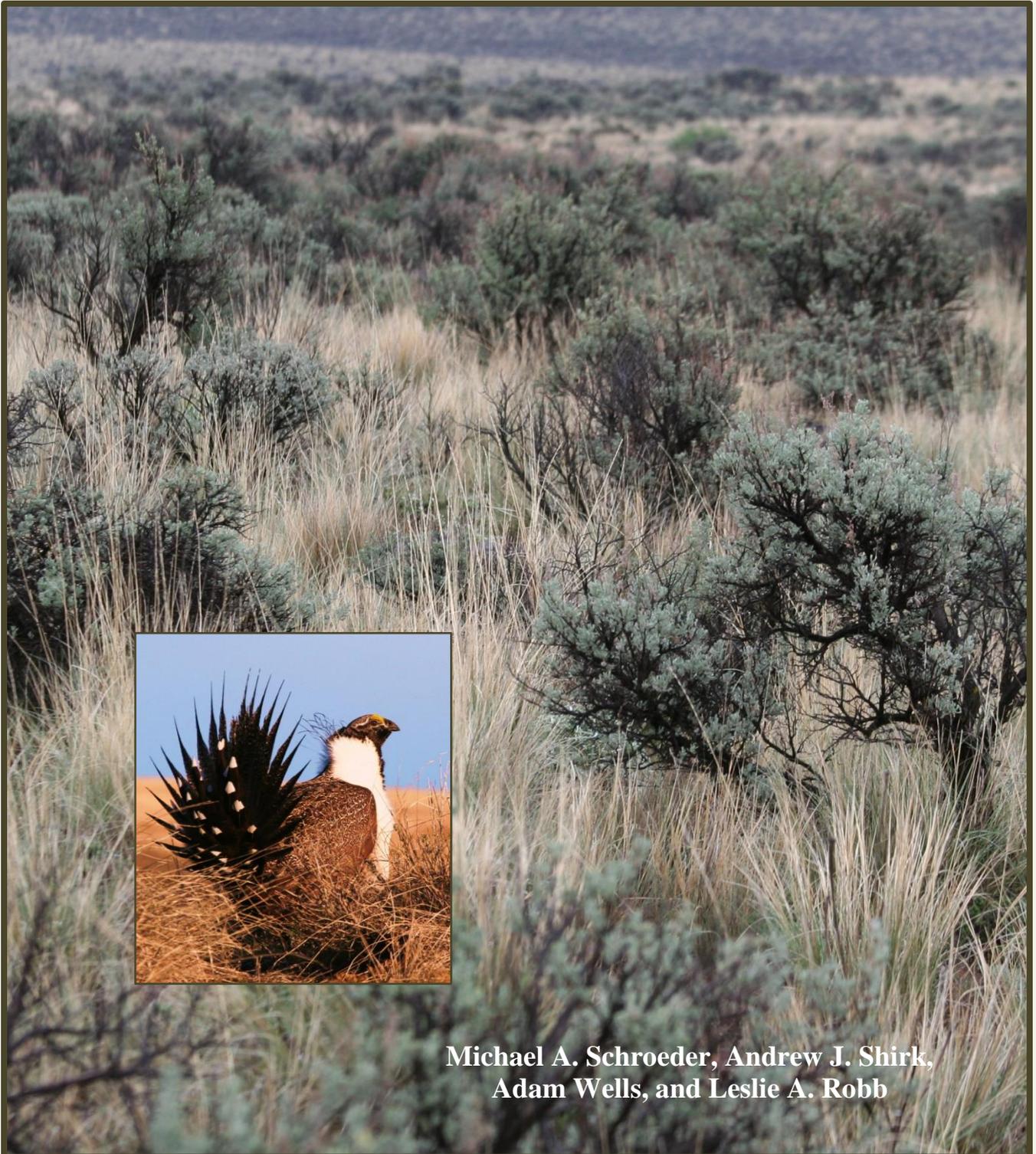


Habitat Occupancy and Movements by Greater Sage-Grouse in Washington State



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Cover photo of male Greater Sage-Grouse by Michael A. Schroeder. Title page and TOC page illustrations by Brian Maxfield.

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December 2015

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Acknowledgements

This project would not have been possible without the long-term data collected for Greater Sage-Grouse by Washington Department of Fish and Wildlife field biologists and we thank the numerous people who have contributed to this effort. We especially thank Jason Lowe (BLM) for acquiring GPS transmitters and Mike Atamian (WDFW) for managing the GPS dataset.

Funding

This report builds upon connectivity models developed by the Washington Wildlife Habitat Connectivity Working Group (WHCWG). In addition to funding provided by WHCWG organizations the following entities provided additional support:

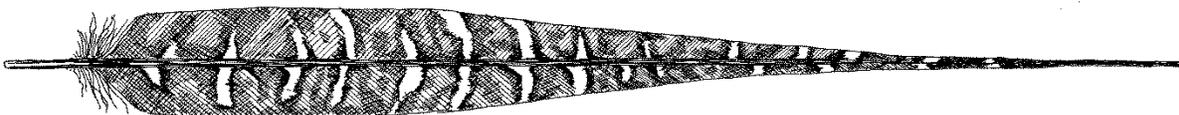
- ❖ Bureau of Land Management
- ❖ Department of Defense, Yakima Training Center
- ❖ Great Northern Landscape Conservation Cooperative



Columbia Plateau Ecoregion. Photo by Joe Rocchio.

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Abstract

Local extirpations drive species' range contractions, and are often precursors of extinction. Understanding the dynamics underlying these processes is critical for devising effective conservation strategies. The Greater Sage-Grouse (*Centrocercus urophasianus*) is an example of a species undergoing range contraction, with local extirpations occurring over nearly half of the historically occupied habitat. The Columbia Basin population in Washington State, USA, is particularly threatened, as it persists in a highly modified agricultural landscape that other studies have characterized as similar to extirpated range. Yet declines in this population have stabilized, and unoccupied habitat is being successfully recolonized via translocations. In this study, we used species distribution modeling to quantify environmental variables constraining sage grouse distribution in Washington, with the primary objective to understand how this species may persist in agricultural landscapes. We also used GPS location data collected from translocated birds to understand how natural and anthropogenic features of the landscape influence movement patterns. We found that fields planted to perennial vegetation as part of the Conservation Reserve Program (CRP) are critical in providing year-round habitat for sage grouse (and likely many other species) when intermixed with native sagebrush. Without this program, we estimate 63% of sage grouse habitat in Washington would become unsuitable. Conversely, if CRP allotments were redistributed to better support sage grouse, we estimate the area of habitat could be increased by 66%. In addition to the area of native sagebrush and CRP lands, we also found that climate variability, the patch configuration of sagebrush, and development impacts constrain the distribution within the study area. With careful consideration of the multiple intended uses of the program, it may be possible to strategically allocate a portion of CRP allowances over space and time to reduce the risk of extirpation in agricultural areas, and to facilitate sage grouse range shifts in response to climate-driven changes in the sagebrush biome. With regard to GPS data, we did not find evidence that perception of the landscape, as represented by the alternative resistance models, was different between early-mortalities and long-surviving sage grouse. A close look at the statistically similar-top 4 movement models showed that the top-ranked model was the null model. This suggested that the least-cost path is found in straight line from the first GPS telemetry point to the last GPS telemetry point of each 5 km path. This process illustrated some potential approaches for future analysis.

This report, submitted by the Washington Connected Landscapes Project, is the **Final Report for Informing Connectivity Conservation Decisions for Greater Sage-Grouse in the Columbia Plateau Ecoregion deliverables outlined in Agreement number F14AP01042** with the United States Fish and Wildlife Service.

Document Overview

This report presents results for the development of a habitat model for Greater Sage-Grouse (*Centrocercus urophasianus*) in Washington State and an analysis of movements by GPS-collared translocated birds. Spatial data layers used in the analyses and supporting information are freely available from <http://www.waconnected.org>. This document is organized as follows:

- 1) **Introduction**—Background information about conservation of sage grouse in the region, habitat associations and movements for Greater Sage-Grouse in Washington State, project objectives, and an overview of Greater Sage-Grouse data used in the analyses.
- 2) **Species distribution modeling**—An assessment of landscape factors associated with the presence of sage grouse in the Columbia Basin of Washington State. We also considered seasonal differences in sage grouse responses to environmental variables, as well as the spatial scale at which these variables were important predictors of occurrence.
- 3) **Movement modeling**—The findings and recommendations of the analysis of existing landscape resistance surfaces in conjunction with GPS data acquired from translocated sage-grouse.
- 4) **Literature cited and Presentations**

Introduction

The Washington Wildlife Habitat Connectivity Working Group (WHCWG) has produced detailed connectivity analyses for the 20 million acre Columbia Plateau, a sage shrub/grassland (WHCWG 2012, 2013). Whereas agriculture and infrastructure dominate the human footprint of the Columbia Plateau Ecoregion, understanding the functional wildlife habitat connectivity in this highly fragmented landscape is in early stages.

Empirical validation of the WHCWG Columbia Plateau sage-grouse resistance model (Shirk et al. 2015) showed that transmission lines convey a stronger impact to landscape resistance than originally predicted by the expert model. While the model testing assessed connectivity between existing sage-grouse populations, it did not consider connectivity between existing populations and unoccupied modeled suitable habitat, i.e., potential translocation sites. This is because range-wide habitat models perform poorly in Washington at predicting presence and absence of sage-grouse (Aldridge et al. 2008; Wisdom et al. 2011; Knick et al. 2013). The poor fit of range-wide models for sage-grouse in the Columbia Plateau has important implications for conservation of this species, limiting management objectives in Washington (Stinson et al. 2004).

The Washington Department of Fish and Wildlife (WDFW) in cooperation with the USFWS have been conducting a translocation effort since 2008 to establish a population of Greater Sage-Grouse on the Swanson Lakes Wildlife Area (Schroeder et al. 2013). In 2014, 20 GPS radio transmitters were provided by the Bureau of Land Management (BLM) to monitor translocated birds. Species based connectivity models make fundamental assumptions as to how animals perceive and move through the landscape. For instance, even though we often record dispersal movements as straight-line distances, we know that species make pathway decisions influenced

by habitat resistance. Understanding patterns of movement through the landscape and the factors that influence movement pathways is important for conservation efforts that address habitat and population connectivity. Translocated birds make exploratory movements within the first few weeks after release. These movements are analogous to dispersal movements and provide the unique opportunity to gain insight as to how sage-grouse perceive natural and anthropogenic (e.g., powerlines, roads, croplands, areas impacted by wildfire) landscape features.

Greater Sage-Grouse

Greater Sage-Grouse are considered a landscape species for shrubsteppe ecosystems (Hanser & Knick 2011). They have large home ranges, are capable of extensive movements, and use a mosaic of habitat patch sizes (Connelly et al. 2004). Greater Sage-Grouse are sensitive to disturbance from human activities as well as the configuration and juxtaposition of suitable habitat in the landscape (Braun 1986; Lyon & Anderson 2003; Connelly et al. 2004; Aldridge 2005; Aldridge & Boyce 2007; Holloran et al. 2010; Johnson et al. 2011; Knick & Hanser 2011; Wisdom et al. 2011). Habitat loss, degradation, and fragmentation of native shrubsteppe vegetation resulting from altered fire regimes, conversion of shrubsteppe to agriculture, urban development, energy development, grazing, mining, military activity, noise, powerlines, roads, fences, and encroachment by invasive plant species threaten the persistence of populations in Washington (Schroeder et al. 2003; Stinson et al. 2004). Additional threats include loss of genetic diversity through population isolation (Stinson et al. 2004) and evidence suggests that Greater Sage-Grouse in Washington have already undergone a genetic bottleneck (Benedict et al. 2003; Oyler-McCance et al. 2005; Oyler-McCance & Quinn 2011).

Greater Sage-Grouse were once widely distributed throughout central and eastern Washington, parts of north-central and eastern Oregon, southern Idaho and in the extreme southern portion of British Columbia following the Okanagan valley (Campbell et al. 1990; Schroeder et al. 2000; Aldridge & Brigham 2003; Schroeder et al. 2004). Initial declines of Greater Sage-Grouse distribution in Washington were related to cultivation of shrubsteppe habitat, primarily for production of wheat, and continued as cultivation expanded throughout the Columbia Basin (Schroeder et al. 2000). The estimated range of Greater Sage-Grouse in Washington is approximately 4683 km² or 8% of the historical range (Schroeder et al. 2000). Current estimates place the state population at approximately 1000 birds (2015 estimate; MAS).

There are two endemic populations of Greater Sage-Grouse in Washington (Fig. 1). One is located in the Moses Coulee area in Douglas/Grant counties and one is on the U.S. Army's Yakima Training Center (YTC) in Yakima/Kittitas counties (Schroeder et al. 2000; Stinson et al. 2004). These populations are isolated from each other by approximately 50 km and from populations in Oregon and Idaho by about 250 km and 350 km respectively. In 2008 WDFW initiated a translocation project to release birds at the Swanson Lakes Wildlife Area, Lincoln County, Washington (Fig. 1 Crab Creek, Schroeder et al. 2008, 2013). Greater Sage-Grouse were also extirpated from the Yakama Reservation, though the timeline was likely at least 20 years earlier than for Lincoln County. Greater Sage-Grouse were translocated to the Yakama Reservation in 2006 and again in 2013 and 2014. One lek has been observed to be still active in 2015.

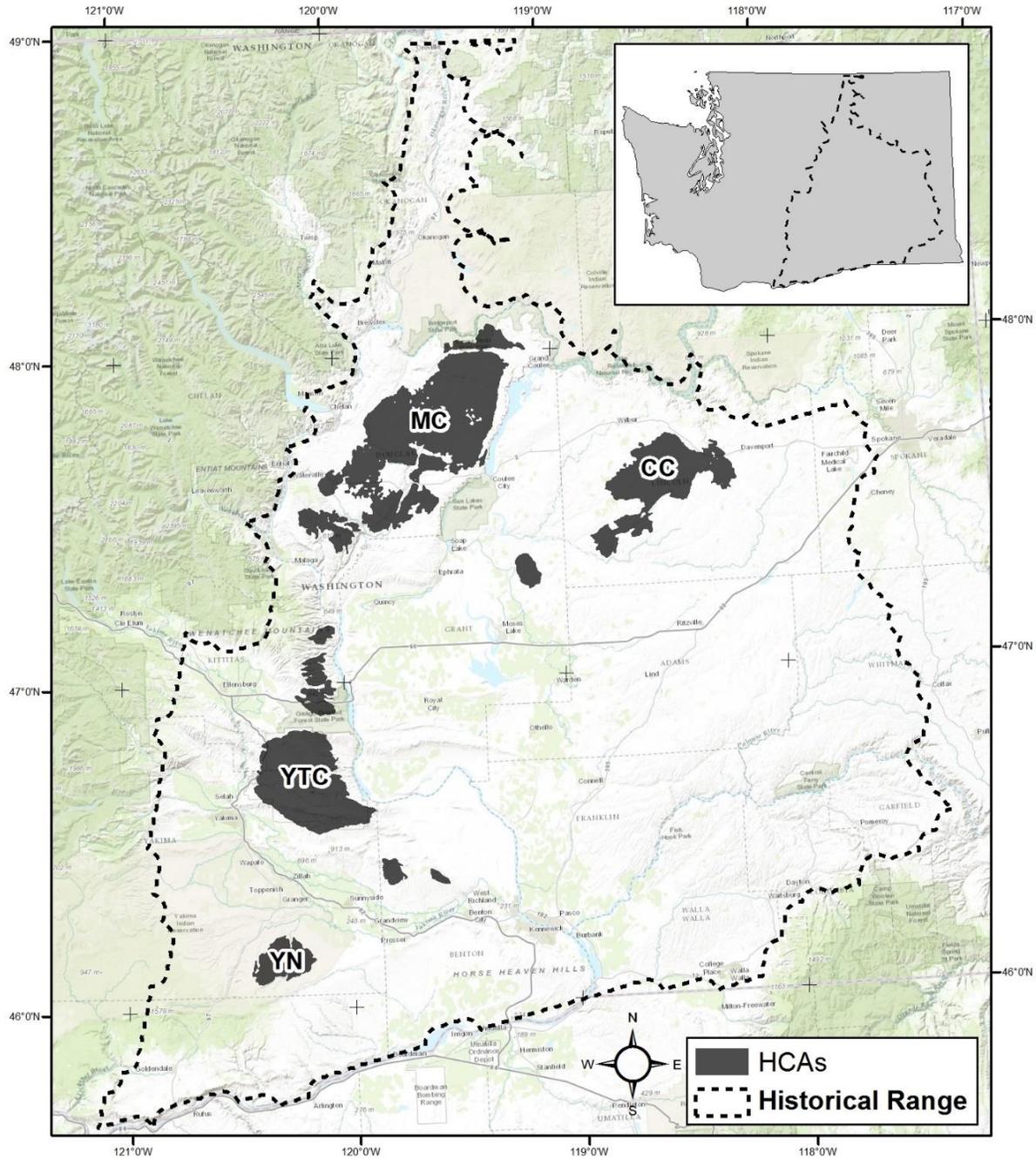


Figure 1. Estimated historical and current distribution of Greater Sage-Grouse habitat in Washington. The current population is distributed among four subpopulations located in Crab Creek (CC), Moses Coulee (MC), the Yakima Training Center (YTC), and the Yakama Nation (YN). The YN and CC populations were recently established by reintroductions to formerly occupied habitat. The Habitat Concentration Areas (HCAs) shown are revisions of previous delineations of core habitat areas and were based on the species distribution models described in Objective 1.

Describing the relationship between landscape pattern and how Greater Sage-Grouse perceive that pattern will help further our understanding of how landscape patterns influence Greater Sage-Grouse mobility, and ultimately gene flow. Recent genetic analysis indicates that the YTC population has only 1 haplotype and the Moses Coulee population 3 haplotypes (2 unique) compared to an average of 6.4 for other populations range-wide reflecting little gene flow between these populations (Benedict et al. 2003; Oyler-McCance et al. 2005).

Greater Sage-Grouse are considered a state Threatened species by the WDFW and are considered a Priority Species by the WDFW Priority Habitats and Species Program (Hays et al. 1998; Schroeder et al. 2003; Stinson et al. 2004). WDFW is currently developing standards to implement a Candidate Conservation Agreement with Assurances for Greater Sage-Grouse in Washington.

Habitat Associations

GENERAL

The distribution of Greater Sage-Grouse is closely allied to the distribution of sagebrush, particularly big sagebrush (*Artemisia tridentata*) in the western U.S. Sagebrush habitat types demonstrate considerable variation across the range in terms of vegetative composition, fragmentation, topography, substrate, weather, and frequency of fire (Schroeder et al. 1999). Because Greater Sage-Grouse use a variety of habitat patches within a larger landscape, the juxtaposition and quality of these habitat types is critical.

In Washington, Greater Sage-Grouse habitat includes the shrubsteppe and meadowsteppe plant communities (Stinson et al. 2004). Shrubsteppe plant communities are characterized by bunchgrasses, big sagebrush, three-tipped sagebrush (*A. tripartita*), bitterbrush (*Purshia tridentata*) and forbs. Meadowsteppe habitat is characterized by dense grass and forb cover and fewer shrubs (Stinson et al. 2004). The quality of the shrubsteppe and diversity of the vegetation is critical. Many uncultivated areas are not suitable for Greater Sage-Grouse because of lack of sagebrush, perennial grasses, and forbs (Schroeder et al. 1999). Greater Sage-Grouse may use alfalfa (*Medicago sativa*), wheat (*Triticum* spp.), and crested wheatgrass but use of these altered habitats depends primarily on their configuration (proximity) with native habitat (Schroeder et al. 1999).

BREEDING

Leks are traditional breeding areas where males congregate in the spring and perform courtship displays. They are typically situated near nesting habitat and close to relatively dense stands of sagebrush used for cover and feeding (Connelly et al. 2004). Leks tend to be located in natural openings such as ridge-tops, grassy swales, and dry stream channels as well as openings created by human disturbance, including cultivated fields, airstrips, gravel pits, roads, burned areas, and edges of stock ponds (Schroeder et al. 1999; Connelly et al. 2004).

Sagebrush/bunchgrass habitat is used for nesting (Stinson et al. 2004); nests tend to be situated under the tallest sagebrush within a stand (Connelly et al. 2000). Good quality brood habitat is characterized by abundant forbs, insects and high plant diversity (Connelly et al. 2000).

WINTER

Winter habitat for Greater Sage-Grouse consists of large stands of good quality sagebrush that provide food and cover. Presence of sagebrush is essential for survival as it is 100% of the winter diet (Schroeder et al. 1999). Spatial distribution of Greater Sage-Grouse in winter is related to snow depth as sagebrush must be exposed to be accessible for forage (Connelly et al. 2004). Sagebrush stands with canopy cover 10–30% and heights of at least 25–35cm are considered minimal for winter habitat (Connelly et al. 2000).

AGRICULTURE

The reduction in distribution of Greater Sage-Grouse range in Washington is largely a consequence of habitat loss due to conversion of shrubsteppe to cropland. Less than 50% of historical shrubsteppe remains in Washington and what is left is often degraded, fragmented, or isolated (Schroeder & Vander Haegen 2011). Interestingly, the Moses Coulee population of Greater Sage-Grouse occupies a landscape highly fragmented by dryland agriculture, unlike most other populations in North America (Aldridge et al. 2008; Wisdom et



Male Greater-Sage Grouse, Moses Coulee, Photo by Michael A. Schroeder.

al. 2011). The remnant patches of native shrubsteppe in this matrix often are of good quality for Greater Sage-Grouse while larger areas of intact shrubsteppe can be over-grazed by livestock.

The Conservation Reserve Program (CRP) is a voluntary program (administered by the United States Department of Agriculture) that pays farmers to take agricultural lands out of production to achieve specific conservation objectives, one of which is improved wildlife habitat. Active CRP lands totaled 564,829 ha (1,395,724 ac) for Washington State as of December 2014 (USDA 2015). The vast majority of CRP (including State Acres for Wildlife Enhancement) in the state occurs in eastern Washington; Douglas County alone had 73,353 ha (181,260 ac). When Aldridge et al. (2008) modeled range-wide patterns of Greater Sage-Grouse populations the Moses Coulee (Douglas/Grant) population exceeded the cropland thresholds, while also having lower than expected sagebrush habitat. They suggested that habitat loss may have been mitigated through conversion of cultivated agricultural lands to CRP. For example, in the Moses Coulee population of Greater Sage-Grouse females nest in CRP more than expected by its availability. In general, the “usefulness” of CRP for Greater Sage-Grouse is influenced by maturity of the planting, species planted, presence of sagebrush, and juxtaposition to native habitat (Schroeder & Vander Haegen 2011). Lands enrolled in the Conservation Reserve Program in Washington can reduce resistance to movement in the landscape for Greater Sage-Grouse by providing suitable habitat.

Dryland wheat is the dominant agricultural crop within the distribution of the Douglas/Grant population of Greater Sage-Grouse. In spring, males often display in wheat fields that are adjacent to native shrubsteppe. These display sites are situated within 500 m of native habitat (MAS.), suggesting a threshold distance beyond which Greater Sage-Grouse are reluctant to move.

Movements

Migratory corridors for Greater Sage-Grouse are determined by the seasonal patterns of Greater Sage-Grouse movement (Connelly et al. 2004) and the distribution of required habitats. Greater Sage-Grouse intensively monitored during seasonal migration followed shrubsteppe corridors at higher elevations, close to breeding habitat. Birds tended to deviate from a minimal “straight-line” route, instead choosing longer routes in or close to shrubsteppe vegetation (Schroeder & Vander Hagen 2003).

Project Objectives

The analyses presented in this report had two primary objectives: (1) use species distribution modeling to quantify environmental variables constraining sage grouse distribution in Washington to understand how this species may persist in agricultural landscapes, and (2) use GPS location data collected from translocated birds to understand how natural and anthropogenic features of the landscape influence movement patterns.

Overview of Data Used

SPATIAL DATA LAYERS

Resistance surfaces—The resistance models used as hypotheses for the analysis of GPS telemetry data and space use were based on the fine-scale models described in Shirk et al. (2015). These resistance models were based on natural and anthropogenic landscape features that potentially influence sage grouse movements, including land cover, elevation, slope, highways, roads, transmission lines, railroads, and wind turbines. Two examples of these resistance models are shown in Figure 2. In total, 30 fine-scale resistance models (30-m pixel resolution) were included in this study. A null model with a resistance of 1 in all pixels was also included. This null model predicts that the best path through the landscape between two points is a straight line.

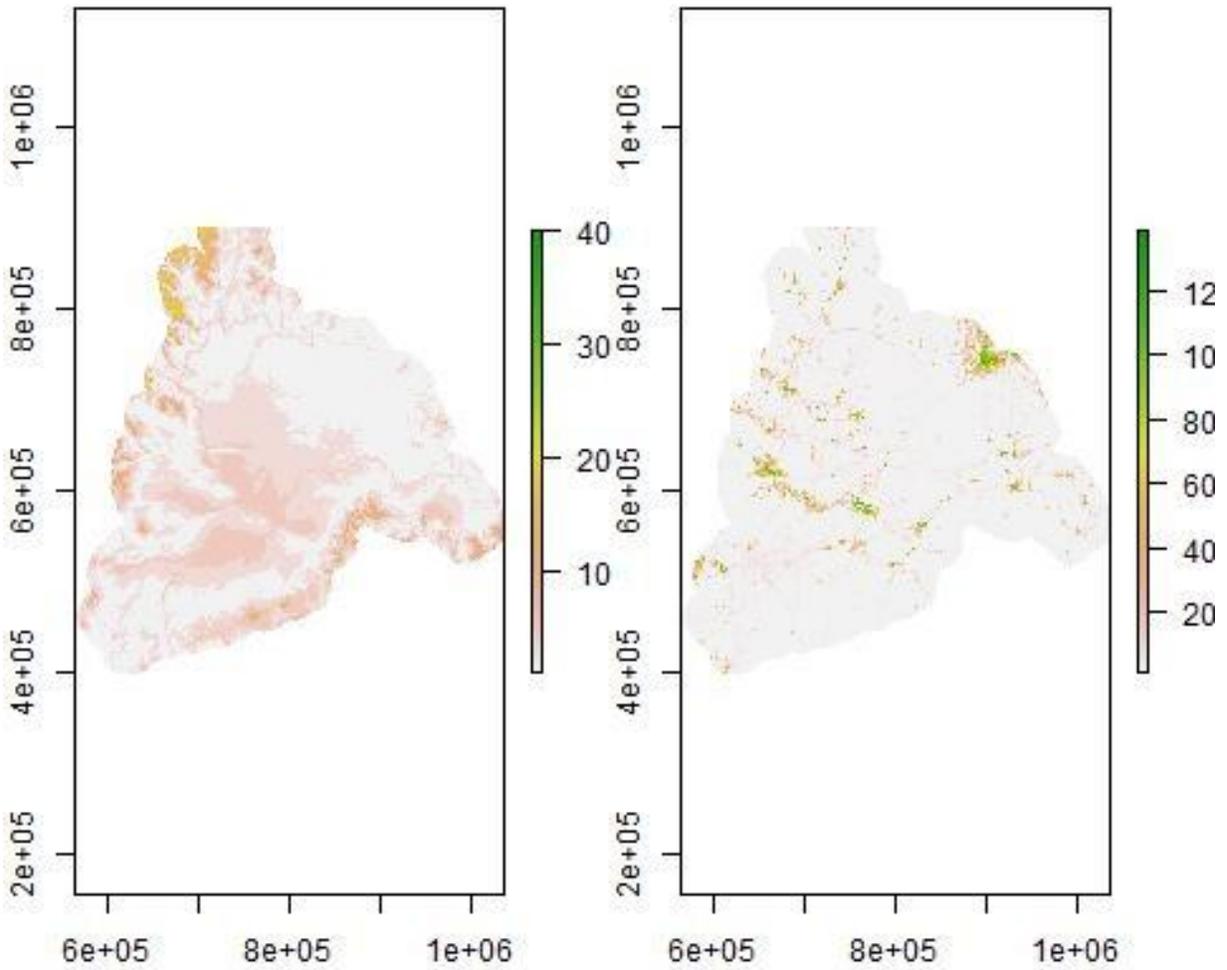


Figure 2. Examples of 2 alternative resistance models used as the basis for evaluating Greater Sage-Grouse movements across the landscape with higher resistance values shown in green (Model #74 on left and # 55 on the right).

GREATER SAGE-GROUSE LOCATION DATA

Species distribution models—These models were based on all available occurrence data collected by Washington Department of Fish and Wildlife field biologists from 1992 to 2014, including observations collected during lek surveys, opportunistic sightings, and radio-telemetry.

Movement models— The GPS data used to relate Greater Sage-Grouse movements to resistance hypotheses came from a translocation effort conducted in the spring of 2014. Twenty male sage grouse were released carrying GPS receivers recording positional information multiple times per day. Of the initial 20 sage grouse released, 11 suffered early mortalities within the first 35 days, while the other 9 sage grouse all lived at least 100 days or more, with 4 individuals surviving well over a year. The GPS receivers recorded more than 12,200 telemetry locations over the duration of the study. For the 9 sage-grouse that lived well beyond the initial release date, number of telemetry locations ranged from 686 to 2497 locations per individual, with an average of ~1700 locations per individual. These telemetry locations were then screened to identify serial locations that amounted to a movement path greater than 5 km. The movement path data provided the basis for analyzing the response of Greater Sage-Grouse to landscape resistance while moving across a novel environment.



Attaching a GPS transmitter to a male Greater Sage-Grouse. Photo by Heather McPherron.

Objective 1: Species Distribution Modeling

Introduction

The WHCWG Columbia Plateau Analysis (WHCWG 2012) of sage grouse habitat connectivity in Washington was based on coarse delineations of Habitat Concentration Areas (HCAs) where sage grouse were known to be present. Ideally, HCA boundaries would be drawn from an empirical species distribution model (SDM; Elith & Leathwick 2009) that spatially quantifies areas on the landscape suitable for Greater Sage-Grouse. In addition to providing a more rigorous delineation of the true extent of core areas, species distribution modeling can potentially identify new areas that are suitable but currently unoccupied. Such areas might be targets for establishing new subpopulations through natural colonization if they are accessible to occupied habitat, or by translocations if they are too isolated. In addition, species distribution models may also reveal important landscape variables and thresholds that are related to habitat occupancy.

In this study, we used species distribution modeling to identify factors associated with the presence of sage grouse in the Columbia Basin of Washington State. We were also interested in seasonal differences in sage grouse responses to environmental variables, as well as the spatial scale at which these variables were important predictors of occurrence. Specifically, we sought to (1) delineate suitable habitat areas throughout the Columbia Basin of Washington for each biological season (breeding, nesting, brood-rearing, and winter), (2) update the WHCWG Columbia Plateau Analysis Habitat Concentration Areas (HCAs) based on the mean habitat suitability value across all seasons, (3) update the WHCWG Columbia Plateau Analysis barrier, pinch point, and centrality models based on the new definition of HCAs, and (4) compare the updated models to the original WHCWG Columbia Plateau Analysis to determine the extent of change and the conservation implications.

Methods

The methods used to produce the species distribution models for sage grouse are described in the attached manuscript titled *Persistence of Greater Sage-Grouse (Centrocercus urophasianus) in an Agricultural Landscape*.

To produce new HCAs from the seasonal Greater Sage-Grouse habitat models, we first averaged all four seasonal models (breeding, nesting, brood-rearing, and winter). We then used this mean year-round probability of occurrence as an input for the GIS algorithm used to delineate HCAs, as described in WHCWG (2012). Specifically, we used a 500 m moving window radius, required an average habitat value of at least 0.2 within the window and per pixel, expanded the cores by 1000 m to connect nearby patches, and required a minimum core area size of 1000 ha.

We then used these empirically derived HCAs as the cores for assessing connectivity. We used the Linkage Mapper toolkit to map linkages, barriers, pinch-points, and calculate centrality scores for HCAs and linkages, as described in WHCWG (2012, 2013).

Results

The results from the species distribution modeling are described in the attached manuscript. Updating sage grouse HCAs with the empirical distribution model resulted in a total of 10 HCAs (Fig. 1, Figs. 3–6), compared to 4 HCAs defined in the WHCWG Columbia Plateau Analysis

(2012). The 4 largest HCAs (numbered 1, 2, 5, and 6 in Figs. 3–6 respectively) roughly corresponded to the WHCWG (2012) HCA locations and the 4 subpopulations in the state (Moses Coulee, Crab Creek, Yakima Training Center, and Yakama Nation). The 6 new HCAs (mean area = 8159 ha) were much smaller than the 4 largest HCAs (mean area = 93,485 ha), raising the issue of whether they were large enough to support a breeding population. Regardless, their distribution between the larger cores makes them potential stepping stones that could serve as stopovers for long-distance dispersers moving between the large HCAs.

Linkages connecting these HCAs followed a similar pattern to the WHCWG (2012) HCA models, connecting each of the 4 largest HCAs and running through the smaller stepping stones described above (Fig. 3). The presence of the stepping stones reduces the cost-weighted distance between the 4 largest HCAs, underscoring their value as stopovers for Greater Sage-Grouse dispersing between subpopulations.

The major barriers which added significant cost-distance to the linkages over small areas corresponded to major transmission lines (Fig. 4). Transmission lines in this analysis and our prior analysis of resistance (Shirk et al. 2015) appear to be major determinants of habitat suitability and movement within the study area.

Within the linkages, major pinch-points appeared in several places where high resistance funneled movement paths into narrow constrictions (Fig. 5). The most significant bottlenecks appeared south of HCAs 1 and 3 (Moses Coulee) in a gap between a major transmission line and a region of intensive agriculture, west of HCA 5 (Yakima Training Center) where the linkage crosses highway 410, and east of HCA 6 (Yakama Nation) where the linkage passes through intensive agricultural areas and across Interstate Highway 82.

The most central linkages and HCAs in the network, based on circuit theory current flow, were comprised of the Yakima Training Center (HCA 5) and Colockum (HCA 7 and 8) HCAs and the linkage between them (Fig. 6). Any loss of HCAs or linkages in this region would fragment the population into two disconnected regions.

Discussion

There were several key findings from this analysis that can be used to guide conservation of habitat and connectivity for Greater Sage-Grouse in the Columbia Basin. The attached manuscript describes several habitat requirements that are strongly associated with sage grouse occupancy, including a minimum of about 30% of the landscape comprised of native shrubsteppe within a 5 km moving window, at least 2 km from the nearest transmission line, and a configuration of habitat (both native shrubsteppe and CRP) characterized by large cores rather than small isolated patches. Additionally, we found that when CRP was about 25% or more of the landscape within a 5 km moving window, it significantly increased the suitability of areas where native shrubsteppe was less extensive and more fragmented. At least some native shrubsteppe was required in the local landscape for this benefit, however (i.e., CRP was not a substitute for native habitat). The importance of the CRP program in augmenting habitat was demonstrated by the ‘No CRP’ alternative scenario, which revealed a loss of 66% of suitable habitat when CRP lands in our species distribution models were converted to wheat fields (see attached manuscript). These relationships between landscape attributes and occupancy (including

the shape of the relationship as well as the scale of selection) provide a means to better manage the landscape to best support a viable population of sage grouse.

Another benefit of the species distribution models we have produced is a more rigorous delineation of areas that support sage grouse habitat requirements over the seasons of breeding, nesting, brood-rearing, and winter. Not only does this provide a more spatially accurate representation of HCAs associated with the four known breeding subpopulations, but it also identified several smaller HCAs that could serve as stepping stones between the largest cores. This revised set of HCAs (including the stepping stones) provides a slightly different network for modeling connectivity, and this led to modest changes in the linkages, pinch-points, barriers, and centrality models compared to the Columbia Plateau analysis (WHCWG 2012, 2013).

The biggest implication of this new network of habitat is presence of the stepping stone HCAs, which reduce cost-distances between the larger occupied HCAs. If these stepping stones do, in fact, serve as seasonal stopovers for long-distance dispersal events, they may serve a key role in connecting the larger network, and these areas may warrant additional survey effort and protections. Moreover, it is possible some of the larger stepping stones may even support a breeding population.

Even when including stepping stones southeast of the YTC HCA, our revised linkage models still predict very large cost-weighted distances (well over 100 km) between the YTC and the newly introduced Yakama Nation population to the south. These large distances suggest the Yakama Nation population is isolated from the rest of the network, perhaps explaining why modeled habitat there was not naturally recolonized (the population was instead introduced via translocation).

The current network of habitat and linkages is threatened by potential future changes in climate and climate-related disturbance regimes. A recent analysis of five climatic niche models (i.e., spatial models that correlate species distributions with climate variables and make future projections given climate change scenarios) predicts a contraction of between 37% and 79% of the current sagebrush steppe biome in the Columbia Basin by the end of the century, and these models generally agree that contraction is most likely to occur in the southwest portion of the basin (Michalak et al. 2014). This region encompasses the Yakama Nation and the Yakima Training Center HCAs (numbered 5, 6, 9, and 10 in Figs. 3–6). Contraction of the sagebrush biome to exclude the YTC would be a major loss, as it represents about a third of the population and the largest block of native shrubsteppe habitat in the state. However, the above study projected expansion of sagebrush steppe by between 63% and 165% of the current area (depending on the climate change scenario), mainly in the northern portion of the basin (Michalak et al. 2014). If the current population was connected to expanding habitat in the north, it may provide a means to offset the loss of habitat where the YTC population resides and allow the population to shift its range and track its climate envelope.

The Lund-Potsdam-Jena Dynamic Global Vegetation Model, a mechanistic model based on biological processes, population dynamics, and species competition, projects a very different future Columbia Basin biome distribution by the end of the century. Under this approach, 4 of the 5 climate models described above agree that most of the sagebrush steppe biome will

transition to grasslands and open forests (Michalak et al. 2014). Indeed, encroachment of forests into sagebrush habitats has already been observed (Hyerdahl et al. 2006). If the future Columbia Basin matches the mechanistic model projections, the current network of HCAs and linkage would be unsuitable for sage grouse. Monitoring of forest encroachment appears warranted and adaptation responses may include suppression of forests to maintain shrubsteppe.

The frequency and intensity of wildfire in the future will likely be a major influence on the sagebrush biome. Historically fire suppression and reduction in fuels due to grazing and conversion to agriculture has resulted in low fire frequency and intensities. Sagebrush can recolonize burned areas if the intensity is sufficiently low that some plants survive and can re-seed, and if seedlings have time to establish. The frequency and intensity of fires is projected to increase in the region, although climate models differ in the magnitude and timing of these changes (Rogers et al. 2011). If the future fire regime exceeds the intensity and frequency thresholds for survival and establishment of sagebrush species, fire could be a major factor driving transition of sagebrush to grasslands, as predicted by the mechanistic model described above.

Clearly there is great uncertainty about the future distribution of sagebrush steppe in the Columbia Basin landscape. However, regardless of how the future unfolds, habitat connectivity to existing and future habitat areas will almost certainly be critical to maintaining a viable population of Greater Sage-Grouse in this landscape. Habitat connectivity will allow the population to track its shifting habitat and maintain robust demographic and genetic exchange that is key to functional metapopulations. This analysis demonstrates the degree to which human modification of the landscape, particularly agriculture and transmission lines, has fragmented the population and limited connectivity among the major remaining remnant patches. Our observation that CRP lands are valuable in augmenting habitat suitability (see attached manuscript) and offer low resistance to movement (Shirk et al. 2015) suggests a means by which the area of habitat and connectivity may be increased through reallocation of CRP enrollments. The allocation of CRP in this landscape could be shifted over time to reflect the changing distribution of the sagebrush steppe biome, and thereby provide an adaptive management tool for sage grouse conservation in a changing climate and landscape.

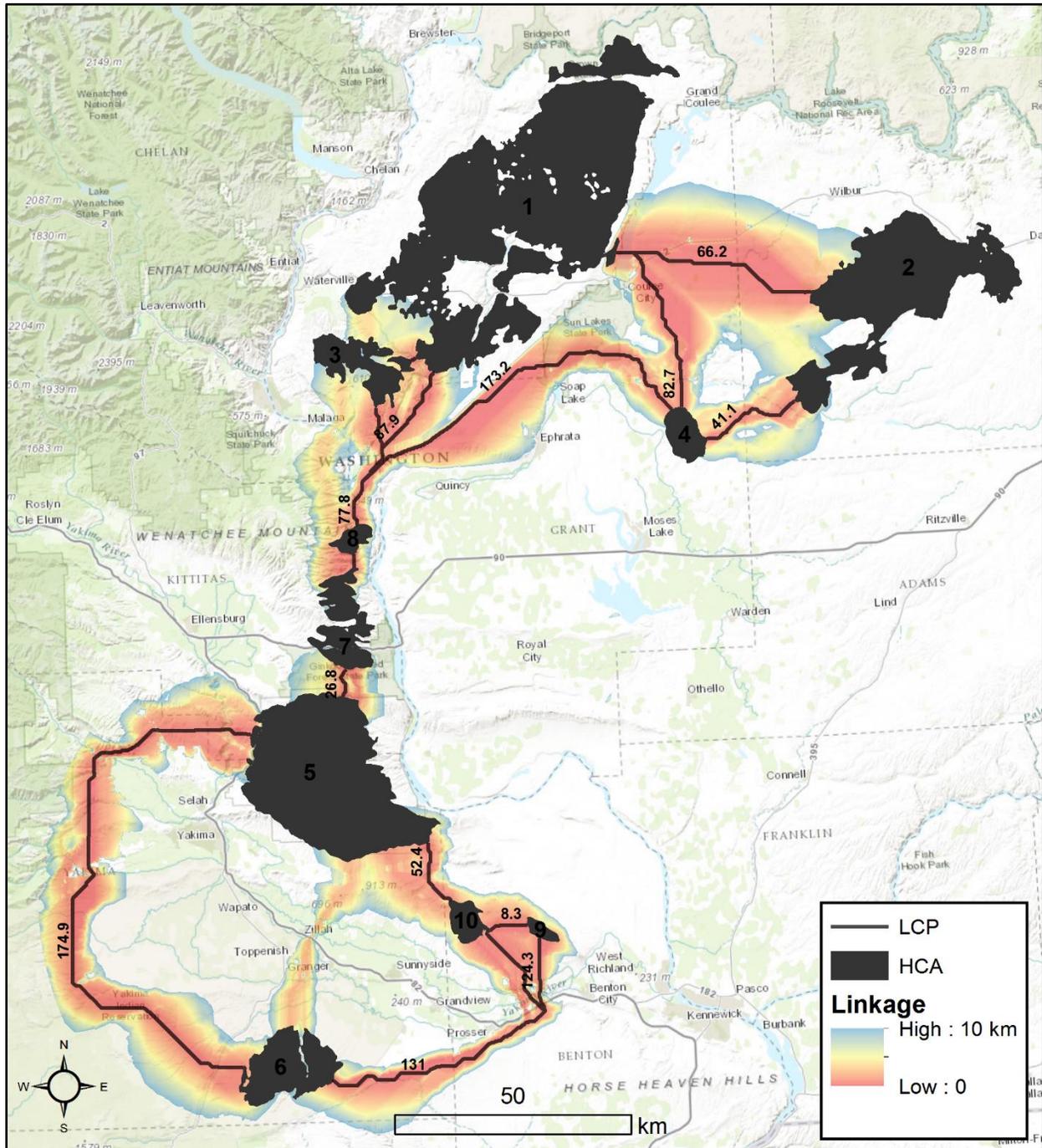


Figure 3. Linkages connecting HCAs followed a similar pattern to the WHCWG (2012) HCA models connecting each of the 4 largest HCAs (numbered 1, 2, 5, and 6) and running through the smaller stepping stones (HCAs 3, 4, 7, 8, 9, and 10).

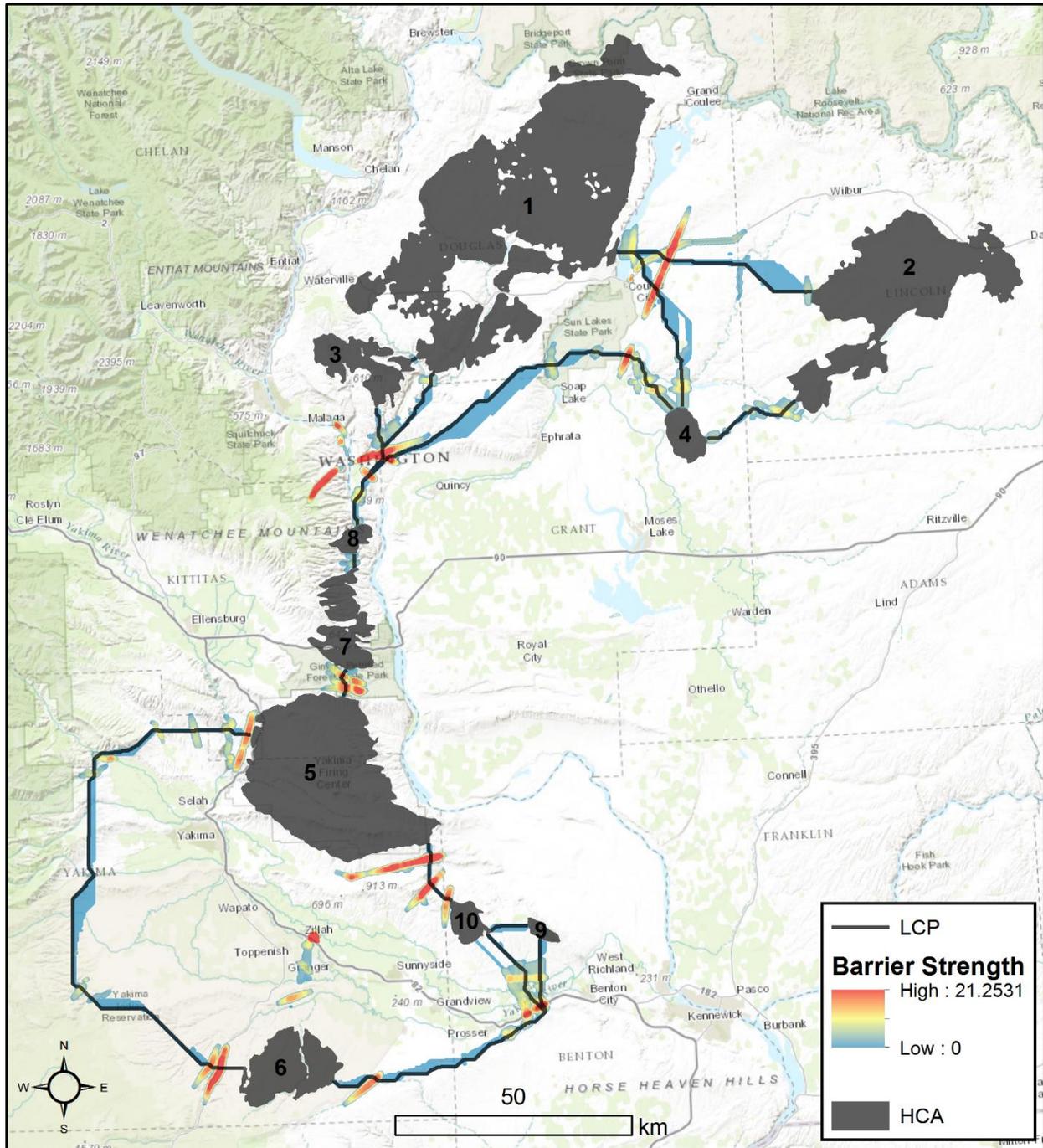


Figure 4. Barriers which added cost-weighted distance to linkages for Greater Sage-Grouse. Areas of highest barrier strength correspond to locations of major transmission lines.

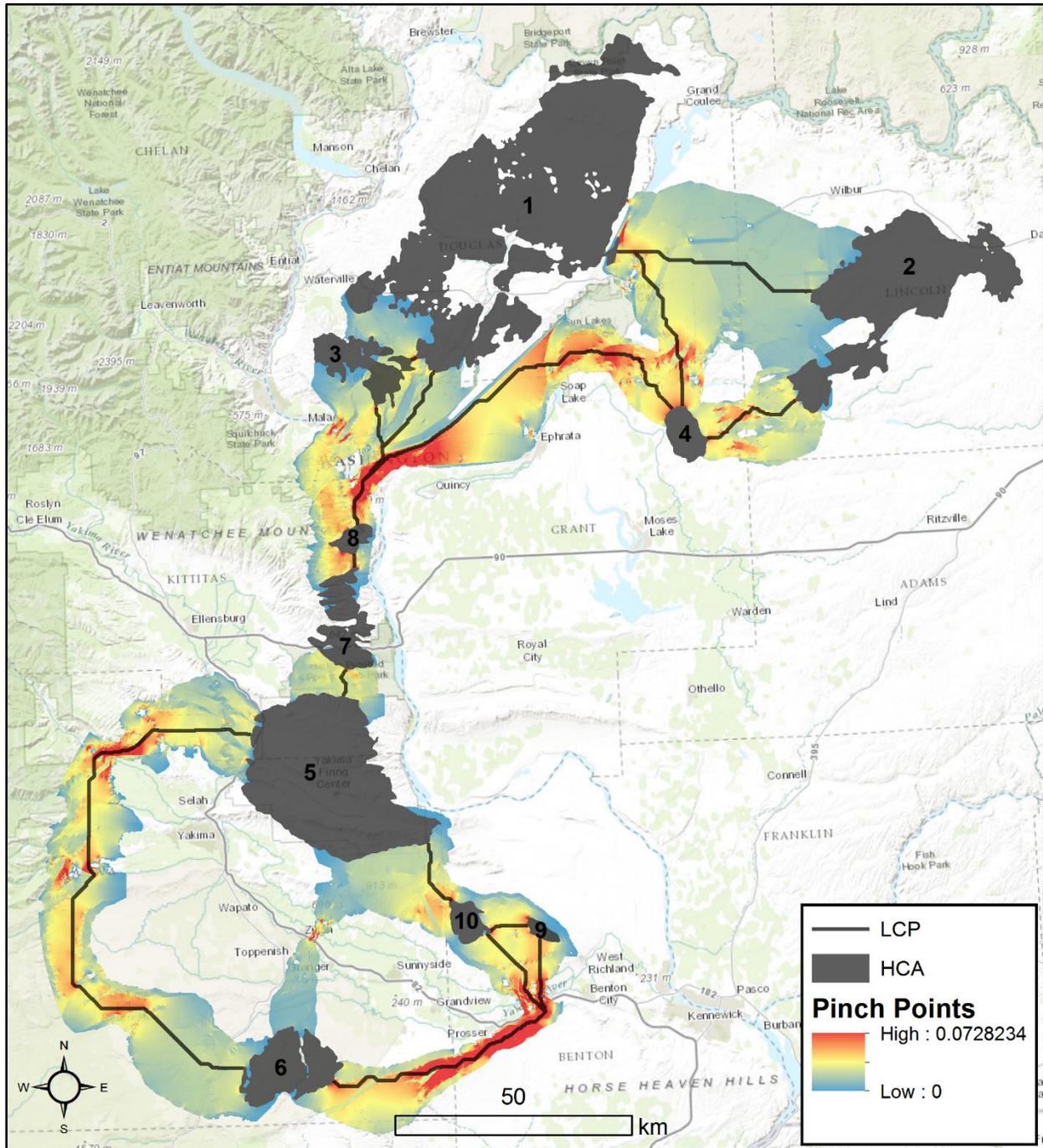


Figure 5. Linkage pinch-points for movement of Greater Sage-Grouse.

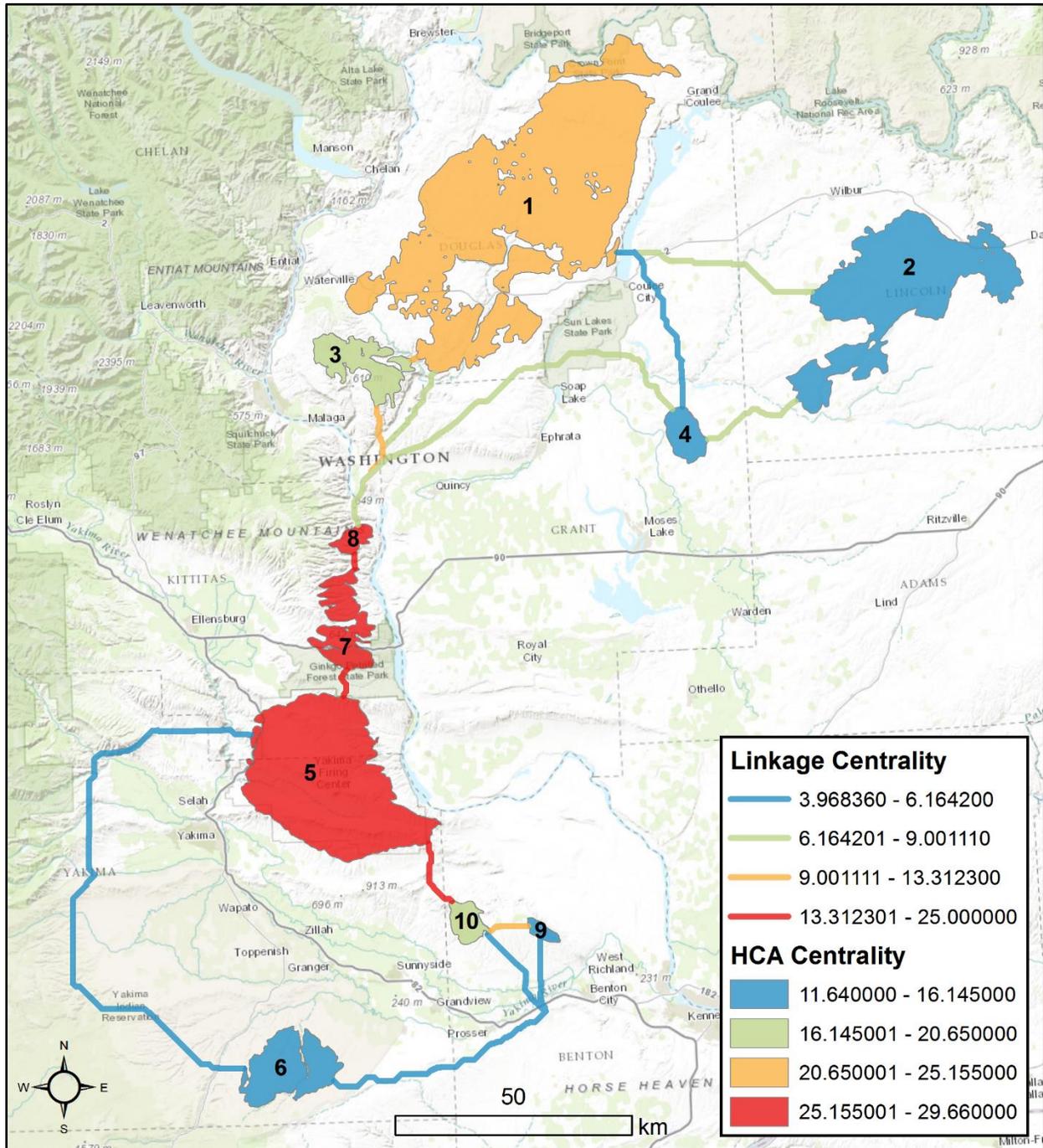


Figure 6. Linkage network centrality for Greater Sage-Grouse.

Objective 2: Movement Modeling

Introduction

The translocation effort conducted by WDFW provided a unique opportunity to analyze GPS telemetry data from radio-marked Greater Sage-Grouse in conjunction with existing and ongoing research. As well, the release offered a chance to evaluate existing models of landscape resistance based on previous studies of sage grouse landscape connectivity (Shirk et al 2015). Essentially, the analysis of GPS location data for translocated Greater Sage-Grouse was a test of alternative hypotheses developed to explain and understand how sage grouse respond to landscape features. We theorized that after release sage grouse would move around or explore the landscape for periods of time before eventually settling or establishing a localized home range. These exploratory moves were the basis for evaluating the different resistance surfaces and landscape connectivity.

Methods

Characterization and estimation of the exploratory movements was done with the use of the Brownian bridge movement model of space use (Horne et al. 2008). The Brownian bridge movement model (BBMM) offers a convenient and spatially explicit estimation of probabilities of space use between known telemetry locations. Initially, the telemetry data were screened to identify consecutive locations that exceed 5 km in length, thereby representing an exploratory movement path. A minimum of 3 locations were used per path, with up to 10 telemetry locations per path in total. Once each path was identified the probability of use along the path was estimated with the BBMM package in program R (R Core Team 2015). Each individual path was then combined and evaluated against each hypothesis as characterized by landscape resistance surfaces.

Each of the hypotheses described by landscape connectivity was represented as a 30-m GIS raster layer representative of the resistance surface (Fig. 7). These resistance surfaces are previously described by Shirk et al. (2015). For this portion of the study we focused on the 30 fine-scale models in Supplement 2 of Shirk et al. (2015), including a null model, where landscape resistance for the entire landscape was set to 1. Prior to combination with the BBMM, for each of the 30 resistance surfaces, and for each individual path, least-cost corridors (LCC) were generated from accumulated cost surfaces. Accumulated costs surfaces were derived from a transitional layer, or graph, based upon the original resistance surface using the raster (Hijaman and van Etten 2012) and *gdistance* (van Etten 2015) packages in R. Each resistance surface was initially cropped to the extent of each of the BBMM paths. This greatly reduced processing time and allowed for the summation of weighted costs for each BBMM from the first telemetry location in the path to the last. Each LCC was also normalized, with the least-cost path equal to zero, so comparisons among paths and hypotheses could be done, as well as population averaging. Each BBMM, for each path, was multiplied by the corresponding LCC generating a weighted LCC based on the BBMM probabilities. These weighted probability values were averaged and divided by the average BBMM probability of each path to give an average probability weighted LCC value for each path. Subsequent compilation and analysis of results were based on these weighted probability values of average LCC across the BBMM distribution for each path.

With the spatial analysis complete, further statistical analysis was required to establish any patterns in the results and for further inference to landscape and anthropogenic features. Therefore, to compare the average, probability weighted LCC values of each path and hypothesis, we ranked the averaged values combined over all paths and used non-parametric statistics to test for differences among hypotheses. We also tested for differences between those sage grouse that lived well beyond the release and those which died shortly after release. We used the Kruskal-Wallis test to test for difference between early mortalities and survivors, and for overall difference of hypotheses. Multiple comparisons after the Kruskal-Wallis test were done in R with the *kruskalmc* command from package *pgirmess* in R (2015 R Core Development Team) based on the Siegel and Castellan (1988). Once differences among hypotheses were defined and understood, the hypotheses could be interpreted in relation to the GPS telemetry data and further spatial dynamics related to sage grouse landscape connectivity could be explored. Initially, we expected to update existing models of spatial dynamics including linkage, pinch-point, barrier and centrality models to reflect testing of the GPS data and resistance surfaces. This however, proved not to be warranted as discussed below.

Updating the linkage, pinch-point, barrier and centrality models for sage grouse in those historical areas where current conservation is ongoing can be done relatively quickly and is straightforward (McRae et al. 2008, WHCWG 2013). The software and programs used for creating these layers is available from circuitscape.org and requires the additional data input of core habitat areas, provided by WHCWG (2013). The resistance surfaces used were those of the Shirk et al. (2015) and selected based upon the average weighted least-cost corridor values. Circuitscape also offers a program to create new resistance surfaces. However, as will be discussed, we did not find merit in updating existing linkage models based on our findings.

Results

Comparison of results between sage grouse that suffered early mortality and sage grouse that survived for more than 100 days, showed no difference overall in probability weighted LLC. (Kruskal-Wallis $X^2 = 2.08$; $p = 0.15$). Sage grouse that died shortly after release did not have a different response to the resistance layers, in general, than those that survived well beyond release. Although, the smaller sample size of BBMM paths for early mortalities ($n = 59$) than those of survivors BBMM paths ($n = 317$) could well play a part in this finding. Since the overall goal was to discern how sage grouse responded to the landscape, understanding if the resistance surfaces could characterize the difference in survivorship was a relevant analysis. Had there been a statistically significant difference in probability weighted LLC between early mortalities and survivors some further analysis and conclusion may have been inferred. However, the fact that no differences were found is in itself an informative finding for gleaning down future decision making. It appears that the use of the landscape, as portrayed by the combination of sage grouse movement paths and landscape resistance surfaces in this study, did not differ between early mortalities and long surviving sage grouse.

The averaged probability weighted LLCs for each path and hypothesis were tallied and ranked (Table 1). These values represent the average probability weighted LLC value of each cell, or pixel, for each resistance surface, or hypothesis. Or in other words, the LLC for each pixel after being weighted by the probability of use as defined by the BBMM. The tally and ranking of the resistance surfaces for the early mortalities (Table 1) are similar to those of the survivors. The

first 3 resistance surfaces and the last 4 were identical between early mortalities and long-surviving sage grouse. Slight differences in rank position are shown by the double-sided arrows in Table 1 and show only minor discrepancies. The greatest difference in rank is only six places for resistance surface 54. The resistance surface number directly correlates with the models shown in the tables of Shirk et al. (2015).

Further analysis based on non-parametric statistics showed there was a difference in probability weighted LLC among the resistance layers for those sage grouse surviving more than 100 days (Kruskal-Wallis $X^2 = 136.22$; $p = >7.9e -16$). Contrary, there was no difference in probability weighted LLC (Kruskal-Wallis $X^2 = 31.86$; $p = 0.326$) for those that died early on, shown in red in Table 1. Therefore, no further multiple comparisons were conducted for the early mortalities, but were conducted on the longer surviving sage grouse. Multiple comparisons of the long-surviving sage grouse showed three distinct groupings of different weighted probability LLCs among the resistance surfaces. The highlighted text in Table 1, illustrate which models showed differences. Essentially the first 4 resistance surfaces highlighted in yellow were all significantly different than the last 5 resistance surfaces shown in yellow. None of these however, showed any significant difference with those models ranked between the 2 groupings, lacking any highlighting. Nor were there any differences within the first 4, nor within the last 5 resistance surfaces. The null model, # 52, showed significant differences with all those ranked 18th place, and are shown in boldface. Examples of the Greater Sage-Grouse GPS telemetry data with contoured or rasterized BBMM paths overlaid on an example resistance surface are shown in Figures 7–11 below. These examples are all of sage grouse that survived well beyond the initial release.



Male Greater Sage-Grouse wearing GPS transmitter. Photo by Michael A. Schroeder.

Discussion

The highest ranked resistance surfaces correspond to models representing differing features on the landscape. In this case, the null model had the lowest overall average LLC values. This was the case for both long-surviving Greater Sage-Grouse and sage grouse that suffered early mortality. In general, there did not appear to be much difference in the overall ranking of early mortality sage grouse and long-surviving sage grouse. We did not find evidence that perception of the landscape, as represented by the alternative resistance models, was different between early-mortalities and long-surviving sage grouse. Nor was a significant difference among the early-mortality results based on the Kruskal-Wallis test. This may be due to the much smaller sample size and the actual nature of the mortalities, i.e., via predation, translocation-stress, GPS unit complications, etc. The limited data on the early mortalities appeared no different than surviving sage grouse in this analysis.

Beyond the null model, the lowest average LLC values for long surviving sage grouse corresponded to models 74, 55, 76 & 79. Notably these 5 models (null included) all differed significantly from the highest average values found at the bottom of Table 1. Finding the null model as the lowest resistance surface offers an important context for interpretation of the results. There are a variety of possible explanations and implications that can be inferred from this finding, however there are additional avenues of research that need to be done to verify and either collate or to question these findings. Keeping the finding of the null model in relation to the other 29 resistance surfaces is important, as is understanding the findings of the 29 resistance models without considering the null. As will be discussed below, the magnitude of the initial resistance values may bias the results in favor of the null.

A closer look at the next four highest ranked models showed some similarities in their patterns of resistance. The highest ranked resistance surface, # 74 was developed based on expert opinion and also included elevation as a main resistance factor. The second highest ranked model, # 55 included pasture converted to Conservation Reserve Program land (CRP) as the major resistance factor, with minor resistance due to major highways, secondary highways, railways, transmission lines, and wind turbines. The third highest ranked resistance surface, # 76, represents the combination of the highest ranked, # 74, and the second highest ranked, # 76. The fourth highest resistance model, # 79, was similar to the highest rank model, # 76, except for the resistance values of the transmission lines were doubled. The null model however, represents a landscape where the resistance was initially set to 1 and the least-cost corridor. Actual resistance values from the 4 top ranked resistance surfaces ranged from 0 to 99.

The multiple comparison of means suggested however that these models really were not any different than the null model. This could be due to a variety of reasons. Given the initial broad extent of the resistance surfaces (Fig. 1), and the greatly reduced extent of individual BBMMs, each of the resistance surfaces that did not differ from the null, may have actually been approximating the null model. If, due to the limited extent of the BBMM, there were only original values of 1 in the alternative resistance surface, then each alternative is really on average no different than the null. In other words, there could be a lack of heterogeneity in the resistance surfaces and accumulated cost surfaces at the fine scale that the BBMM estimates within.

Looking deeper however, we find that the null model suggests that the lowest resistance and consequently the least-cost path is found in straight line from the first GPS telemetry point to the last GPS telemetry point of each 5 km path. Now in theory, were the middle GPS points(s), and the corresponding BBMM, not along or that straight, and for example in a large C-shaped curve, then an alternative resistance model that truly was the “correct” model would have a least-cost path that follows the C-shaped curve, and consequently, a lower overall average LCC. The minimum values along the least-cost path are zero. Deviations away from the LCC, as reflected in the accumulated cost surface, result in an increase in LCC values. In particular, if the straight line between the first and last point crossed through a particularly resistant surface, for example, a small mountain range, a town, or even a large body of water the accumulated cost values for that straight line, could in theory become quite large for the null hypothesis. How large those accumulated cost values becomes depends on how far spatially the deviation to the null straight line path is from the alternative LCC, and also the resistance values themselves. In this study, resistance values range from 0 to 99, while the null was set to 1. If these values are not commensurate with the null and how sage grouse actually travel through space and time then the very magnitude of the resistance values may in fact be too large to detect a deviation from the straight line path, or the null model. Basically, as deviations from the LCP are created in an accumulated cost surface, the values may become so large that only C-shaped curves which are heavily exaggerated could possibly have lower average LCP values. In particular, exaggerated C-shaped moves by sage grouse may occur relatively quickly in time, thereby narrowing the BBMM probability distribution. Movement paths of 5 km that were relatively straight have less of an opportunity to have a lower average LCP than the null model due to the magnitude of resistance values, thus possibly biasing the findings in favor of the null.

The evidence supporting the null model as the resistance surface with the lowest average weighted LLC may in fact be biased based upon the very resistance values themselves. Or possibly the extent of the BBMM has actually reduced the heterogeneity of the resistance surfaces to such a point that the resistance surfaces are approximating the null resistance model. In either case, further refinement in the modeling process to assess the potential for bias and for developing fine-scale resistance models that have sufficient heterogeneity at the extent of the sage grouse BBMM needs to be done. Likewise given the likely changes in behavior as a sage grouse moves along a 5 km path, additional consideration should be given to including the results of the habitat analysis into the resistance models. Therefore, future investigation of these GPS data and resistance models needs to be completed prior to updating linkage, pinch-point, barrier, and centrality models based on circuitscape theory (McRae et al.2008). Proceeding to the intended analysis and revaluation of linkage, pinch-points, barriers, and centrality models were not warranted based upon the findings of the null model being lowest ranked. Preliminary linkage models were developed based on the average values of the top 4 resistance surfaces, but were not presented here to do the shortcomings of our findings. Existing linkage, pinch-point, barrier and centrality model were nearly identical to those preliminary models developed.

None the less, this data analysis has provided a streamlined methodology for evaluating probabilities of space use by GPS collared Greater Sage-Grouse with resistance models and circuit theory of animal movement. This demonstration has provided insight into the modeling process and a possible bias for further development and research into patterns of sage grouse movement. The preliminary results also suggest, at least out of the ranked ordering, which

resistance models should be included in further evaluation and possible factors impacting sage grouse as they explored this novel landscape.

Future Direction

The particular refinements to our approach that need to be done include exploring the bias towards the null due to magnitude of resistance values and bringing the results of the habitat model into the resistance surface creation. Adjusting the magnitude of resistance values can be done systematically to see if and when there is any evidence of a resistance surface having a lower LLC than the null. If there is a point at which this takes place, some simulated data and analysis may be helpful in determine the extent of deviations that need to occur spatially, prior to having an expectation for accumulated cost distances to tend lower for alternative resistance surfaces. Exploration of resistance magnitude and the overall shape of movements paths, i.e., straight or curved, should be done to follow up and advance the findings presented here. Simulation analysis can provide a relatively quick way to understand these potential biases.

Additionally, given the linear nature of roads and transmission lines across the landscape, it is reasonable to assume that as a sage grouse travels across the landscape, the easiest and best way to cross the linear feature is directly and quickly. In this case, the high resistance values of those features, may not be reflected by the accumulated, weighted LCC values, and essentially missed. The large contiguous portions of the resistance surface and accumulated cost surface may override any signal that could be expected from a linear feature. Especially if the crossing took place quickly, as the greater the distance traveled per unit of time tends to narrow a BBMM thereby lowering the accumulated cost of the linear feature. Therefore, attempting to understand how sage grouse respond to these linear features might more appropriately be addressed following the example of Horne et al. (2007). Future analysis of these data could follow up with a general linear modeling of BBMM in response to covariates describing known crossings of roads, transmission lines, and any other linear feature of interest. This may provide a more direct assessment of the influence of linear features like roads and transmission lines on space-use by sage grouse than the evaluation of landscape resistance model, where the influence of the linear features are essentially nested in the resistance model and not specifically addressed.

Table 1. Ranking of landscape resistance surfaces based on the weighting of least-cost corridors (LCC) by the Brownian bridge movement model (BBMM) probabilities showing the average LCC values of each resistance surface, the differences in ranks between Greater Sage-Grouse suffering early mortality vs. long-surviving sage grouse (arrows), and the groupings based on multiple comparison of means (yellow highlight).

Rank	Resistance surface	Long-surviving		Resistance surface	Early mortalities
NULL	52	67.3112		52	61.2073
1	74	70.0215		74	61.9035
2	55	75.6457		55	71.1334
3	76	78.6056		76	72.1578
4	79	78.8219	←	60	73.5116
5	60	80.8701	←	77	74.2688
6	78	81.8346	←	79	78.8085
7	77	83.9195	←	58	79.0326
8	71	85.0327	←	78	79.9790
9	57	85.4671	←	57	81.7647
10	58	87.5237	←	71	82.9909
11	56	89.9008		56	84.2900
12	53	91.0386	←	72	85.0257
13	59	91.0386	←	53	85.9124
14	67	91.0386	←	59	85.9124
15	64	92.0174	←	67	85.9124
16	72	92.5659	←	64	86.5626
17	73	94.3585		73	86.9517
18	66	94.6480	←	65	90.2494
19	65	96.5712	←	61	90.5123
20	61	97.2027	←	54	92.4628
21	80	98.0375	←	66	93.8775
22	68	101.3546	←	80	95.0265
23	62	102.5289		62	97.2812
24	63	103.8187	←	68	98.9202
25	54	104.2356	←	63	99.3746
26	81	104.8488		81	100.1432
27	69	113.9205		69	111.0471
28	70	115.2346		70	113.4254
29	75	118.8686		75	114.6158

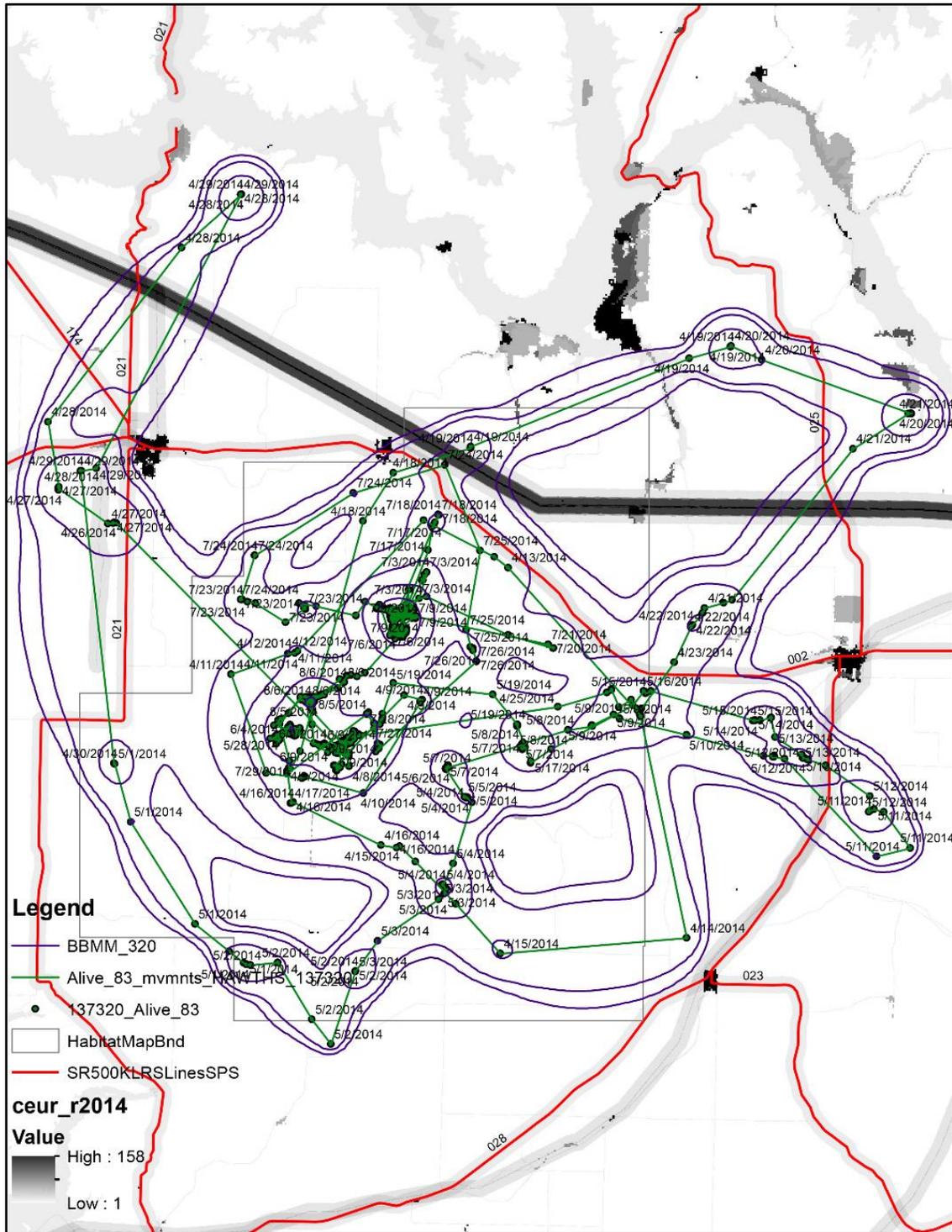


Figure 7. Example map showing Greater Sage-Grouse GPS telemetry data with contoured or rasterized BBMM paths overlaid on an example resistance surface (sage grouse ID # 13720). Darker areas of the background landscape indicate higher resistance values, while the red lines indicated state highways and roads.

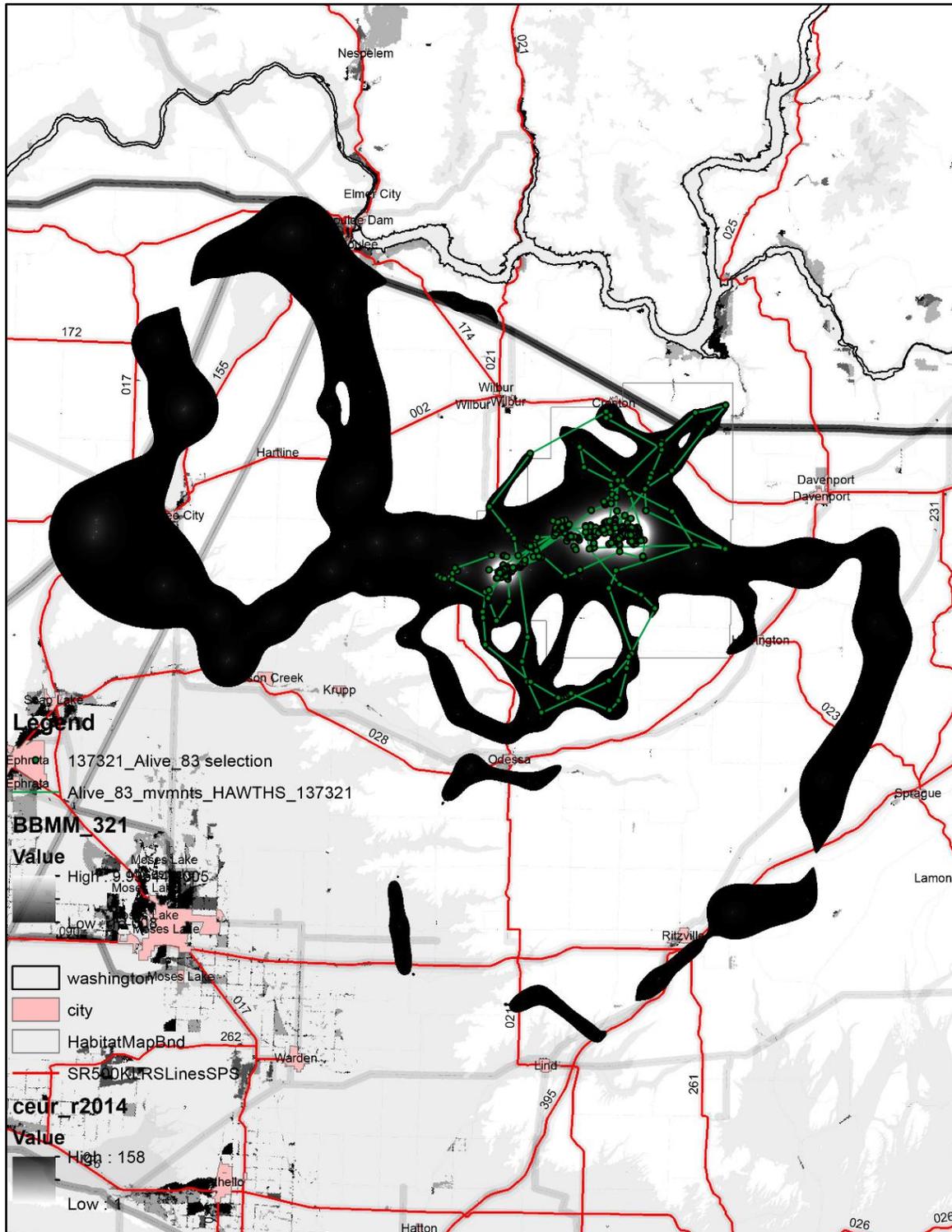


Figure 8. Example map showing Greater Sage-Grouse GPS telemetry data with contoured or rasterized BBMM paths overlaid on an example resistance surface (sage grouse ID # 13721; some telemetry data removed). Darker areas of the background landscape indicate higher resistance values, while the red lines indicated state highways and roads.

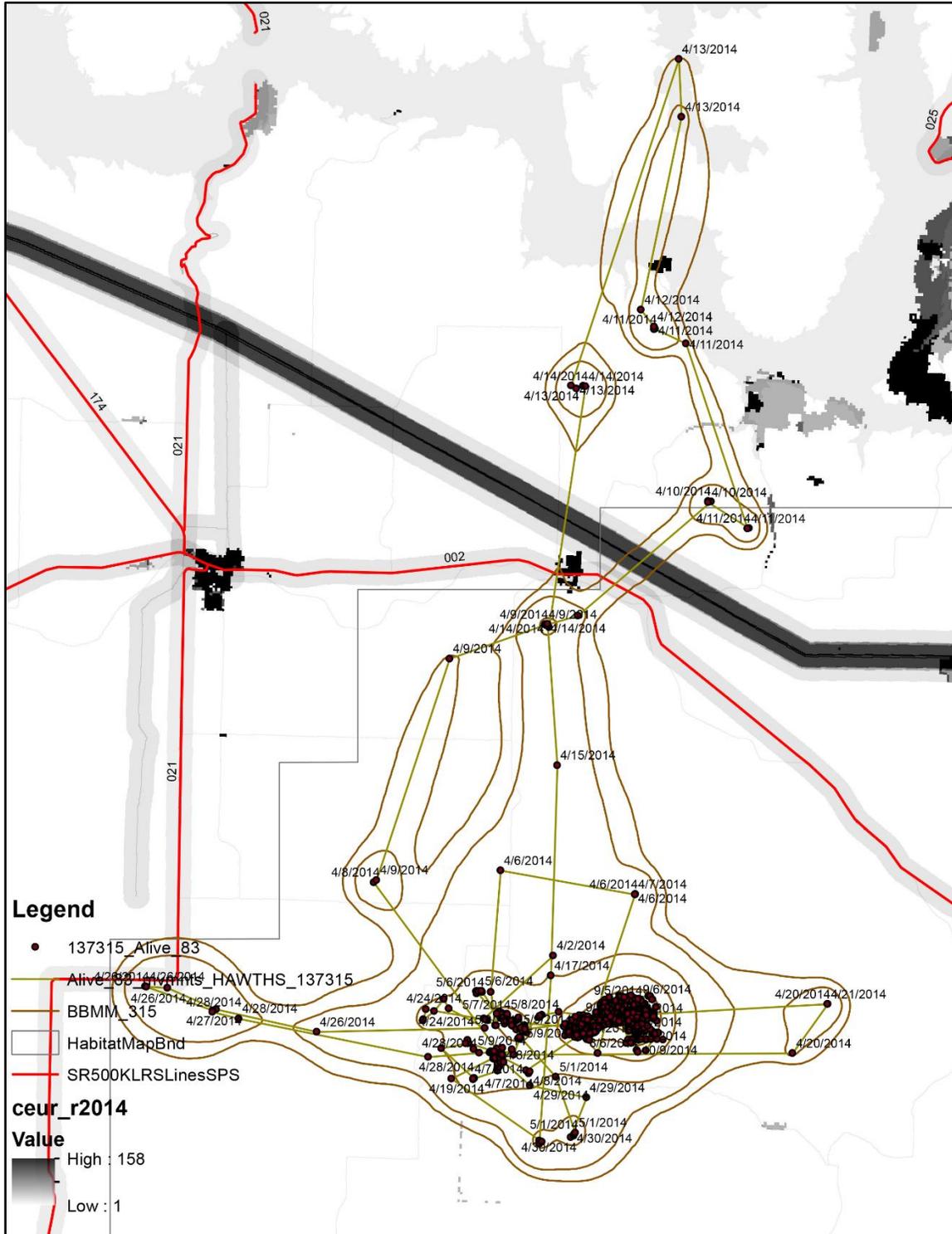


Figure 9. Example map showing Greater Sage-Grouse GPS telemetry data with contoured or rasterized BBMM paths overlaid on an example resistance surface (sage grouse ID # 13715). Darker areas of the background landscape indicate higher resistance values, while the red lines indicated state highways and roads.

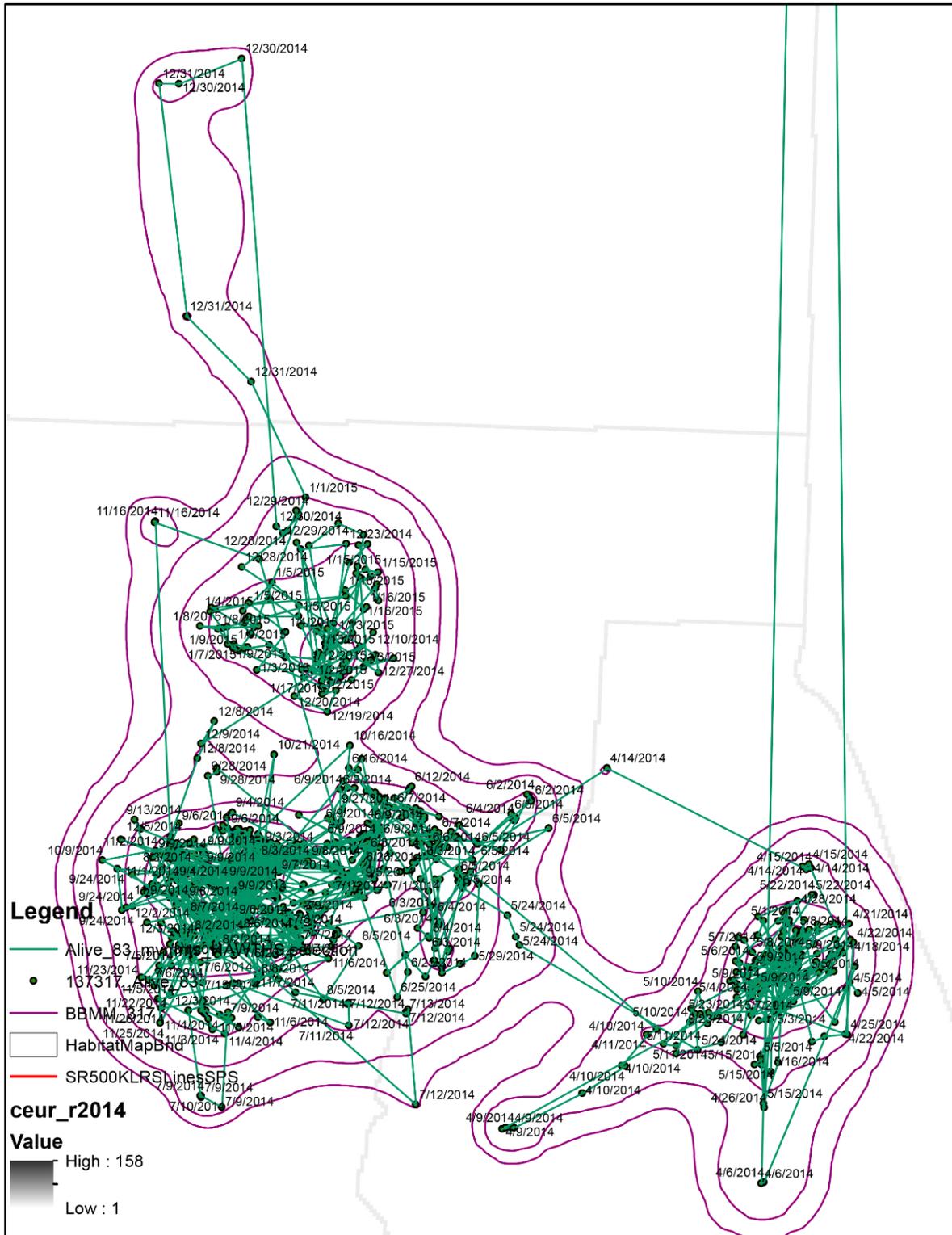


Figure 10. Example map showing Greater Sage-Grouse GPS telemetry data with contoured or rasterized BBMM paths overlaid on an example resistance surface (sage grouse ID # 13717). Darker areas of the background landscape indicate higher resistance values, while the red lines indicated state highways and roads.

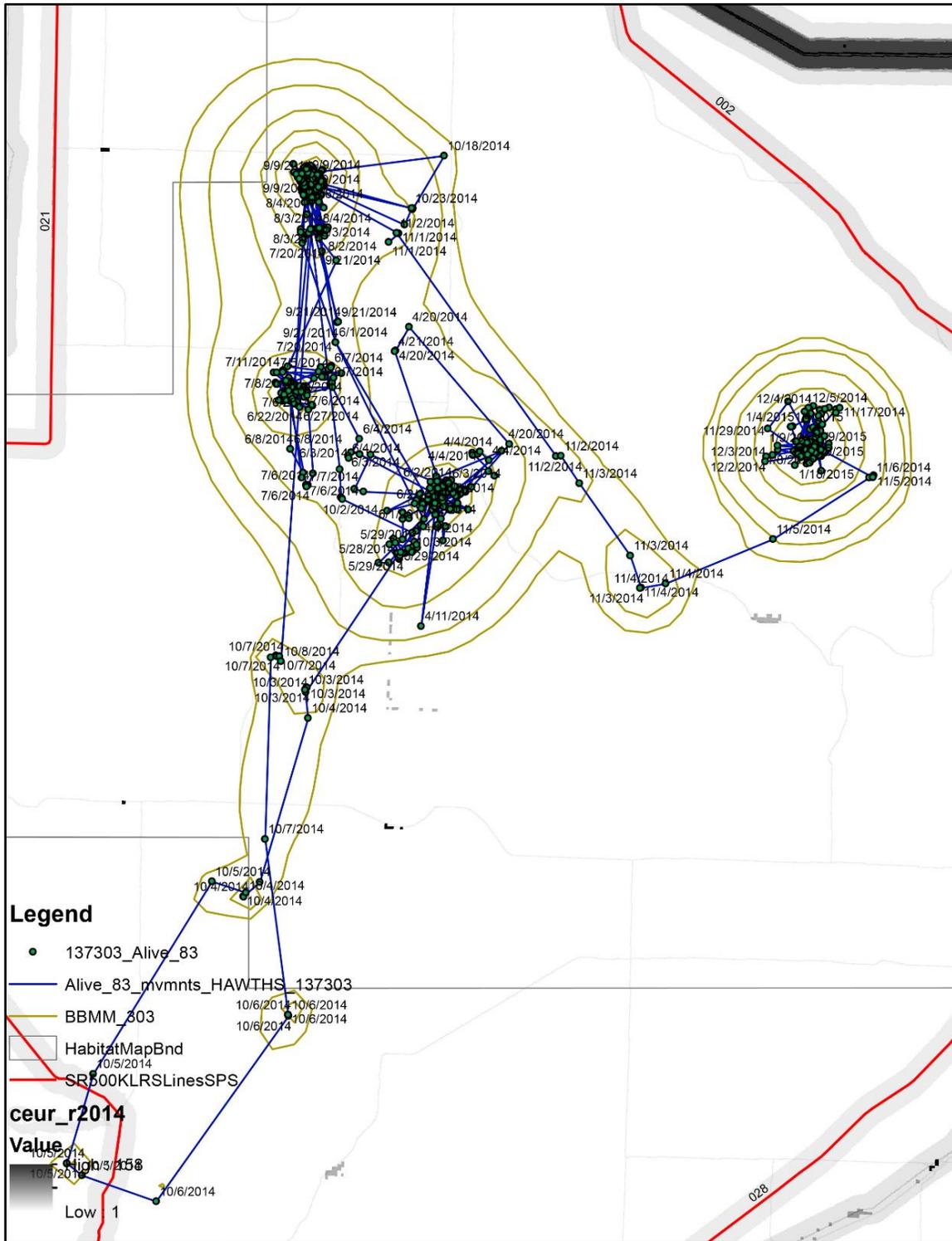


Figure 11. Example map showing Greater Sage-Grouse GPS telemetry data with contoured or rasterized BBMM paths overlaid on an example resistance surface (sage grouse ID # 13703). Darker areas of the background landscape indicate higher resistance values, while the red lines indicated state highways and roads.

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