Aldridge et al. (2012). Hirzel et al. (2006) showed that continuous scale maps are often misleading because all predictive models suffer from some level of uncertainty. Therefore, a reclassified map showing only a few classes may be more appropriate for depicting the map's actual information content. In addition, evaluation of our models required quantification of how accurately the model predicted presence of sage-grouse in Wyoming (Buckland and Elston 1993, Manel et al. 2001, Hirzel et al. 2006), as given by our set of evaluation points.

Based on the initial classification methods proposed by Hirzel et al. (2006), Gummer and Aldridge (Parks Canada and Colorado State University, unpublished data) developed an approach to optimize the RSF classification point for a given model by identifying the highest predicted habitat that contains the maximum proportion of use locations while minimizing the proportion of the landscape implicated. This approach evaluates all potential classification points (i.e., RSF values) and the user applies 1 of several principles to identify the classification threshold best suited to a given species or management target(s).

For every predicted RSF value for observed calibration and evaluation locations (RSF_i), we applied a binary classification to the continuous RSF surface based on all pixel values that were $\leq RSF_i$. We calculated the proportion of locations contained within each binary map (Absolute Validation Index sensu Hirzel et al. 2006; AVI, range = 0–1) and the proportion of the entire landscape implicated at that cutoff within the study site SAEs (AVI_0). For each RSF_i value, we calculated the contrast validation index (CVI; Hirzel et al. 2006): $CVI = AVI - AVI_0$, and estimated lower and upper 95% confidence limits from the *F* distribution. The CVI indicated how efficiently the model identified used habitat in comparison with a hypothetical random model that predicted presence everywhere. For all models, CVI was consistently positive at each RSF threshold value.

We identified the maximum CVI value (i.e., the value where the highest number of use locations were captured in the smallest total area; Fig. 5). Colloquially, this value provides the most "bang for your buck." We then determined the lowest RSF value (farthest right on plot) for which the CVI confidence intervals overlapped with those of the maximum CVI point estimate (i.e., not statistically different from the maximum CVI; Fig. 5). Overall, this approach enabled us to generate binary maps that contained the greatest number of use locations in the smallest footprint of predicted habitat. We refer to these areas as the identified important habitat areas throughout.

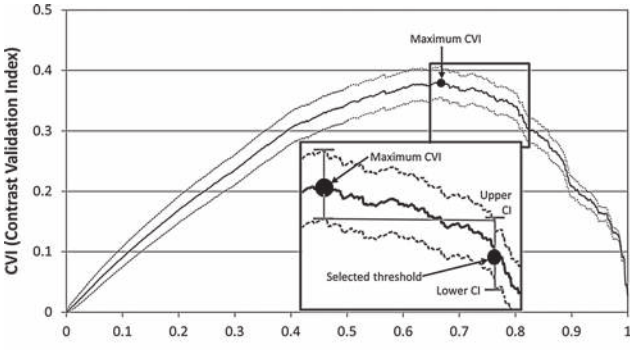

Figure 5. An example of a threshold selection figure. Results presented are for the top nest-season statewide-combined (landscape × patch) averaged model. The absolute validation index is along the *x*-axis and the *y*-axis is the contrast validation index (CVI). Values presented are based on the calibration nest data associated with each resource selection function value. The black line represents the estimated CVI and the dotted lines represent the upper and lower 95% confidence intervals. The maximum CVI is indicated. We classified all habitat indicated above the lower 95% confidence interval as important.

We summarized the ability of each model to capture both the calibration data and our withheld evaluation locations in the binary classified maps. This independent evaluation of the classification approach assesses the ability of each individual model to predict seasonal sage-grouse habitat selection. Given our goal of producing regional models for each life stage, which included both patch- and landscape-scale selection, we similarly took the combined scales as 1 modeled surface (landscape × patch) and applied the above thresholding approach to evaluate model fit and predictive capabilities for combined-scale models.

We assessed model performance based on 2 fundamental metrics: discrimination and validation. The CVI provides an estimate of the discriminatory power of the models. To validate our models, we calculated the proportion of locations that fell within our identified important areas. We did this calculation for both the calibration and the evaluation datasets for each seasonal and regional combination.

We also validated our nesting models using a lek dataset for Wyoming (Fig. 6), following Doherty et al. (2010*a*). The hotspot hypothesis of lek evolution suggests that leks are typically located in nesting habitat where males will most likely encounter pre-nesting females (Schroeder and White 1993, Gibson 1996). Additionally, leks are usually located in close proximity to nesting habitat (Holloran and Anderson 2005*a*, Aldridge and Boyce 2007, Doherty et al. 2010*a*). "Thus, more nesting habitat is expected to occur around leks than around random points in the landscape" (Doherty et al. 2010*a*). We quantified the amount of area classified as important nesting habitat within 3, 5, 10, and 20 km of active leks and available locations. We obtained locations and counts of displaying males from a lek database maintained by the Wyoming Game and Fish Department. We selected the peak male count in 2008 and if a site was not surveyed in 2008, we took the peak count from the next closest year, going back a maximum of 5 years (i.e., 2003). We used 1,033 leks across Wyoming that had ≥ 5 males. For comparison, we randomly selected 1,033 available locations within the sage-grouse distribution in Wyoming.

For the spatial presentation of the final habitat models, we classified habitat into several categories around that selected threshold RSF value, based on the confidence intervals (CI) of the CVI point estimate (see above for identification of that point). We considered RSF values greater than the upper CI to be category 1 habitat, values between the selected RSF threshold and the upper CI were category 2 habitat, and values between the selected RSF threshold and the lower CI were category 3 (Fig. 5). We assigned values below the lower confidence interval a null value, or non-crucial habitat.

Application of Nesting Models to Novel Areas

We defined novel areas as the areas outside of our SAEs and not used in the development of the models. Again, we used leks as a proxy for nesting habitats. We calculated the proportion of leks contained within the identified important habitat both within and outside of our SAEs.

Although we applied models to novel areas across each region for management purposes, we examined a test case of applying

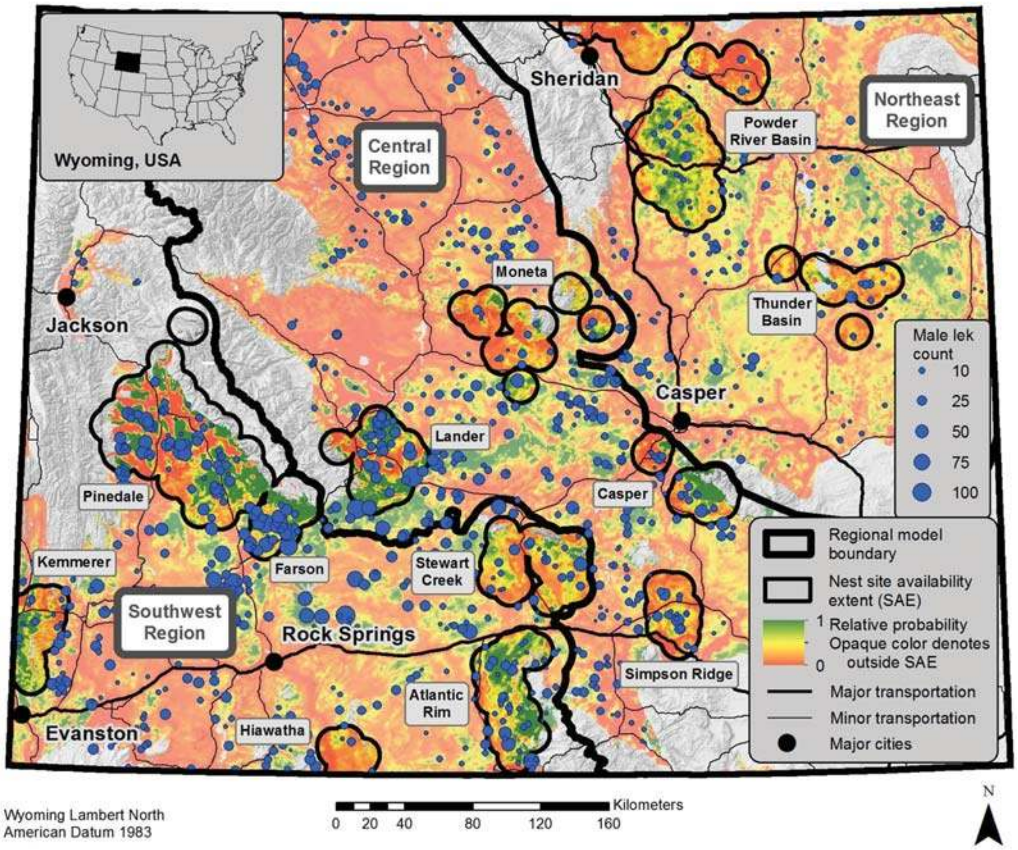

Figure 6. Statewide nesting greater sage-grouse model applied to Wyoming, USA, and represented as a continuous surface. The colors range from red to green to represent the range of probability values from 0 (low relative probability of selection) to 1 (high relative probability of selection). Study site boundaries are indicated by the black line. Areas of gray hill shade represent the areas masked out in the model predicted surfaces. Areas outside of the study sites are novel areas and slightly grayed to indicate the inherent lower confidence in model predictions in these areas. Lek locations and counts based on 2008 peak male counts (Wyoming Game and Fish Department, unpublished data) are represented by the blue circles. Regional boundaries are indicated by the thick black lines and were delineated based primarily on hydrologic units and sage-grouse management zones.

the nesting models to a novel area. Nest data were collected in the Bighorn Basin (BHB) area of north-central Wyoming (2011; Fig. 7). These data were collected after the initiation of our modeling efforts and we did not include them in developing any of the seasonal models. The region where the nest data were collected was also outside all study site SAEs used in the development of the habitat selection models. Preference for particular habitat components is scale-dependent and functional responses in preference can result from changing availability (Beyer et al. 2010). Therefore, the most appropriate model to apply to novel areas should be the model that was developed using similar available habitat. To test this prediction, we calculated the availability of key habitat components posthoc in the BHB. We defined availability for the BHB data in the same way as all nesting datasets. We then compared the distribution of key habitat components in the BHB to the availability of the same components in our nest models. We applied all nesting models to the BHB study site and thresholded these models as described above. We calculated the number of independent BHB nest sites that fell within the areas identified as important habitat by each model. We also calculated the number of lek sites in the BHB study site that fell within the important habitat identified by each model, as well as the distance of lek sites to important habitat.

RESULTS

Nesting

We incorporated 1,584 nest locations from 13 study sites collected during 1994–2009 in our nesting models (Table 2; Fig. 2), with 1,388 nest locations for model calibration and 196 locations withheld for model evaluation (Fig. 2). We generated 8 model sets across regions (state and 3 regions) and scales (patch and landscape) for the nesting season (Tables 4 and 5).

None of the variables included in this suite of models had confidence intervals that overlapped 0, indicating they were all informative, with the exception of mean herbaceous cover in the southwest patch model (Table 5). Herbaceous cover in the southwest patch model was included in the final models because of the inclusion of the standard deviation of the mean herbaceous cover, which, based on our rule set (above), could not be present without the mean herbaceous estimate. Sage-grouse demonstrated consistently positive nest site associations with sagebrush and consistently negative associations with roads class 1 and 2 across all 8 models (Table 6). Agriculture variables also showed consistently negative associations (with the exception of the central landscape model, which included Euclidean distance to agriculture) and were present in 6 of 8 models, and were represented in all 4 regions in at least 1 of the 2 scales (Table 6).

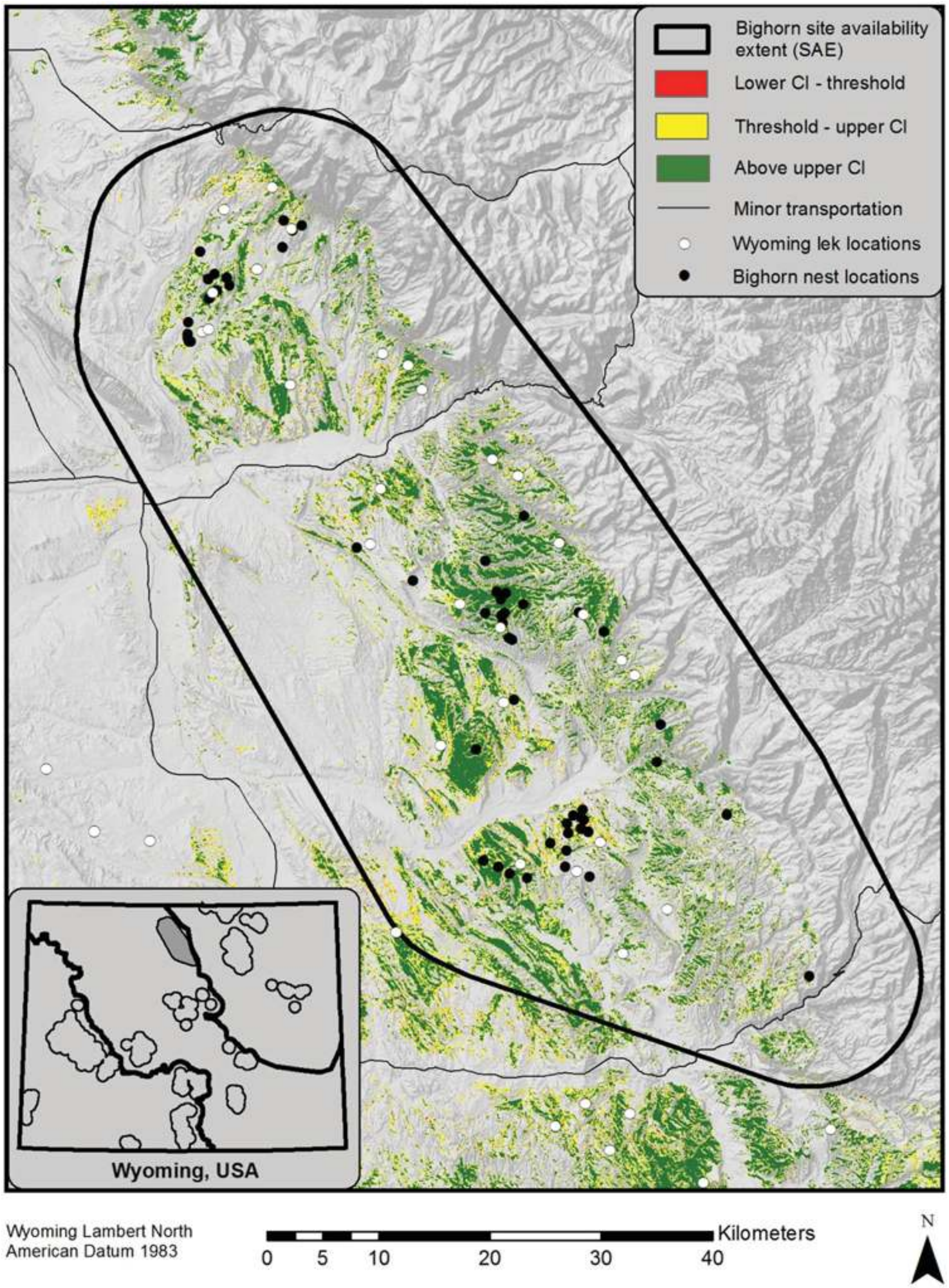

Figure 7. Map of the central region nest-season patch model applied to the Bighorn Basin. The habitat categories 1 through 3 are coded by green (category 1, above the upper confidence interval), yellow (category 2, between the maximum value and the upper confidence interval), and red (category 3, between the maximum value and the lower confidence interval). Habitats with values below the chosen threshold are represented as gray hill shade. Black dots represent independent nest locations from 2011, and white dots represent 2008 lek sites.

Models suggested consistent avoidance of forests (with the exception of the central landscape model, which included Euclidean distance to forests), and forest variables occurred in 5 of the 8 final models. Herbaceous cover and TRI occurred in a single averaged model, each indicating selection for greater herbaceous cover, and avoidance of rough terrain (Table 6). Shrub height was present in only the statewide patch model and indicated birds were selecting nest sites with taller shrub cover. The density of wells occurred in 1 model and indicated avoidance of landscapes with higher well densities.

The nest models demonstrated good discriminatory power within the study site SAEs (Figs. 8–10). Across all regions and scales, the models captured an average of 84% of the evaluation nest locations in an average of 50% of the landscape within each study site SAE (Table 7; Fig. 10). The CVI was similar across scales with an average CVI of 40% for landscape models, 36% for patch models, and 42% for combined landscape and patch models. On average, the statewide and regional models had similar discriminatory capabilities based on CVI (statewide = 38%, regional = 39%). The southwest model had the best discriminatory capabilities of all combined landscape and patch models, capturing 92% of the calibration locations in only 45% of the landscape (Table 7). The central combined (landscape × patch) nesting model captured 94% of the calibration locations

Table 4. Comparison of the top patch and landscape models used to characterize sage-grouse nest occurrence (1994–2009) across Wyoming. Models are presented for the statewide data and each regional division. The final 3 digits (x.xx) of each variable represent the radii (km; rounded to 2 decimals) of the moving window size selected. Models are ranked by the change in the Bayesian Information Criterion (ΔBIC). Weights (w_i) indicate the likelihood of the model being the best of those evaluated (*n* model set) and *K* indicates the number of parameters in the model. The models represent the 90% confidence set and were incorporated in the model-averaging procedure. Models *N* presents the total number of models evaluated in the model set after removing unstable variables.

Model	Model structure[a]	*K*	BIC	ΔBIC	w_i	Models *N*
Statewide						
Landscape	Agr1.50 + Forest_dist1.50 + Paved_road_dens3.20 + Sage1.50	5	3,204.21	0.00	0.90	63
Patch	Agr_dist0.56 + Forest_dist0.56 + Paved_road_dist0.56 + Sage0.56 + Shrub_height0.05	6	3,214.13	0.00	0.63	127
	Agr_dist0.56 + Forest_dist0.56 + Paved_road_dist0.56 + Sage0.56	5	3,215.45	1.32	0.33	
Southwest						
Landscape	Agr_dist_Euclidean + Forest_dist1.50 + Paved_road_dens3.20 + Sage3.20	5	1,761.00	0.00	1.00	127
Patch	Forest_dist0.56 + Herb0.56 + Herb_SD0.56 + Paved_road_dist0.56 + Sage0.56	6	1,830.91	0.00	0.77	31
	Forest_dist0.56 + Herb0.56 + Herb_SD0.56 + Paved_road_dist0.56 + TRI0.56 + Sage0.56	7	1,834.84	3.94	0.11	
Central						
Landscape	Agr_dist_Euclidean + Paved_road_dens6.44 + Sage3.20 + Well3.20	5	604.86	0.00	0.46	127
	Agr_dist_Euclidean + Forest_dist_Euclidean + Paved_road_dens6.44 + Sage3.20 + Well3.20	6	605.76	0.90	0.30	
	Agr_dist_Euclidean + Sage3.20 + Well3.20	4	608.58	3.73	0.07	
	Agr_dist_Euclidean + Forest_dist_Euclidean + Paved_road_dens6.44 + Sage3.20	5	608.67	3.81	0.07	
Patch	Paved_road_dist0.56 + Sage0.05	3	615.02	0.00	0.67	15
	Sage0.05	2	617.06	2.04	0.24	
Northeast						
Landscape	Agr_dist1.50 + Paved_road_dens6.44 + Sage6.44	4	774.17	0.00	0.95	31
Patch	Agr_dist0.56 + Paved_road_dist0.56 + Sage0.56	4	783.27	0.00	0.70	31
	Agr_dist0.56 + Sage0.56	3	786.35	3.08	0.27	

[a] Agr, agriculture including irrigated and non-irrigated lands; Herb, herbaceous cover; Sage, sagebrush cover.

within 59% of the landscape, and the northeast models captured 95% of the calibration datasets in 50% of the landscape (Table 7). The statewide model had similar discriminatory capabilities with 88% of locations in 49% of the landscape. Overall, the nest models captured 84% of the independent evaluation locations (Fig. 10).

We used lek sites as a proxy for nesting habitat. Overall, the abundance of predicted nesting habitat corresponded with active lek locations at large spatial scales (3–20 km; Fig. 6; Table 8). Landscapes with active leks contained a consistently higher proportion of predicted important nesting habitat and the confidence intervals did not overlap between leks and random locations (Table 8; Fig. 6) for the statewide and the regional models. For the statewide model alone, landscapes with active leks contained 1.2–1.6 times greater predicted important nesting habitat than random locations (Table 8). For regional models, landscapes with active leks contained 1.1–1.5 times greater predicted nesting habitat than random locations (Table 8). Also, for both statewide and regional models, as distance from lek increased, the percent of the landscape classified as important nesting habitat decreased.

Application of Nesting Models to Novel Areas

The nesting models predicted important habitat both within the SAEs and outside the SAEs in novel areas. Generally, a greater proportion of known lek sites were contained within important habitat inside the SAE boundaries than outside (Table 9). Within the SAE, the statewide models captured 78% of known leks and 83% of males. The regional models captured 76% of known leks and 76% of males within the SAEs. As predicted, the models were not as efficient at capturing lek locations and males in novel areas outside of the SAEs, capturing between 45% and 53% of all leks or males in the novel areas. However, we also considered how far the leks and attending males were from the nearest identified important habitat. The proportion of leks and males increased substantially when we considered a 1.5-km buffer surrounding important habitat (Table 9). For example, 72% of all leks outside of the SAEs were within 1.5 km of important habitat and these leks represented 77–78% of all males attending leks in novel areas. The nesting models consistently captured a greater proportion of males than leks both within and outside the SAEs. These results seem to indicate the model-identified important habitat may be capturing the larger leks.

The distributions of key habitat variables (sagebrush and road metrics) in the BHB study site were most similar to those used to develop the northeast nesting models (Table 10). The BHB study area contained 55 nest locations and 28 lek sites. The central patch model applied to the BHB contained the highest number of nest sites ($n = 27$) and lek sites ($n = 7$) captured by identified important habitat (Fig. 7). The second best model was the northeast patch model, which captured 16 of the nest locations and 7 leks within important habitats. All other models captured 0–4 nests and 0–2 leks. We also calculated the distance to the nearest identified habitat for nests that fell outside of the classified habitat for the central patch model. Most nests outside of important habitat were located <500 m from classified habitat ($n = 28/29$). Thus, 98% of nests ($n = 54/55$) were within important habitat or <500 m from important habitat. The pattern was the same for lek sites, with only 1 site >500 m from important habitat identified by the central patch model. The thresholded northeast patch model captured 16 nest locations and 7 lek locations. The combined central model captured 6 nest and 1 lek location and the combined northeast

Table 5. Model-averaged beta coefficients and associated standard errors for variables included in the top 90% model set for Wyoming greater sage-grouse nesting. Results are presented for each region and both patch and landscape scales. Data included in the nesting modeling effort were collected from 1994 to 2009. The metric column presents the metric used to represent the variable estimated and summarized for each window size. Extent presents the radii (km) and decays of the various window sizes for patch and landscape scales. An extent value of na indicates the metric was not summarized across a window size and either represents Euclidean distance for distance metrics, or a pixel estimate for other metrics. Note that a positive association with distance decays suggested selection for proximity to a habitat feature as values were 1 at a feature of interest, and decay farther from the feature. Also presented are the odds ratios and associated confidence intervals.

Category	Metric	Extent	β_i	SE	Odds ratio	Lower CI	Upper CI
Statewide							
Landscape							
Agriculture	Mean cover	1.50	−4.08	1.48	0.02	0.00	0.31
Forest	Decay	1.50	−1.29	0.15	0.27	0.20	0.37
Paved roads	Line density	3.20	-0.53×10^{-4}	0.08×10^{-4}	0.58×10^{-4}	0.49×10^{-4}	0.67×10^{-4}
Sagebrush	Mean cover	1.50	0.22	0.01	1.25	1.22	1.28
Patch							
Agriculture	Decay	0.56	−1.99	0.34	0.14	0.07	0.27
Forest	Decay	0.56	−1.52	0.18	0.22	0.15	0.31
Paved roads	Decay	0.56	−3.00	0.61	0.05	0.02	0.16
Sagebrush	Mean cover	0.56	0.20	0.01	1.22	1.19	1.25
Shrub height	Mean height	0.05	0.13×10	0.04×10	1.14×10	1.05×10	1.25×10
Southwest							
Landscape							
Agriculture	Distance	6.44	0.12×10^{4}	0.02×10^{4}	1.12×10^{4}	1.08×10^{4}	1.15×10^{4}
Forest	Decay	1.50	−1.42	0.24	0.24	0.15	0.38
Paved roads	Line density	3.20	-0.70×10^{-4}	0.11×10^{-4}	0.47×10^{-4}	0.38×10^{-4}	0.58×10^{-4}
Sagebrush	Mean cover	1.50	0.22	0.02	1.25	1.21	1.29
Patch							
Forest	Decay	0.56	−1.63	0.31	0.20	0.11	0.36
Herbaceous	Mean cover	0.56	0.01	0.01	1.01	0.99	1.04
Herbaceous	SD mean cover	0.56	−0.16	0.04	0.85	0.78	0.92
Paved roads	Decay	0.56	−3.36	0.81	0.03	0.01	0.17
Ruggedness	Mean value	0.56	−2.70	1.49	0.07	0.00	1.24
Sagebrush	Mean cover	0.56	0.21	0.02	1.23	1.20	1.27
Central							
Landscape							
Agriculture	Distance	na	0.23×10^{4}	0.05×10^{4}	1.26×10^{4}	1.42×10^{4}	1.38×10^{4}
Forest	Distance	na	-0.64×10^{4}	0.28×10^{4}	0.53×10^{4}	0.31×10^{4}	0.90×10^{4}
Paved roads	Line density	6.44	-0.64×10^{-4}	0.21×10^{-4}	0.53×10^{-4}	0.35×10^{-4}	0.79×10^{-4}
Sagebrush	Mean cover	3.20	0.17	0.03	1.18	1.12	1.24
Wells	Density	3.20	-0.49×10^{-7}	0.26×10^{-7}	0.61×10^{-7}	0.37×10^{-7}	1.02×10^{-7}
Patch							
Paved roads	Decay	0.56	−2.63	1.10	0.07	0.01	0.62
Sagebrush	Mean cover	0.05	0.18	0.02	1.20	1.15	1.25
Northeast							
Landscape							
Agriculture	Decay	1.50	−1.72	0.42	0.18	0.08	0.41
Paved roads	Line density	6.44	-0.79×10^{-4}	0.23×10^{-4}	0.45×10^{-4}	0.29×10^{-4}	0.71×10^{-4}
Sagebrush	Mean cover	6.44	0.43	0.06	1.54	1.38	1.72
Patch							
Agriculture	Decay	0.56	−3.36	0.74	0.03	0.01	0.15
Paved roads	Decay	0.56	−0.37	0.22	0.69	0.45	1.05
Sagebrush	Mean cover	0.56	0.34	0.04	1.41	1.29	1.53

model captured 3 nest locations. The only other model that captured nest or lek locations was the statewide patch model ($n = 4$ nests; $n = 2$ leks).

Summer

We incorporated 6,478 late summer locations from 12 study sites spanning 1998–2008 in our summer models (Table 2; Fig. 3), with 5,577 summer locations for model calibration and 901 withheld for model evaluation. We generated 8 model sets across regions (state and 3 regions) and scales (patch and landscape) for the summer season (Tables 11 and 12).

None of the variables included in the top models had confidence intervals that overlapped 0, with the exception of sagebrush cover in the central landscape model. Sagebrush cover was the only variable included in all top models, and it was positively related to sage-grouse locations across scales and regions (Table 13). Avoidance of forests was indicated in 7 of 8 top models as either a proportion of habitat or a distance metric (Tables 12 and 13). Roads class 1 and 2 (negative), roads class 4 and 5 (positive), agriculture (negative), shrub cover (positive), precipitation (positive), and TRI (negative) variables were all consistent in their interpretation across all regions and scales in which they were included (Table 13); whereas associations with herbaceous cover and NDVI were inconsistent across models (Table 13). However, the relative importance of each of these variables changed across regions and scales as indicated by their inclusion or exclusion from certain top models (Table 13) and by the variation in the magnitude of the coefficient estimates (Table 12).

Table 6. Summary of variables included in top models for Wyoming greater sage-grouse nest models and their influence on the probability of selection, 1994–2009. Results are presented for each region and both patch and landscape (land) scales. A plus symbol indicates a positive association and a minus symbol indicates a negative association. Lack of a symbol means the covariate did not enter the top model.

	State		Southwest		Central		Northeast	
Covariate	**Patch**	**Land**	**Patch**	**Land**	**Patch**	**Land**	**Patch**	**Land**
Sagebrush	+	+	+	+	+	+	+	+
Paved roads	−	−	−	−	−	−	−	−
Agriculture	−	−		−		+	−	−
Forest	−	−	−	−		+		
Wells						−		
Herbaceous			−					
Shrub height	+							
Ruggedness			−					

Precipitation was always selected in its quadratic form when included in a model.

The summer models also demonstrated good discriminatory power within the study-site SAEs (Figs. 11–13). Across all regions and scales, the models captured an average of 82% of the evaluation summer locations in an average of 45% of the landscape within each study site SAE (Table 14; Fig. 13). The discriminatory power was similar across scales with an average CVI of 38% for the landscape models, 34% for the patch models, and 38% for the combined landscape and patch models (Table 14). On average, the statewide and regional models had similar discriminatory capabilities (state CVI = 38%, regional mean CVI = 37%). Unlike the nesting models, which consistently performed best in the southwest, the northeast regional summer models had consistently higher discriminatory capabilities compared to other regions (Table 14).

Winter

We incorporated 2,338 locations from 7 study sites during 2005–2010 in our winter models (Table 2; Fig. 4), with 2,092 winter locations for model calibration and 246 withheld for model evaluation. We generated 8 model sets across regions (state and 3

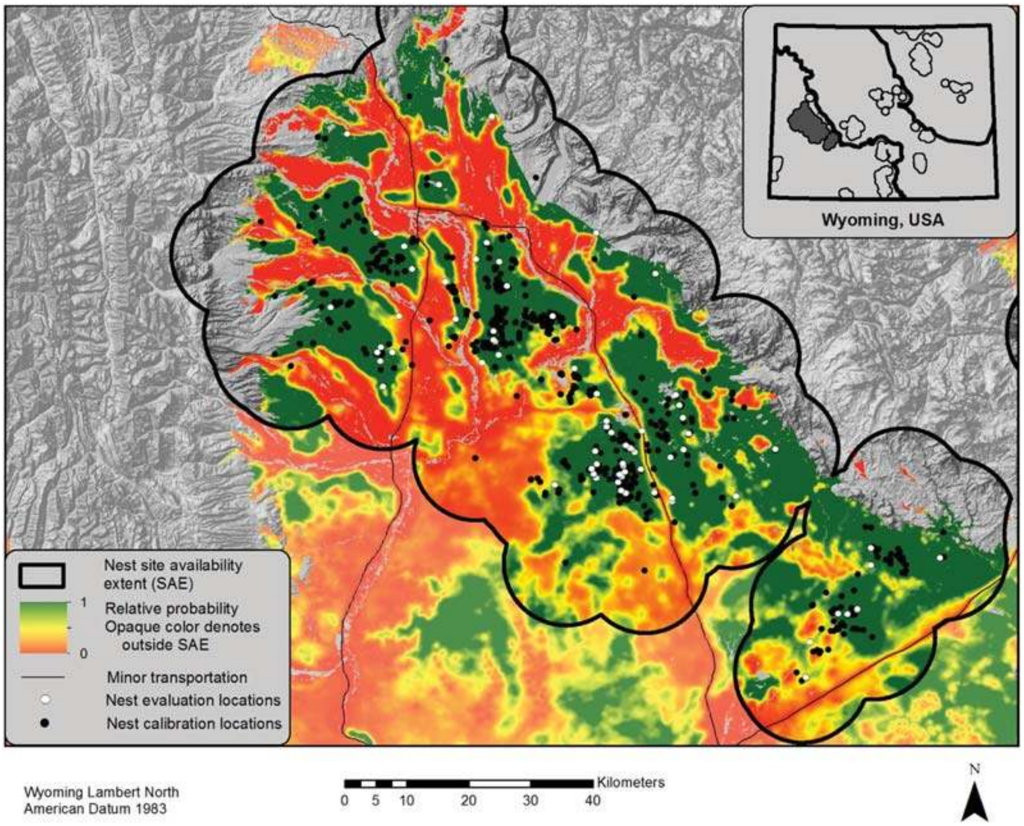

Figure 8. Statewide nesting greater sage-grouse model applied to Wyoming, USA, and represented as a continuous surface. The map is zoomed into the Pinedale study-site-availability extent (SAE) to provide an example of statewide model performance within study site SAEs. The colors range from red to green to represent the range of probability values from 0 (low relative probability of selection) to 1 (high relative probability of selection). The black circles represent nest locations used for model calibration and the white circles represent nest locations used for model evaluation, 1998–2009. The Pinedale study site boundary is indicated by the black line. Areas of gray hill shade represent the areas masked out in the model predicted surfaces. Areas outside of the study sites are novel areas and slightly grayed to indicate the inherent lower confidence in model predictions in these areas.

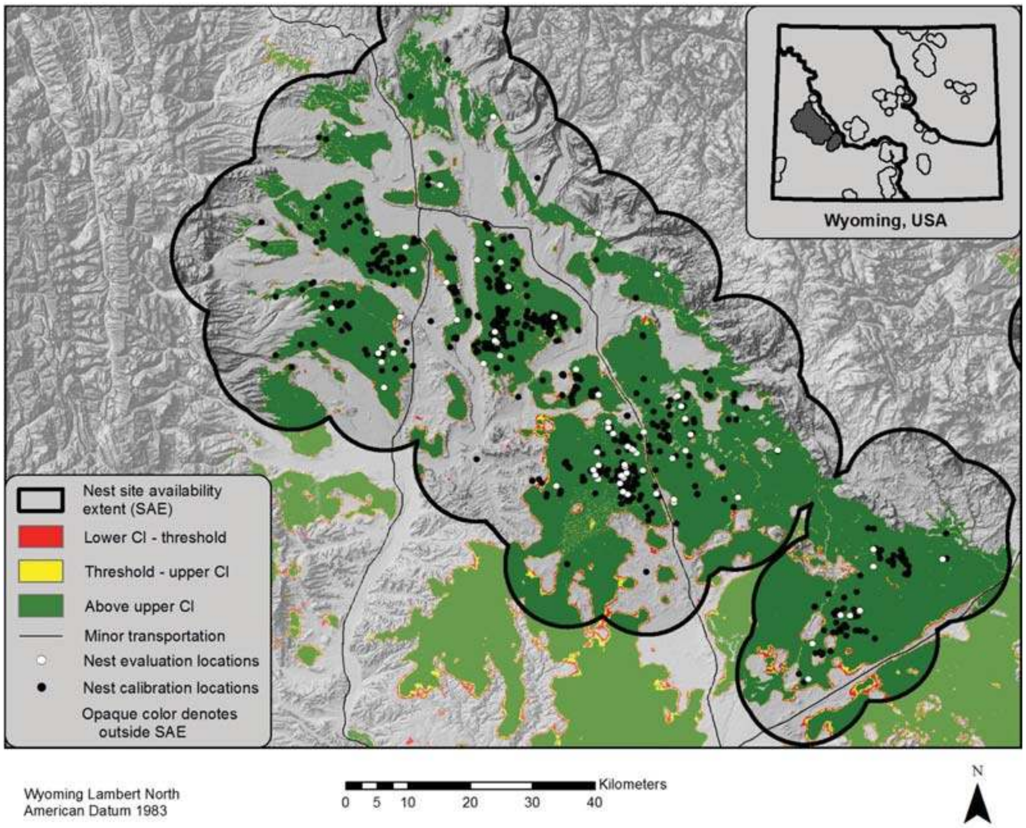

Figure 9. Important nesting habitat for greater sage-grouse in Wyoming. The map is zoomed into the Pinedale study-site-availability extent (SAE) to provide an example of statewide model performance within study site SAEs. The habitat categories 1 through 3 are coded by green (category 1, above the upper confidence interval), yellow (category 2, between the maximum value and the upper confidence interval), and red (category 3, between the maximum value and the lower confidence interval). Habitats with values below the chosen threshold are represented as gray hill shade. The map is the southwest top, model-averaged, landscape × patch model. Study site boundaries are indicated by the thick black lines. The black circles represent nest locations used for model calibration and the white circles represent nest locations used for model evaluation, 1998–2009. We did not make predictions outside of the greater sage-grouse distribution in Wyoming. Areas outside of the study sites are novel areas and slightly grayed to indicate the inherent lower confidence in model predictions in these areas.

regions) and scales (patch and landscape) for the winter season (Tables 15 and 16).

Sagebrush cover, roads class 1 and 2, forest, and ruggedness variables were the most common covariates included in the top model sets. Sage-grouse demonstrated consistently positive selection for sagebrush and consistent avoidance of roads class 1 and 2, forest, and rugged terrain. The only variable that occurred in all 8 top model-averaged sets was TRI (Table 17). Well variables were included in half of the top model sets. The models suggested birds consistently avoided landscapes with higher well densities. When agriculture variables were included in a top model set, they indicated consistent avoidance across regions and scales. Shrub height was included in the state patch models and indicated selection for lower shrub heights at that scale. Shrub height was also included in the central landscape models as both the mean and standard deviation. The standard deviation metric was the more important of the 2 metrics and indicated selection for areas with less variation in shrub height.

The winter models demonstrated reasonable discriminatory power within the study site SAEs (Figs. 14 and 15). The winter models, as thresholded using the approach outlined here, did not discriminate well outside of the SAEs (Fig. 16). Across all regions and scales, the models captured an average of 93% of the evaluation winter locations in an average of 50% of the landscape within each study site SAE (Table 18). The discriminatory power was similar across scales with an average CVI of 39% for the landscape models, 37% for the patch models, and 39% for the combined landscape × patch models. The regional and statewide models had the same similar discriminatory capabilities of 38%. The winter models had a CVI range (33–48%) similar to the nesting and summer models. The central models had the best discriminatory capabilities of all combined landscape and patch models capturing 96% of the calibration locations in 54% of the landscape (Table 18), although the statewide and regional models also had discriminatory ability.

Multiscale Models and Variance Decomposition

We produced models at both patch and landscape scales. However, the multiscale models had higher statistical support (Table 19). Variance decomposition showed that for all seasons and all regions, the percent deviance explained was always higher in the shared component of the deviance than in either the patch or landscape scales alone (Table 19). The percent deviance explained in the shared component ranged from 52% to 92% (Table 19).

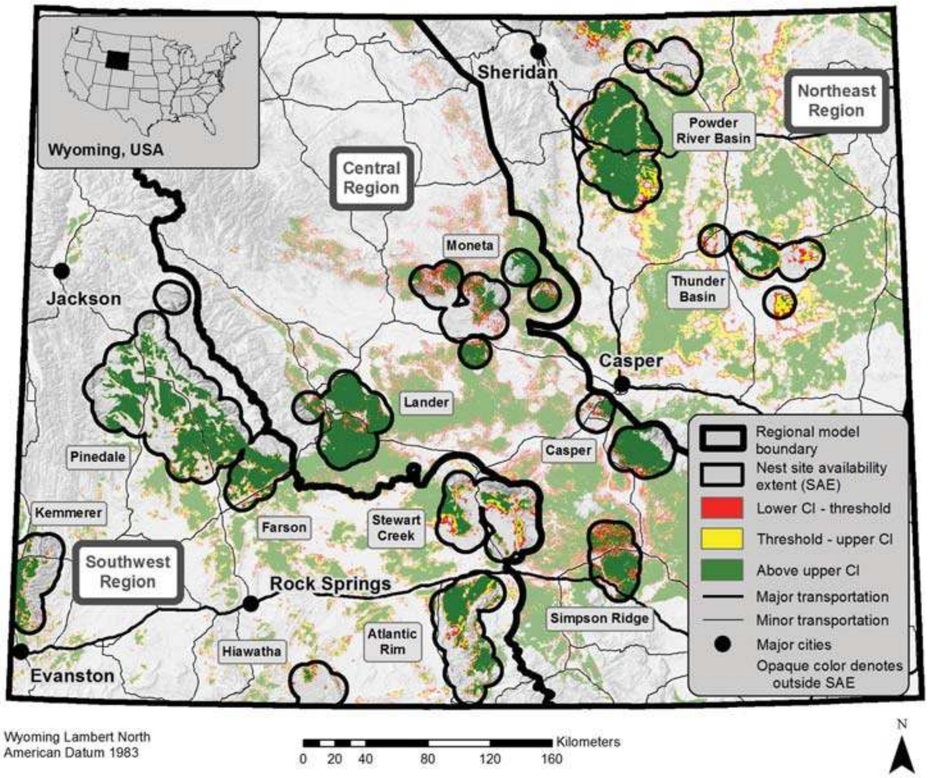

Figure 10. Important nesting habitat for greater sage-grouse in Wyoming. The map represents the 3 regional nest models stitched together across the state. The habitat categories 1 through 3 are coded by green (category 1, above the upper confidence interval), yellow (category 2, between the maximum value and the upper confidence interval), and red (category 3, between the maximum value and the lower confidence interval). Habitats with values below the chosen threshold are represented as gray hill shade. The map is a composite of each of the 3 regional nesting models (e.g., the southwest top, model-averaged, landscape × patch model was applied to the southwest region). Study site boundaries are indicated by the thick black lines and included nesting data from 1994 to 2009. We did not make predictions outside of the greater sage-grouse distribution in Wyoming. Areas outside of the study sites are novel areas and thus we have inherently lower confidence in model predictions in these areas.

Table 7. Evaluation and discrimination results for all models used to characterize sage-grouse nesting habitat use in Wyoming, 1994–2009. We chose all model resource selection function (RSF) thresholds by selecting the RSF value associated with the maximum contrast validation index (CVI). Data are presented for each region and scale, and for the combined landscape × patch (L × P) models. Choice of the threshold resulted in the identification of important habitats. Data presented summarize the percent of all locations that fell within the identified important habitats, from the evaluation dataset. Also presented are values that represent the percent of landscape implicated by RSF values above the chosen threshold (i.e., designated as important). The CVI represents the difference between the percent of locations captured and the percent of landscape implicated. Higher CVI values represent greater discriminatory capabilities.

Region	Scale	Locations captured (%)	Landscape implicated (%)	Contrast validation index
Statewide	Landscape	89	49	40
Southwest	Landscape	93	46	47
Central	Landscape	83	58	25
Northeast	Landscape	93	44	49
Statewide	Patch	84	48	36
Southwest	Patch	91	46	45
Central	Patch	100	72	28
Northeast	Patch	95	61	34
Statewide	L × P	88	49	39
Southwest	L × P	92	45	47
Central	L × P	94	59	35
Northeast	L × P	95	50	45
Average		84	50	34

DISCUSSION

Despite considerable variation in the distribution of key habitat components across sage-grouse range in Wyoming, we developed habitat selection models with good predictive capabilities when applied to numerous large study sites across Wyoming

Table 8. Percent of the landscape classified as important nesting habitat for sage-grouse within 3 km, 5 km, 10 km, and 20 km of leks and random locations, Wyoming, USA. Leks used in the habitat analyses had ≥5 displaying males ($n = 1{,}033$). Number of males attending a lek was based on peak male lek count in 2008. If a lek was not counted in 2008, we used the peak number of males attending the lek during the next most recent year—going back a maximum of 5 years (i.e., 2003). We defined percent predicted nesting habitat as resource selection values ≥ the maximum threshold (i.e., important habitat). Values are presented for the statewide nesting model, and a summary of the regional nesting models (southwest, central, and northeast).

	3 km	5 km	10 km	20 km
Statewide				
Leks	52.5	48.1	42.5	38.6
95% CI	50.2, 54.8	46.0, 50.12	40.8, 44.3	37.3, 40.0
Random	32.8	32.7	32.3	32.1
95% CI	30.6, 35.0	30.6, 34.7	30.6, 34.0	30.8, 33.5
Regional				
Leks	49.1	45.7	40.7	37
95% CI	46.8, 51.5	43.5, 47.9	38.9, 43.0	35.5, 38.5
Random	33.2	32.8	32.5	32.7
95% CI	30.9, 35.4	30.8, 34.9	30.7, 34.3	31.2, 34.2

Table 9. The proportion of males and leks contained within identified important habitat and within 3 different Euclidean distances (1.5 km, 3 km, and 5 km) to the nearest identified important habitat. All leks included in the analysis were active ($\geq$2 displaying males) in 2008. Results are presented for the statewide model. Values presented for the regional models represent the average across the southwest, central, and northeast regional models. Leks represent the proportion of lek sites and males represent the proportion of males. We also present the study site extent (SAE). We calculated all values for leks within the SAE and outside the SAE. We considered sites outside of the SAEs to be novel areas because they were not included in the model development. Results for proportion of leks and males contained within important habitat are represented in the 0 km column.

Nest model	Metric	SAE	0 km	1.5 km	3 km	5 km
Statewide	Leks	Within	0.78	0.96	0.96	1.00
		Outside	0.48	0.72	0.80	0.90
	Males	Within	0.83	0.98	0.98	0.99
		Outside	0.53	0.77	0.84	0.87
Regional	Leks	Within	0.76	0.90	0.92	0.95
		Outside	0.45	0.72	0.80	0.84
	Males	Within	0.76	0.90	0.92	0.96
		Outside	0.49	0.78	0.85	0.89

(Tables 7, 14, and 18; Figs. 9, 12, and 15). Adequately sampling the range of variation in sagebrush habitats to produce state-wide management tools across Wyoming would not have been possible without collaboration from many independent research efforts. A collaboration of such a scale is uncommon but should not be the exception. Evaluation of our models using independent seasonal sage-grouse locations showed we could capture 82–93% of all telemetry locations while implicating roughly 45–50% of the landscape, on average. Further, using lek sites as an independent test for nesting habitat, we showed our nesting models performed well in novel areas outside of our SAEs (Tables 8 and 10; Fig. 6). Quantitatively assessing the performance of the summer and winter models outside of the SAEs where models were calibrated was difficult because of the limited data available on summer and winter habitat use outside of the study site boundaries. Therefore, additional uncertainties exist in extrapolated areas, particularly for summer and winter models. However, the large landscapes implicated in the un-sampled areas for the winter models in the southwest and northeast regions (Fig. 16) suggest limited discriminatory capabilities for these models using the threshold methods presented here.

Our analyses showed habitat selection maps using landscape-scale GIS can provide powerful tools for conservation planning. Doherty et al. (2010*a*) compared local- and landscape-scale habitat needs for nesting sage-grouse, and found local-scale habitat variables that cannot currently be mapped in a GIS (e.g., visual obstruction, grass height) captured the largest amount of pure variation in habitat selection and strongly influenced sage-grouse nest-site selection. However, they found this result was only true within priority nesting habitats defined at the landscape scale (Doherty et al. 2010*a*). "GIS habitat models will only explain part of the variation in habitat selection for some time because current technological limitations and cost of new remote sensing platforms preclude remote mapping at the fine-scale level of detail that can be obtained from ground-based habitat measures (e.g., grass cover, species-specific shrub cover)" (Doherty et al. 2010*a*). However, the maps produced by our models are accurate at the scale of prioritizing regions for management. Managers must ensure the tools (e.g., our models) match the scale of the objective or question of interest.

Models and Considerations

The habitat models presented here were developed using extensive radiotelemetry data and the best available GIS data. Based upon model evaluation statistics and prediction of independent seasonal locations, we show that we have adequately sampled the range of used and available habitats to produce an RSF with high discriminatory capabilities, particularly within our study-site SAEs. However, when model coefficients are applied using coarse spatial data, localized predictions will only be as accurate and reliable as the underlying data in that area. Therefore, predictive accuracy for robust statistical models may vary spatially if GIS data are not of similar resolution or accuracy across large extents. We assessed these assumptions qualitatively and quantitatively through inspection of all data inputs. Fundamental species habitat relationships used to discriminate habitat selection can be robust and correct; however, when spatial predictions are used by managers at smaller scales (e.g., project-level scales, particularly in areas far removed from the sage-grouse data available for generating models), limitations apply.

Managers should recognize that local inaccuracies of spatial input layers exist and understand that finer resolution assessments are not possible with models developed from coarser resolution spatial inputs. Acknowledging these local inaccuracies will help to recognize ecological boundaries for these models and identify potential biases in model predictions. For example, the most

Table 10. All sagebrush and road metric estimates included in the top sage-grouse nesting models for each region. Mean and standard deviation are presented for each variable within each region across Wyoming, 1994–2009. We calculated values from geographic information systems data layers. Sagebrush cover is summarized and presented at 4 moving window radii (0.05 km, 0.56 km, 1.5 km, and 3.2 km). The density of paved roads is summarized and presented at 3 moving window radii (0.56 km, 3.2 km, and 6.44 km). The canopy cover estimates are not directly comparable to local on-the-ground measured canopy cover estimates. See Homer et al. (2012) for more discussion.

	Sagebrush								Paved roads					
	0.05 km		0.56 km		1.5 km		3.2 km		0.56 km		3.20 km[a]		6.44 km[a]	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Bighorn Basin	6.6	2.8	6.3	1.7	6.0	1.4	5.6	1.0	0.002	0.008	0.061	0.378	0.121	0.257
Statewide	10.2	5.1	10.2	4.5	10.2	4.3	10.2	3.8	0.037	0.128	0.365	0.789	0.370	0.545
Southwest	11.0	5.7	11.0	5.0	11.0	4.8	11.0	4.2	0.039	0.130	0.362	0.729	0.366	0.494
Central	10.4	5.4	10.4	4.8	10.4	4.6	10.4	4.2	0.039	0.131	0.386	0.823	0.393	0.571
Northeast	8.8	3.3	8.7	2.5	8.7	2.3	8.7	1.9	0.033	0.122	0.350	0.849	0.354	0.597

[a] The variable was multiplied by 10,000 for display and summary purposes.

Table 11. Comparison of the top patch and landscape models used to characterize sage-grouse summer habitat use (1998–2009) across Wyoming. Models are presented for the statewide data and each regional division. The final 3 digits (x.xx) of each variable represent the radii (rounded to 2 decimals) of the moving window size selected. Models are ranked by the change in the Bayesian Information Criterion (ΔBIC). Weights (w_i) indicate the likelihood of the model being the best of those evaluated (*n* model set) and *K* indicates the number of parameters in the model. The models represent the 90% confidence set and were incorporated in the model-averaging procedure. Models *N* presents the total number of models evaluated in the model set after removing unstable variables. Parenthetical referencing of variables indicates those terms could not enter the candidate model set independent of each other.

Model	Model structure[a]	*K*	BIC	ΔBIC	w_i	Models *N*
Statewide						
Landscape	Non_irrigated6.44 + Forest3.20 + Herb6.44 + (Precip1.50 + Precip1.50^2) + Paved_road_dens3.20 + Unpaved_road_dens1.50 + (Sage3.20 + Sage_SD3.20) + Shrub_height6.44	11	13,023.23	0.00	1.00	255
Patch	Non_irrigated_dist0.56 + Forest_dist0.56 + Herb0.05 + (Precip0.05 + Precip0.05^2) + Paved_road_dist0.05 + Unpaved_road_dens0.05 + (Sage0.05 + Sage_SD0.05)	10	13,279.41	0.00	1.00	1,023
Southwest						
Landscape	Non_irrigated6.44 + Forest3.20 + (Precip1.50 + Precip1.50^2) + TRI1.50 + (Sage3.20 + Sage_SD3.20)	8	2,964.43	0.00	1.00	32
Patch	Forest0.56 + NDVI_2004 + (Precip0.05 + Precip0.05^2) + TRI0.05 + (Sage0.05 + Sage_SD0.05)	8	3,146.68	0.00	1.00	511
Central						
Landscape	Non_irrigated_dist6.44 + Herb6.44 + (Precip3.20 + Precip3.20^2) + Paved_road_dens3.20 + TRI1.50	7	2,388.69	0.00	0.64	511
	Non_irrigated_dist6.44 + Herb6.44 + (Precip3.20 + Precip3.20^2) + Paved_road_dens3.20 + Unpaved_road_dens1.50 + TRI1.50	8	2,391.24	2.55	0.18	
	Non_irrigated_dist6.44 + Herb6.44 + (Precip3.20 + Precip3.20^2) + Paved_road_dens3.20 + TRI1.50 + Sage6.44 + Sage_SD6.44	9	2,392.29	3.60	0.11	
Patch	Forest_dist0.56 + (Herb0.56 + Herb_SD0.56) + (Precip0.56 + Precip0.56^2) + Paved_road_dist0.56 + TRI0.56 + Sage0.05	9	2,415.42	0.00	0.90	255
Northeast						
Landscape	Non_irrigated6.44 + Forest3.20 + NDVI_2004 + Paved_road_dist3.20 + Unpaved_road_dens1.50 + (Sage6.44 + Sage_SD6.44)	8	6,879.55	0.00	0.91	31
Patch	Non_irrigated_dist0.56 + Forest_dist0.56 + ndvi_04 + Paved_road_dist0.56 + Unpaved_road_dens0.56 + (Sage0.56 + Sage_SD0.56) + (Shrub_height0.05 + Shrub_height_SD0.05)	10	2,415.42	0.00	0.90	31

[a] Agr, agriculture including irrigated and non-irrigated lands; Herb, herbaceous cover; NDVI, Normalized Difference Vegetation Index; Non_irrigated, non-irrigated agricultural lands; Sage, sagebrush cover; TRI, Terrain Ruggedness Index.

current sagebrush map products we used were noted to overpredict sagebrush cover in some areas of northeastern Wyoming, primarily because of difficulties in capturing sparse sagebrush cover in contiguous landscapes of northern mixed grasses (Homer et al. 2012). However, this sampling variation did not overwhelm the strong biological selection for sagebrush in the northeast. In fact, sagebrush was consistently a strong predictor that contributed to our ability to identify important habitats across all 3 life stages within this region. Nevertheless, localized identification of important habitats where the GIS sagebrush layer overestimates actual sagebrush cover may, by extension, be overpredicted. This challenge is not unique to analyses that encompass large extents but must be explained when working with managers who are tasked to use predictive maps in decision-making.

The models and predicted maps we developed represent significant advancement in spatial identification of important habitats, giving managers a more comprehensive tool for conservation planning, habitat prioritization, and restoration, particularly for statewide management of the species. Our large-scale analysis revealed some challenges that likely would not have caused issues within individual study sites but emerged when working at larger extents such as the entire state and the 3 sub-state regions. Challenges exist in developing spatial predictor layers that represent the same biological processes across such a large landscape, and special attention needs to be given to both the biological or mapping consistency of predictor variables (e.g., CTI, hydrologic flowlines, snow). Our work highlights some emergent challenges that arise when working at large extents and extrapolating habitat relationships into novel areas. Clearly, improvements in the accuracy of spatial layers representing ecologically relevant variables would improve such modeling efforts. We encourage other researchers pursuing this type of large-extent habitat selection modeling to carefully consider the behavior and accuracy of all GIS spatial layers and generated metrics.

Sage-grouse winter habitat use has been successfully characterized using similar modeling approaches (Doherty et al. 2008, Carpenter et al. 2010). Our winter habitat selection models performed well within our study sites (Table 18, Figs. 14 and 15). However, unlike the previous studies, we applied our models over large extents outside of our study sites and found that winter models seem to suffer from lack of discrimination outside study sites where they were developed using the threshold approach described here (Fig. 16). We caution against the application and use of these models outside of the study sites. However, exploration of alternative thresholds may result in more site-relevant discrimination in areas of interest. Winter habitat selection for sage-grouse is strongly dependent on food availability, which in many cases is determined by snow depth in relation to shrub height (Remington and Braun 1985, Homer et al. 1993, Schroeder et al. 1999, Connelly et al. 2000, Crawford et al. 2004). Patterns of snow accumulation are highly variable and difficult to predict and thus, prediction to novel areas during this stage of the annual cycle is more difficult than other periods when animals rely on less variable resources. The snow data that we gathered were not capable of capturing these ephemeral, but important, processes of local variability in non-persistent snow cover.

Table 12. Model-averaged beta coefficients and standard errors for variables included in the top 90% model set for Wyoming greater sage-grouse summer season. Results are presented for each region and both patch and landscape scales. Data included in the modeling effort were collected from 1998 to 2009. The metric column presents the metric used to represent the variable estimated and summarized for each window size. Extent presents the radii (km) of the various window sizes for patch and landscape scales. A radius value of na indicates the metric was not summarized across a window size and either represents Euclidean distance for distance metrics, or a pixel estimate for other metrics. Note that a positive association with distance decays suggested selection for proximity to a habitat feature as values were 1 at a feature of interest, and decay farther from the feature. Also presented are the estimated odds ratios and associated confidence intervals.

Category	Metric	Extent	β_i	SE	Odds ratio	Lower CI	Upper CI
Statewide							
Landscape							
Agriculture	Mean cover	6.44	-0.37×10^{-2}	0.04×10^{-2}	0.69×10^{-2}	0.64×10^{-2}	0.74×10^{-2}
Forest	Mean cover	3.20	-0.19×10^{-2}	0.01×10^{-2}	0.83×10^{-2}	0.81×10^{-2}	0.84×10^{-2}
Herbaceous	Mean cover	1.50	0.03	0.00	1.03	1.02	1.03
Precipitation	Mean	1.50	0.11	0.02	1.11	1.08	1.15
Precipitation	Mean^2	1.50	-0.81×10^{3}	0.18×10^{3}	0.44×10^{3}	0.31×10^{3}	0.63×10^{3}
Paved roads	Line density	3.20	-0.40×10^{-4}	0.03×10^{-4}	0.67×10^{-4}	0.63×10^{-4}	0.71×10^{-4}
Unpaved roads	Line density	1.50	0.27×10^{-3}	0.02×10^{-3}	1.32×10^{-3}	1.25×10^{-3}	1.38×10^{-3}
Sagebrush	Mean cover	3.20	0.06	0.01	1.06	1.04	1.08
Sagebrush	SD mean cover	3.20	0.12	0.02	1.13	1.09	1.17
Shrub height	Mean height	6.44	0.05	0.01	1.05	1.04	1.06
Patch							
Agriculture	Decay	0.56	−4.82	0.55	0.01	0.00	0.02
Forest	Decay	0.56	−2.67	0.10	0.07	0.06	0.08
Herbaceous	Mean cover	0.05	0.03	0.00	1.03	1.02	1.03
Precipitation	Mean	0.05	0.17	0.02	1.18	1.15	1.22
Precipitation	Mean^2	0.05	0.00	0.00	1.00	1.00	1.00
Paved roads	Decay	0.56	−1.00	0.17	0.37	0.26	0.52
Unpaved roads	Line density	0.56	0.14×10^{-3}	0.02×10^{-3}	1.15×10^{-3}	1.11×10^{-3}	1.19×10^{-3}
Sagebrush	Mean cover	0.56	0.09	0.01	1.09	1.08	1.10
Sagebrush	SD mean cover	0.56	0.14	0.02	1.15	1.11	1.19
Southwest							
Landscape							
Agriculture	Euclidean	na	0.12×10^{4}	0.01×10^{4}	1.13×10^{4}	1.10×10^{4}	1.16×10^{4}
Forest	Mean cover	3.20	-0.12×10^{-2}	0.02×10^{-2}	0.89×10^{-2}	0.85×10^{-2}	0.92×10^{-2}
Precipitation	Mean	1.50	0.33	0.03	1.39	1.31	1.48
Precipitation	Mean^2	1.50	0.00	0.00	1.00	1.00	1.00
Ruggedness	Mean value	1.50	-0.73×10^{-2}	0.11×10^{-2}	0.48×10^{-2}	0.39×10^{-2}	0.60×10^{-2}
Sagebrush	Mean cover	3.20	0.09	0.01	1.09	1.06	1.12
Sagebrush	SD mean cover	3.20	0.09	0.03	1.09	1.04	1.15
Patch							
Forest	Mean cover	0.56	−6.16	1.71	0.00	0.00	0.06
NDVI	Pixel	na	0.27×10^{3}	0.03×10^{3}	1.31×10^{3}	1.22×10^{3}	1.40×10^{3}
Precipitation	Mean	0.05	0.25	0.03	1.29	1.22	1.36
Precipitation	Mean^2	0.05	0.00	0.00	1.00	1.00	1.00
Ruggedness	Mean value	0.56	-0.13×10^{-3}	0.01×10^{-3}	0.88×10^{-3}	0.86×10^{-3}	0.90×10^{-3}
Sagebrush	Mean cover	0.05	0.06	0.01	1.07	1.05	1.08
Sagebrush	SD mean cover	0.05	−0.01	0.03	0.99	0.93	1.05
Central							
Landscape							
Agriculture	Decay	6.44	−6.80	1.29	0.00	0.00	0.01
Herbaceous	Mean cover	6.44	−0.06	0.01	0.94	0.92	0.96
Precipitation	Mean	3.20	0.25	0.04	1.29	1.19	1.40
Precipitation	Mean^2	3.20	0.00	0.00	1.00	1.00	1.00
Paved roads	Line density	3.20	-0.68×10^{-4}	0.10×10^{-4}	0.51×10^{-4}	0.41×10^{-4}	0.62×10^{-4}
Unpaved roads	Line density	1.50	0.29×10^{-2}	0.13×10^{-2}	1.34×10^{-2}	1.04×10^{-2}	1.72×10^{-2}
Ruggedness	Mean value	1.50	-0.83×10^{-2}	0.09×10^{-2}	0.44×10^{-2}	0.37×10^{-2}	0.52×10^{-2}
Sagebrush	Mean cover	6.44	0.08×10^{-2}	0.22	1.08	0.70	1.67
Sagebrush	SD mean cover	6.44	0.02	0.01	1.02	1.01	1.04
Patch							
Forest	Decay	0.56	−1.32	0.24	0.27	0.17	0.42
Herbaceous	Mean cover	0.56	−0.06	0.01	0.94	0.92	0.96
Herbaceous	SD mean cover	0.56	0.25	0.03	1.28	1.21	1.36
Precipitation	Mean	0.56	0.19	0.04	1.21	1.11	1.32
Precipitation	Mean^2	0.56	0.00	0.00	1.00	1.00	1.00
Paved roads	Decay	0.56	−3.83	0.76	0.02	0.00	0.10
Ruggedness	Mean value	0.56	-0.63×10^{-2}	0.10×10^{-2}	0.53×10^{-2}	0.44×10^{-2}	0.65×10^{-2}
Sagebrush	Mean cover	0.05	0.06	0.01	1.06	1.03	1.08
Northeast							
Landscape							
Agriculture	Mean cover	6.44	-0.51×10^{-2}	0.04×10^{-2}	0.60×10^{-2}	0.55×10^{-2}	0.65×10^{-2}
Forest	Mean cover	3.20	-0.17×10^{-2}	0.02×10^{-2}	0.84×10^{-2}	0.82×10^{-2}	0.87×10^{-2}
NDVI	Mean value	na	-0.21×10^{3}	0.05×10^{3}	0.81×10^{3}	0.73×10^{3}	0.89×10^{3}
Paved roads	Decay	3.20	−2.53	0.15	0.08	0.06	0.11

Table 12. (*Continued*)

Category	Metric	Extent	β_i	SE	Odds ratio	Lower CI	Upper CI
Unpaved roads	Line density	1.50	0.39×10^{-3}	0.04×10^{-3}	0.04×10^{-3}	1.37×10^{-3}	1.59×10^{-3}
Sagebrush	Mean cover	6.44	0.24	0.02	1.27	1.23	1.32
Sagebrush	SD mean cover	6.44	0.62	0.04	1.86	1.71	2.01
Patch							
Agriculture	Decay	0.56	−5.63	0.60	0.00	0.00	0.01
Forest	Decay	0.56	−2.30	0.16	0.10	0.07	0.14
NDVI	Mean value	na	-0.30×10^{3}	0.05×10^{3}	0.74×10^{3}	0.67×10^{3}	0.82×10^{3}
Paved roads	Decay	0.56	−2.87	0.32	0.06	0.03	0.11
Unpaved roads	Line density	0.56	0.19×10^{-3}	0.03×10^{-3}	1.21×10^{-3}	1.15×10^{-3}	1.27×10^{-3}
Sagebrush	Mean cover	0.56	0.06	0.01	1.07	1.04	1.10
Sagebrush	SD mean cover	0.56	0.50	0.03	1.64	1.55	1.75
Shrub height	Mean height	0.05	0.02	0.01	1.02	1.01	1.03
Shrub height	SD mean height	0.05	0.06	0.01	1.06	1.03	1.09

NDVI, Normalized Difference Vegetation Index.

The probability of brood habitat use by sage-grouse in Alberta increased with the density of primitive, unpaved roads (Aldridge and Boyce 2007). Our summer models also demonstrated increasing probability of selection with unpaved roads classed 4 and 5. Aldridge and Boyce (2007) suggested this pattern could be related to the increased abundance of succulent invasive species (e.g., dandelions, *Taraxacum* sp.), which can serve as an important food source. Alternatively, in western rangelands, roads in this class often lead to riparian areas or track riparian areas. The positive association with this road class was not necessarily selection for roads but more for the riparian areas they are near. As mentioned, we were not able to include riparian areas as a potential covariate and therefore, were unable to quantitatively assess this explanation. Finally, radio-telemetry is often conducted from motorized vehicles and thus radio-marked grouse may easier to detect when closer to roads.

Seasonal and Regional Variation

The diversity of model structures observed across seasons confirmed concerns that pooling data across seasons can mask variation in habitat selection (Schooley 1994). Thus, the suite of variables having the most consistent influence on important resources selected by sage-grouse varied among seasons and each season was characterized by a unique set of covariates (Tables 6, 13, and 17).

Selection for habitat components can change across scales and with restricted availability in some species (Boyce et al. 2003). In others, selection has been consistent across scales (Schaefer and Messier 1995). Many of the variables included in the top model sets were represented by several different metrics. For example, sage-grouse demonstrated consistent avoidance of agriculture during the nesting season; however, in some models this was represented by all agriculture, whereas others included only non-irrigated agriculture and different metrics. For example, avoidance was represented by proximity (e.g., decay distance, Euclidean distance) or mean proportion cover of agriculture on the landscape. Therefore, direct comparison in the strength of selection was not possible in most cases.

We found considerable regional variation in the strength of selection for some key covariates. Most notably, the β-estimates for sagebrush cover were considerably higher in the northeast nesting models than the other top models. Census of GIS layers within the 4 extents showed the amount of sagebrush varied across the regions with the lowest availability of sagebrush corresponding with the largest selection coefficient for sagebrush (Tables 5 and 9). Southwestern Wyoming has the highest densities of sage-grouse in North America (Doherty et al. 2010*b*), yet coefficients are approximately 50% of those for the more fragmented northeast region, suggesting availability affected the strength of selection (Aarts et al. 2008). Changing the proportion

Table 13. Summary of variables included in top models for Wyoming greater sage-grouse summer models and their influence on the probability of selection, 1998–2009. Results are presented for each region and both patch and landscape (land) scales. A plus symbol indicates a positive association and a minus symbol indicates a negative association. Lack of a symbol means the covariate did not enter the top model.

	State		Southwest		Central		Northeast	
Covariate	Patch	Land	Patch	Land	Patch	Land	Patch	Land
Sagebrush	+	+	+	+	+	+	+	+
Paved roads	−	−			−	−	−	−
Unpaved roads	+	+				+	+	+
Agriculture	−	−	−			−	−	−
Forest	−	−	−	−	−		−	−
Herbaceous	+	+			+	−		
Shrub height		+					+	
NDVI	+						−	−
Precipitation	+	+	+	+	+	+		
Ruggedness	−	−	−	−				

NDVI, Normalized Difference Vegetation Index.

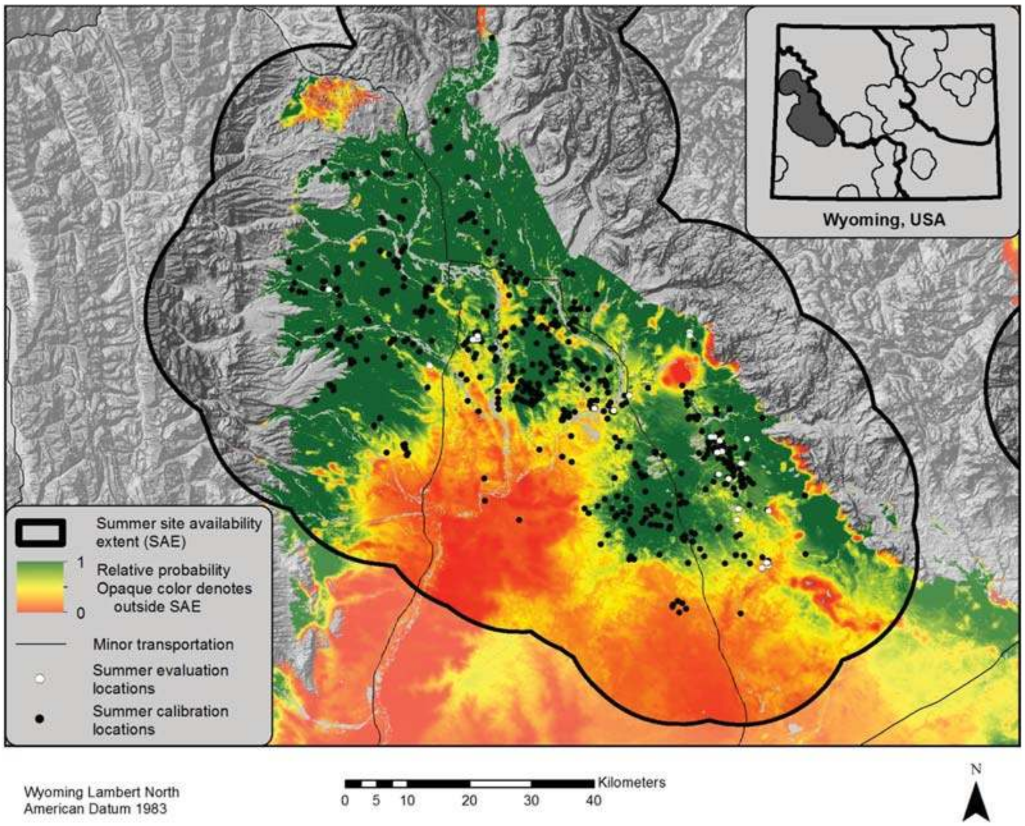

Figure 11. Statewide summer greater sage-grouse model applied to Wyoming, USA, and represented as a continuous surface. The map is zoomed into the Pinedale study-site-availability extent (SAE) to provide an example of statewide model performance within study site SAEs. The colors range from red to green to represent the range of probability values from 0 (low relative probability of selection) to 1 (high relative probability of selection). The black circles represent summer locations used for model calibration and the white circles represent summer locations used for model evaluation, 1998–2007. The Pinedale study site boundary is indicated by the black line. Areas of gray hill shade represent the areas masked out in the model predicted surfaces. Areas outside of the study sites are novel areas and slightly grayed to indicate the inherent lower confidence in model predictions in these areas.

of available habitat within areas (or study sites) can influence relative use in trade-off situations, referred to as the functional response in habitat use (Mysterud and Ims 1998). In this case, the strength of habitat selection (i.e., steepness of the functional response) increases with the amount of non-used habitat sampled (Mysterud and Ims 1998). Thus, our work further illustrates the importance of understanding the difference between mathematical versus biological strength of relationships. Conversely, density of major roads (classes 1 and 2) was also included in all top nesting models at the landscape scale and the coefficient estimates were relatively stable across regions (Tables 5, 12, and 16). Assessment of road variables within the 4 regions modeled showed that the available samples were also stable across the state (Table 10).

Multiscale Models and Variance Decomposition

Habitat selection is fundamentally a hierarchical process (Johnson 1980), which has been demonstrated for greater sage-grouse (Doherty et al. 2010*a*) and Gunnison sage-grouse nesting habitats (Aldridge et al. 2012). Hence, we developed models at both the patch and landscape scales. The percent deviance explained for all models was higher in the shared component of the models than in either the patch- or landscape-scale components individually (Table 19). Thus, a considerable amount of the explained deviance in the models could not be attributed to factors at any 1 spatial scale but were instead shared by explanatory factors from both the patch and landscape models. We suggest using the combined models for identification of important habitats, following the recommendations of others (Johnson 1980, Boyce 2006). Sage-grouse are commonly referred to as a "landscape species" (Knick and Connelly 2011) because evidence indicates that this species relies on large landscapes to meet life-history requirements. In further support of this concept and the role of extensive habitat assessments, the percent deviance explained was higher in the landscape than in the patch components for 10 of 12 season and regional combinations (Table 19). Furthermore, in 7 of 10 models where percent deviance was higher for the landscape component, landscape models explained more than double the patch-level deviance. These results do not dismiss the importance of local-scale habitat needs for sage-grouse, which are well documented (Hagen et al. 2007); rather, we simply could not assess such local vegetation characteristics as accurately in our broad-scale analyses.

Regional and Statewide Model Performance

We predicted the 3 regionally specific model sets would perform considerably better than the models developed statewide.

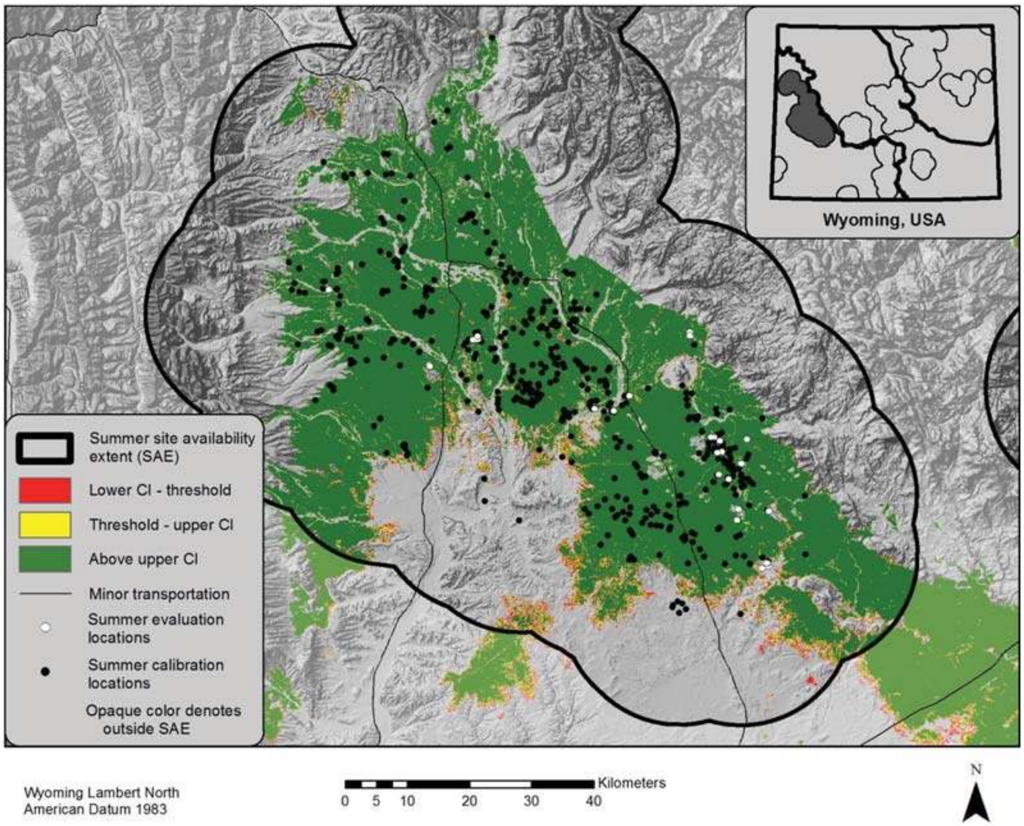

Figure 12. Important summer habitat for greater sage-grouse in Wyoming. The map is zoomed into the Pinedale study-site-availability extent (SAE) to provide an example of the southwest regional model performance within study site SAEs. The habitat categories 1 through 3 are coded by green (category 1, above the upper confidence interval), yellow (category 2, between the maximum value and the upper confidence interval), and red (category 3, between the maximum value and the lower confidence interval). Habitats with values below the chosen threshold are represented as gray hill shade. Study site boundaries are indicated by the thick black lines. The black circles represent summer locations used for model calibration and the white circles represent summer locations used for model evaluation, 1998–2007. We did not make predictions outside of the greater sage-grouse distribution in Wyoming. Areas outside of the study sites are novel areas and slightly grayed to indicate the inherent lower confidence in model predictions in these areas.

However, this was not the case. Generally, the regional models tended to capture a higher percentage of the evaluation locations. However, the regional models also tended to implicate a greater percentage of the landscape within each of the SAEs across seasons. Therefore, the average CVI for the regional landscape × patch models was essentially the same as the statewide landscape × patch models for the nesting (statewide = 38%, regional = 39%), summer (statewide = 38%, regional = 37%), and winter (statewide = 38%, regional = 38%) data.

We used lek sites as an independent assessment of nesting model performance (Table 9). Contrary to our predictions, the statewide model generally captured more leks and more males within the identified important habitat than the regional models. This pattern was true for both within the SAEs and in novel areas outside the SAEs. However, the differences were generally not large (range 2–7% within 0 km). Thus, the statewide modeling approach seemed as efficient as the regional models for the nesting season.

Application to Novel Areas

Application of models to novel areas is a challenging issue when predicting ecological processes, such as habitat selection, for management purposes (Miller et al. 2004, Aldridge et al. 2012). Managers rarely have data in all areas important for conservation planning, yet challenges arise related to many of the modeling issues discussed above. We developed the means to apply and assess these models when required to use them for management in unique areas. Ideally, evaluation with independent datasets and tests of predictions are required to assure model performance to inform management decisions in novel areas. New, independent, seasonally explicit, location data for species of interest are the best test of model accuracy. Conservation of species of concern is often a crisis science, but realistically, such data may not always be available, and decisions may ultimately need to be made in the absence of independent data.

We demonstrated that alternative, but readily available, data sources can be used to evaluate models, as illustrated by our assessment of how well nest models captured lek (breeding) locations (Table 9; Fig. 6). We recognize the percentages of leks in areas outside SAEs that fell directly within identified important habitat were not overly impressive (e.g., 48% of leks, and 53% of males for the statewide landscape × patch model). However, 72% of leks and 77% of males were within 1.5 km of important habitat identified by the statewide nesting model. If we extend that value to 3 km, we captured 80% of leks and 84% of males counted across the state in novel areas. We feel this represents good performance of the models in novel areas and provides evidence these models are useful tools for habitat

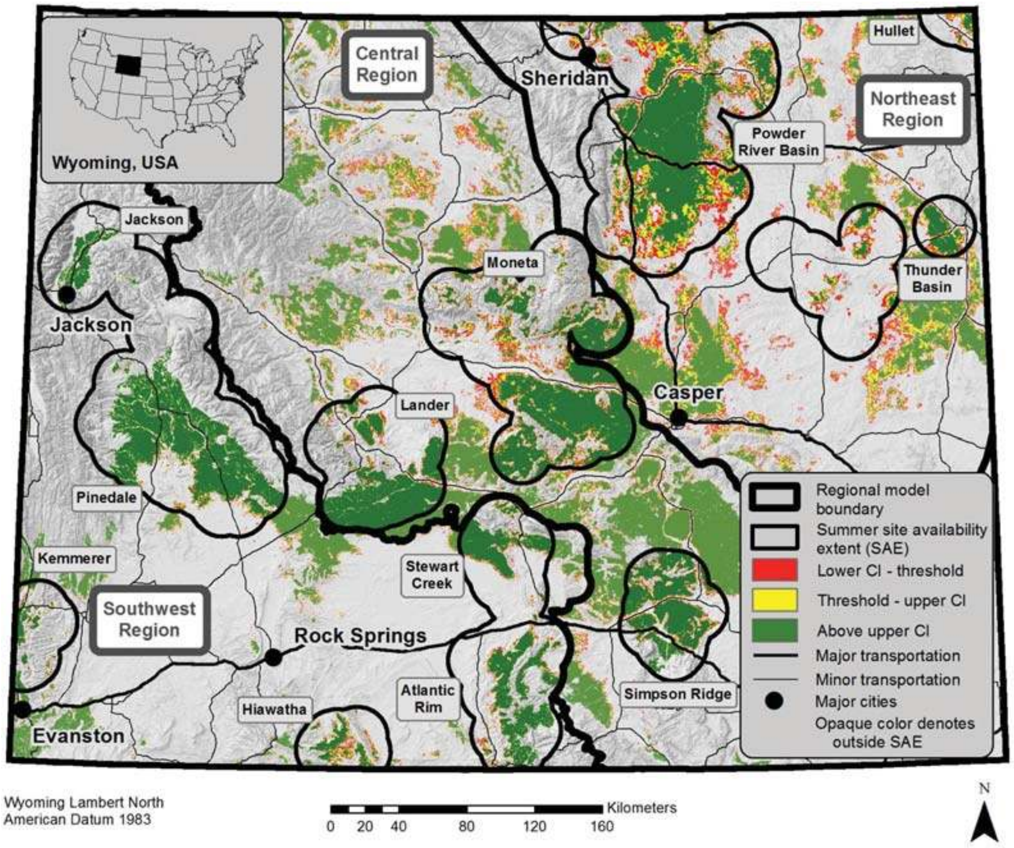

Figure 13. Important summer habitat for greater sage-grouse in Wyoming, USA. The map represents the 3 regional summer models stitched together across the state. The habitat categories 1 through 3 are coded by green (category 1, above the upper confidence interval), yellow (category 2, between the maximum value and the upper confidence interval), and red (category 3, between the maximum value and the lower confidence interval). Habitats with values below the chosen threshold are represented as gray hill shade. The map is a composite of each of the 3 regional summer models (e.g., the southwest top, model-averaged, landscape × patch model was applied to the southwest region). Study site boundaries are indicated by the thick black lines and included summer location data from 1998 to 2009. We did not make predictions outside of the greater sage-grouse distribution in Wyoming. Areas outside of the study sites are novel areas and thus we have inherently lower confidence in model predictions in these areas. Regional boundaries are indicated by the thick black lines and were delineated based primarily on hydrologic units and sage-grouse management zones.

prioritization in novel areas. Additionally, lek sites were consistently located in areas considered important nesting habitat at all evaluated distances.

Access to independent sage-grouse nesting data that were obtained after our modeling effort, allowed for a direct assessment of the capacity of our nesting models to predict important nesting habitat in a completely novel area. The BHB is ecologically unique within Wyoming with lower-than-average percent sagebrush cover (Table 1). Additionally, the BHB has experienced extensive burning and mowing which has influenced sage-grouse habitat in the area (Hess and Beck 2012). As a result of the differences in habitat and availability of resources compared to those from modeled populations, we expected models to have reduced predictive capacity (Table 10). Because habitat availability is known to affect the functional response of species in a habitat selection modeling context (Boyce et al. 2003, Boyce 2006), we tried to identify the best-performing model a priori based on habitat availability. The availability of key habitat components in the northeast nesting models was most similar to the availability in the BHB (Table 10). However, the best-performing model, as measured by predicting independent data, was the central patch model. This result was contrary to our predictions, and could be due to a number of factors. First, other habitat components that we could not summarize may affect nest site selection and better characterize the similarities among sites. Also, this result could have been influenced by the threshold approach used here and defining new site-specific thresholds for the BHB may have resulted in better model performance.

Our results highlighted the importance of independent data to validate a priori assumptions. Thus, when selecting the best nesting model (from the suite we developed) to apply in a novel area, we suggest using lek locations as proxy for nesting habitat and applying the model that captures the greatest proportion of lek locations within or near the boundaries of the new area of interest. However, we caution that this approach could be limited in areas where nesting habitats are highly fragmented and high-quality nesting habitat may not be widely distributed or closely tied to leks. In the absence of independent data (either direct locations of individual birds or lek locations), we suggest applying the model(s) that were developed using the most similar distribution of important modeled habitat components in the available sample locations. Overall, the capacity to test our nesting models using independent lek locations provides greater confidence in the nesting models than the other seasons.

Table 14. Evaluation and discrimination results for all models used to characterize sage-grouse summer habitat use in Wyoming, 1998–2009. We chose all model resource selection function (RSF) thresholds by selecting the RSF value associated with the maximum contrast validation index (CVI). Data are presented for each region and scale, and for the combined landscape × patch (L × P) models. Choice of the threshold resulted in the identification of important habitats. Data presented summarize the percent of all locations that fell within the identified important habitats, from the evaluation dataset. Also presented are values that represent the percent of landscape implicated by RSF values above the chosen threshold (i.e., designated as important). The CVI represents the difference between the percent of locations captured and the percent of landscape implicated. Higher CVI values represent greater discriminatory capabilities.

Region	Scale	Locations captured (%)	Landscape implicated (%)	Contrast validation index
Statewide	Landscape	83	43	40
Southwest	Landscape	74	45	29
Central	Landscape	83	55	28
Northeast	Landscape	91	35	56
Statewide	Patch	83	48	35
Southwest	Patch	74	46	28
Central	Patch	77	54	23
Northeast	Patch	93	41	52
Statewide	L × P	86	48	38
Southwest	L × P	72	43	29
Central	L × P	79	49	30
Northeast	L × P	92	38	54
Average		82	45	37

In our assessment of model performance in novel areas, our assessment of performance in novel areas is based on only 1 approach to establishing habitat thresholds. The approach we used maximizes model performance within the areas of interest—in our case, within our SAEs. Inspection of the continuous surface RSF demonstrated the models potentially contained much more information than what was captured in the binary threshold approach. Re-thresholding these models to better-fit local conditions within novel areas of interest is possible. We recommend the generation of new, site-specific thresholds in novel areas where the important habitat identified by the thresholds presented here does not agree with independent data. Re-defining thresholds on a case-by-case basis in novel areas would increase model performance.

Other modeling approaches may have resulted in more accurate predictions to novel areas. For example, Matthiopoulos et al. (2011) suggested a generalized selection function in a mixed model context would better predict to novel areas. However, in our study with large sample sizes and extents, the inclusion of random effects in a mixed model context including random intercepts, and random coefficients was unfeasible.

The predictive ability of our resource selection models for sage-grouse might be improved with the inclusion of a number of different factors. Primarily, additional location data for novel areas outside of our study sites would likely improve model performance in novel areas and would allow for selection of the best model, as demonstrated by our example application for the nesting season in the BHB region. Riparian areas can be important to sage-grouse during the summer season (Hagen et al. 2007) and more consistent, higher quality, riparian data across the state would likely assist with model performance in novel areas. Sage-grouse avoid leks with increased levels of anthropogenic noise (Blickley et al. 2012) and inclusion of soundscapes within developed areas may also improve model predictive capabilities. State and federal agencies in Wyoming regularly conduct winter aerial surveys for sage-grouse. The winter models could potentially be improved through the inclusion of the many winter flight data collected across Wyoming. However, the distribution of winter habitats can vary substantially among years because of variation in snowfall and accumulation. Ultimately, agencies and organizations using habitat selection models to identify priority winter habitats will have to determine whether they prefer to predict habitat in

Table 15. Comparison of the top patch and landscape models used to characterize sage-grouse winter habitat use (2001–2010) across Wyoming. Models are presented for the statewide data and each regional division. The final 3 digits (x.xx) of each variable represent the radii (rounded to 2 decimals) of the moving window size selected. Models are ranked by the change in the Bayesian Information Criterion (ΔBIC). Weights (w_i) indicate the likelihood of the model being the best of those evaluated (*n* model set) and *K* indicates the number of parameters in the model. The models represent the 90% confidence set and were incorporated in the model-averaging procedure. Models *N* presents the total number of models evaluated in the model set after removing unstable variables. Parenthetical referencing of variables indicates those terms could not enter the candidate model set independent of each other.

Model	Model structure[a]	*K*	BIC	ΔBIC	w_i	Models *N*
Statewide						
Landscape	Agr_dist3.20 + Forest_dist1.50 + Paved_road_dist1.50 + TRI1.50 + Well6.44	6	5,850.08	0.00	0.60	64
	Agr_dist3.20 + Forest_dist1.50 + Paved_road_dist1.50 + TRI1.50 + (Sage6.44 + Sage_SD6.44) + Well6.44	8	5,850.88	0.80	0.40	64
Patch	Agr_dist0.56 + Forest_dist0.56 + Paved_road_dist0.56 + TRI0.56 + Sage0.56 + Well0.56 + Shrub_height0.56 + TRI0.56	9	5,825.99	0.00	1.00	127
Southwest						
Landscape	Forest_dist1.50 + Paved_road_dist1.50 + TRI1.50 + (Sage6.44 + Sage_SD6.44) + Well1.50	7	3,083.53	0.00	1.00	31
Patch	Forest_dist0.56 + Paved_road_dist0.56 + TRI0.56 + Well0.56	5	3,187.28	0.00	0.93	31
Central						
Landscape	TRI1.50 + (Shrub_height6.44 + Shrub_height_SD6.44)	4	737.20	0.00	0.82	7
	TRI1.50 + (Shrub_height6.44 + Shrub_height_SD6.44) + (Sage6.44 + Sage_SD6.44)	6	741.62	4.41	0.09	
Patch	TRI0.56 + Sage0.56	3	746.35	0.00	0.92	7
Northeast						
Landscape	Forest3.20 + Paved_road_dist3.20 + TRI1.50 + Sage3.20 + Agr6.44	6	1,100.15	0.00	0.77	63
	Forest3.20 + Paved_road_dist3.20 + TRI1.50 + Sage3.20	5	1,068.58	2.70	0.21	
Patch	Agr_dist0.56 + Forest_dist0.56 + Paved_road_dist0.56 + TRI0.56 + Sage0.56	5	1,127.14	0.00	0.90	31

[a] Agr, agriculture including irrigated and non-irrigated lands; Sage, sagebrush cover; TRI, Terrain Ruggedness Index.

Table 16. Model-averaged beta coefficients and associated standard errors for variables included in the top 90% model set for Wyoming greater sage-grouse winter season. Results are presented for each region and both patch and landscape scales. Data included in the winter modeling effort were collected from 2001 to 2010. The metric column presents the metric used to represent the variable estimated and summarized for each window size. Extent presents the radii (km) and decays of the various window sizes for patch and landscape scales. Note that a positive association with distance decays suggested selection for proximity to a habitat feature as values were 1 at a feature of interest, and decay farther from the feature. Also presented are the estimated odds ratios and associated confidence intervals.

Category	Metric	Extent	β_i	SE	Odds ratio	Lower CI	Upper CI
Statewide							
Landscape							
Agriculture	Decay	3.20	−1.00	0.12	0.37	0.29	0.46
Forest	Decay	1.50	−1.82	0.15	0.16	0.12	0.22
Paved roads	Decay	1.50	−3.60	0.32	0.03	0.01	0.05
Ruggedness	Mean value	1.50	-0.84×10^{-2}	0.07×10^{-2}	0.43×10^{-2}	0.38×10^{-2}	0.50×10^{-2}
Sagebrush	Mean cover	6.44	0.01	0.00	1.02	1.01	1.02
Sagebrush	SD mean cover	6.44	0.01	0.01	1.01	0.99	1.04
Wells	Density	6.44	-0.23×10^{-6}	0.05×10^{-6}	0.80×10^{-6}	0.73×10^{-6}	0.87×10^{-6}
Patch							
Agriculture	Decay	0.56	−1.95	0.21	0.14	0.09	0.21
Forest	Decay	0.56	−2.92	0.25	0.05	0.03	0.09
Paved roads	Decay	0.56	−7.53	0.99	0.00	0.00	0.00
Ruggedness	Mean value	0.56	-0.73×10^{-2}	0.08×10^{-2}	0.48×10^{-2}	0.41×10^{-2}	0.56×10^{-2}
Sagebrush	Mean cover	0.56	0.10	0.01	1.11	1.08	1.14
Wells	Density	0.56	-0.95×10^{-5}	0.27×10^{-5}	0.39×10^{-5}	0.23×10^{-5}	0.65×10^{-5}
Shrub height	Mean height	0.56	−0.05	0.01	0.95	0.94	0.96
Southwest							
Landscape							
Forest	Decay	1.50	−2.17	0.22	0.11	0.07	0.18
Paved roads	Decay	1.50	−3.04	0.37	0.05	0.02	0.10
Ruggedness	Mean value	1.50	-0.64×10^{-2}	0.13×10^{-2}	0.53×10^{-2}	0.41×10^{-2}	0.67×10^{-2}
Sagebrush	Mean cover	6.44	0.01	0.02	1.01	0.98	1.05
Sagebrush	SD mean cover	6.44	0.04	0.04	1.04	0.96	1.12
Wells	Density	1.50	-0.27×10^{-6}	0.07×10^{-6}	0.77×10^{-6}	0.67×10^{-6}	0.87×10^{-6}
Patch							
Forest	Decay	0.56	−3.17	0.34	0.04	0.02	0.08
Paved roads	Decay	0.56	−7.07	1.05	0.00	0.00	0.01
Ruggedness	Mean value	0.56	-0.81×10^{-2}	0.13×10^{-2}	0.44×10^{-2}	0.34×10^{-2}	0.57×10^{-2}
Wells	Density	0.56	-0.13×10^{-6}	0.04×10^{-6}	0.88×10^{-6}	0.81×10^{-6}	0.95×10^{-6}
Central							
Landscape							
Ruggedness	Mean value	1.50	-0.24×10^{-3}	0.04×10^{-3}	0.79×10^{-3}	0.85×10^{-3}	0.73×10^{-3}
Sagebrush	Mean cover	6.44	0.05	0.01	1.05	1.02	1.08
Sagebrush	SD cover	6.44	-0.29×10^{2}	0.08×10^{2}	1.34×10^{2}	1.14×10^{2}	1.57×10^{2}
Shrub height	Mean height	6.44	−0.01	0.02	0.99	0.95	1.04
Shrub height	SD height	6.44	−0.25	0.07	0.78	0.68	0.89
Patch							
Ruggedness	Mean value	0.56	-0.34×10^{-3}	0.04×10^{-3}	0.71×10^{-3}	0.66×10^{-3}	0.77×10^{-3}
Sagebrush	Mean cover	0.56	0.08	0.02	1.08	1.03	1.14
Northeast							
Landscape							
Agriculture	Mean cover	6.44	−4.63	1.57	0.01	0.00	0.21
Forest	Mean cover	3.20	-0.17×10^{-2}	0.05×10^{-2}	0.84×10^{-2}	0.77×10^{-2}	0.92×10^{-2}
Paved roads	Decay	3.20	−3.06	0.44	0.05	0.02	0.11
Ruggedness	Mean value	1.50	-0.61×10^{-2}	0.12×10^{-2}	0.54×10^{-2}	0.43×10^{-2}	0.69×10^{-2}
Sagebrush	Mean cover	3.20	0.26	0.04	1.29	1.19	1.41
Patch							
Agriculture	Decay	0.56	−1.93	0.41	0.15	0.06	0.32
Forest	Decay	0.56	−1.36	0.42	0.26	0.11	0.59
Paved roads	Decay	0.56	-0.10×10^{-2}	0.03×10^{-2}	0.90×10^{-2}	0.85×10^{-2}	0.95×10^{-2}
Ruggedness	Mean value	0.56	-0.68×10^{-2}	0.12×10^{-2}	0.51×10^{-2}	0.40×10^{-2}	0.65×10^{-2}
Sagebrush	Mean cover	0.56	0.19	0.03	1.21	1.13	1.30

specific years or snow cover (e.g., severe winters; Dzialak et al. 2013) or to predict winter habitat more generally, even if those areas are not used every year.

MANAGEMENT IMPLICATIONS

Our models identified important habitats across the entire sage-grouse distribution in Wyoming. Data resolution and planning-unit resolution are often considered separate issues. For example, coarse-resolution data can be used to prioritize small planning units, but the results may not accurately convey habitat distribution within small land units. Conversely, fine-resolution data can be aggregated into large planning units, but the outcome of prioritization will likely be the same as if coarse-resolution data were used (Arponen et al. 2012). We worked in close collaboration with our management partners to ensure the resolution of our data and models corresponded with the resolution of the planning units.

Table 17. Summary of variables included in top models for Wyoming greater sage-grouse winter models and their influence on the probability of selection, 2001–2010. Results are presented for each region and both patch and landscape (land) scales. A plus symbol indicates a positive association and a minus symbol indicates a negative association. Lack of a symbol means the covariate did not enter the top model.

	State		Southwest		Central		Northeast	
Category	**Patch**	**Land**	**Patch**	**Land**	**Patch**	**Land**	**Patch**	**Land**
Sagebrush	+	+		+	+	+	+	+
Paved roads	–	–	–	–			–	–
Agriculture	–	–					–	–
Forest	–	–	–	–			–	–
Wells	–	–	–	–				
Ruggedness	–	–	–	–	–	–	–	–
Shrub height	–					–		

One significant goal of our research was to provide planning tools for managing seasonal sage-grouse habitat and resources at scales similar to those developed for identifying sage-grouse core regions (e.g., planning units) in Wyoming. However, the collection of models presented here represents a significant advancement in terms of both spatial and temporal resolution. We have included explicit consideration of many habitat components and requirements throughout the annual life-cycle, and illustrated the ability to apply these models to novel spatial extents with measured success. These models will be useful in understanding the habitat requirements of sage-grouse in Wyoming at the level of the home range of an individual, the population level, and within and across management zones.

A quantitative assessment of how our seasonal models could revise the current core regions recognized in Wyoming (State of Wyoming 2011) is beyond the scope of this research. However, we suggest the core regions could be assessed on a case-by-case basis in light of our seasonal predictions. Our models can refine sage-grouse core areas and better inform habitat prioritization and management actions (Aldridge and Boyce 2008) for sage-grouse in Wyoming. Our models rely on the sagebrush GIS layers developed by Homer et al. (2012). If these spatial data are generated for other regions within the sage-grouse range,

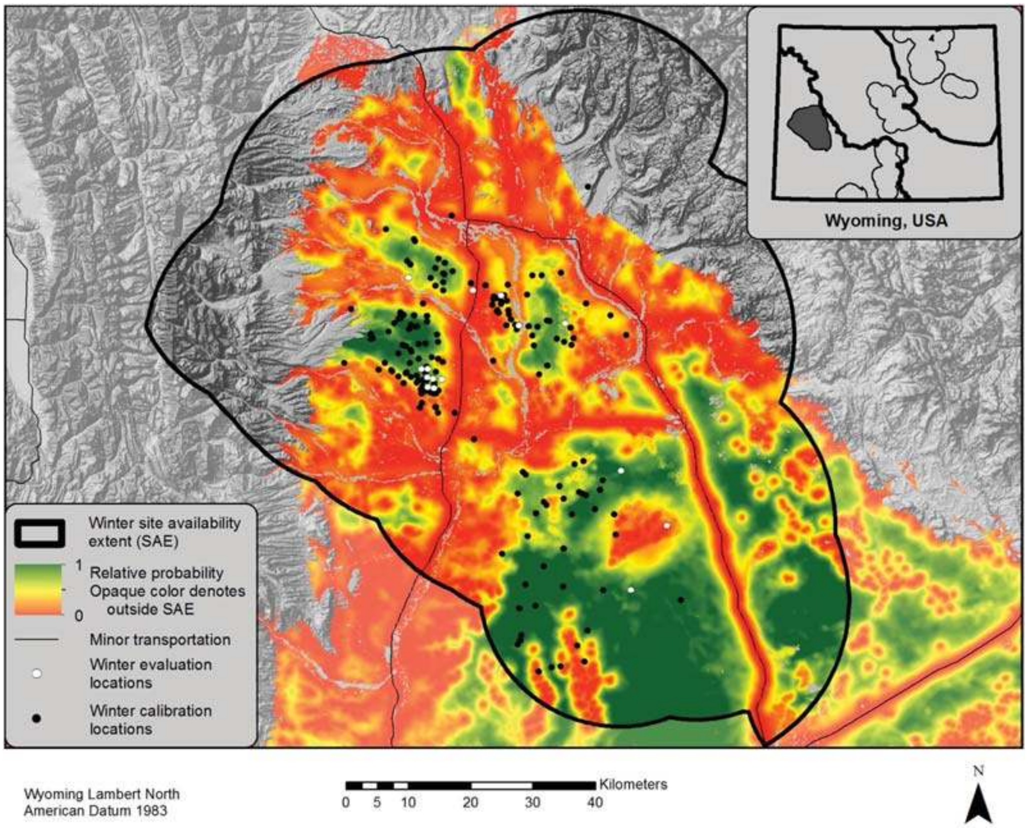

Figure 14. Statewide winter greater sage-grouse model applied to Wyoming, USA, and represented as a continuous surface. The map is zoomed into the Pinedale study-site-availability extent (SAE) to provide an example of statewide model performance within study site SAEs. The colors range from red to green to represent the range of probability values from 0 (low relative probability of selection) to 1 (high relative probability of selection). The black circles represent winter locations used for model calibration and the white circles represent winter locations used for model evaluation, 2006–2008. The Pinedale study site boundary is indicated by the thick black line. Areas of gray hill shade represent the areas masked out in the model predicted surfaces. Areas outside of the study sites are novel areas and slightly grayed to indicate the inherent lower confidence in model predictions in these areas.

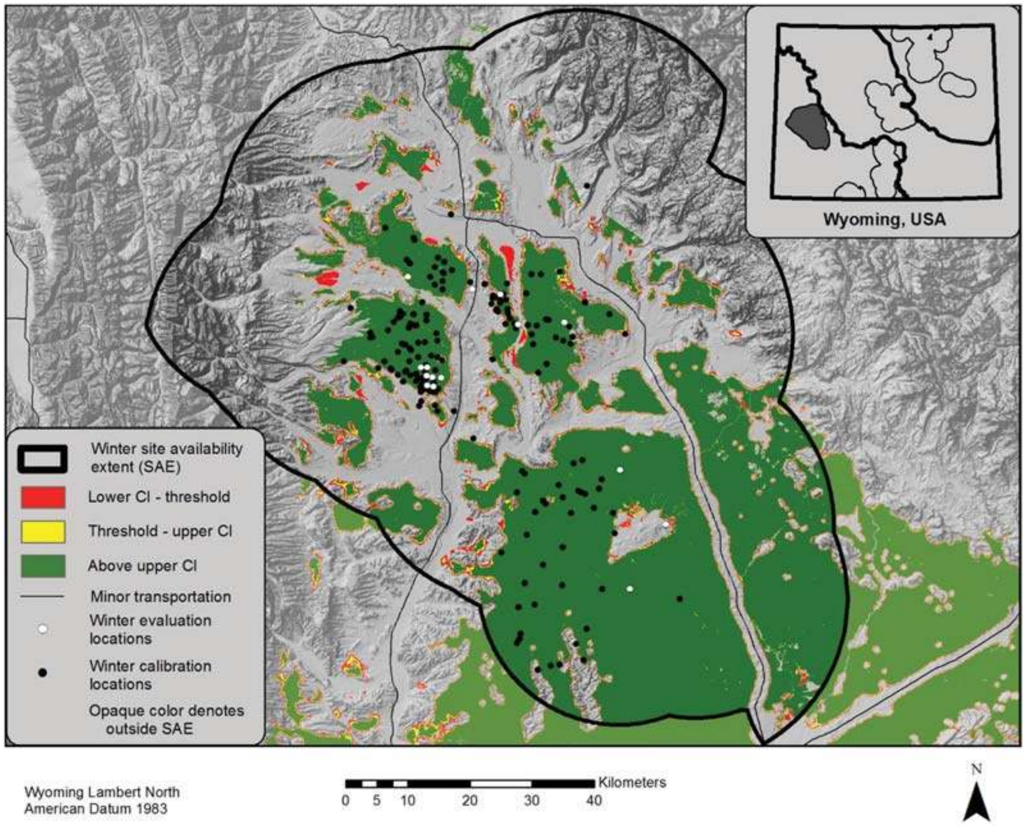

Figure 15. Important winter habitat for greater sage-grouse in Wyoming, USA. The map is zoomed into the Pinedale study-site-availability extent (SAE) to provide an example of southwest regional model performance within study site SAEs. The habitat categories 1 through 3 are coded by green (category 1, above the upper confidence interval), yellow (category 2, between the maximum value and the upper confidence interval), and red (category 3, between the maximum value and the lower confidence interval). Habitats with values below the chosen threshold are represented as gray hill shade. Study site boundaries are indicated by thick black lines. The black circles represent winter locations used for model calibration and the white circles represent winter locations used for model evaluation, 2006–2008. We did not make predictions outside of the greater sage-grouse distribution in Wyoming. Areas outside of the study sites are novel areas and slightly grayed to indicate the inherent lower confidence in model predictions in these areas.

managers could apply our models to those areas. Model performance outside of Wyoming could be assessed using existing telemetry data or lek locations, in the case of the nesting models. Our modeling efforts have included many additional landscape features known to influence sage-grouse habitat use such as anthropogenic influences, and allow the assessment of multiple seasons, as suggested in the original work that formed the basis for the core regions concept (Doherty et al. 2011, Kiesecker et al. 2011).

Inherent in land-use management is the inclusion or exclusion of areas as conservation priorities. In many cases, complex approaches and statistical predictions are summarized as lines on a map. From a species perspective, boundaries are most relevant when grounded in the biology of the species and supported in transparent, empirically driven models fitted to species data. Providing model predictions on continuous mapped surfaces provides flexibility for stakeholders to adjust habitat perimeters with ancillary data. We presented 1 method of thresholding continuous predictive surfaces of sage-grouse nesting, brood rearing, and wintering areas. The approach was biologically meaningful and identified important priority habitats for sage-grouse in each season. These thresholds could be adjusted to include other metrics, such as the percent of sage-grouse seasonal populations contained, land management regulations, or policy. The underlying statistically supported biological relationships and resulting continuous predicted surfaces we developed would not change under this type of boundary modification scenario (i.e., thresholding). The criteria for grouping predictions into classes and determining boundaries for important habitat would simply be revised to include additional information and priorities. Interaction between stakeholders, local managers, and researchers is critical to informing such decisions.

One strength to our approach of identifying important habitats was the use of species and habitat data in a transparent and biologically sound application across a wide variety of landscapes to support management decisions. We believe the thresholding process will be strengthened if conducted in conjunction with field managers who have knowledge of local site conditions that were not represented in a GIS. The inclusion or exclusion of land can have major implications for stakeholders; therefore, stakeholders should agree to a process of delineating important habitats before final maps are seen to encourage a non-arbitrary habitat delineation process.

Landscape-scale models are powerful tools that can help decision makers better understand and quantify the ramifications of including or excluding habitat for conservation. Careful explanation of modeling and thresholding processes is necessary to ensure the strength of the approaches is conveyed and

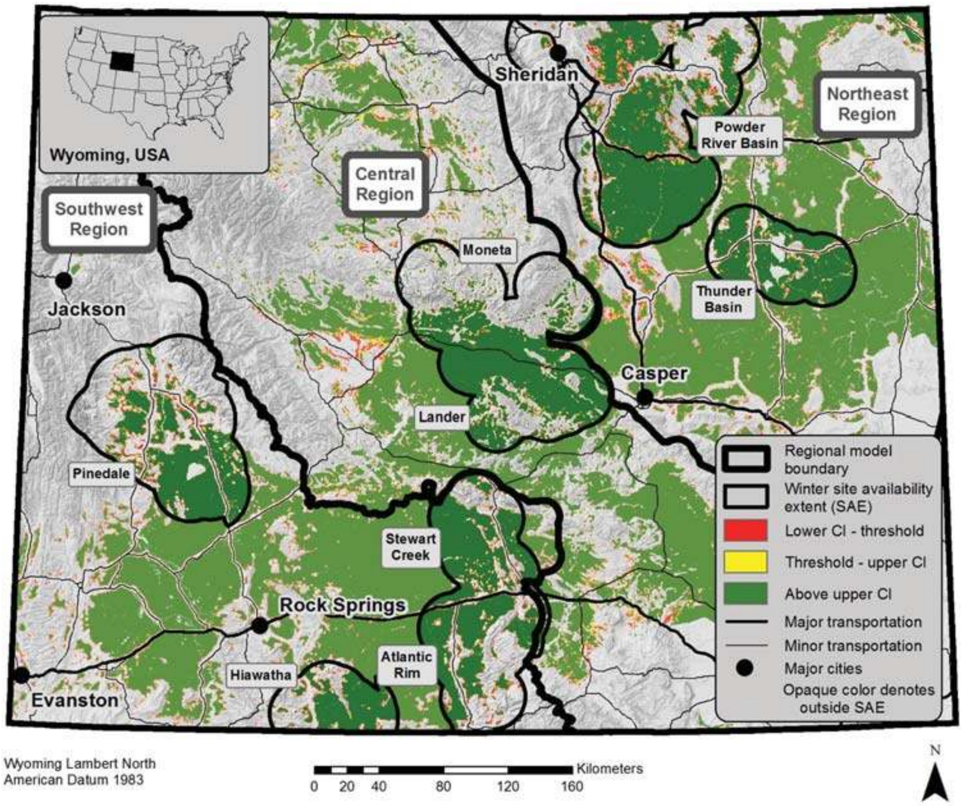

Figure 16. Important winter habitat for greater sage-grouse in Wyoming. The map represents the 3 regional winter models stitched together across the state. The habitat categories 1 through 3 are coded by green (category 1, above the upper confidence interval), yellow (category 2, between the maximum value and the upper confidence interval), and red (category 3, between the maximum value and the lower confidence interval). Habitats with values below the chosen threshold are represented as gray hill shade. The map is a composite of each of the 3 regional winter models (e.g., the southwest top, model-averaged, landscape × patch model was applied to the southwest region). Regional and study site boundaries are indicated by the black lines and included winter location data from 2001 to 2010. We did not make predictions outside of the greater sage-grouse distribution in Wyoming. Areas outside of the study sites are novel areas and thus we have inherently lower confidence in model predictions in these areas. Regional boundaries are indicated by the thick black lines and were delineated based primarily on hydrologic units and sage-grouse management zones.

contextualized for local managers, who are often concerned with habitat quality at the local scale. One of the primary goals for our models was to define areas that have high importance for the seasonal needs of sage-grouse, thus giving managers a tool to help focus efforts aimed at minimizing disturbance. In our experience, careful explanation of what models are—and are not—intended for may alleviate miscommunications among those that develop models, stakeholder groups that use them to guide policy decisions, and resource managers on the ground who are tasked with making decisions at pasture scales.

Differences in the scales at which people are thinking about problems also can cause miscommunication between field and regional managers. This issue is extremely important, because models can work well across an ecoregion or a state, such as our models did, but predictions can be inaccurate at the local level. This uncoupling is critical because it may affect the credibility of the larger process, especially for non-technical stakeholders. When modeling at extents as large as the state of Wyoming, inevitably the GIS habitat layers will not accurately represent actual conditions in some localized areas because of GIS-based habitat misclassification in portions of the base data within localized areas. These misclassifications can be a result of inaccurate GIS data inputs or localized differences that are not captured within study areas used for training the models (i.e., relative habitat quality differences). Consequently, anticipation of localized habitat inaccuracies and agreement upon a systematic approach to correct prediction errors before defining conservation thresholds through a stakeholder process can minimize conflicts resulting from different needs. Careful consideration of landscape planning objectives should result in clear articulation of spatial and temporal scales relevant to conservation and management and models should not be expected to perform at scales for which the data are not relevant.

Data-driven planning tools can facilitate landscape conservation planning and provide transparency and credibility to land management decisions that are generally made by a few individuals but implicitly affect many individuals. Prioritization of landscape for conservation treatments, land-use policy, resource extraction, and other uses is an inherently political process that involves various stakeholder groups with diverse priorities. The generation of seamless maps that inform the value of specific areas for sage-grouse seasonal habitat selection is an important step toward generating a conservation plan for sage-grouse. The next critical step is working with managers and explaining models so that discussions center on strengths, weaknesses, and potential uses of models to ground their decisions. Land-management decisions with high potential for conflict are best supported and informed by processes that are

Table 18. Evaluation and discrimination results for all models used to characterize sage-grouse winter habitat use in Wyoming, 2001–2010. We chose all model resource selection function (RSF) thresholds by selecting the RSF value associated with the maximum contrast validation index (CVI). Data are presented for each region and scale, and for the combined landscape × patch (L × P) models. Choice of the threshold resulted in the identification of important habitats. Data presented summarize the percent of all locations that fell within the identified important habitats, from the evaluation dataset. Also presented are values that represent the percent of landscape implicated by RSF values above the chosen threshold (i.e., designated as important). The CVI represents the difference between the percent of locations captured and the percent of landscape implicated. Higher CVI values represent greater discriminatory capabilities.

Region	Scale	Locations captured (%)	Landscape implicated (%)	Contrast validation index
Statewide	Landscape	88	52	36
Southwest	Landscape	94	60	34
Central	Landscape	96	48	48
Northeast	Landscape	100	62	38
Statewide	Patch	94	55	39
Southwest	Patch	97	62	35
Central	Patch	97	57	40
Northeast	Patch	95	62	33
Statewide	L × P	91	52	39
Southwest	L × P	97	59	38
Central	L × P	96	54	42
Northeast	L × P	97	62	35
Average		93	50	43

transparent, data driven, and scientifically credible. We hope this type of collaboration between independent researchers and stakeholders will continue for large conservation challenges in the future.

SUMMARY

- We developed habitat selection models to map priority habitats for sage-grouse across Wyoming at 2 scales (patch and landscape), 4 extents (statewide, southwest, central, northeast), and 3 seasons (nesting, summer, winter).
- Strength of selection for sagebrush varied regionally, with stronger selection in the northeast region, likely because of more limited availability. Sage-grouse avoidance of areas with high road density was fairly consistent across regions.
- Sage-grouse consistently preferred areas with greater sagebrush cover and avoided paved roads, agriculture, and forested areas across seasons and regions. In the summer, birds consistently preferred areas with higher precipitation across regions. Likewise in the winter, birds consistently avoided rugged terrain across regions.
- Statewide models seemed to perform as well as regional models both within study sites and in novel areas.
- Sage-grouse selection was consistent across seasons and regions for certain key habitat components. However, model structure and some habitat components (e.g., terrain ruggedness) varied across seasons, highlighting the importance of seasonal variation in life-history requirements on model development.
- The use of independent location data resulted in the selection of the most predictive models for application in novel areas. In the absence of such location data, we recommend determination of the most appropriate model using lek locations as a proxy for nesting habitat. For summer and winter seasons with no location data, the best approach is likely to apply the regional or statewide models with habitat distributions similar to the new area of interest.
- We compiled high-quality GIS data that covered the sage-grouse distribution in Wyoming and allowed for the development of accurate habitat selection models. We were unable to include certain data layers biologically relevant to sage-grouse because of inaccuracies in those layers (e.g., urban and hydrologic GIS data).
- The apparent low discriminatory capabilities of the winter models in novel areas demonstrated the need to develop new habitat thresholds on a case-by-case basis or more localized studies to provide better-quality local management tools in some cases.
- Emphasis on local studies and collaboration among studies with regional interests is imperative to developing tools for landscape-scale habitat prioritization for sage-grouse.

Table 19. Estimates of percent deviance explained for each season and regional model for greater sage-grouse in Wyoming (1994–2010). Percent deviance is presented for the pure patch, pure landscape (land), and shared components of the full model.

		% Deviance		
Season	Region	Patch	Land	Shared
Nest	State	4	4	92
	Southwest	4	15	81
	Central	11	28	61
	Northeast	8	14	78
Summer	State	10	20	70
	Southwest	8	25	67
	Central	21	27	52
	Northeast	7	27	66
Winter	State	9	7	84
	Southwest	2	24	74
	Central	19	26	55
	Northeast	7	17	76

ACKNOWLEDGMENTS

Synthesis: We are grateful to E. Hellgren, J. Connelly, and S. Knick whose many useful comments improved the manuscript. Funding for the synthesis of these studies and the conceptual development of these models and analyses was provided by Arch Coal, Cameco Resources, Devon Energy, Foundation Coal West, Pathfinder Energy, Petroleum Association of Wyoming, Powder River Coal, RioTinto, Rocky Mountain Power, Wyoming Sage Grouse Local Working Groups, Wyoming Game and Fish Department (WGFD), Bureau of Land Management (BLM), U.S. Fish and Wildlife Service (USFWS), and the U.S. Geological Survey. We appreciated the cooperation of numerous landowners in each study area who provided access to their private lands to collect field data. We also thank the many individuals who provided logistical and field support on the individual projects listed below. The manuscript was improved through comments by T. Christiansen, the Petroleum Association of Wyoming, Peabody Energy, and R. Taylor. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the USFWS. *Atlantic Rim and Stewart Creek*: Funding was provided by Anadarko Petroleum Corporation, U.S. Department of the Interior BLM, WGFD–Sage-Grouse Conservation Fund, and the University of Wyoming School of Energy Resources. *Hiawatha*: Funding was provided by the Colorado Division of Wildlife (now Colorado Division of Parks and Wildlife) and Questar Exploration and Production. *Hulett*: Funding for this study was provided by Federal Aid in Wildlife Restoration Act (W 67 R) through North Dakota Game and Fish Department, BLM (ESA000013), USFS Rocky Mountain Research Station (05 JV 11221609 127), USFS Dakota Prairie National Grasslands (05 CS 11011800 022), and support from South Dakota State University. *Jackson*: Funding was provided by the WGFD (Upper Snake River Sage-Grouse Working Group), the Jackson Hole Airport, Grand Teton National Park, USFS, and a variety of private individuals and foundations. *Lander and Pinedale*: Financial support provided by the WGFD, BLM, U.S. Department of Energy, Yellowstone-to-Yukon Initiative, EnCana Oil & Gas, Inc., Ultra Resources, Inc., and Shell Rocky Mountain Production. *Moneta*: The Moneta study area was a combination of data collected from 2 separately funded projects: Hayden-Wing Associates and a project funded by BLM and WGFD and referred to as the Western Natrona County Sage-Grouse Distribution Project. The Hayden-Wing Associates study was funded by ConocoPhillips, EnCana Natural Gas, and Noble Energy. Financial support, equipment, and trapping personnel for the Western Natrona County Sage-Grouse Distribution Project were provided by the BLM, WGFD, Bates Hole and Shirley Basin Sage-Grouse Working Group, University of Wyoming, and Casper College. Telemetry flights were conducted by Laird Flying Service, Ekalaka MT. *PRB*: Funding was provided by the BLM in Montana and Wyoming. Additional project support came from the BLM in Washington, D.C., U.S. Department of Energy, Montana Fish, Wildlife and Parks, WGFD, National Fish and Wildlife Foundation, National Science Foundation (EPS–CORE program), Montana Cooperative Fish and Wildlife Research Unit, Petroleum Association of Wyoming, Western Gas Resources Incorporated, Wolf Creek Charitable Foundation, Bighorn Environmental Consulting, Anheuser-Busch Companies, Inc., Liz Claiborne and Art Ortenberg Foundation, the Hewlett Foundation, and the University of Montana. The Hayden-Wing and Associates study was funded by Fidelity Exploration and Production Company. *Simpson Ridge*: Funding for this project was received from Horizon Wind Energy, Iberdrola Renewables, the Bates Hole and Shirley Basin Local Sage-Grouse Working Group, the U.S. Department of Energy, and the University of Wyoming School of Energy Resources. *Thunder Basin*: Initial work (2001–2003) was supported primarily by Peabody Energy Company's North Antelope Rochelle Mine (NARM) and the Abandoned Coal Mine Lands Research Program (ACMLRP) at the University of Wyoming. The ACMLRP support was administered by the Wyoming Department of Environmental Quality from funds returned to Wyoming by the Office of Surface Mining of the U.S. Department of the Interior. The Triton Coal Company and Thunder Basin Coal Company also provided financial assistance for the initial project work, and the WGFD provided valuable field assistance, equipment, digital land-cover data, and funding for aerial telemetry for project needs from 2001 to 2003. Beginning in 2004, NARM provided all project funding. All data for this study area were collected and contributed by Thunderbird Wildlife Consulting, Inc. *Bighorn Basin*: Funding for this project was received from the American Colloid Company.

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