RESEARCH ARTICLE

Range-wide connectivity of priority areas for Greater Sage-Grouse: Implications for long-term conservation from graph theory

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ABSTRACT

The delineation of priority areas in western North America for managing Greater Sage-Grouse (*Centrocercus urophasianus*) represents a broad-scale experiment in conservation biology. The strategy of limiting spatial disturbance and focusing conservation actions within delineated areas may benefit the greatest proportion of Greater Sage-Grouse. However, land use under normal restrictions outside priority areas potentially limits dispersal and gene flow, which can isolate priority areas and lead to spatially disjunct populations. We used graph theory, representing priority areas as spatially distributed nodes interconnected by movement corridors, to understand the capacity of priority areas to function as connected networks in the Bi-State, Central, and Washington regions of the Greater Sage-Grouse range. The Bi-State and Central networks were highly centralized; the dominant pathways and shortest linkages primarily connected a small number of large and centrally located priority areas. These priority areas are likely strongholds for Greater Sage-Grouse populations and might also function as refugia and sources. Priority areas in the Central network were more connected than those in the Bi-State and Washington networks. Almost 90% of the priority areas in the Central network had ≥ 2 pathways to other priority areas when movement through the landscape was set at an upper threshold (effective resistance, ER_{12}). At a lower threshold (ER_4), 83 of 123 priority areas in the Central network were clustered in 9 interconnected subgroups. The current conservation strategy has risks; 45 of 61 priority areas in the Bi-State network, 68 of 123 in the Central network, and all 4 priority areas in the Washington network had ≤ 1 connection to another priority area at the lower ER_4 threshold. Priority areas with few linkages also averaged greater environmental resistance to movement along connecting pathways. Without maintaining corridors to larger priority areas or a clustered group, isolation of small priority areas could lead to regional loss of Greater Sage-Grouse.

Keywords: *Centrocercus urophasianus*, conservation reserve design, graph theory, Greater Sage-Grouse, network, priority areas, conservation

Conectividad de áreas prioritarias a lo largo de todo el rango de distribución de *Centrocercus urophasianus*: implicancias para la conservación a largo plazo a partir de la teoría de grafos

RESUMEN

La delimitación de áreas prioritarias en el oeste de América del Norte para el manejo de *Centrocercus urophasianus* constituye un experimento a gran escala para la biología de la conservación. La estrategia de limitar la perturbación espacial y de enfocar las acciones de conservación dentro de áreas delimitadas podría beneficiar a la mayor proporción de *C. urophasianus*. Sin embargo, el uso del suelo bajo restricciones normales afuera de las áreas prioritarias potencialmente limita la dispersión y el flujo génico, lo que puede aislar a las áreas prioritarias y generar poblaciones espacialmente disyuntas. Usamos la teoría de grafos, representando a las áreas prioritarias como nodos espacialmente distribuidos interconectados por corredores de movimiento, para entender la capacidad de las áreas prioritarias de funcionar como redes conectadas en las regiones Bi-Estatal, Central y de Washington dentro del rango de distribución de *C. urophasianus*. Las redes Bi-Estatal y Central estuvieron altamente centralizadas; un pequeño número de áreas prioritarias grandes y localizadas en el centro representaron las conexiones primarias y las vías de conexión más cortas. Estas áreas prioritarias son probablemente bastiones para las poblaciones de *C. urophasianus* y también podrían funcionar como refugios y fuentes. La red Central estuvo más altamente conectada que las redes Bi-Estatal y de Washington. Casi el 90% de las áreas prioritarias en la red Central tuvo ≥ 2 vías de conexión con otras áreas prioritarias cuando el movimiento a través del paisaje fue establecido en un umbral superior (resistencia efectiva, RE_{12}). En un umbral inferior (RE_4), 83 de las 123 áreas prioritarias en la red Central se agruparon en nueve subgrupos interconectados. La estrategia actual de conservación es riesgosa; 45 de las 61 áreas prioritarias en la red Bi-Estatal, 68 de las 123 en la red Central, y las 4 áreas prioritarias en la red de Washington tuvieron ≤ 1 conexión a otra área

prioritaria en el umbral inferior ER_4. Las áreas prioritarias con menos vínculos también tuvieron en promedio mayor resistencia ambiental al movimiento a lo largo de las vías de conexión. Sin el mantenimiento de los corredores hacia las áreas prioritarias más grandes o hacia una agrupación, el aislamiento de áreas prioritarias pequeñas puede llevar a la pérdida regional de *C. urophasianus*.

Palabras clave: áreas prioritarias para conservación, *Centrocercus urophasianus*, diseño de reservas para conservación, red, teoría de grafos

INTRODUCTION

The Greater Sage-Grouse (*Centrocercus urophasianus*) is a galliform endemic to arid and semiarid sagebrush (*Artemisia* spp.) landscapes of western North America (Schroeder et al. 1999). Greater Sage-Grouse currently occupy approximately half of their presettlement habitat distribution and have recently received much attention for their long-term population declines (Schroeder et al. 2004, Garton et al. 2011). Broad-scale habitat loss and fragmentation from synergistic cycles of wildfire and conversion to invasive plant communities as well as from human land use are the primary causes of population declines (Knick and Connelly 2011). Therefore, the most pressing challenge to long-term Greater Sage-Grouse persistence is conservation of remaining large, intact sagebrush landscapes (Stiver et al. 2006, Connelly et al. 2011a).

The U.S. Fish and Wildlife Service (USFWS 2015) recently reviewed the status of Greater Sage-Grouse in the United States and determined that listing under the Endangered Species Act was not warranted. As part of the strategy to avert current and future listings, the 11 western state and federal management agencies within the Greater Sage-Grouse range developed conservation plans adopting the concept of core or priority areas (Priority Areas for Conservation [PACs; USFWS 2013], or equivalent terms designated in individual state agency plans). Within priority areas, the allowable spatial area of disturbance due to human land use, such as energy development, is tightly restricted. Land use is allowed to continue outside priority areas under normal regulations. Conservation strategies focused on priority areas can potentially have the greatest benefit by targeting areas containing the highest numbers of Greater Sage-Grouse (Doherty et al. 2010).

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 terrestrial species. Individual priority areas range in size from <1 to ~79,500 km^2 and encompass the broad spectrum of reserve design paradigms from single large to several small reserves. We do not know the minimum area required to support Greater Sage-Grouse populations, although the largest priority areas likely can sustain viable populations completely within their boundaries. However, the smallest priority areas clearly enclose much less than the annual range of a Greater Sage-Grouse (4–615 km^2; Connelly et al. 2011b). Thus, different spatial and temporal scales of connectivity among priority areas may be necessary for dispersal, generally <30 km for marked individuals (Knick and Hanser 2011, Thompson 2012), gene flow, or movement among seasonal habitats that can be separated by up to 160 km (Connelly et al. 2011b, Smith 2013).

The Greater Sage-Grouse is a landscape species; individuals often use a mosaic of widely separated seasonal habitats embedded within large annual ranges to meet their resource requirements (Knick and Connelly 2011). Maintaining the persistence of wide-ranging species, such as the Greater Sage-Grouse, experiencing population and habitat fragmentation is challenging (Harris 1984, Margules et al. 1994). Individual priority areas, even large ones, may not be able to fully mitigate the effects of internal disturbances (Pickett and Thompson 1978, Lindenmayer et al. 2008), which for Greater Sage-Grouse include habitat loss to recent wildfires (Miller et al. 2011) and threats to populations from West Nile virus (Walker and Naugle 2011).

We propose that the network of priority areas might be best understood from the conceptual foundation of conservation reserve design, in which the configuration of existing high-quality patches in relation to potential movement pathways and barriers is an important component (Noss and Harris 1986). Delineating and managing priority areas as a network, rather than as a collection of individual priority areas, could be an effective strategy to link high-quality priority areas into a larger whole to increase the likelihood of long-term survival of Greater Sage-Grouse populations.

We used graph theory (Horary 1969) to understand how the spatial arrangement of priority areas might function as a network of connected reserves. Graph theory characterizes node and linkage relationships to provide insights into network function and has been applied across a diverse spectrum of networks, such as those describing people, organizations, computers, and internet hubs (Freeman 2004, Wasserman and Faust 2004, Newman 2010). In ecology, graph theoretic applications can describe potential network connectivity, particularly at large spatial scales, using basic inputs of patch distribution and animal movements (Urban and Keitt 2001, Calabrese and Fagan

2004). Network structures can vary from scale-free distributions, which are dominated by a few centralized and highly connected nodes that serve as hubs, to widely dispersed configurations, in which connections are distributed equally among all nodes. Each different configuration has implications or consequences for ecological function (Minor and Urban 2007, 2008).

We described the basic characteristics of the Bi-State, Central, and Washington networks of priority areas designated for Greater Sage-Grouse. We then modeled connectivity within each network by combining centrality metrics and the potential for movement among priority areas across an effective resistance surface that combined distance and habitat suitability. Quantifying these network features has important implications for the ongoing conservation effort for Greater Sage-Grouse by highlighting (1) the relative importance and configuration of priority areas within each network, (2) the implications for how the network might function, implied from its structure, and (3) the relative isolation among priority areas based on the potential for movement through their surrounding environment. As such, our analysis presents a working hypothesis of how the network of priority areas might function to conserve Greater Sage-Grouse populations.

METHODS

Study Area

We included 2,030,230 km^2 of the western United States in our analysis of designated priority areas across the current Greater Sage-Grouse range (Schroeder et al. 2004). The area contains a diversity of shrubland types, of which landscapes dominated by sagebrush are the most important to Greater Sage-Grouse (Connelly et al. 2000). Mountain ranges, forest communities, and agricultural regions, particularly those within broad plains of large river systems, are not used by Greater Sage-Grouse and can act as barriers to their movements (Fedy et al. 2014). Lands used by Greater Sage-Grouse are of mixed administration and ownership (Knick 2011). Public lands dominate the western region and are managed primarily by the U.S. Bureau of Land Management and the U.S. Forest Service for multiple uses. Private lands, which characteristically are fertile lands with deep soils and access to water, constitute the greatest proportion of ownership in the northern and eastern parts of the Greater Sage-Grouse range and can comprise more than two-thirds of the landscapes used by Greater Sage-Grouse (Doherty et al. 2010, Knick 2011).

Each state has used different criteria for delineating the boundaries of priority areas, but each generally has incorporated metrics for Greater Sage-Grouse populations (lek [breeding] locations and breeding bird densities; Doherty et al. 2010) and habitat areas (identified from known Greater Sage-Grouse distributions, or seasonal habitats for breeding, nesting, brood-rearing, or wintering derived from observations or telemetry data). In some cases, states have also adjusted boundaries to exclude private lands, federal lands approved for or in the process of being developed for energy or other management activities, or preexisting development.

We created a range-wide map of priority areas in western North America by merging the 11 individual state coverages delineating priority areas in the Greater Sage-Grouse range (Supplemental Material Figure S1, Supplemental Material Table S1). Boundaries of polygons were merged across state lines when shared, but followed state lines when adjacent priority areas did not match across borders. We also merged or removed priority areas of <1 km^2, which typically were slivers left over after a state's original delineation and subsequent edits. The final map contained 188 priority areas; average size was 16,842 km^2 and ranged from 1.1 to 79,495 km^2. The frequency distribution consisted predominantly of small priority areas; almost half (93 of 188) of the priority areas were <125 km^2 and 90% were <3,300 km^2. The total land area contained within priority areas was ~316,000 km^2 and included ~16% of our study area.

Priority Areas as Spatial Networks

We constructed a graph network consisting of priority areas (nodes) and interconnecting movement pathways (links) defined by environmental suitability (Bunn et al. 2000, Urban and Keitt 2001, Diestel 2005). The graph was undirected: we assumed that movement was equal between pairs of priority areas regardless of direction or relative difference in area and presumed population size. We developed separate networks for the Bi-State distinct population segment and the Washington state populations because Greater Sage-Grouse in these regions are genetically isolated from those in the Central range (Oyler-McCance et al. 2005, 2014).

Connectivity among nodes is a function of distance and environmental resistance, both of which impose costs on movement through the interstitial landscape (Cushman et al. 2009, Spear et al. 2010). We modeled environmental resistance to movement relative to an index of habitat suitability (Zeller et al. 2012). Greater Sage-Grouse may perceive a landscape differently when moving within a range, moving between seasonal ranges, or when dispersing. Similarly, connectivity of areas for individual movements obtained from telemetry data might be different from connectivity derived from genetic information or breeding locations (Shirk et al. 2015). We assumed that the likelihood that Greater Sage-Grouse would move through a habitat mosaic was related to the suitability of those habitats.

We first created a range-wide map of habitat suitability for Greater Sage-Grouse at 1-km^2 resolution from a model of ecological minimum requirements following the protocol developed previously for the western portion of the range (Knick et al. 2013) and described in the Appendix. We then transformed the map of habitat suitability to environmental resistance under the untested assumption that the likelihood of sage-grouse movement through a 1-km^2 grid cell followed an inverse relationship to habitat suitability.

We used circuit theory to model potential movement pathways between priority areas based on an effective resistance (ER) that combined distance and environmental resistance (R: McRae et al. 2008; Γ_{ij}: Hanks and Hooten 2013). ER is a measurement on a scale between complete absence of environmental resistance (in which all priority areas are interconnected because there is no cost of movement) to total barrier (all priority areas are isolated from each other). Circuit theory uses electrical current flow between nodes connected by resistors to model movement potential. In an ecological context, linear distance and impedance by habitat or landscape features that constrain movements across a linkage increase resistance. In contrast, resistance decreases when multiple corridors or broad pathways provide options for movement. Whereas Euclidean or least-cost methods delineate single pathways independent of linkage width, circuit theory offers the advantage that multiple pathways can be simultaneously evaluated across heterogeneous landscapes to estimate effective resistance (McRae 2006, McRae et al. 2008).

We used Circuitscape 4.0 (http://www.circuitscape.org, McRae and Shah 2008) to estimate ER iteratively between all pairwise combinations of priority areas. We treated priority areas as focal patches, which permitted pathways from polygon boundaries of priority areas rather than points, to capture the influence of reserve patch configuration and size on movement potential. A low ER between pairs of priority areas represented a relatively high potential pathway for Greater Sage-Grouse movement. Resulting ER values described the links, or connecting movement pathways, in our graph.

A final map of maximum current density derived from summing all pairwise pathways across the range-wide raster surface represented the spatial structure of connectivity for the network of priority areas. We used maximum current density to reduce the confounding effects of network configuration (halo effect) in the Circuitscape results. Locations of high current densities may function as bottlenecks (pinch points) to Greater Sage-Grouse connectivity if movement is constricted or alternative pathways are not available (McRae et al. 2008, Dickson et al. 2013). These locations potentially represent conservation priorities for Greater Sage-Grouse because their

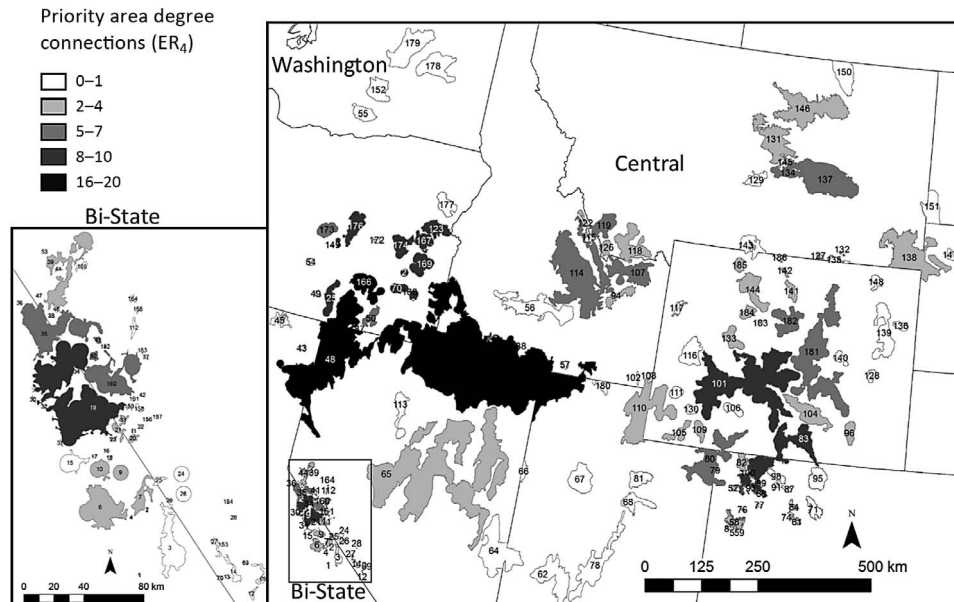loss may disrupt connectivity within the network and isolate priority areas.

Network Analysis

We used 2 centrality metrics, degree and betweenness, to describe the network of priority areas (Wasserman and Faust 2004). Degree centrality measures the relative importance and configuration of nodes within the network based simply on the number of connections to other nodes (Freeman 2004, Wasserman and Faust 2004, Newman 2010); more connections indicate greater influence and a more central position in the network (Erdos and Gallai 1960, Diestel 2005). We also measured the total and average degree resistance for each node by summing the ER of connections.

We restricted the potential for priority areas to be connected based on 2 thresholds of ER. An upper threshold of 12 (ER$_{12}$) was the minimum ER separating priority areas in the Bi-State and the Central Greater Sage-Grouse ranges; populations in the Bi-State distinct population segment have been genetically isolated for thousands of years (Oyler-McCance et al. 2014). More recently, Greater Sage-Grouse in Jackson Hole, Wyoming (priority area ID 117), have shown genetic differentiation from neighboring populations (Schulwitz et al. 2014). The ER between priority areas corresponding to their sampling locations ranged from 12 to 17. Although ER$_{12}$ on our scale may represent an upper threshold, genetic separation may also occur across much lower thresholds. Priority areas in southeastern Montana–North Dakota (ID 151; ER = 5) and South Dakota (ID 138; ER = 3) were genetically separated from priority areas in east-central Montana (ID 137; Cross et al. in press). We also characterized network structure at ER$_4$ to represent a lower threshold of environmental resistance that might restrict movement.

Betweenness quantifies the number of times that a node acts as a bridge along the shortest path (minimum set of connecting links) between 2 other nodes (Freeman et al. 1991, Brandes 2008). Nodes with high scores for betweenness 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, Carroll et al. 2012).

We estimated the number of components and identified the priority areas that comprised their membership within each network for the 2 ER thresholds. Components were subsets of priority areas that were interconnected below the ER threshold but isolated from the rest of the network by an ER exceeding the threshold (Minor and Urban 2007). In concept, a Greater Sage-Grouse could traverse the greatest length of a component without exceeding the ER threshold, but could not disperse outside the component

FIGURE 1. Number of degree connections for priority areas for Greater Sage-Grouse across their range in the western U.S. within the Bi-State, Central, and Washington networks having an effective resistance <4 (ER_4) for movement pathways to other priority areas. Effective resistance is a measurement on a scale between complete absence of environmental resistance (in which all priority areas are interconnected because there is no cost of movement) to total barrier (all priority areas are isolated from each other). Degree connections are the total number of connections for each priority area and thus measure relative importance and configuration within the network. Numbers for each priority area correspond to the ID in Supplemental Material Table S1.

to any other nodes. We calculated centrality metrics using the igraph package (Csardi and Nepusz 2006) and computed summary statistics using R (R Core Team 2015).

RESULTS

Network Configuration
The Bi-State network was characterized by a few large priority areas surrounded by numerous smaller priority areas that were largely unconnected (Figure 1). The median size of the 61 priority areas was 5 km^2 and ranged from 1 to 1,870 km^2 (Supplemental Material Table S2). At the lower ER_4 threshold for connectivity, almost 75% (45 of 61) of the priority areas had ≤1 connection to other areas (Table 1, Figure 2). Even when the upper threshold of ER_{12} (based on genetic separation between the Bi-State and Central populations) was used, 19 of 61 priority areas had ≤1 connection. Two primary components (subgroups within the network) dominated the Bi-State network, consisting of separate clusters enclosing 6 and 16 priority areas at the threshold of ER_4, and containing 5 and 45 priority areas at ER_{12} (Figure 3). The majority of components at ER_4, and 20% at ER_{12}, consisted of individual priority areas (Table 1). Priority areas that had few links (Deg_n) also averaged a greater ER per connection ($Deg_{ER} = -0.09(Deg_n) + 9.7$; $F_{1,48} = 10.1$, $P = 0.003$) that further increased their potential isolation.

The Central network contained 123 priority areas, including the largest single priority area (ID = 48; 79,495 km^2; Supplemental Material Table S3) in the Greater Sage-Grouse range (Figure 1). A greater proportion of priority areas were more highly connected than in the Bi-State network; almost half ($n = 55$) had >1 connection at ER_4, and 107 priority areas were connected by >1 link at ER_{12} (Table 1). The Central network had 49 components when connections did not exceed the ER_4 threshold, which were mostly clustered into 9 components of >1 priority area. The network was almost completely connected at the higher threshold of ER_{12} (Figure 3). Two separate clusters contained 110 and 5 priority areas; only 8 components had single membership (Table 1). Similarly to the Bi-State network, the average ER increased with a decrease in the number of connections ($Deg_{ER} = -0.05(Deg_n) + 8.3$; $F_{1,113} = 7.2$, $P = 0.008$).

The Washington network exhibited little connectivity among its 4 priority areas that ranged in size from 1,285 to 4,437 km^2 (Supplemental Material Table S4). Two components consisted of 2 priority areas each at ER_{12} (Table 1). At the lower ER_4 threshold, the 4 priority areas were unconnected to each other (Figure 3). The minimum ER separating Washington priority areas and those in the Central network was 24, indicating a low potential for any connectivity between these 2 regions.
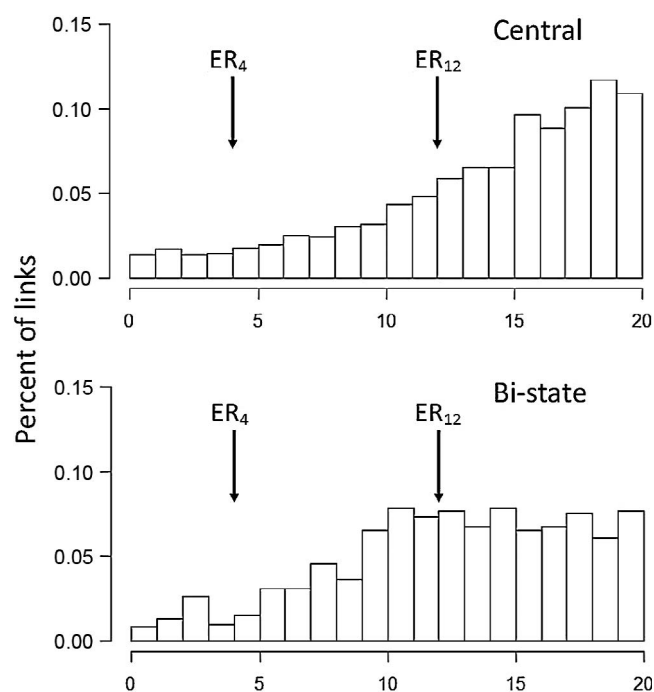
TABLE 1. Structure of the Bi-State ($n = 61$ priority areas), Central ($n = 123$), and Washington ($n = 4$) networks of priority areas in the Greater Sage-Grouse range (western U.S.).

	Bi-State		Central		Washington	
Effective resistance [a]	ER_4	ER_{12}	ER_4	ER_{12}	ER_4	ER_{12}
Degree linkages [b]						
n	70	530	336	1,714	0	4
Maximum	10	31	20	47	—	1
Degree resistance (mean)	2.2	8.1	2.0	7.4	—	8.5
Priority areas ≤ 1	45	19	68	16	4	4
Components [c]						
n	41	13	49	10	4	2
Membership $= 1$	39	11	40	8	4	0

[a] Effective resistance (ER) was estimated from Circuitscape (McRae and Shah 2008) using pairwise sets of priority areas overlaid on a surface of environmental suitability (Appendix). See Figure 1 for explanation of ER. Thresholds were derived from models of genetic population structure in Montana for ER_4 (Cross et al. in press) and from genetic isolation of the Bi-State priority areas from the Central network for ER_{12} (Oyler-McCance et al. 2014).

[b] Degree linkages included only connections between priority areas that did not exceed the ER threshold. Frequency distribution of linkage ER is shown in Figure 2. Degree resistance is the average ER of all linkages in the network.

[c] Components were subsets of networks that consisted of groupings of priority areas that were interconnected below the ER threshold but isolated from the rest of the network by an ER exceeding the threshold (Minor and Urban 2007). In concept, a Greater Sage-Grouse could traverse the greatest length of a component without exceeding the ER threshold, but could not disperse outside the component to any others. Membership $= 1$ indicates the number of components that included only 1 priority area.
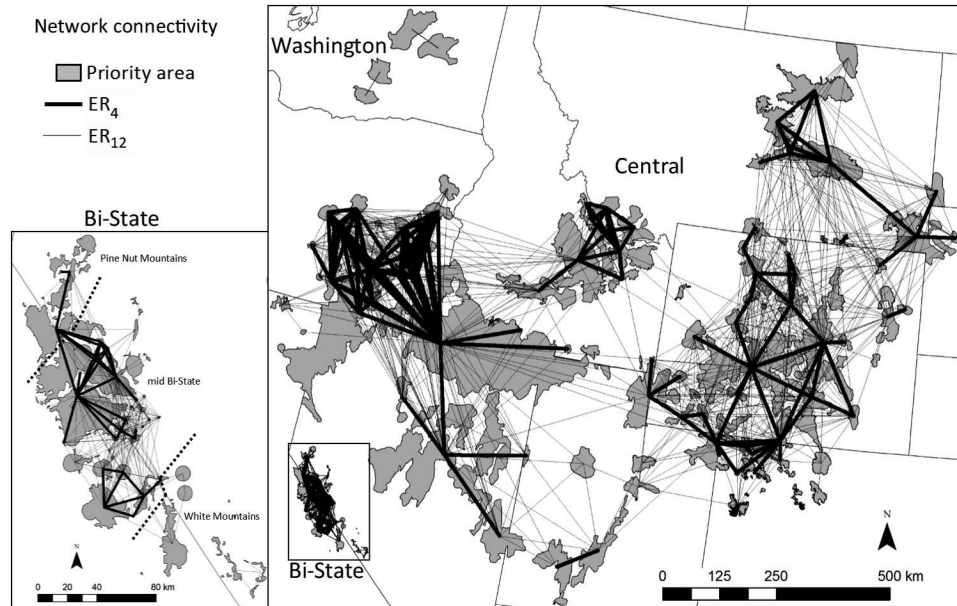

FIGURE 2. Frequency distribution of linkage effective resistance (ER) for the Central and Bi-State networks of priority areas for Greater Sage-Grouse across their range in the western U.S. relative to our ER_4 and ER_{12} thresholds (see Figure 1 for explanation of ER). Thresholds were truncated at ER_{20} because these links often represent pairwise connections through an intermediate priority area.

Network Structure and Movement Dynamics

Connectivity in the Bi-State and Central networks was primarily directed through a small number of large priority areas (Figure 3). In the Bi-State network, 71% of the shortest pathways (percent of cumulative betweenness scores) went through 3 priority areas (ID = 19, 21, and 35) at the ER_4 threshold. Forty priority areas in the Bi-State network were not located on any of the shortest pathways at ER_{12} (betweenness = 0). In the Central network, 5 priority areas at ER_4 accounted for 58% of the cumulative betweenness scores; 98 of 123 priority areas had a 0 betweenness score at ER_{12}. Priority areas that scored a 0 for betweenness (none of the shortest pathways went through these nodes) were small and averaged 23.4 km^2 ($n = 52$) at ER_4 and 4.4 km^2 ($n = 31$) at ER_{12} in the Bi-State network and 796.6 km^2 ($n = 88$) at ER_4 and 307.6 km^2 ($n = 41$) at ER_{12} in the Central network.

Movement potential, estimated by maximum Circuitscape current densities, highlighted connectivity across the network characterized by numerous and multiple pathways between most of the priority areas (Figure 4). Pinch points between priority areas delineated by high current densities may indicate important habitat linkages where connectivity is constrained due to surrounding natural or anthropogenic barriers to sage-grouse movements. Habitat change or loss at these locations may result in disconnections among nodes or in the use of less efficient (more costly) habitat pathways connecting priority areas.
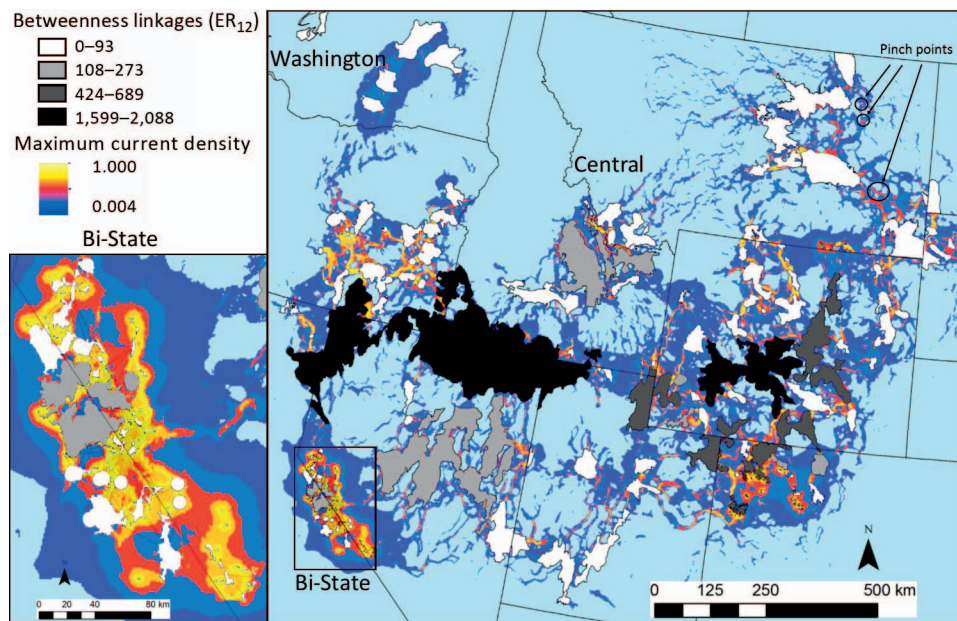
Low current densities delineated areas where habitat was broadly or diffusely connected. Average maximum current density across the entire study area was low (≈ 0.1)

FIGURE 3. Degree connectivity among priority areas for Greater Sage-Grouse across their range in the western U.S. within the Bi-State, Central, and Washington networks at effective resistance thresholds of 4 (ER_4) and 12 (ER_{12}) for movement (see Figure 1 for explanations of degree connectivity and effective resistance). The 3 subpopulations in the Bi-State network (Pine Nut Mountains, mid Bi-State, and White Mountains) were delineated from genetic structure (Oyler-McCance et al. 2014).

because the study area included large expanses of high-elevation mountain ranges, forested communities, highly populated areas, agriculture development, and other areas of low habitat value for Greater Sage-Grouse. For example, the Snake River Plain in southern Idaho, which contains

Interstate 84, large areas of developed private lands, and significant tracts of cheatgrass (*Bromus tectorum*) and recently burned areas, may present a major barrier for Greater Sage-Grouse movements at an ER_4 threshold among priority areas (Figure 3) and for movements among

FIGURE 4. Betweenness connectivity (number of shortest pathways) for the Bi-State, Central, and Washington networks of priority areas for Greater Sage-Grouse across their range in the western U.S. Movement corridors among priority areas were delineated from the maximum current density using Circuitscape (McRae and Shah 2008). High to medium current densities represent areas where movement potential is high and possible pinch points where constricted.

all potential pathways delineated by current densities (Figure 4).

DISCUSSION

Graph theory provides a framework for understanding network function and characterizing the importance of priority areas within a network by using basic inputs of population units and movement behavior (Calabrese and Fagan 2004). To evaluate priority areas as a connected network for Greater Sage-Grouse, we produced a range-wide model of habitat suitability from which we estimated environmental resistance to movement, identified linkages between priority areas, and determined the relative importance of priority areas for facilitating Greater Sage-Grouse movement. Our results at the ER_{12} threshold to movement corresponded to the range-wide genetic model that demonstrated a high degree of connectivity across the Central network, but isolation of the Washington and Bi-state populations (Oyler-McCance et al. 2005). We compared our results from graph theory with the genetic structure recently delineated for the Bi-State distinct population segment of Greater Sage-Grouse (Oyler-McCance et al. 2014) which suggested that 3 subpopulations occurred in the Bi-State segment (Figure 3). Although our graph delineated 2 primary components, only 1 link at the ER_4 threshold connected the genetic subpopulation in the Pine Nut Mountains with the mid Bi-State subpopulation. The separation of the southern White Mountain subpopulation from the mid Bi-State population by singleleaf pinyon (*Pinus monophylla*) and juniper (*Juniperus* spp.) woodlands and steep mountain ranges, which are unsuitable for Greater Sage-Grouse, was reflected in both the graph and genetic data.

The Bi-State and Central networks of priority areas for conserving Greater Sage-Grouse were highly centralized and were characteristic of scale-free networks (Li et al. 2005, Minor and Urban 2008). A few large priority areas accounted for a high proportion of the linkages and movement pathways within each network. In contrast, a relatively high proportion of priority areas had few linkages, particularly at the ER_4 threshold, and most were not linked along the shortest pathways between priority areas within the network. In accordance with the properties of scale-free networks, loss of priority areas with few connections has little consequence for maintaining connectivity across the entire network. In fact, the U.S. Fish and Wildlife Service decision that listing Greater Sage-Grouse under the Endangered Species Act in 2005 was not warranted (USFWS 2005) was based in part on the relative stability of core populations (now corresponding to the large, highly connected priority areas in our Central network) that would ensure long-term persistence even though peripheral populations might be lost. The more recent thinking, if not the network implication and ecological reality, is that all populations and priority areas are of equal conservation importance across the range and that each priority area bounds a homogeneous patch of sagebrush habitat (USFWS 2010, 2013). Our results for the Bi-State and Central networks of priority areas for Greater Sage-Grouse provide an interesting contrast between implications derived from a graph theoretic approach and its application in managing a species of conservation concern.

The Achilles heel of scale-free networks (Li et al. 2005) is that the loss of central hubs can fragment the entire configuration, or that their high connectivity and control of pathways can aggressively spread unwanted agents such as disease. The large priority areas, particularly those in the Central network, likely can sustain viable year-round Greater Sage-Grouse populations because of the expansive sagebrush regions within their boundaries. Large priority areas also might function as sources to augment adjacent populations, either in priority areas too small to support persistent sage-grouse populations or in nonpriority areas. Large size is also correlated with longer boundaries that allow for more opportunities for dispersal to 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. As expected from network characteristics, loss or fragmentation of these large priority areas or their associated connections would have a disproportionally large influence across the entire network.

Priority areas that have limited connectivity from a network perspective are not unimportant for conserving Greater Sage-Grouse populations. Priority areas with few connections in this study generally were smaller and were distributed in peripheral regions surrounding the larger and more central priority areas. These small priority areas collectively contained a large amount of the sagebrush habitat across the network. Although they may not be critical stepping-stones along primary pathways identified by betweenness metrics (Bodin et al. 2006, Saura et al. 2014), their connections to surrounding priority areas are likely important for the functioning of clusters toward maintaining Greater Sage-Grouse populations.

The formal conservation strategy, which is focused on priority areas, has not designated connecting corridors among priority areas, which could effectively isolate priority areas or regions. Landscape connectivity is often assessed in the form of least-cost paths, corridors, and graph networks to identify critical habitat connections that, if severed, could potentially isolate populations (Bunn et al. 2000, Urban and Keitt 2001, LaPoint et al. 2013). Our analyses also highlighted important features between priority areas, such as pinch points, that land managers can target for conservation to help secure Greater Sage-

Grouse seasonal and dispersal movements. Although pinch points identify critical locations where movement is constrained, we note that the entire corridor, including broader areas where movement is less constrained, is important for network connectivity. If resources are limited, sagebrush restoration at pinch points between priority areas might enhance potential corridors and preserve the likelihood of population persistence by facilitating movements that sustain or augment populations, dispersal, and gene flow.

The parameters defining connectivity in our study were based on a habitat suitability metric measured at 1-km^2 resolution. We assumed that movement through a cell was inversely proportional to our measure of habitat suitability. This assumption has not been tested by movement data. However, we emphasize that connectivity involves more than assessing movement between sequential points, but must be interpreted within the context of genetic, individual, and population levels, as well as taking into account behavioral differences between seasonal and dispersal movements. We used genetic separation to define our thresholds of connectivity. However, the primary concern for Greater Sage-Grouse may not be genetic diversity (which can be maintained by few dispersers over time spans of multiple generations), but rather connectivity that allows the exchange of individuals at sufficient rates to recolonize or augment populations (Crooks and Sanjayan 2006, Luque et al. 2012, Davis et al. 2015).

Synthesis and Application

The strategy currently implemented for conserving Greater Sage-Grouse is based on designated priority areas in each of the 11 states across its range (USFWS 2013). Focusing conservation actions on a relatively small (<15%) 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 no longer retain the characteristics necessary to sustain Greater Sage-Grouse populations, similar to what now exists in the Washington network.

The current network of priority areas has many important characteristics for maintaining Greater Sage-Grouse populations. The Bi-state and Central networks contain a range of large-and small-sized priority areas that might provide different functions, particularly as sources and connecting habitat along movement corridors. The current network also contains connected clusters of areas that might be too small individually to sustain viable populations. Our analysis focused on 3 major regions within the Greater Sage-Grouse distribution. However, there is likely a hierarchical system within the Bi-State and Central networks for both priority areas and metapopu-

lations. These smaller groups might have different structures and functions independent of their positions within the larger distribution.

Conservation based on a system of static reserves may fail in rapidly changing landscapes (Bengtsson et al. 2003). Numerous factors, both natural and anthropogenic, make it unlikely that the network of priority areas can be sustained as currently delineated (Knick and Connelly 2011, Miller et al. 2011). Our degree and betweenness centrality measures could be used to rank priority areas for conservation and help to predict impacts to connectivity when priority areas are lost, degraded, or fragmented (Blazquez-Cabrera et al. 2014; Supplemental Material Tables S2–S4). Thus, the boundaries of priority areas might need to be fluid and new sagebrush landscapes suitable for Greater Sage-Grouse identified to create a more dynamic network of reserves (Hanski 1999, Lindenmayer et al. 2008).

Adopting a range-wide conservation plan for Greater Sage-Grouse based on a network of priority areas has risks as well. Different conservation and management priorities among administrative units could disrupt the metapopulation structure, leading to greater isolation, and may 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. Priorities and land use plans often differ among state and federal management agencies, both within and outside the proposed priority area structure (Knick 2011, Copeland et al. 2014). However, the graph structure of this network suggests that Greater Sage-Grouse are likely to persist, even with the loss of smaller priority areas, as long as the large central hubs are maintained. Under this scenario, population numbers likely would be reduced and Greater Sage-Grouse would occupy a smaller range. The current strategy represents an exciting experiment in conservation reserve design and the opportunity to understand how network configuration can influence population dynamics and persistence for a species of conservation concern.

Ethics statement: We did not handle animals, thus no ethics protocols were required to be followed.

Author contributions: S.T.K., S.E.H., and M.R.C. developed the concept for the study; M.R.C., S.T.K., and S.E.H. conducted the analysis and wrote the paper.

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APPENDIX

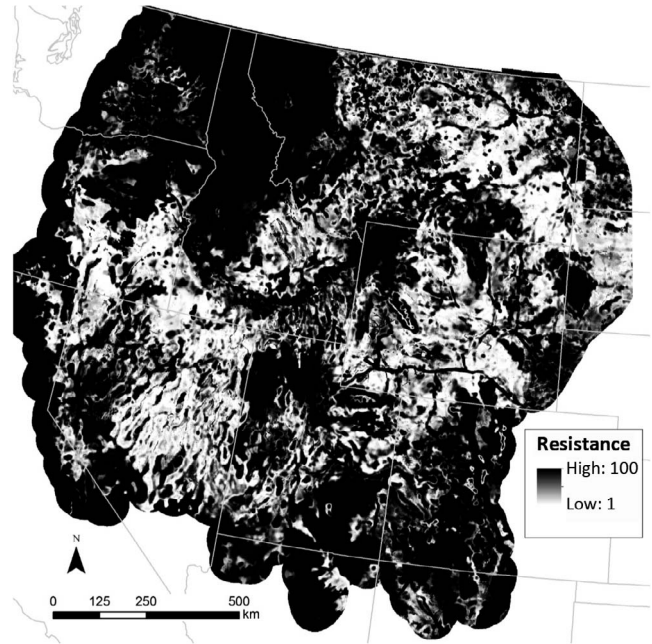### A Range-wide Model of Ecological Minimum Requirements for Greater Sage-Grouse

Our modeling of ecological minimum requirements for the range-wide distribution of Greater Sage-Grouse followed a similar protocol used previously for the western region (Knick et al. 2013). We used 23 variables to describe land cover, fire history (area burned from 1980 to 2013), terrain (topographic accessibility; Sappington et al. 2007), climate, and edaphic and anthropogenic features measured at our minimum mapping unit of 1-km^2 resolution across the Greater Sage-Grouse range. Land-cover variables consisted of combined classes in the Landfire Existing Vegetation Type (http://www.landfire.gov/, Rollins 2009) for big sagebrush (*Artemisia tridentata*), black sagebrush (*A. nova*), little sagebrush (*A. arbuscula*), saltbush (*Atriplex* spp.), exotic grassland (primarily *Bromus tectorum*), native grassland, pinyon–juniper (*Pinus–Juniperus* spp.) woodland, conifer forest, and riparian associations. Climate variables were obtained from the PRISM Climate Group (Daly et al. 2004, Prism Climate Group 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 (http://websoilsurvey.nrcs.usda.gov/). 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.

An ecological minimum represents a multivariate construct of the basic requirements for a species (Rotenberry et al. 2002). We calculated the multivariate vector of ecological minimums from a partitioned Mahalanobis D^2 model of presence only data (Dunn and Duncan 2000, Rotenberry et al. 2002). Lek locations were used to indicate presence in a previous model of Greater Sage-Grouse ecological minimums across their western range (Knick et al. 2013). We did not have permission to use lek location data from all states across the Greater Sage-Grouse range. Therefore, we assumed that the priority areas delineated by states included a large proportion of the Greater Sage-Grouse population and also captured higher-quality habitat than that occurring outside the defined priority areas, despite having some areas excluded because of ownership or forecast disturbance. We randomly selected 1,669 points within individual priority areas as presence data and extracted values for corresponding environmental variables to calibrate models.

Mahalanobis D^2 is the standardized difference between the multivariate means of environmental variables and the values of those variables at locations where a species occurs. Smaller D^2 values indicate similarity to the vector of multivariate means; dissimilarity increases with greater D^2 distance. We partitioned Mahalanobis D^2 into k separate components that each represented a multivariate relationship between the environmental variable and a species occurrence. To derive partitions, we performed a principal components analysis (PCA) on 1,000 iterative samples created by bootstrapping the calibration data. The

APPENDIX TABLE 2. 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

APPENDIX FIGURE 5. Environmental resistance surface to movement for the Greater Sage-Grouse range in the western U.S. We used Circuitscape (McRae and Shah 2008) to estimate effective resistance (ER) values (see Figure 1 for explanation of ER) from environmental resistance, which was a transformation of the similarity of environmental values at map locations to the multivariate mean vector of minimum habitat requirements for Greater Sage-Grouse.

final model was created by subsequently averaging the PCA output after correcting for sign ambiguity (Bro et al. 2008) across all iterations.

We evaluated the performance of the habitat suitability index (HSI) model derived for priority areas using a separate but related spatial layer of Greater Sage-Grouse breeding densities (Doherty et al. 2010). We used 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 nonhabitat points predicted to be habitat; Fielding and Bell 1997). To generate the sample of presence data for model evaluation, we overlaid the 100% Greater Sage-Grouse breeding densities (Doherty et al. 2010), representing spatial locations of all known Greater Sage-Grouse breeding sites, onto 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 the breeding density boundaries. To calculate the AUC, we randomly sampled 5,000 presence points and 20,000 absence points from the Greater Sage-Grouse breeding density map. 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 2 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 2 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.

We used principal component partition 14 to model ecological minimums across the sage-grouse range. Partition 14 met our criteria of having an eigenvalue ≤ 1, a relative difference in eigenvalues among adjacent partitions (Appendix Table 2), and performance against evaluation data (AUC = 0.80, null AUC = 0.50, 95% CL = 0.49 and 0.50; t-test between the null AUC and true AUC = $-3,775.0$; $P << 0.001$), and met our subjective assessment of mapped results from different model partitions. We rescaled an inverse of the mapped output to range continuously from 0 to 1 based on a chi-square distribution with p-1 degrees of freedom of the D^2 distance (Rotenberry et al. 2002); 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.

We scaled the inverse of the habitat suitability scores by multiplying habitat values in each grid cell by 100 and using the function ((habitat value − maximum habitat value) * −1) + minimum habitat value to create a resistance surface (Appendix Figure 5). Resistance values assigned to each 1-km^2 grid cell ranged from 1 (lowest resistance, or

highest habitat value) to 100 (highest resistance, or lowest habitat value). Although the range of resistance values was linear from 1 to 100, the underlying suitability surface from which resistance was derived was scaled as a chi-square probability distribution (Rotenberry et al. 2002).

Thus, the multivariate vector describing the environment in any grid cell became increasingly dissimilar to the vector of ecological minimums with incremental decreases in similarity. We assumed that environmental resistance to movement followed a similar inverse function.