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Range-Wide Network of Priority Areas for Greater Sage-Grouse—A Design for Conserving Connected Distributions or Isolating Individual Zoos?

Open-File Report 2015–1158

U.S. Department of the Interior
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Conversion Factors

International System of Units to Inch/Pound

Multiply	By	To obtain
	Length	
kilometer (km)	0.6214	mile (mi)
	Area	
hectare (ha)	2.471	acre
square hectometer (hm^2)	2.471	acre
square kilometer (km^2)	247.1	acre
square kilometer (km^2)	0.3861	square mile (mi^2)

Vertical coordinate information is referenced to the North American Vertical Datum of 1988 (NAVD 88).

Horizontal coordinate information is referenced to the North American Datum of 1983 (NAD 83).

Elevation, as used in this report, refers to distance above the vertical datum.

Range-Wide Network of Priority Areas for Greater Sage-Grouse—A Design for Conserving Connected Distributions or Isolating Individual Zoos?

By Michele R. Crist, Steven T. Knick, and Steven E. Hanser

Abstract

The network of areas delineated in 11 Western States for prioritizing management of greater sage-grouse (*Centrocercus urophasianus*) represents a grand experiment in conservation biology and reserve design. We used centrality metrics from social network theory to gain insights into how this priority area network might function. The network was highly centralized. Twenty of 188 priority areas accounted for 80 percent of the total centrality scores. These priority areas, characterized by large size and a central location in the range-wide distribution, are strongholds for greater sage-grouse populations and also might function as sources. Mid-ranking priority areas may serve as stepping stones because of their location between large central and smaller peripheral priority areas. The current network design and conservation strategy has risks. The contribution of almost one-half (n = 93) of the priority areas combined for less than 1 percent of the cumulative centrality scores for the network. These priority areas individually are likely too small to support viable sage-grouse populations within their boundary. Without habitat corridors to connect small priority areas either to larger priority areas or as a clustered group within the network, their isolation could lead to loss of sage-grouse within these regions of the network.

Introduction

Greater sage-grouse (*Centrocercus urophasianus*; hereinafter, sage-grouse) is an endemic Galliform to arid and semiarid sagebrush (*Artemisia* spp.) landscapes of Western North America (Schroeder and others, 1999). Sage-grouse currently occupy approximately one-half of their presettlement habitat distribution and have recently received much attention for their long-term population declines (Schroeder and others, 2004; Garton and others, 2011). The U.S. Fish and Wildlife Service listed sage-grouse as a candidate species under the Endangered Species Act in 2010 concluding that protection was warranted although immediate conservation actions were precluded due to other higher priority species (U.S. Fish and Wildlife Service, 2010). Broad-scale habitat loss and fragmentation from synergistic cycles of wildfire and conversion to invasive plant communities as well as from human land use is the primary cause of population declines (Knick and Connelly, 2011). The most pressing challenge to long-term sage-grouse persistence is conservation of remaining large and intact sagebrush landscapes (Stiver and others, 2006).

The U.S. Fish and Wildlife Service, faced with legal challenges for delaying full protection under the Endangered Species Act, is currently reviewing the bird's status and is scheduled to issue an updated listing decision in September 2015. In an effort to avoid listing, the 11 Western States and Federal management agencies within the sage-grouse range have developed conservation plans embracing the concept of core or priority areas (Priority Areas for Conservation, PACs [U.S. Fish and Wildlife Service, 2013], or equivalent terms designated in individual State agency plans)—allowable spatial area of disturbance due to human land use, such as energy development, is tightly regulated and conservation actions are focused in areas with the highest number of sage-grouse and potentially the greatest benefit to the species. Land use is allowed to continue outside of priority areas under normal regulations.

The delineation of an entire species range spanning more than 2 million km^2 (excluding the Canadian portion) into a binary division of priority and nonpriority areas may represent one of the largest experiments in conservation reserve design for a single species. Individual priority areas range in size from less than 1 to more than 83,000 km^2 and encompass the broad spectrum of reserve design paradigms from single large to several small reserves. Although we do not know the minimum area required, the largest priority areas likely can support viable sage-grouse populations completely within their boundaries. However, the smallest priority areas clearly enclose much less than the annual range of a sage-grouse (4–615 km^2; Connelly and others, 2011). Much scientific literature addressing conservation reserve design has stressed the importance of the inclusion and protection of habitat connectivity between conservation reserves to ensure individual movements, opportunity to shift habitats when needed, and facilitate genetic exchange (Crooks and Sanjayan, 2006). Therefore, numerous connected priority areas also may be necessary to provide seasonal habitats that can be separated by up to 160 km (Connelly and others, 2011; Smith, 2013). The two primary factors that influence populations, area and isolation (MacArthur and Wilson, 1967; Hanski and Gilpin, 1991; Hanski, 1999), are important metrics in understanding the efficacy of this conservation approach.

We used social network theory and centrality metrics (Moreno, 1932, 1934; Freeman, 1979, 2004) to quantify and understand the potential for the delineated priority areas to function as a connected network to conserve sage-grouse populations. Our objectives were to:

1. Identify high-ranking priority areas within the network based on their location and number of connections to other priority areas,
2. Estimate the ability of other lower ranking priority areas within the network to function as stepping stones for maintaining connectivity among clusters of priority areas, and
3. Model relative isolation among priority areas based on movement potential in their surrounding environment.

Description of Study Area

We included 2,030,230 km^2 of the Western United States in our analysis of designated priority areas across the current sage-grouse range (Schroeder and others, 2004). The sage-grouse range is divided into seven management zones based on similar floristic and environmental characteristics (Stiver and others, 2006). The area contains a diversity of shrubland types of which landscapes dominated by sagebrush are the most important to sage-grouse. Mountain ranges, forest communities, and agricultural regions, particularly in broad plains of large river systems, are not used by sage-grouse and can act as barriers to their movements (Fedy and others, 2014). Lands used by sage-grouse are of mixed ownership (Knick, 2011). Public lands are dominant in the Western States and are managed primarily by the Bureau of Land Management and U.S. Forest Service for multiple uses. Private lands, characteristically those fertile lands with deep soils and access to water, constitute the greatest proportion of ownership in the northern and eastern parts of the sage-grouse range and can comprise more than two-thirds of the landscape used by sage-grouse (Doherty and others, 2010; Knick, 2011).

Each State used different criteria for delineating boundaries of priority areas but each generally incorporated metrics for sage-grouse populations (lek locations and breeding bird densities [Doherty and others, 2010]) and habitat areas (identified from known sage-grouse distributions or seasonal habitats for breeding, nesting, brood-rearing, or wintering areas derived from observations or telemetry data). In some cases, States also adjusted boundaries to exclude private lands, Federal lands approved for or in the process of being developed for energy and other management activities, and pre-existing development. The current range-wide management strategy, if not the ecological reality, is that each priority area bounds a homogeneous patch and that all priority areas are of equal importance.

We created a range-wide map of priority areas by combining the spatial boundaries of priority areas as delineated by the 11 States in Western North America (fig. 1, appendix A). Boundaries of polygons were merged between States when shared but followed State lines when adjoining priority areas did not match across borders. We also merged or removed priority areas less than 1 km^2 that typically were slivers left after the State's original delineations and subsequent edits. The final map contained 188 priority areas ranging in size from approximately 1.1 to 83,000 km^2 (appendix B). Mean size was approximately 16,600 km^2. The frequency distribution consisted predominantly of smaller priority areas; 50 percent of the priority areas were less than 125 km^2 and 90 percent were less than 3,300 km^2. Total area included within priority areas was approximately 310,000 km^2 and included 15 percent of our study area.

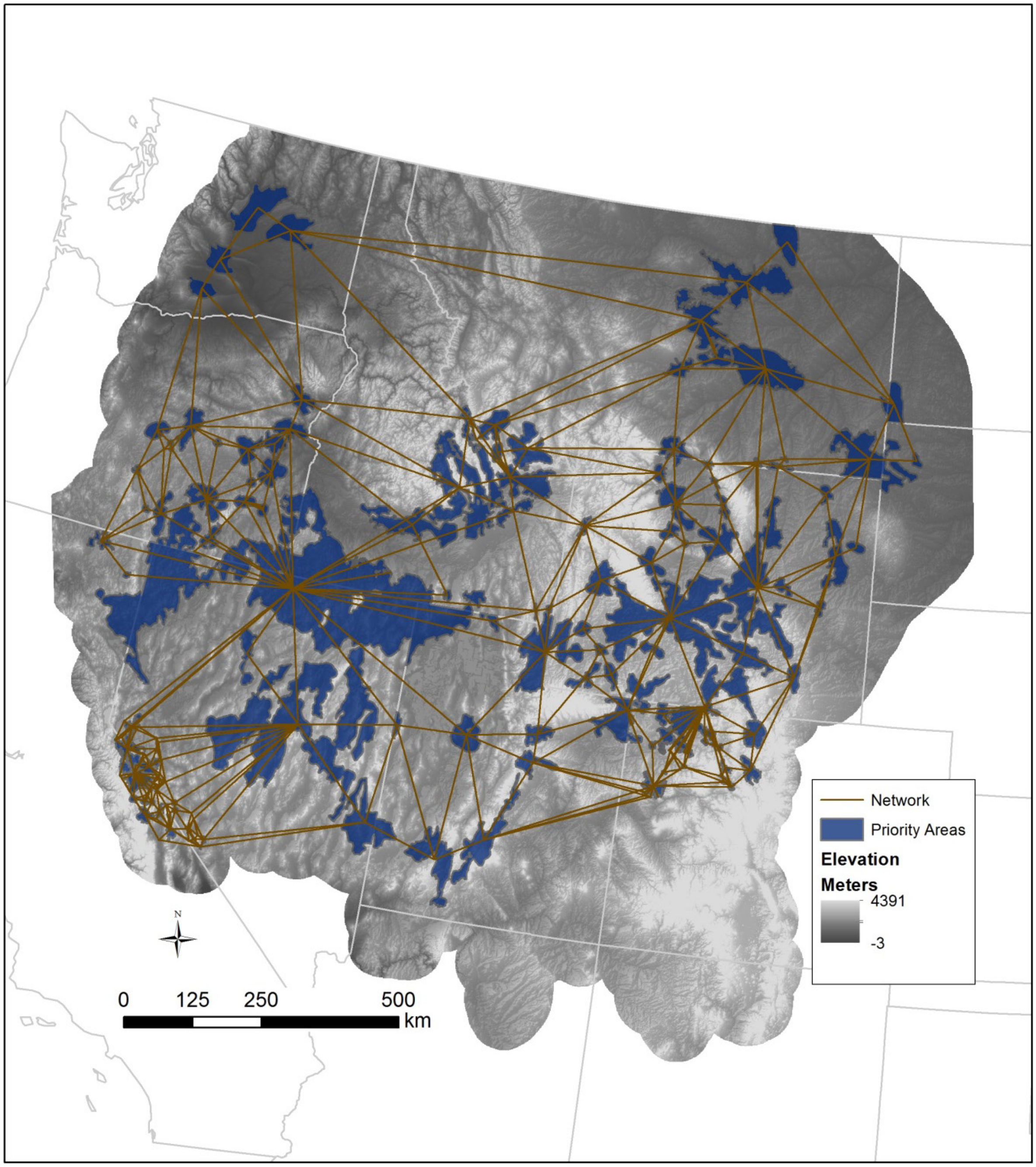

Figure 1. Study area and designated priority areas across the sage-grouse range in Western North America represented as a network of nodes and links. Background map is from U.S. Geological Survey National Elevation Data (NED; 2011; http://seamless.usgs.gov).

Methods

Priority Areas as a Spatial Network

We described the spatial network of priority areas as a graph structured by nodes and connecting links (Diestel, 2005). To identify adjacencies, we delineated individual polygons around each priority area by creating Thiessen polygons where boundaries encompassed grid cells closest to each priority area relative to all other priority areas. Shared boundaries between Thiessen polygons identified neighboring priority areas. We then added links between each priority area and its neighbor’s centroid. Thus, the network of conservation reserves currently designed for the sage-grouse range was represented by nodes and links across all priority areas (fig. 1).

We used analyses derived from social network theory (Wasserman and Faust, 2004) to identify priority areas that were highly important for connectivity within the range-wide network. Social network theory combines graph theory and centrality indices to characterize network structures by mapping and measuring relationships and flows (links) between people, groups, organizations, computers, and other entities (nodes) (Freeman, 2004; Wasserman and Faust, 2004; Diestel, 2005; Newman, 2010). Quantifying network centrality provides insight into the overall structure, connection, and function of a network, and is considered to be the fundamental characteristic describing a node’s position in a network. Relative importance in social networks is measured by centrality metrics that emphasize number of connections to indicate relative position within the network. Networks can range from highly centralized, dominated by a few highly connected nodes, to more widely dispersed configurations in which connections are equally shared among all nodes.

We used two centrality metrics, degree and betweenness, to assess the relative importance of individual priority areas based on their position and number of connections within the overall range-wide network (Freeman, 1977, 2004; Wasserman and Faust, 2004; Newman, 2010). Relative importance estimated by degree centrality is based simply on number of connections to other nodes in the network; more connections indicate greater influence and a more central position in the network (Erdos and Gallai, 1960; Diestel, 2005). However, a priority area also might be important because its relative position connects clusters or groups of priority areas located in close proximity. Betweenness centrality quantifies the number of times a node acts as a bridge along the shortest path between two other nodes, thus indicating its importance in maintaining the network (Freeman, 1977; Freeman and others, 1991; Estrada, 2007; Brandes, 2008; González-Pereira and others, 2010). Nodes with high scores of betweenness centrality represent the primary foundation of the network’s structure because a disproportionately high number of the shortest pathways go through them. These nodes funnel movement not only from adjacent nodes but also from nodes that could be located far away in the landscape (Bodin and Norberg, 2007).

Movement Potential among Priority Areas

Connections in ecological networks are not without dimensions (as in social networks) but rather have a distance and environmental cost to move between nodes (Bunn and others, 2000; McRae and others, 2008; Carroll and others, 2012; LaPointe and others, 2013). To assess the relative importance of priority areas, we needed to combine number of connections with the ability to traverse the interstitial landscape matrix.

We calibrated movement potential by sage-grouse through the landscape by mapping a model of ecological minimum requirements (Knick and others, 2013). Sage-grouse may perceive a landscape quite differently when moving within a range, moving between seasonal ranges, or when dispersing. Similarly, connectivity for individual movements obtained from telemetry data might be different than connectivity derived from genetic information. For our study, we made the basic assumption that movement would be more likely in suitable environments that could be modeled across the entire range.

An ecological minimum, in concept, represents a multivariate construct of the basic requirements for a species. The model was developed from 23 variables describing land cover, fire history (area burned from 1980 to 2013), terrain (topographic accessibility [Sappington and others, 2007]), climate, edaphic, and anthropogenic features measured at our minimum mapping unit of 1-km^2 resolution across the sage-grouse range. Land-cover variables consisted of combined Landfire Existing Vegetation Type (http://www.landfire.gov/; Rollins, 2009) for big sagebrush, low sagebrush, salt desert shrub, exotic grassland, native grassland, pinyon-juniper woodland, conifer forest, and riparian associations. Climate variables were obtained from the PRISM Climate Group (Daly and others, 2004; Oregon State University, 2011) measured from 1998 to 2010 and included mean annual maximum and minimum temperatures, and mean annual precipitation. We described soils using available water capacity, salinity, and depth to rock (U.S. Department of Agriculture, 2011). Anthropogenic features included agriculture and development land cover (http://www.landfire.gov/), transmission lines, tall structures (communication towers, wind towers), roads, pipelines, and oil and gas wells. We produced a smoothed, continuous surface for most variables by averaging individual cell values within a 5-km radius moving window. We used mapped values for soils, which were in vector format, measured at the center of each 1-km grid cell in the map.

We derived estimates of the ecological minimums using a partitioned Mahalanobis D^2 model of presence only data (Dunn and Duncan, 2000; Rotenberry and others, 2002). Lek (breeding area) locations were used to indicate presence for a previous model of sage-grouse ecological minimums across their western range (Knick and others, 2013). However, we did not have permission to use lek data from all States across the sage-grouse range. Therefore, we assumed that the priority areas delineated by States captured higher quality habitat than occurred outside, despite having some areas excluded because of ownership or forecasted disturbance, and a large proportion of the sage-grouse population. We randomly selected 1,669 points within individual priority areas as presence data and extracted values for corresponding variables to calibrate models. Total number of presence points was obtained by proportional area expansion to the eastern part of the sage-grouse range after an initial 1,000 point random sample in a preliminary comparison of results from priority areas compared to the lek-based map in our previous study of the western range (Knick and others, 2013). We then performed a principal components analysis on 1,000 iterative samples created by bootstrapping the calibration data. The final model was created by subsequently averaging the PCA output after correcting for sign ambiguity (Bro and others, 2008) across all iterations.

We evaluated model performance from the area under the curve (AUC) for a receiver operating characteristic (ROC) to assess sensitivity (fraction of habitat points correctly classified) and specificity (fraction of non-habitat points predicted as habitat) (Fielding and Bell, 1997). To generate presence data, we overlaid the 100 percent sage-grouse breeding densities (Doherty and others, 2010) representing spatial locations of all known sage-grouse breeding sites with our map of ecological minimums and selected all values that fell within the density boundaries. For absence data, we selected all values that fell outside of the breeding density boundaries. To calculate the AUC, we randomly sampled 5,000 presence points and 20,000 absence points. We also created a null presence/absence dataset by randomly sampling 20,000 points 1,000 times from the ecological minimums map. For each iteration, we divided the resulting sample into two datasets (null presence and null absence) based on a relatively equal proportion of the total rows and columns. We then sampled 10,000 points from each of the two datasets and computed a mean AUC score and distribution from all null samples. Means and distributions for model and null AUC scores then were used in a t-test for significance.

Principal component partition 14 met our criteria of having an eigenvalue ≤ 1, a relative difference in eigenvalues among adjacent partitions (table 1), performance against evaluation data (AUC = 0.80; null AUC = 0.50; 95% CI = 0.49 and 0.50; t-test between the null AUC and true AUC = -3,775.0; $p \ll 0.001$), and our subjective assessment of mapped results from different model partitions. We rescaled the mapped output to range continuously from 0 to 1 based on a χ^2 distribution of the D^2 distance; a value of 1 indicated environmental conditions identical to the mean vector of ecological minimum requirements, whereas a value near 0 indicated very dissimilar conditions (fig. 2).

We used circuit theory (McRae and others, 2008) to model movement pathways between all priority areas across our network. We assumed that sage-grouse moved more readily through areas meeting their ecological minimum requirements and used a scaled inverse of our mapped scores as a resistance surface (McRae and others, 2008; Spear and others, 2010; Beier and others, 2011; Zeller and others, 2012). Our resistance surface was calculated by multiplying habitat values by 100 and using the following function: ((habitat value – maximum habitat value) * -1) + minimum habitat value). Resistance values ranged from 1, representing the lowest resistance/highest habitat value, to 100 (high resistance/lowest habitat value). We ran Circuitscape (Circuitscape version 4.0, http://www.circuitscape.org; McRae and Shah, 2008) using the pairwise mode to calculate connectivity between all pairs of priority areas. We treated priority areas as focal patches instead of individual nodes in the modeling process: evaluating habitat pathways from priority area polygon boundaries rather than nodes captured the influence of priority area structure and size in influencing current flow. Effective resistance distances, the relative distance that incorporates the resistance to a species movements across a heterogeneous landscape and used as an estimate of connectivity, were calculated iteratively between all priority area pairs and maps of current densities. We calculated electric current flowing through the resistance landscape between each pair to produce cumulative and maximum current densities across all pair-wise combinations. Our approach thus incorporated multiple dispersal pathways and landscape heterogeneity.

Table 1. Partitions (*k*) in a Mahalanobis D^2 model describing ecological minimums for the range-wide distribution of greater sage-grouse.

Partition (*k*)	Eigenvalue
1	3.18
2	2.89
3	1.87
4	1.76
5	1.68
6	1.42
7	1.31
8	0.99
9	0.96
10	0.93
11	0.85
12	0.80
13	0.76
14	0.63
15	0.59
16	0.49
17	0.44
18	0.40
19	0.34
20	0.32
21	0.24
22	0.14
23	0.04

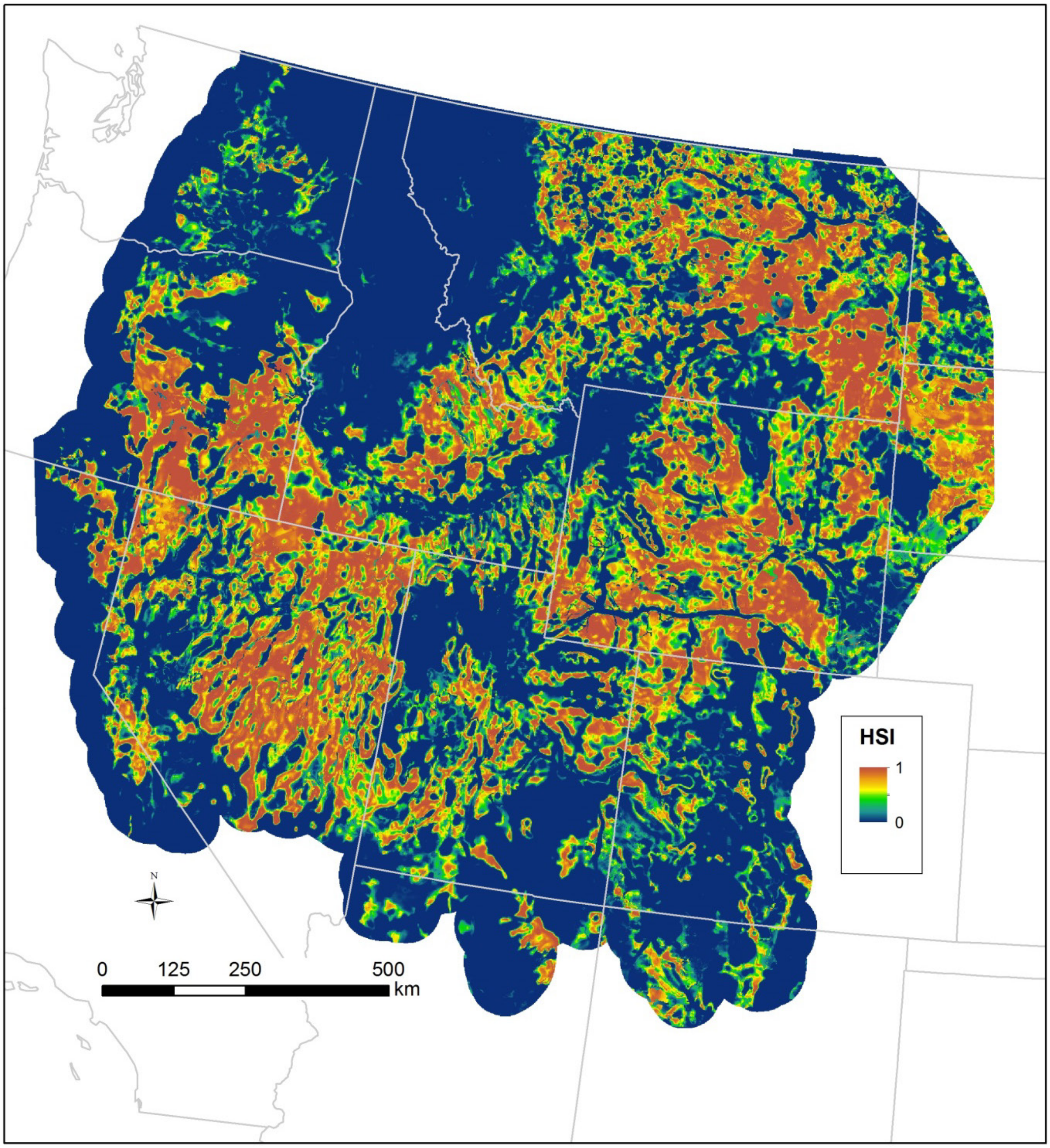

Figure 2. Habitat similarity index (HSI) values for greater sage-grouse across their historical range. HSI values represent the relationship of environmental values at map locations to the multivariate mean vector of minimum requirements for sage-grouse defined by land cover, anthropogenic variables, soil, topography, and climate.

Network Analysis

We applied the effective resistance distances calculated between priority areas to our priority area network. We exported the attribute table of our line network shapefile and built a matrix based on priority area IDs, where “0” was assigned to indicate non-adjacency for a priority area pair (where the two priority areas are not linked in the network), and a “1” indicates adjacency (priority area pairs are linked). We assigned the resulting pair-wise effective resistance distances as a cost between adjacent priority areas in the matrix to all priority pair adjacencies labeled with a “1”. For example, a low effective resistance distance represents a relative capability for sage-grouse movements between the priority area pair based on similarity to habitats within priority areas. We rebuilt our node and link network from our matrices using the igraph package in R (Csardi and Nepusz, 2006; R Core Team, 2013) to calculate centrality. Links connecting adjacent priority areas represent a relation between the priority areas based on the effective resistance distance. The final graph represented the priority area network’s spatial structure of connectivity.

We calculated our centrality metrics, degree and betweenness, using the igraph package and computed summary statistics of our centrality results using R (Csardi and Nepusz, 2006; R Core Team, 2013). We also computed a cumulative distribution curve for resulting betweenness centrality values and used the incremental contribution by each priority areas to assess its contribution to overall network centrality. We used the distribution to rank and identify central priority areas that contribute the most in maintaining a connected network and to identify priority areas that function as stepping stones in promoting connectivity to the central priority areas.

Relative Isolation

Our final objective was to model the relative isolation of priority areas across the historical range of sage-grouse. Results from Circuitscape were used to map habitat linkages among all priority areas and identify clusters of connected priority areas within our network. Circuit theory is advantageous for quantifying connectivity in this manner because of its ability to simultaneously evaluate the combined contributions of multiple pathways to dispersal in heterogeneous landscapes, and identify areas important for connectivity conservation (McRae, 2006; McRae and others, 2008). We used visual observations of the maximum current densities and computed effective resistance distances resulting from Circuitscape to identify areas where habitat connectivity is high or low between priority areas. We chose to evaluate the maximum current density map because maximum values help to remove the confounding effects of network configuration (halo effect) in the Circuitscape results. Again, greater connectivity among priority areas was reflected by a larger number of connected pathways and lower effective resistance distance values (McRae and Shah, 2008; McRae and others, 2008). We also visually identified locations of high current densities that may function as bottlenecks (pinch points) to sage-grouse movements where alternative pathways are not available (McRae and others, 2008). These locations may represent conservation priorities for sage-grouse because their loss may disrupt connectivity among the priority area network.

Results

Priority Areas as a Spatial Network

Average number of connections from each priority area to adjacent neighbors averaged 11 and ranged from 2 to 50 (fig. 3). Betweenness centrality scores ranged from 0 to 11,414 (table 2; appendix B); the average betweenness centrality was 475 (table 2), indicating that most priority areas were contributing little to the range-wide centrality. The largest priority area (Priority Area ID 48), which combined individual State polygons in northeastern Oregon, western California, northern Nevada, southern Idaho, and western Utah, exhibited the highest number of adjacent neighbors (n = 50) and highest betweenness centrality value, signifying its importance in connecting the network.

Twenty priority areas explained 80 percent of the total betweenness centrality value and were likely the central priority areas for maintaining a connected reserve network (fig. 4). Two priority areas that exhibited the highest betweenness centrality scores and explained 20 percent of total centrality were the largest single polygon (Priority Area ID 48) and a priority area centrally located in Wyoming (Priority Area ID 110). Priority areas that were within the 80–99 percent cumulative distribution scored lower in centrality compared to the central priority areas but may still contribute largely by functioning as stepping stones maintaining connections across the most central 20 priority areas. These priority areas typically were located between the highest- and lowest-scoring priority areas, mid-sized in area, and were distributed across the entire range rather than having a more central location.

Ninety-three priority areas that scored a 0 for betweenness centrality were characterized by small size (averaging approximately 350 km^2), and were either isolated between large priority areas where the shape of the surrounding large priority areas limited the number of connections, or were located on the periphery of the range. Although these small priority areas were not central in maintaining the overall network, most scored low in the effective resistance distance results (figs. 4 and 5; appendix B) indicating high connectivity to their neighboring priority areas.

Table 2. Summary statistics calculated for degree and betweenness centrality, and effective resistance and maximum current densities from Circuitscape (McRae and others, 2008).

Priority Areas	Mean	Minimum	Maximum
Distance between Priority Areas (km)	99.3	2.7	843.3
Degree Centrality Metric	10.6	2.0	50.0
Betweenness Centrality Metric	475	0	11,414
Priority Area Effective Resistance	4.4	<0.1	35.8
Maximum Current Densities	0.1	0.0	1.0

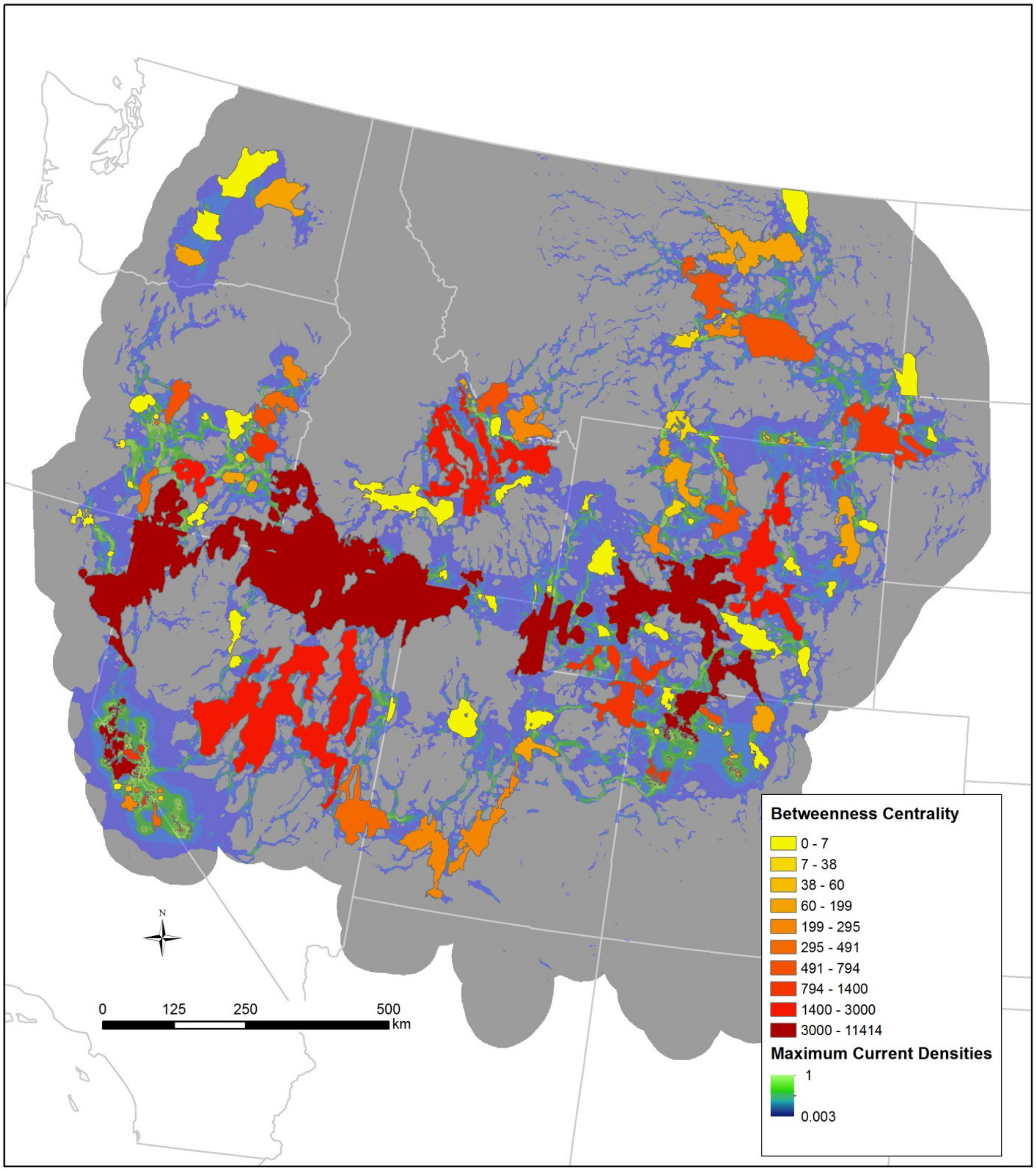

Figure 3. Priority area importance and connectivity for betweenness centrality and ranked across the network. Potential for sage-grouse movements was estimated between priority areas and used to determine each priority area's centrality based on the number of movement pathways available between priority areas. Current densities were displayed using a histogram equalize stretch.

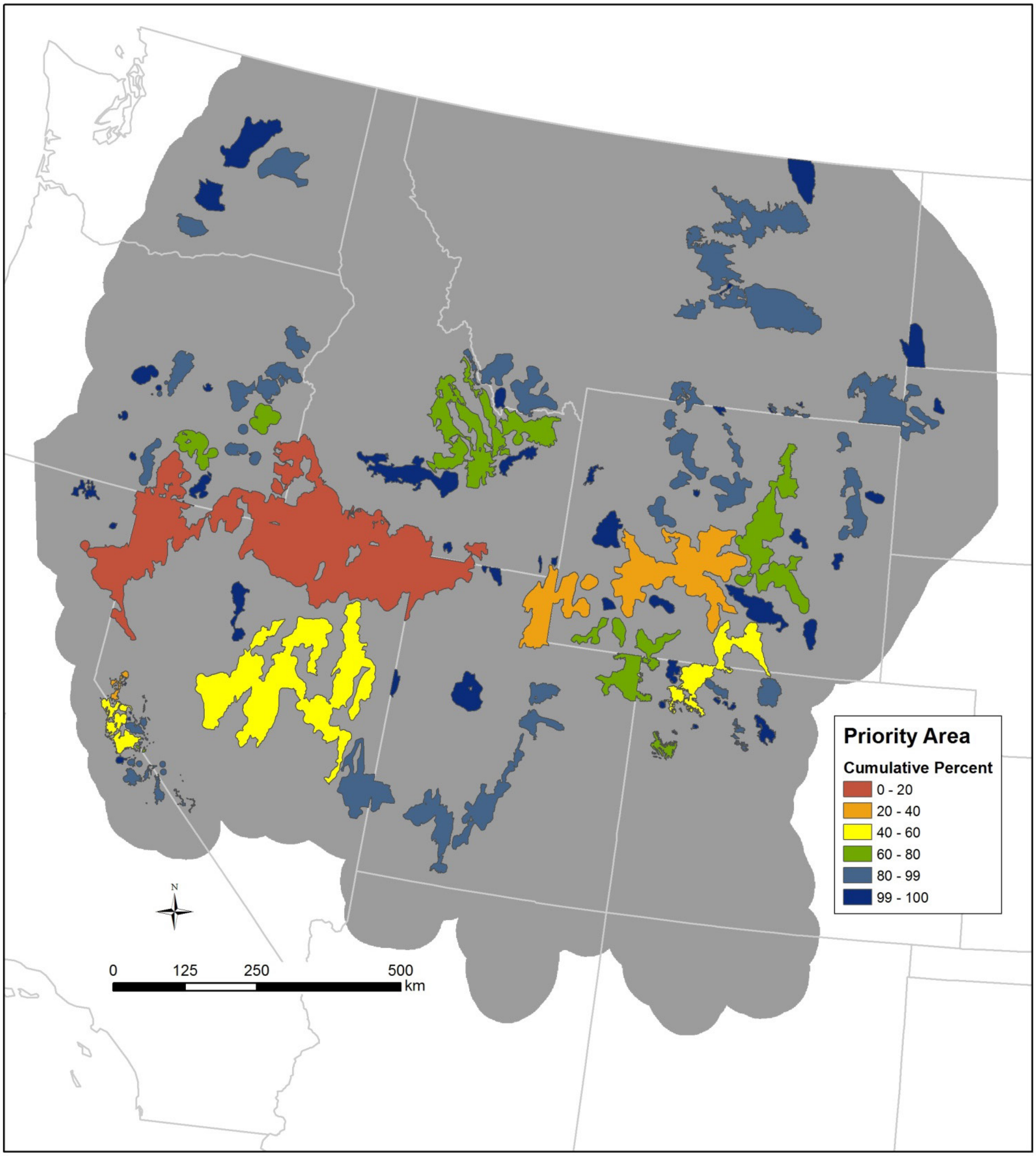

Figure 4. Relative contribution of each priority area to range-wide cumulative percent betweenness centrality. Priority area colors in map correspond with figure 5.

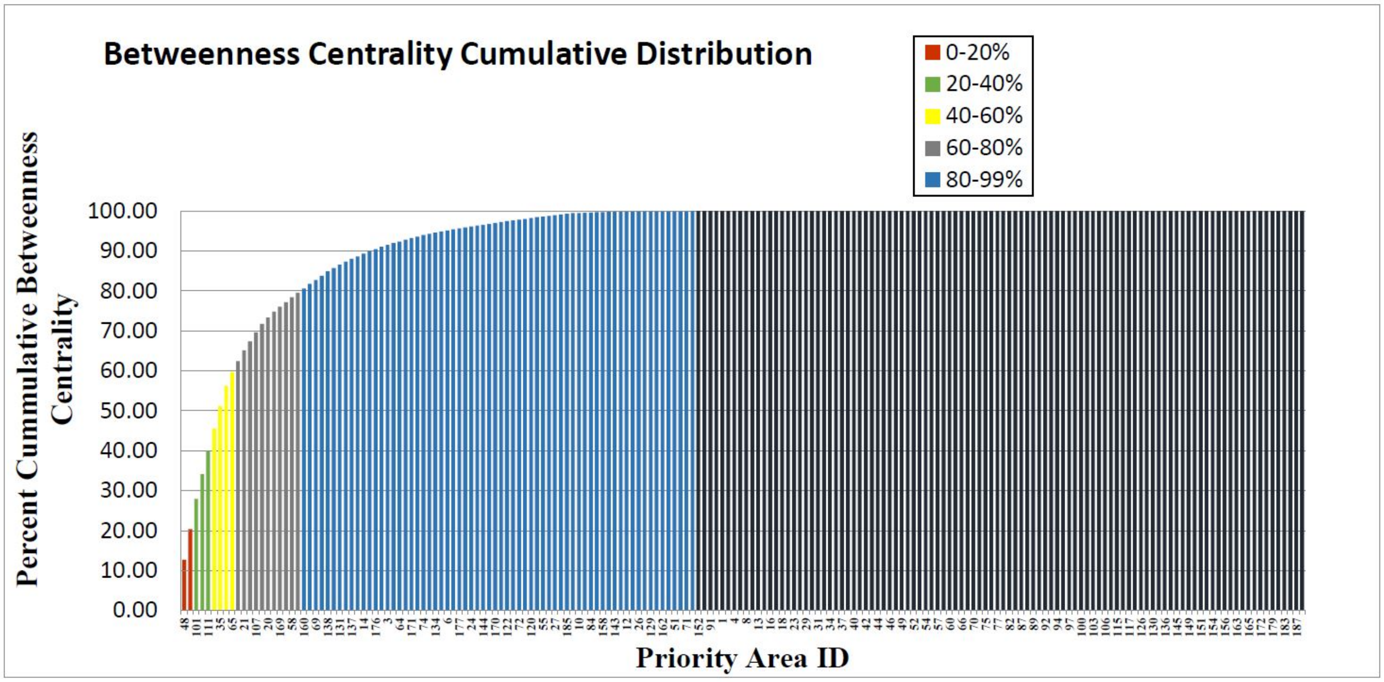

Figure 5. Cumulative distribution of each priority area's contribution to total betweenness centrality. Graph colors correspond to mapped priority areas in figure 4.

Connectivity among Priority Areas

Movement potential, estimated by Circuitscape current densities (fig. 6), coupled with the relatively low mean for priority area effective resistance distance (mean = 4.4; table 2) indicated a high degree of connectivity across the network characterized by numerous and multiple pathways between most of the priority areas. The map reflecting maximum current densities highlighted areas of high current flow between priority areas that may be important habitat linkages (pinch points). Their loss may result in disconnections across the entire network or result in the use of less efficient (more costly) habitat pathways connecting priority areas (fig. 6). A number of linkages have portions of high current densities that depict pinch points where connectivity is high but constrained due to either natural or anthropogenic barriers to sage-grouse movements surrounding the pinch points. Our map of maximum current densities also highlighted priority area clusters where current flow was high between priority areas and low surrounding a group of priority areas.

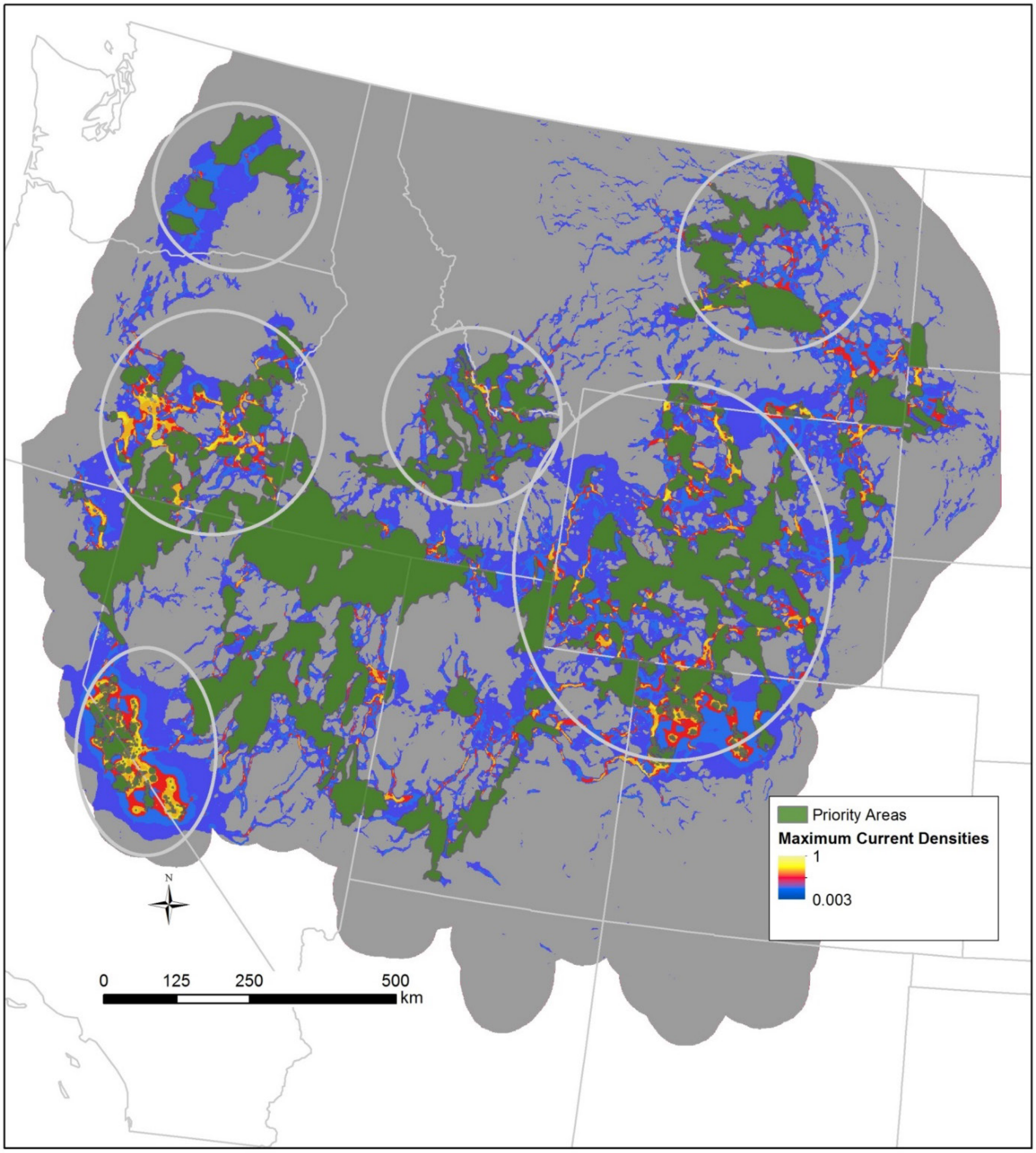

Figure 6. Relative isolation of priority areas based on estimated potential for sage-grouse movement (Circuitscape; McRae and Shah, 2008). Inverted HSI values were used as a measure of landscape resistance. Six clusters of priority areas are circled where connectivity between priority areas was high in comparison to surrounding environment. High to medium current densities represent pinch points.

Relative Isolation

Low current densities highlighted areas where habitat quality was more fragmented or where barriers for sage-grouse movements may exist. Mean maximum current density across the study area was low (mean = 0.1; table 2) because the study area included large expanses for high elevation mountain ranges, forested communities, highly populated areas, agriculture development, and other areas of low habitat value for sage-grouse that composed a large portion of our study area. For example, the Snake River Plain in southern Idaho, which contains Interstate 84 and large areas of developed private lands, may function as a barrier for sage-grouse movements between two adjoining priority areas. The Snake River Plain also has experienced significant areas of cheatgrass (*Bromus tectorum*) invasions and recent fire activity resulting in higher habitat loss and fragmentation in comparison to other regions across the historical range.

Discussion

The strategy currently implemented for conserving greater sage-grouse is based on designated priority areas in each of the 11 States across its range (U.S. Fish and Wildlife Service, 2013). Focusing conservation actions on a relatively small (<15 percent) total area containing a large proportion of the range-wide population can have the greatest benefit with limited resources. However, continued management under normal regulations in regions surrounding priority areas can potentially lead to a spatially disjunct set of areas that retain the characteristics necessary to sustain sage-grouse populations. We assumed that the priority areas serve as a system of reserves and function within the context of island biogeography theory (MacArthur and Wilson, 1967; Wiens, 1997).

We used two primary factors, size and connectivity of priority areas, to understand how this network functions. We ranked priority areas for their relative importance within the network and identified important habitat linkages that may help maintain connected sage-grouse populations across their range. However, our approach was a simple metric based on a social theory relating importance to number of connections. The critical component to assessing viability is not just size of priority area and number of connections but how individuals are linked together to function as a viable population.

Priority Areas as a Spatial Network

Centrality measures derived from social network theory provided an interpretable analysis for characterizing the importance of priority areas within a network. Centrality measures also produced a ranking metric for identifying key areas to conserve to minimize network connectivity loss (Freeman, 2004; Blazquez-Cabrera and others, 2014). A highly centralized network is dominated by one or a few very central nodes. If these nodes are removed, the network may quickly fragment into unconnected sub-networks by isolating individual or clusters of nodes. In contrast, a less centralized network might be more resilient because many links or nodes can fail while allowing the remaining nodes to remain connected through other network paths.

High centrality scores for 20 of 188 priority areas indicated that the network was highly centralized. Highly ranked priority areas were characterized by large size, a more central spatial location within the network, and were surrounded by many other priority areas of various sizes. The highest ranked priority area (Priority Area ID 48) was the largest and most centrally located in the network. Large size also correlates with longer boundaries that allow for more dispersal opportunity with adjacent priority areas. Similarly, a central position in the network facilitates movement to reach numerous other priority areas, thus increasing overall connectivity across the network. Loss or fragmentation of these large priority areas, or their associated connections, would have a disproportionally large influence across the entire network. Delineating priority areas with these characteristics may be important in further conservation strategies because they play a strong role in the range-wide network connectivity.

Approximately 80 percent of the priority areas scored betweenness centrality values of (near) zero despite being well-connected to surrounding priority areas. These priority areas generally were smaller and were distributed across the network surrounding the central larger priority areas. Although these individual priority areas were small, their total area contained a large amount of the habitat across the entire sage-grouse range. Their size and location likely allows them to function as stepping stones and may be critical for individuals moving from larger neighboring priority areas needed to maintain smaller sage-grouse populations (Bodin and others, 2006; Saura and others, 2014).

Connectivity among Priority Areas

Maintaining connectivity by conserving habitat between separated populations or reserves is an important strategy to mitigate against impacts of land-use change. Landscape connectivity is often assessed in the form of least-cost paths, corridors, and graph networks to identify critical habitat connections where, if severed, could potentially isolate populations (Bunn and others, 2000; Urban and Keitt, 2001; LaPoint and others, 2013). Our primary objective was to evaluate the capability of the network of priority areas to serve as a connected reserve network for sage-grouse. To do that, we also needed to produce the first range-wide landscape-scale analysis to quantify habitat quality and connectivity across their range. This approach, incorporating an effective resistance surface, enhanced our assessment of the priority area network by permitting multiple dispersal pathways and recognizing landscape heterogeneity in estimating movement cost. Our maps highlighted important habitat corridors and pinch points between priority areas that land managers can target for conservation to help ensure sage-grouse seasonal and dispersal movements. These locations also might be considered for future priority areas to ensure connectivity.

We emphasize that the parameters defining connectivity in our study were based on a habitat suitability metric measured at a 1-km^2 resolution. The interpretation of connectivity requires an understanding of genetic, individual, and population levels as well as recognizing behavioral differences between seasonal and dispersal movements. Connectivity to maintain genetic diversity might have different requirements than the connectivity necessary to recolonize areas or augment declining populations. Characteristics of sage-grouse dispersal are relatively unknown (Connelly and others, 2011); patterns from telemetry, satellite, and genetic studies would provide valuable information in assessing landscape-scale connectivity for conservation planning.

Relative Isolation

The cost of movement across a landscape is a combined function of distance and resistance to movement (McRae, 2006). Connectivity, measured by the effective resistance distance, varied widely across the sage-grouse range. Some geographically distant priority areas were highly connected to the network through corridors of low resistance to movement. In contrast, other priority areas in close proximity were disconnected because of resistance created by unsuitable environments.

The formal conservation strategy focused on priority areas did not designate connecting corridors among priority areas, which could effectively isolate priority areas or regions. Therefore, we identified linkages and pinch-points that may be important for sustaining sage-grouse movements among priority areas (Bengtsson and others, 2003; Beier and others, 2011; Dickson and others, 2013; LaPoint and others, 2013). Most techniques for analyzing landscape connectivity identify one primary route based on a least cost pathway that becomes the focus for conservation efforts. Our approach for characterizing connectivity based on a resistance surface and circuit theory allowed for the quantitative and simultaneous evaluation of multiple alternative habitat linkages important for maintaining connected sage-grouse populations (McRae and others, 2008; Knick and others, 2013).

Synthesis and Application

The current network of priority areas has many important characteristics for maintaining sage-grouse populations. This network contained a range of large and small sizes of priority areas that might provide different functions. The structure of the network of priority areas for conserving greater sage-grouse was highly centralized. A relatively few large and more central priority areas accounted for a large proportion of cumulative centrality ranking. These large priority areas likely can self-sustain viable sage-grouse populations because of the large sagebrush regions within their boundaries. Large priority areas also might function as sources to augment adjacent populations, either those in priority areas too small to support persistent sage-grouse populations or in nonpriority areas.

The network also contained connected clusters of priority areas that otherwise might be too small individually to sustain viable populations. For example, a cluster of priority areas in Wyoming were highly connected and centered on one large priority area. A priority area cluster in Montana appears geographically isolated but is highly connected to the Wyoming cluster through habitat linkages in North and South Dakota. High current densities between priority areas in Oregon connect with priority areas across Idaho, Nevada, and California. The Bi-State cluster on the border of Nevada and California was isolated from all other clusters but exhibited a high degree of connectivity among the priority areas within it. Although our analysis focused on the range-wide network, there is likely a hierarchical system of networks for both priority areas and metapopulations of sage-grouse. These smaller clusters might function independently and an analysis of these smaller clusters as networks might provide important insights into regional centrality and linkages.

Designating clustered areas in close proximity is one of the central tenets of reserve design (Diamond, 1975; Williams and others, 2004). Clustering helps to promote frequent dispersal movements for genetic exchange. Clustering also might enhance migration that might rescue declining or isolated populations, allow for seasonal movements, or egress away from areas that have become degraded or lost (Cabeza and Moilanen, 2001). Maintaining connectivity within and among the clusters potentially allows for dispersal to augment declining populations and maintain genetic exchange across the entire network reducing the chance for the creation of isolated or genetically distinct populations in the long-term (Crooks and Sanjayan, 2006).

Priority areas that scored lower in the centrality metrics were mid-sized and widely distributed across the entire range. Their function as stepping stones to reduce overall distance for sage-grouse movements among the central priority areas is an important consideration for sustaining a connected network.

Adopting a range-wide conservation plan for sage-grouse based on a network of priority areas has risks. Different conservation and management priorities among administrative units could disrupt the metapopulation structure leading to greater isolation and potentially initiate or accelerate population declines. Many priority areas share a boundary on State jurisdictional lines and many important habitat linkages presented here occur across State and Federal jurisdictional boundaries. Yet, priorities and land use plans often differ among State and Federal management agencies both within and outside of the proposed priority area structure (Copeland and others, 2014). Understanding the functions of the priority area network and recognizing the importance of connecting corridors can help sustain sage-grouse populations.

Designing reserve networks is challenging because of combined needs to protect the largest habitat or population areas in a landscape, ensure that those areas are close enough to sustain effective dispersal rates, and also ensure that a sufficient number of areas exist so that individual losses can be absorbed within the entire network (Diamond, 1975; Cabeza and Moilanen, 2001; Williams and others, 2004). Our centrality results may help predict impacts to connectivity when priority areas are lost, degraded, or fragmented. Numerous factors, both natural and anthropogenic, make it unlikely that the current network of priority areas can be sustained (Knick and Connelly, 2011). Focusing conservation actions on important and highly connected priority areas and corresponding habitat linkages may help to mitigate future landscape change and enhance the long-term viability of sage-grouse populations.

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Appendix A. Crosswalk Table Depicting Priority Area Identifiers, U.S. Fish and Wildlife Service Unique Identifiers, Sage-Grouse Population Name, and Management Zone

[Data for crosswalk table was obtained from the U.S. Fish and Wildlife Service (FWS). ID, identifier]

Priority Area ID	FWS Unique ID	Sage-grouse Population	Management Zone	FWS Name
1	401	Bi-State	MZ3	401-Bi-State-MZ3
2	395	Bi-State	MZ3	395-Bi-State-MZ3
3	358	Bi-State	MZ3	358-Bi-State-MZ3
4	396	Bi-State	MZ3	396-Bi-State-MZ3
5	334	Parachute Piceance Roan	MZ7	334-Parachute Piceance Roan-MZ7
6	353	Bi-State	MZ3	353-Bi-State-MZ3
7	354	Bi-State	MZ3	354-Bi-State-MZ3
8	332	Parachute Piceance Roan	MZ7	332-Parachute Piceance Roan-MZ7
9	352	Bi-State	MZ3	352-Bi-State-MZ3
10	351	Bi-State	MZ3	351-Bi-State-MZ3
11	385	Bi-State	MZ3	385-Bi-State-MZ3
12	362	Bi-State	MZ3	362-Bi-State-MZ3
13	399	Bi-State	MZ3	399-Bi-State-MZ3
14	360	Bi-State	MZ3	360-Bi-State-MZ3
15	350	Bi-State	MZ3	350-Bi-State-MZ3
16	388	Bi-State	MZ3	388-Bi-State-MZ3
17	391	Bi-State	MZ3	391-Bi-State-MZ3
18	390	Bi-State	MZ3	390-Bi-State-MZ3
19	345	Bi-State	MZ3	345-Bi-State-MZ3
20	386	Bi-State	MZ3	386-Bi-State-MZ3
21	349	Bi-State	MZ3	349-Bi-State-MZ3
22	383	Bi-State	MZ3	383-Bi-State-MZ3
23	387	Bi-State	MZ3	387-Bi-State-MZ3
24	356	Bi-State	MZ3	356-Bi-State-MZ3
25	355	Bi-State	MZ3	355-Bi-State-MZ3
26	357	Bi-State	MZ3	357-Bi-State-MZ3
27	359	Bi-State	MZ3	359-Bi-State-MZ3
28	394	Bi-State	MZ3	394-Bi-State-MZ3
29	393	Bi-State	MZ3	393-Bi-State-MZ3
30	382	Bi-State	MZ3	382-Bi-State-MZ3
31	389	Bi-State	MZ3	389-Bi-State-MZ3
32	384	Bi-State	MZ3	384-Bi-State-MZ3
33	381	Bi-State	MZ3	381-Bi-State-MZ3
34	374	Bi-State	MZ3	374-Bi-State-MZ3
35	344	Bi-State	MZ3	344-Bi-State-MZ3
36	369	Bi-State	MZ3	369-Bi-State-MZ3

Priority Area ID	FWS Unique ID	Sage-grouse Population	Management Zone	FWS Name
37	372	Bi-State	MZ3	372-Bi-State-MZ3
38	370	Bi-State	MZ3	370-Bi-State-MZ3
39	341	Bi-State	MZ3	341-Bi-State-MZ3
40	347	Bi-State	MZ3	347-Bi-State-MZ3
41	346	Bi-State	MZ3	346-Bi-State-MZ3
42	375	Bi-State	MZ3	375-Bi-State-MZ3
43	314	Western Great Basin	MZ5	314-Western Great Basin-MZ5
44	343	Bi-State	MZ3	343-Bi-State-MZ3
45	317	Klamath OR/CA	MZ5	317-Klamath OR/CA-MZ5
46	368	Bi-State	MZ3	368-Bi-State-MZ3
47	367	Bi-State	MZ3	367-Bi-State-MZ3
48	316	Western Great Basin	MZ5	316-Western Great Basin-MZ5
49	309	Western Great Basin	MZ5	309-Western Great Basin-MZ5
50	312	Western Great Basin	MZ5	312-Western Great Basin-MZ5
51	223	Eagle/S Routt CO	MZ2	223-Eagle/S Routt CO-MZ2
52	156	Wyoming Basin	MZ2	156-Wyoming Basin-MZ2
53	363	Bi-State	MZ3	363-Bi-State-MZ3
54	306	Central	MZ5	306-Central-MZ5
55	322	Yakama Indian Nation	MZ6	322-Yakama Indian Nation-MZ6
56	253	Snake, Salmon, and Beaverhead	MZ4	253-Snake, Salmon, and Beaverhead-MZ4
57	279	Northern Great Basin	MZ4	279-Northern Great Basin-MZ4
58	329	Parachute Piceance Roan	MZ7	329-Parachute Piceance Roan-MZ7
59	340	Parachute Piceance Roan	MZ7	340-Parachute Piceance Roan-MZ7
60	331	Parachute Piceance Roan	MZ7	331-Parachute Piceance Roan-MZ7
61	224	Eagle/S Routt CO	MZ2	224-Eagle/S Routt CO-MZ2
62	239	Panguitch	MZ3	239-Panguitch-MZ3
63	398	Bi-State	MZ3	398-Bi-State-MZ3
64	242	Southern Great Basin	MZ3	242-Southern Great Basin-MZ3
65	243	Southern Great Basin	MZ3	243-Southern Great Basin-MZ3
66	241	Southern Great Basin	MZ3	241-Southern Great Basin-MZ3
67	232	Sheeprock Mountains	MZ3	232-Sheeprock Mountains-MZ3
68	237	Carbon	MZ3	237-Carbon-MZ3
69	361	Bi-State	MZ3	361-Bi-State-MZ3
70	400	Bi-State	MZ3	400-Bi-State-MZ3
71	214	Middle Park CO	MZ2	214-Middle Park CO-MZ2
72	221	Eagle/S Routt CO	MZ2	221-Eagle/S Routt CO-MZ2
73	222	Eagle/S Routt CO	MZ2	222-Eagle/S Routt CO-MZ2
74	220	Eagle/S Routt CO	MZ2	220-Eagle/S Routt CO-MZ2
75	326	Meeker - White River	MZ7	326-Meeker - White River-MZ7
76	327	Parachute Piceance Roan	MZ7	327-Parachute Piceance Roan-MZ7
77	323	Meeker - White River	MZ7	323-Meeker - White River-MZ7

Priority Area ID	FWS Unique ID	Sage-grouse Population	Management Zone	FWS Name
78	238	Parker Mountain-Emery	MZ3	238-Parker Mountain-Emery-MZ3
79	153	Wyoming Basin	MZ2	153-Wyoming Basin-MZ2
80	152	Wyoming Basin	MZ2	152-Wyoming Basin-MZ2
81	235	Strawberry	MZ3	235-Strawberry-MZ3
82	154	Wyoming Basin	MZ2	154-Wyoming Basin-MZ2
83	183	Wyoming Basin	MZ2	183-Wyoming Basin-MZ2
84	219	Eagle/S Routt CO	MZ2	219-Eagle/S Routt CO-MZ2
85	204	Wyoming Basin	MZ2	204-Wyoming Basin-MZ2
86	198	Wyoming Basin	MZ2	198-Wyoming Basin-MZ2
87	160	Wyoming Basin	MZ2	160-Wyoming Basin-MZ2
88	193	Wyoming Basin	MZ2	193-Wyoming Basin-MZ2
89	199	Wyoming Basin	MZ2	199-Wyoming Basin-MZ2
90	195	Wyoming Basin	MZ2	195-Wyoming Basin-MZ2
91	158	Wyoming Basin	MZ2	158-Wyoming Basin-MZ2
92	191	Wyoming Basin	MZ2	191-Wyoming Basin-MZ2
93	182	Wyoming Basin	MZ2	182-Wyoming Basin-MZ2
94	266	Snake, Salmon, and Beaverhead	MZ4	266-Snake, Salmon, and Beaverhead-MZ4
95	213	North Park	MZ2	213-North Park-MZ2
96	142	Wyoming Basin	MZ2	142-Wyoming Basin-MZ2
97	159	Wyoming Basin	MZ2	159-Wyoming Basin-MZ2
98	157	Wyoming Basin	MZ2	157-Wyoming Basin-MZ2
99	178	Wyoming Basin	MZ2	178-Wyoming Basin-MZ2
100	169	Wyoming Basin	MZ2	169-Wyoming Basin-MZ2
101	139	Wyoming Basin	MZ2	139-Wyoming Basin-MZ2
102	143	Wyoming Basin	MZ2	143-Wyoming Basin-MZ2
103	114	Powder River Basin	MZ1	114-Powder River Basin-MZ1
104	141	Wyoming Basin	MZ2	141-Wyoming Basin-MZ2
105	148	Wyoming Basin	MZ2	148-Wyoming Basin-MZ2
106	150	Wyoming Basin	MZ2	150-Wyoming Basin-MZ2
107	264	Snake, Salmon, and Beaverhead	MZ4	264-Snake, Salmon, and Beaverhead-MZ4
108	144	Wyoming Basin	MZ2	144-Wyoming Basin-MZ2
109	149	Wyoming Basin	MZ2	149-Wyoming Basin-MZ2
110	145	Wyoming Basin	MZ2	145-Wyoming Basin-MZ2
111	146	Wyoming Basin	MZ2	146-Wyoming Basin-MZ2
112	366	Bi-State	MZ3	366-Bi-State-MZ3
113	244	NW-Interior NV	MZ3	244-NW-Interior NV-MZ3
114	267	Snake, Salmon, and Beaverhead	MZ4	267-Snake, Salmon, and Beaverhead-MZ4
115	263	Snake, Salmon, and Beaverhead	MZ4	263-Snake, Salmon, and Beaverhead-MZ4
116	138	Wyoming Basin	MZ2	138-Wyoming Basin-MZ2

Priority Area ID	FWS Unique ID	Sage-grouse Population	Management Zone	FWS Name
117	126	Jackson Hole WY	MZ2	126-Jackson Hole WY-MZ2
118	246	Southwest Montana	MZ4	246-Southwest Montana-MZ4
119	245	Southwest Montana	MZ4	245-Southwest Montana-MZ4
120	275	Northern Great Basin	MZ4	275-Northern Great Basin-MZ4
121	273	Northern Great Basin	MZ4	273-Northern Great Basin-MZ4
122	248	Snake, Salmon, and Beaverhead	MZ4	248-Snake, Salmon, and Beaverhead-MZ4
123	269	Northern Great Basin	MZ4	269-Northern Great Basin-MZ4
124	277	Northern Great Basin	MZ4	277-Northern Great Basin-MZ4
125	310	Western Great Basin	MZ5	310-Western Great Basin-MZ5
126	247	Southwest Montana	MZ4	247-Southwest Montana-MZ4
127	115	Powder River Basin	MZ1	115-Powder River Basin-MZ1
128	121	Powder River Basin	MZ1	121-Powder River Basin-MZ1
129	108	Yellowstone Watershed	MZ1	108-Yellowstone Watershed-MZ1
130	147	Wyoming Basin	MZ2	147-Wyoming Basin-MZ2
131	104	Yellowstone Watershed	MZ1	104-Yellowstone Watershed-MZ1
132	117	Powder River Basin	MZ1	117-Powder River Basin-MZ1
133	137	Wyoming Basin	MZ2	137-Wyoming Basin-MZ2
134	106	Yellowstone Watershed	MZ1	106-Yellowstone Watershed-MZ1
135	116	Powder River Basin	MZ1	116-Powder River Basin-MZ1
136	120	Powder River Basin	MZ1	120-Powder River Basin-MZ1
137	107	Yellowstone Watershed	MZ1	107-Yellowstone Watershed-MZ1
138	110	Yellowstone Watershed	MZ1	110-Yellowstone Watershed-MZ1
139	119	Powder River Basin	MZ1	119-Powder River Basin-MZ1
140	123	Powder River Basin	MZ1	123-Powder River Basin-MZ1
141	135	Wyoming Basin	MZ2	135-Wyoming Basin-MZ2
142	134	Wyoming Basin	MZ2	134-Wyoming Basin-MZ2
143	128	Wyoming Basin	MZ2	128-Wyoming Basin-MZ2
144	130	Wyoming Basin	MZ2	130-Wyoming Basin-MZ2
145	105	Yellowstone Watershed	MZ1	105-Yellowstone Watershed-MZ1
146	102	Northern Montana	MZ1	102-Northern Montana-MZ1
147	113	Dakotas	MZ1	113-Dakotas-MZ1
148	118	Powder River Basin	MZ1	118-Powder River Basin-MZ1
149	305	Central	MZ5	305-Central-MZ5
150	101	Northern Montana	MZ1	101-Northern Montana-MZ1
151	111	Dakotas	MZ1	111-Dakotas-MZ1
152	321	Yakama Training Center	MZ6	321-Yakama Training Center-MZ6
153	397	Bi-State	MZ3	397-Bi-State-MZ3
154	392	Bi-State	MZ3	392-Bi-State-MZ3
155	365	Bi-State	MZ3	365-Bi-State-MZ3
156	380	Bi-State	MZ3	380-Bi-State-MZ3
157	379	Bi-State	MZ3	379-Bi-State-MZ3

Priority Area ID	FWS Unique ID	Sage-grouse Population	Management Zone	FWS Name
158	377	Bi-State	MZ3	377-Bi-State-MZ3
159	378	Bi-State	MZ3	378-Bi-State-MZ3
160	348	Bi-State	MZ3	348-Bi-State-MZ3
161	376	Bi-State	MZ3	376-Bi-State-MZ3
162	373	Bi-State	MZ3	373-Bi-State-MZ3
163	371	Bi-State	MZ3	371-Bi-State-MZ3
164	364	Bi-State	MZ3	364-Bi-State-MZ3
165	342	Bi-State	MZ3	342-Bi-State-MZ3
166	308	Western Great Basin	MZ5	308-Western Great Basin-MZ5
167	270	Northern Great Basin	MZ4	270-Northern Great Basin-MZ4
168	276	Northern Great Basin	MZ4	276-Northern Great Basin-MZ4
169	272	Northern Great Basin	MZ4	272-Northern Great Basin-MZ4
170	274	Northern Great Basin	MZ4	274-Northern Great Basin-MZ4
171	304	Central	MZ5	304-Central-MZ5
172	300	Central	MZ5	300-Central-MZ5
173	302	Central	MZ5	302-Central-MZ5
174	271	Northern Great Basin	MZ4	271-Northern Great Basin-MZ4
175	303	Central	MZ5	303-Central-MZ5
176	301	Central	MZ5	301-Central-MZ5
177	268	Baker	MZ4	268-Baker-MZ4
178	320	Crab Creek	MZ6	320-Crab Creek-MZ6
179	319	Moses Coulee	MZ6	319-Moses Coulee-MZ6
180	298	Northern Great Basin	MZ4	298-Northern Great Basin-MZ4
181	140	Wyoming Basin	MZ2	140-Wyoming Basin-MZ2
182	136	Wyoming Basin	MZ2	136-Wyoming Basin-MZ2
183	132	Wyoming Basin	MZ2	132-Wyoming Basin-MZ2
184	131	Wyoming Basin	MZ2	131-Wyoming Basin-MZ2
185	129	Wyoming Basin	MZ2	129-Wyoming Basin-MZ2
186	133	Wyoming Basin	MZ2	133-Wyoming Basin-MZ2
187	315	Western Great Basin	MZ5	315-Western Great Basin-MZ5
188	288	Northern Great Basin	MZ4	288-Northern Great Basin-MZ4

Appendix B. Centrality Results for Degree and Betweenness Metrics for Each Priority Area

[Priority areas are ranked from highest to lowest betweenness centrality value. Cumulative percent of betweenness centrality was calculated to provide each priority area's contribution to total betweenness centrality. ID, identifier]

Priority Area ID	Area (km^2)	Degree Centrality	Betweenness Centrality	Betweenness Centrality Rank	Cumulative Percent
48	78,218	50	11,414	1	12.8
110	7,673	20	6,820	2	20.4
101	18,607	24	6,740	3	27.9
39	440	22	5,537	4	34.1
111	608	8	5,178	5	39.9
19	1,847	32	5,072	6	45.6
35	717	24	5,048	7	51.3
83	7,316	48	4,455	8	56.2
65	33,892	26	3,000	9	59.6
181	11,999	24	2,554	10	62.5
21	40	16	2,415	11	65.2
114	9,548	14	2,024	12	67.4
107	6,133	18	2,009	13	69.7
166	2,570	18	1,907	14	71.8
20	24	16	1,400	15	73.4
80	5,593	22	1,291	16	74.8
169	1,760	14	1,093	17	76.0
105	950	10	1,068	18	77.2
58	839	28	1,048	19	78.4
109	753	8	1,029	20	79.6
160	560	18	992	21	80.7
7	132	14	961	22	81.7
69	33	12	948	23	82.8
148	493	8	945	24	83.9
138	7,677	16	926	25	84.9
182	2,601	10	794	26	85.8
131	4,448	16	711	27	86.6
119	1,894	14	670	28	87.3
137	7,376	20	626	29	88.0
167	1,132	6	577	30	88.7
14	48	14	574	31	89.3
98	554	10	542	32	89.9
176	1,788	18	524	33	90.5
9	82	12	491	34	91.1
3	400	22	458	35	91.6
123	1,492	16	400	36	92.0

Priority Area ID	Area (km²)	Degree Centrality	Betweenness Centrality	Betweenness Centrality Rank	Cumulative Percent
64	5,783	10	366	37	92.4
125	1,336	14	366	38	92.8
171	56	10	364	39	93.3
141	585	10	338	40	93.6
74	50	10	325	41	94.0
157	2	16	295	42	94.3
134	1,422	8	268	43	94.6
62	4,606	8	257	44	94.9
6	541	14	233	45	95.2
133	1,260	10	225	46	95.4
177	1,362	14	222	47	95.7
118	3,264	12	218	48	95.9
24	82	12	210	49	96.2
78	4,563	12	210	50	96.4
144	2,464	18	199	51	96.6
139	3,122	14	198	52	96.8
170	669	16	193	53	97.0
178	3,273	12	193	54	97.3
122	316	14	192	55	97.5
146	6,796	10	185	56	97.7
72	37	12	180	57	97.9
95	1,529	10	178	58	98.1
120	336	10	174	59	98.3
135	284	10	172	60	98.5
55	1,285	8	164	61	98.7
142	147	8	155	62	98.8
27	26	14	149	63	99.0
68	1,442	14	148	64	99.2
185	523	10	142	65	99.3
61	81	10	128	66	99.5
10	120	12	60	67	99.5
33	23	12	60	68	99.6
84	214	12	60	69	99.7
112	24	12	51	70	99.7
158	17	14	38	71	99.8
25	24	12	30	72	99.8
143	1,487	12	29	73	99.8
121	227	8	24	74	99.9
12	14	12	23	75	99.9
127	79	12	18	76	99.9
26	82	12	16	77	99.9

Priority Area ID	Area (km²)	Degree Centrality	Betweenness Centrality	Betweenness Centrality Rank	Cumulative Percent
161	4	10	14	78	99.9
129	965	12	13	79	100.0
184	661	8	12	80	100.0
162	2	10	7	81	100.0
174	1,492	14	7	82	100.0
51	27	10	6	83	100.0
81	1,309	10	4	84	100.0
71	888	10	3	85	100.0
108	117	8	3	86	100.0
152	1,933	8	2	87	100.0
86	8	8	1	88	100.0
91	78	8	1	89	100.0
175	81	8	1	90	100.0
1	2	6	0	91	100.0
2	1	4	0	92	100.0
4	1	6	0	93	100.0
5	5	6	0	94	100.0
8	8	10	0	95	100.0
11	4	8	0	96	100.0
13	4	4	0	97	100.0
15	153	12	0	98	100.0
16	1	12	0	99	100.0
17	2	8	0	100	100.0
18	4	8	0	101	100.0
22	2	12	0	102	100.0
23	7	6	0	103	100.0
28	2	12	0	104	100.0
29	2	6	0	105	100.0
30	2	8	0	106	100.0
31	3	6	0	107	100.0
32	2	2	0	108	100.0
34	1	4	0	109	100.0
36	2	10	0	110	100.0
37	5	12	0	111	100.0
38	5	6	0	112	100.0
40	27	8	0	113	100.0
41	15	8	0	114	100.0
42	3	10	0	115	100.0
43	103	4	0	116	100.0
44	5	2	0	117	100.0
45	658	10	0	118	100.0

Priority Area ID	Area (km^2)	Degree Centrality	Betweenness Centrality	Betweenness Centrality Rank	Cumulative Percent
46	2	6	0	119	100.0
47	2	6	0	120	100.0
49	128	6	0	121	100.0
50	845	8	0	122	100.0
52	108	6	0	123	100.0
53	2	6	0	124	100.0
54	172	10	0	125	100.0
56	4,967	8	0	126	100.0
57	200	4	0	127	100.0
59	1	2	0	128	100.0
60	15	6	0	129	100.0
63	2	8	0	130	100.0
66	399	10	0	131	100.0
67	2,474	14	0	132	100.0
70	2	10	0	133	100.0
73	1	4	0	134	100.0
75	1	8	0	135	100.0
76	31	8	0	136	100.0
77	58	14	0	137	100.0
79	6	2	0	138	100.0
82	648	6	0	139	100.0
85	1	4	0	140	100.0
87	145	12	0	141	100.0
88	12	12	0	142	100.0
89	2	4	0	143	100.0
90	3	4	0	144	100.0
92	1	2	0	145	100.0
93	6	4	0	146	100.0
94	1,046	10	0	147	100.0
96	891	14	0	148	100.0
97	7	4	0	149	100.0
99	1	2	0	150	100.0
100	2	4	0	151	100.0
102	109	12	0	152	100.0
103	37	10	0	153	100.0
104	2,960	8	0	154	100.0
106	697	4	0	155	100.0
113	1,504	4	0	156	100.0
115	7	6	0	157	100.0
116	2,071	12	0	158	100.0
117	342	18	0	159	100.0

Priority Area ID	Area (km^2)	Degree Centrality	Betweenness Centrality	Betweenness Centrality Rank	Cumulative Percent
124	2	6	0	160	100.0
126	555	6	0	161	100.0
128	357	8	0	162	100.0
130	352	10	0	163	100.0
132	48	8	0	164	100.0
136	481	4	0	165	100.0
140	556	6	0	166	100.0
145	125	4	0	167	100.0
147	316	4	0	168	100.0
149	7	10	0	169	100.0
150	2,456	4	0	170	100.0
151	2,121	10	0	171	100.0
153	2	8	0	172	100.0
154	2	10	0	173	100.0
155	7	10	0	174	100.0
156	2	6	0	175	100.0
159	5	8	0	176	100.0
163	1	8	0	177	100.0
164	8	12	0	178	100.0
165	21	6	0	179	100.0
168	11	6	0	180	100.0
172	145	6	0	181	100.0
173	1,044	10	0	182	100.0
179	4,437	4	0	183	100.0
180	490	6	0	184	100.0
183	105	10	0	185	100.0
186	199	12	0	186	100.0
187	6	4	0	187	100.0
188	17	2	0	188	100.0

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