

A large-scale multi-seasonal habitat prioritization and an
analysis of structural connectivity for the conservation of greater
sage-grouse in Wyoming

by

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Author's Declaration

I, hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners. I understand that my thesis may be made electronically available to the public.

Abstract

Habitat loss is widely recognized as the primary cause of global declines in biodiversity and is linked to human disturbances through widespread land-use changes (Menon et al., 2001). As a consequence, wildlife species must persist on landscapes that are greatly modified and fragmented (Moilanen et al., 2005). Disruptions affecting the structural connectivity can hinder ecological flows of energy, nutrients and the natural dispersal of species across the landscape. Therefore, in order to conserve wildlife populations, we are challenged with securing areas where species are most likely to survive in the long run while maintaining habitat connectivity to facilitate natural ecological processes and meta-population dynamics (Gardner et al., 1993; Early and Thomas, 2007).

Identifying conservation priority areas is an essential step in wildlife conservation planning. In order to achieve long term conservation success amid increasing developments and environmental degradation, we must aim for biologically and ecologically comprehensive and justifiable approaches that take multiple factors into consideration when defining conservation priority areas. In addition, when prioritizing the landscape, we must also account for the variations in habitat use caused by seasonal changes throughout the annual cycle in order to protect indispensable habitat across all seasons and life-stages. Thus, my first objective was to develop an annual habitat prioritization for greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) in Wyoming, USA by combining nesting, summer and winter habitat selection models in an ecologically meaningful way using a quantitative spatial prioritization tool. I assessed the capacity of Wyoming's current sage-grouse protected areas for capturing priority areas across the full annual cycle in order to quantify the importance of a multi-seasonal (i.e., annual) habitat prioritization. While, the annual habitat prioritized substantial as well as very similar fractions of the best habitat from each individual season, results indicated that the protected

areas did not account for 52% of the top 25% of best annual habitat. As expected, the individual seasonal analysis confirmed that the protected areas contained more nesting priority habitat and failed to capture substantial fractions of summer and winter priority habitat.

My second objective was to model connectivity between sage-grouse lek sites by applying circuit theory across the annual habitat model. I calculated the correlation between connectivity and habitat use across the annual and nesting habitat selection models to test if greater connectivity resulted in larger and more stable populations independent of habitat. I examined these trends across years of high population as well as years of low population. The structural connectivity of the landscape was not strongly correlated with the relative probability of habitat use across both nesting and annual habitat models ($r = 0.3$). Increasing connectivity was associated with increasing population sizes at leks and decreasing variability in lek counts; thus signifying that structural connectivity has a positive influence on population abundance and supports greater stability at lek sites. These trends also extended across years of high population as well as years of population declines, therefore indicating the importance of structural connectivity across the full cycle.

Overall, my research explicitly integrates across all seasonal habitats supporting a multi-seasonal approach over a single-season approach for identifying priority areas in order to shield sage-grouse from human induced disturbances across the full annual cycle. Furthermore, I found that the structural connectivity of the landscape is beyond a simple summarization of habitat availability; therefore, when prioritizing the landscape and identifying core areas for protection, considering areas of high structural connectivity in addition to good quality habitat would enhance overall conservation outcomes across the full annual cycle.

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Chapter 1 General Introduction

Due to irreversible and increasing loss of global biodiversity caused by human induced wide spread land-use changes, setting priorities in an effort to conserve species has been a recurrent topic for the last two decades (e.g. Myers, 1990; Pressey et al., 1993; Williams et al., 1996; Reid, 1998; Sala et al., 2000; Sanderson et al., 2002; Green et al., 2005; Brooks et al., 2006; Early and Thomas, 2007; Buchanan et al., 2011; Mokany et al., 2014). Natural habitats are increasingly degraded and species are extirpated by disturbances associated with urbanization, agriculture, energy extractions and forestry practices in addition to the affects of climate change (Sinclair et al., 1995). In conservation prioritization literature, establishing protected areas is the oldest and most commonly undertaken action in conservation planning (Kremen et al., 2008; Proctor et al., 2011; Leroux and Rayfield, 2013). However, with increasing development and impacts of climate change drastically altering habitat quality and natural resources, identifying priority areas for species of conservation concern require more sophisticated methods including multiple factors and sources of biologically meaningful information for more effective and long lasting results. Furthermore, research shows that considerable attention must be given to ensuring that connectivity, spatial structure and seasonal changes are also understood and included in conservation plans (Cerdeira et al., 2005; Brooks et al., 2006; Matisziw and Murray 2009; Fedy et al., 2012; Hostetler et al., 2015).

Traditionally, research studies and conservation efforts for birds have mainly focused on one season – the breeding season. However, different seasonal habitats are typically required for a species to persist with seasonal environmental changes. My research focuses on the development of an annual habitat prioritization by combining multiple seasonal habitats in order to identify conservation priority areas across the full annual cycle. Using greater sage-grouse

(*Centrocercus urophasianus*; hereafter sage-grouse) in Wyoming, USA as an example, my first general goal was to quantify the importance of a multi-seasonal habitat prioritization for identifying priority areas in order to protect sage-grouse from human induced disturbances across the full annual cycle. My next general research goal was to model annual structural connectivity in order to assess the importance of incorporating areas of high structural connectivity in landscape prioritizations for sage-grouse in Wyoming. Overall my thesis research explicitly integrates across all seasonal habitats supporting a multi-seasonal approach over a single-season approach for identifying priority areas and modeling multiple corridors that connect active sage-grouse leks for facilitating density dependent dispersal across the full annual cycle.

Chapter 2 Background Information

2.1 Seasonal Habitats

In species management, understanding the spatial distribution and habitat selection is critical for the long term persistence of a species (Pearce and Boyce, 2006; Austin, 2007). The use of natural resources by species may vary over different temporal scales, including across seasons and stages of life. In addition to migratory species, resident species often change foraging substrates and food sources with the change of seasons (Morrison et al., 2006). Furthermore, the theory of evolution through natural selection, presented by Charles Darwin in 1859 and supported by many scientific disciplines suggests seasonal changes as the main factor influencing population numbers (Darwin, 1859; Darwin, 1964; Betini, 2014). He argued that climate and seasonal changes lead to variations in the abundance of food; thus causing changes in species interactions (Darwin, 1859; Darwin, 1964; Betini, 2014). Therefore, we must consider seasonality and account for the variations in habitat requirements caused by seasonal changes across the annual cycle when identifying priority areas. However, despite Darwin's argument, seasonal changes were largely overlooked and initially ignored in ecology (Darwin, 1859; Darwin, 1964; Levins, 1968; Fretwell, 1972; Betini, 2014). Although it is commonly known that different seasonal habitats are typically required for species throughout the year and across their lifespan, the majority of studies in the past have taken a single season approach when studying habitat relationships (e.g., Chandler et al., 2009, King et al., 2009, Schlossberg et al., 2010; McClure et al., 2013).

As populations tend to be regulated by events occurring across multiple seasonal habitats, the relationship between a habitat used during a single season or life stage and the overall population dynamics could be weak as a result of carrying over effects – where demographic

measures are a reflection of the quality of habitats used during earlier seasons (Morrison and Mathewson, 2015). Certain occurrences or conditions during a single season can inevitably influence and change the behaviour, performance or reproduction in another or subsequent season (Marra et al., 1998; Marra et al., 2005; Reudink et al., 2009). Demographic events caused by natural environmental changes or human induced disturbances during one season may have significant and unpredictable effects on its subsequent seasons; thus affecting other life stages and altering a species' seasonal ranges, reproduction, behaviour, habitat requirements and interseasonal movements (Silleet et al., 2000; Webster and Marra 2005; Calvert et al., 2009; Marra et al., 2011; Fedy et al., 2012). Furthermore, when seasonal interactions exist, demographic measures within one season may not reveal habitat quality as a result of carryover effects from previous seasonal locations (Morrison and Mathewson, 2015). Therefore, taking a single-season approach and neglecting and failing to protect priority areas during other seasons could have a significant impact on the overall population and long term survival of a species.

Temporal variations in habitat use are ignored by many researchers in at least two main ways: 1) while they acknowledge the existence of temporal variations, the samples are usually taken during spring and/or summer – largely due to logistical and funding limitations – making it too time specific that it can only be applied minimally to other situations, and 2) they may take samples from only one season and “average out” the relationships across the time period (Morrison et al., 2006). This tendency and bias towards a single season (or life stage) overlooks the fact that all events and conditions across a species' full life cycle shape population dynamics (Morrison and Mathewson, 2015). Furthermore, as it is difficult to quantify habitat requirements for multiple life stages, and due to the important role reproduction plays in maintaining populations (e.g., Hoekman et al., 2002), the majority of ecological studies on birds have mainly

focussed on prioritizing the breeding habitat (e.g., Chandler et al., 2009, King et al., 2009, Schlossberg et al., 2010; McClure et al., 2013; Rodewald, 2015). However, we know that the functional connectivity across the landscape may be related to habitats other than those areas preferred for breeding (Row et al., 2015). As Morrison et al. (2006) points out, during the fall and winter seasons we would naturally expect resources to decline, animals to be physiologically stressed and under pressure by dispersal or migratory movements, and the weather conditions to be harsher, making these the most difficult seasons for animals to survive in and requires as much attention as the breeding season. Hence, without incorporating the full knowledge of an organism's requirements to adapt, survive and thrive during multiple seasons, management recommendations and future implications are limited and may even be defective.

While prioritizing and protecting areas where there is a significant influence on species persistence and survival over multiple seasons is valuable, the significance of seasonal changes have only been taken into consideration recently (Holt, 2008; Hastings, 2012). In the last decade or so, seasonality has been incorporated in ecological models and its appreciation has been gradually increasing (Yang et al., 2008; Schoener, 2011; Hastings, 2012). With increasing habitat loss and fragmentation drastically degrading natural habitats and resources, taking a multi-seasonal approach in wildlife management and conservation plans is vital now more than ever. However, incorporating multiple factors and sources of data is dependent upon the availability of data and computer-processing limitations. Over the years there have been major advances in large scale habitat prioritizations with the use of Geographic Information Systems (GIS) and spatial conservation planning software (e.g., applying quantitative spatial prioritization methods) for conducting multi-feature landscape prioritizations. With the availability of these advanced technologies and novel methods, wildlife conservation and management efforts should

ideally incorporate multiple seasons of comprehensive data and prioritize the landscape across the full annual cycle in order to shield species against disturbances and threats encountered across all seasons and life stages for long term conservation success.

2.2 Spatial Conservation Prioritization

The process of applying spatial analysis on quantitative data in order to identify locations for protection and conservation investment is known as spatial conservation prioritization (Wilson et al., 2009). With the use of mathematical or logical algorithms, quantitative approaches in spatial conservation prioritization aim to generate priority areas based on spatially mapped quantitative data of relevant attributes or variables representing information such as habitat conditions, species distributions, threats and seasonal requirements (Wilson et al., 2007; Ferrier and Wintle, 2009). Ultimately, the chosen prioritization algorithm prioritizes the study area by planning units or grid cells and generates the results as maps representing the spatial distribution of priority areas (e.g., Moilanen et al., 2011). The early development of these techniques – until the early 1990s – addressed simple but theoretically powerful problems such as the minimum set coverage problem –which aims to achieve a given conservation target at minimum cost - with small data sets targeting single-populations (Moilanen et al., 2009). Over the last decade, there have been major advances in conservation prioritizations with the use of GIS, various different mathematical techniques and remarkable improvements in the ability and capacity of computers to handle and facilitate spatial prioritizations (Moilanen et al., 2009). The expansion of protected areas, development of conservation policies and planning processes have all been influenced by the field of spatial conservation prioritization since its origin in the early 1980s (e.g. Kirkpatrick, 1983; Cocks and Baird, 1989) and there has been a rapid increase in the

number of published studies on the development and application of spatial prioritization techniques in the last two decades (Moilanen et al., 2009; Wilson et al., 2009).

Furthermore, as pointed out in Moilanen et al., (2009), some of the earlier used techniques have been reviewed a number of times (e.g. Vane-Wright et al., 1991; Pressey et al., 1994; Margules and Pressey, 2000; Cabeza and Moilanen, 2001; Sarker et al., 2006; Margules and Sarkar, 2007) under the name “systematic conservation planning”. Systematic conservation planning is a term used for the broader context (operational model) in which spatial conservation prioritization is a fundamental form of assessment (*sensu* Knight et al., 2006) - a technical phase (Kukkala and Moilanen, 2013; Lehtomaki and Moilanen, 2013). Moreover, according to Margules and Pressey (2000), the process of spatial conservation prioritization is viewed as more systematic, thorough and consists more accountability than a convenient and opportunistic way of using conservation funds. It has the potential to better allocate limited conservation funds on areas more likely to achieve the most benefits towards the overall long-term conservation of a species. In addition to identifying priority areas for establishing protected areas, areas can also be identified for investing towards other conservation purposes, such as: fire and invasive species management (e.g. Wilson et al., 2007). Thus, in the recent years, there has been a growing interest in the use of quantitative approaches for spatial prioritizations in conservation planning.

According to Ferrier and Wintle (2009) - one of many publications that explain the process - in order to conduct a spatial conservation prioritization we need to incorporate factors of information and measurable indicators for all variables of interest. Each variable should have information in spatial format with geographically linked data values. Due to the difficulty of obtaining such spatially explicit data relating directly to the variables of interest, other sources of information can be used to predict the variables or to act as a surrogate for the factors of interest;

such as for instance, the use of species distributions as a surrogate in the analysis of spatial patterns for the distribution of biodiversity, or using slope and soil data to predict agricultural potential in a study (Ferrier and Wintle, 2009). Furthermore, in large-scale prioritizations, relevant spatial information are manipulated using spatial interpolation methods or methods of modelling in order to fill in the gaps in the information available and prepared as spatial layers (maps) using GIS (e.g. Ferrier et al., 2004). However, more accurate direct field assessments and on-ground data collections should be opted for whenever possible for smaller regions and extents as feasible (Ferrier and Wintle, 2009).

Over the years there have been two approaches to quantitative conservation prioritization: 1) scoring, and 2) complementarity-based approaches. In scoring, each spatial unit (e.g. grid cell) is scored (e.g. presence/absence) against each of the factors of interest with the option of also applying weights to each of the factors (e.g. Strager and Rosenberger, 2006; Regan et al., 2007) along with either having a single set of scores, or scoring each spatial unit twice (first to determine the conservation value without intervention and second to approximate the value if the specific management action were applied) (Ferrier and Wintle, 2009). However, a very essential limitation of scoring had begun to surface in the mid-1980s with regards to maximizing inclusions (representations). Scoring lacked the ability to optimally maximize the overall number of species represented within reserves (Kirkpatrick, 1983; Ferrier and Wintle, 2009). Thus, in order to focus more on the overall representativeness of the study area rather than local richness of a location; the principle of complementarity was implemented (Justus and Sarkar 2002; Ferrier and Wintle, 2009; Wilson et al., 2009). This approach is based on the fact that the biological diversity is a non-additive property of a set of locations – meaning that total diversity is not simply the sum or average of richness at each location (Ferrier and Wintle, 2009). Scoring

approaches do not possess the capacity to address such non-additive methods; whereas complementarity focuses on collective properties - combinations (Margules and Sarkar, 2007; Ferrier and Wintle, 2009).

2.2.1 Conservation Prioritization Tools

Over the last twenty years, many quantitative approaches of spatial conservation prioritization have surfaced for identifying priority areas (e.g., Moilanen et al., 2009; Lehtomaki, 2014). There have been significant advances in spatial modeling techniques (e.g. Guisan and Zimmerman, 2000) leading to more predictive models representing required information of interest; making it increasingly possible to move from taking a single to an effective multi-feature approach. Furthermore, a number of reliable and publicly available spatial conservation prioritization tools and software have been developed, such as: Zonation (Moilanen et al., 2012), Marxan (Ball and Possingham, 2000; Possingham et al., 2000) and C-Plan (Pressey et al., 2009) that can be used to overcome various goals and purposes in conservation planning. The algorithms implemented in spatial prioritizations have been widely studied over the years by many experts in the field (Possingham et al., 2001; Williams et al., 2005; Sarkar et al., 2006; Moilanen et al., 2009). Reserve selection and habitat prioritization algorithms that have the capability of considering multiple features using data such as: probability of occurrence, habitat suitability and population viability models as inputs (i.e., probability surfaces for species occurrences) are increasingly being applied for land management decisions in conservation planning. Moreover, the majority of modern approaches share the concept of complementarity in common. Overall, two of the most frequently used software over the last decade are: Marxan (see Ball and Possingham, 2000; Hazlitt et al., 2010; Esselman and Allan, 2011; Holland et al.,

2012; Levin et al., 2013) and Zonation (see Moilanen et al., 2005; Early and Thomas, 2007; Kremen et al., 2008; Leathwick et al., 2010; Sharafi et al., 2012; Dobrovolski et al., 2013).

Marxan was developed to assist in systematic reserve design with the capability of identifying a set of spatially aggregated sites to meet multi-feature targets while aiming for minimal costs. Although, Marxan was initially developed for marine initiatives, it has been widely used for landscape prioritizations, with the options of including ecological processes and sociopolitical influences (Franklin et al., 2011). By applying a simulated annealing algorithm, this tool delivers either a number of very good solutions, or information regarding the frequency of selecting planning units from the solutions. Marxan, Marxan with Zones (Watts et al., 2009), and C-Plan are built for stochastic optimizations and target-based planning. Conservation planning often utilizes quantitative targets which are essentially the minimum percentage of the distribution of a species or vegetation or some other feature of interest intended for protection (Carwardine et al., 2008). While a review of published literature indicates the use of targets is internationally accepted in conservation planning, target based approaches have received much scrutiny and skepticism in the conservation community. The most frequently reported limitations as listed in Carwardine et al., (2008) are: setting targets produce perverse outcomes (Soulé & Sanjayan, 1998; Woinarski et al., 2007), target-based plans are inadequate, inflexible and overrule expert judgement (Agardy et al., 2003), target-based plans are unachievable, fails across intact landscapes and cannot incorporate complex factors such as: ecological processes and threats (Woinarski et al., 2007). Furthermore, an often pointed out limitation of target-based conservation planning software is that any set of sites selected as a requirement to achieve the defined targets are merely one of the many possible sets of sites that are capable of achieving the

same targets although the individual sites differing in the specific configuration and composition to some extent (Pressey et al., 2009).

In contrast, Zonation conservation planning software was developed for identifying important areas for retaining habitat quality as well as connectivity for multiple species with the indirect aim of long term species persistence with the smallest possible costs. Zonation has the option of incorporating feature richness and allows species to be weighted based on their importance for achieving conservation goals. By applying a reverse iterative heuristic algorithm, Zonation ultimately “produces a hierarchical prioritization of the landscape based on the conservation value of sites, iteratively removing least valuable cells [on a grid based map] (accounting for complementarity) from the landscape while minimizing loss of both biodiversity and connectivity” (Franklin et al., 2011). Therefore, Zonation’s capability of applying a reserve design algorithm that takes a complementarity-based approach producing a grid-based nested hierarchical ranking of the landscape (Franklin et al., 2011) has made Zonation an ideal tool for conducting multi-feature landscape prioritizations for identifying priority sites for protection. Thus, Zonation Version 3.1 (Moilanen et al, 2012) is used in Chapter 4 of my thesis.

2.3 ZONATION Conservation Planning

The Zonation framework consists of two parts: 1) the Zonation meta-algorithm, and 2) the cell removal rule (Moilanen, et al., 2012). The Zonation meta-algorithm is the general underlying basis of the software for the hierarchical prioritization of the landscape based on conservation value specific to each project. The cell removal rule determines how the marginal loss is calculated; deciding which cells lead to the smallest amount of loss in value when considering all input raster models. With the analysis starting from a full landscape, Zonation

uses minimization of the marginal loss as the criterion to iteratively remove cells beginning with the least valuable remaining cell in order to produce the hierarchical ranking of the landscape based on the conservation value of sites while accounting for generalized complementarity (Moilanen et al., 2012). Ranging from 0 to 1, the Zonation meta-algorithm assigns the lowest rankings (close to 0) to the least useful cells, and the cells most valuable for species conservation are assigned the highest rankings (Lehtomäki and Moilanen, 2013).

The Zonation meta-algorithm is capable of answering two very important questions: which parts of the landscape has the most conservation priority adding up to a given percentage from the area or cost? And which parts of the landscape consists of a given percentage of each of the species distributions? (Moilanen et al., 2012). As Zonation starts the cell removal from the full landscape with the option of removing more cells at once, rather than one cell at a time, the Zonation algorithm is a reverse, accelerated, iterative heuristic (Moilanen et al., 2005; Moilanen et al., 2012). The meta-algorithm works as follows (Moilanen 2007; Moilanen et al., 2012):

- 1) Starts from a full landscape with rank set as $r=1$
- 2) Calculates the marginal loss after removing each remaining site i , δ_i . (This step accounts for complementarity)
- 3) Removes the cell that has the smallest δ_i , with removal rank i set to be r , set $r=r+1$, and if any cells are remaining then return to step 2.

The cell removal order is recorded for analysis as well as for selecting any given top fraction of features (i.e. best 5% of the landscape). Information regarding the decline of representation levels of features is also collected along the way for analysis (Moilanen, et al., 2012). The Zonation meta-algorithm stays the same for all available analyses options; however

the actual order of cell removal depends on the cell removal rule chosen for each study (Moilanen, 2007).

2.3.1 Cell Removal Rule

The definition of marginal loss (step 2 of the meta-algorithm above) controls the Zonation algorithm. Marginal loss is defined (calculated) by the separate cell removal rule one chooses to apply. It is the way of deciding which cells lead to the smallest amount of loss in conservation value; thus implementing the conception of how the aggregation of conservation value is done across the landscape and across features (Moilanen et al., 2012). The main cell removal options available in Zonation are: Basic core-area Zonation and Additive benefit function.

2.3.1.1 Basic core-area Zonation

This rule focuses on minimizing biological loss by selecting cell i which is the least valuable for the most valuable occurrence over all the features within the cell. Thus, even if one feature shows a relatively important occurrence in a cell, that cell would be given a high value – however the removal of that said cell is dependent on the remaining proportion of distribution among all features across the full landscape in order to achieve a balanced coverage of all features in the prioritization. Here, removal is done based on a removal index δ_i , which is defined in the Zonation manual as the minimum marginal loss of biological value. The removal index is calculated for each of the cells in the study area:

$$\delta_i = \max_j \frac{Q_{ij}(S)w_j}{c_i}, \quad (1a)$$

where δ_i is the value of the cell, w_j represents the weight (or priority) given to species j and c_i is the cost for leaving cell i in the reserve network. The most critical part of the equation (1a) is $Q_{ij}(S)$, which is the proportion of the remaining distribution of species j in cell i for the remaining set of cells, S (Moilanen 2007; Moilanen et al., 2012). During the analysis, Zonation goes through all cells in order to calculate and give a value of δ_i based on the species that has the highest proportion of distribution left in a cell. A cell that has a high value of δ_i will have the highest biological value to be lost when that cell is removed. When part of a feature distribution is removed, there is an increase in the proportion located in each remaining cell. In other words, Zonation attempts to maintain core-areas of all species until the end of the analysis (end of cell removal), regardless of the feature being initially common; thus accounting for increasing rarity at each iteration (Lehtomäki, 2014). Finally, the last cell to remain untouched would have the highest weighted richness (Moilanen et al., 2005). The minimum-maximum structure of (1a) aims to retain the best areas with the highest “occurrence” levels of features (Moilanen et al., 2012). However, this cell removal rule does not address probabilities of occurrence as additive; which means ten locations of $p = 0.099$ will not be equaled to one location of $p = 0.99$ (Moilanen, 2007). Furthermore, by giving a weight w_j will decide the level of importance given to a feature with respect to other species; a high weight would retain a relatively high fraction from the distribution of the given feature at any iteration (e.g., Moilanen et al., 2005).

2.3.1.2 Additive Benefit Function

This rule is designed to apply more weight to locations with high species (or feature) richness. Unlike basic core-area Zonation, the additive benefit function sums up all features in

the cell. Thus, the number of features in a given cell would directly have a higher importance here than when using basic core-area Zonation. This rule first calculates the loss of representation for each species or feature as cell i is removed. The algorithm shown below (Moilanen, et al., 2012) is again simply calculating the value of the cell; which is equal to the sum of all features within the cell over feature-specific declines in value as cell i is lost:

$$\delta_i = \frac{1}{c_i} w_j \sum_j \Delta V_j = \frac{1}{c_i} w_j \sum_j [V_j(q_j) - V_j(q_j - i)],$$

(1b)

where δ_i is again equal to the value of the cell, q_j represents the species j in the remaining set of cells, $q_j - i$ is the set of remaining cells minus cell i , w_j is the weight given to the species j , and c_i is the cost or area of planning unit i . The cell with the lowest δ_i value will be removed here as well. When a cell is removed, there is a small fractional decrease ΔR_j in the representation of each feature occurrence in the removed cell along with a decrease in the respective value of that feature by ΔV_j . Thus, in other words, the sum divided by feature-specific losses defines the value of total marginal loss when additive benefit function is being used as the cell removal rule. Furthermore, as equation (1b) sums value over all features, the number of features represented in a cell gets a higher significance here than in the basic core-area cell removal rule. Thus, using additive benefit function as the cell removal rule might lead to scenarios where feature-poor cells will be removed even if those cells contained a high occurrence level for one or two rare features (Moilanen et al., 2012).

2.3.2 Justification

The use of Zonation for the identification of multi-species priority sites is relevant for my research because it allows for a transparent and straightforward identification of optimal as well as least useful conservation areas that could easily be replicated. Zonation directly links with statistical distribution modeling and GIS; therefore quantitative reserve planning can directly link with species distribution modeling (Zonation et al., 2012). This link is also very useful for carrying on further analysis, especially because the results can be used in conjunction with other spatial and statistical data. Most importantly, for the justification of Zonation's appropriateness for my research on identifying multi-seasonal priority sites, its ability to equally consider all features across the landscape and accounting for rarity during the cell removal stands out the most in accordance with my research objectives. Furthermore, its ability to work with large grid-based data sets (up to approximately 50 million grid cells) within a reasonable time is very useful for my research.

2.4 Structural Connectivity

When connectivity is based entirely on the physical structure of a landscape (e.g., Green, 1994; With et al., 1997; Metzger and Décamps, 1997; Tiebout and Anderson, 1997; Girvetz and Greco, 2007) without any direct association to the behavioural attributes of a species, it is referred to as structural connectivity (With et al., 1997; Collinge and Forman, 1998; Collinge, 2000; Kindlmann and Burel, 2008). Disruptions in the structural connectivity of the landscape can impede ecological flows of energy through ecosystems, nutrients and the dispersal of organisms (Gardner et al., 1993). Thus, landscape fragmentation can reduce dispersal success (Gibbs, 1998), increase mortality (Fahrig et al., 1995), reduce genetic diversity (Reh and Seitz,

1990; Wilson and Provan, 2003) and lead to population declines. With increasing developments, wildlife populations become relatively isolated, and if these populations are small and with few individuals, there is a high probability of local extinctions (Richter-Dyn and Goel, 1972; Schippers et al., 1996). Connectivity between habitats must therefore be maintained to facilitate meta-population dispersal (Levins, 1970; Verboom et al., 1993; Schippers et al., 1996). Furthermore, an organism's ability to move across the physical landscape will likely also influence its capacity to respond to changing climates, thus increasing the probability of survival (Heller and Zavaleta, 2009; Spencer et al., 2010; Zeller and Rabinowitz, 2011; Cushman et al., 2013). Therefore, the structural connectivity of the landscape is essential for wildlife management and species conservation.

Corridors facilitate the structural connectivity across the landscape. Corridors are often defined as continuous narrow strips of habitat structurally connecting two (or more) non-contiguous patches of habitat (Tischendorf and Fahrig, 2000; Kindlmann and Burel, 2008). The concept of corridors originated based on the generalized assumption that animals avoid non-habitat (e.g., Forman, 1983; Merriam, 1991; Tischendorf and Fahrig, 2000; Kindlmann and Burel, 2008). Based on ecologically fundamental spatial models developed in past studies (e.g., meta-population and island biogeography models; MacArthur and Wilson, 1967; Levins, 1969; Hanski, 1999), movement amongst patches is expected to result in an increase in population size and persistence (Moilanen and Hanski, 2006). There have been an increasing number of studies exploring how corridors are affecting movement in between habitat patches, which supports the notion that population viability should be enhanced by corridors and stochastic temporal variation will be reduced in local and regional population sizes; thus increasing the rates of movement from high-density to low-density areas (Haddad and Tewksbury, 2006). Moreover,

corridors are expected to cause declines in local extinctions while maintaining stable population dynamics (Brown and Kodric- Brown, 1977; Gonzalez and Chaneton, 2002; Haddad and Tewksbury, 2006). Furthermore, the validity of corridors were confirmed when Quinby (2006) tested the usefulness of a corridor using existing annual breeding bird survey data, and found more birds within the corridor than outside of the corridor. However, the importance of connectivity in comparison to other approaches has been a controversial topic in conservation ecology (e.g., Doerr et al., 2011; Hodgson et al., 2009; Hodgson et al., 2011; Fuller, 2012). The most common concern is that it is difficult to measure the benefits of enhanced connectivity and that the evidence of the derived benefits is ambiguous (Fuller, 2012). There is much debate around whether investing in larger areas of high quality habitat is better than enhancing the structural connectivity of the landscape (Fuller, 2012).

Habitat fragmentation results in spatial separations reducing population connectivity which interferes with critical ecological processes required for the preservation of biodiversity and the health of wildlife populations, consequently compromising the functional integrity of landscapes (With, 1999; Koen et al., 2014). Thus, the lack of undisturbed connectivity across the landscape can seriously threaten the persistence of wildlife populations (Johnson et al., 1992; Schippers et al., 1996; Schumaker, 1996; Koen et al., 2014). Conservation plans for fragmented landscapes require multiple wildlife corridors connecting healthy ecosystems in order to maintain biodiversity and species of conservation concern. While species representativeness is an important factor in conservation, maintaining connectivity amongst habitat patches takes habitat fragmentation and meta-population interactions into account while allowing natural ecological processes (e.g., gene flow) necessary for long term survival (Margules and Pressey, 2000; Gillespie et al., 2008). Therefore, structural connectivity can be identified as one of the most

critical factors in species conservation. Ever increasing human developments will continue to decrease and fragment available habitat. Thus, conservation plans should consider how to maintain and improve population connectivity for wildlife in complex landscapes in order to potentially mitigate impacts of increasing fragmentation and habitat loss.

2.4.1 Methods of Measuring Structural Connectivity

There are many methods available for modeling and measuring connectivity. In the past, habitat connectivity was frequently measured based on simple structural metrics, such as Euclidean distances between selected patches of habitat (Muhlner et al., 2010). In recent years, more ecologically and spatially meaningful measures based on cost-distance metrics have been proposed and utilized (Muhlner et al., 2010), such as: least-cost path (LCP) analysis (e.g., Adriaensen et al., 2003; Larkin et al., 2004; Etherington and Holland, 2013) and circuit theory – also referred to as electric circuit theory (e.g., McRae, 2006; McRae and Beier, 2007; McRae et al., 2008). While Euclidean distance is the calculation of the shortest distance between patches, both LCP and circuit theory are based on graph theory. Graph theory is a powerful approach for understanding connectivity by representing the landscape using a network (or graph) where habitat patches are defined by raster (grid-based) data and represented by nodes (i.e., points representing habitat patches) which then connect based on effective distance pathways provided by edges (Urban and Keitt, 2001; Fagan and Calabrese, 2006; Theobald, 2006). Graphs are models that represent the landscape as a network made up of nodes. Based on graph theory, LCP have been widely used for modeling corridors in ecology (Beier et al., 2009). LCP uses resistance (e.g., high resistance = low habitat suitability) values for cells across a grid representing the degree of difficulty in movement, then the best path between pairs of given

nodes are identified with a calculated cost-weighted distance (Adriaensen et al., 2003). Therefore, connectivity measures based on graph theory can account for landscape characteristics through the resistance values assigned across the raster layers compared to connectivity measures based on just the physical distance (e.g., Melles et al., 2012). Furthermore, a study conducted by Chardon et al., (2003), compared the explanatory power of effective-distance and Euclidean distance connectivity models, and found that cost-distance predicted connectivity better than Euclidean distance.

Between the two methods that integrate graph theory, the most significant (to my research objectives) limitation of LCP over circuit theory is that LCP is not able to identify multiple corridors between points –instead LCP is limited to single sources to single destinations of predicted connectivity (Cushman et al., 2013); thus alternative pathways are overlooked and are not considered even though alternate pathways of comparable costs may exist (Pinto and Keitt, 2009). This is not an issue in circuit theory as all possible routes are accounted for across the resistance surface (McRae, 2006). Therefore, a number of ecological researchers have discouraged the use of LCP and suggested graph-theory-based approaches of circuit-theory-based modeling as an improved, more ecologically meaningful method for modeling animal movements and landscape connectivity (e.g., Bunn et al., 2000; Belisle, 2005; Dale and Fortin, 2010; Fall et al., 2007; Phillips et al., 2008; McRae, 2006; McRae and Beier, 2007; McRae et al., 2008; Pinto and Keitt, 2009; Proulx et al., 2005; Rayfield et al., 2010; Shah and McRae, 2008; Urban and Keitt, 2001; Urban et al., 2009; Howey, 2011).

Circuit theory is increasingly being utilized for modeling connectivity in landscape ecology, evolutionary biology, and conservation biology (McRae, 2006) – and is seen most frequently applied in genetic studies. It is an effective means of modelling habitat connectivity

and dispersal (e.g. Howey 2011; Gimona et al., 2012; Walpole et al., 2012; Pelletier et al., 2014) as it is capable of integrating variable probabilities of connectivity throughout the whole landscape (Koen et al., 2014). This method highlights connectivity across a resistance surface (i.e., cost surface) similar to how an electric current moves through a circuit board. Rather than identifying single corridors between source and destination sites, this method makes it possible to identify multiple pathways between multiple defined points or polygons (i.e., nodes) with current flow analogous to random walkers on the landscape (McRae, 2006; McRae and Beier, 2007; McRae et al., 2008; Koen et al., 2012; Koen et al., 2014). The ability to evaluate multiple dispersal pathways among habitat patches (McRae, 2006; McRae and Beier, 2007; McRae et al., 2008; Koen et al., 2012; Koen et al., 2014), is more efficient and likely more biologically relevant.

2.5 Thesis Outline

This thesis contains 6 chapters, beginning with an overall general introduction in Chapter 1, background information in Chapter 2, and information on my study area in Chapter 3. Chapters 4 and 5 are my research chapters containing their own introduction, methodology, results and discussion sections. Chapter 6 provides a summary of findings from each of the research chapters and provides final conclusions and recommendations for future research and conservation efforts. As this thesis was written in a manuscript-style, there are some repetitions between chapters.

2.5.1 Objectives and Research Questions

Chapter 4 A Quantitative Spatial Prioritization for Combining Multiple Seasons: An Example Using the Greater Sage-Grouse in Wyoming, USA

Research Questions:

- i. Does the annual habitat prioritization capture the best habitat from each individual season?
- ii. Do the current protected areas for sage-grouse in Wyoming protect across all seasonal habitats?

Prediction: The protected areas will not capture significant portions of winter and summer habitats as they are developed mainly based on leks.

Chapter 5 An Analysis of Structural Connectivity for the Conservation of Greater Sage-Grouse in Wyoming, USA

Research Questions:

- i. Is there a correlation between connectivity and habitat quality?
- ii. What is the influence of structural connectivity on lek size?
- iii. How does structural connectivity influence variability in male lek counts?
- iv. Examine the influence of structural connectivity on lek size and variability at leks across peak population years and years of decline.

Chapter 3 Study Site

3.1 Location

With a total area of 253,000 km², my study area is the state of Wyoming (Figure 3.1-1) located in the north central USA – the mountain region of the Western United States - consisting of 23 counties. Wyoming is 360 miles in length and 280 miles in width with a longitude of 104° 3'W to 111° 3'W and latitude of 41°N to 45°N. It is the 10th largest state in America and also one of the states where the Rocky Mountains meet the Great Plains. The state is divided into three geographic areas: the Rocky Mountains, the Great Plains and the Intermontane Basins (land between the state's mountain ranges) (Kummer, 2003).

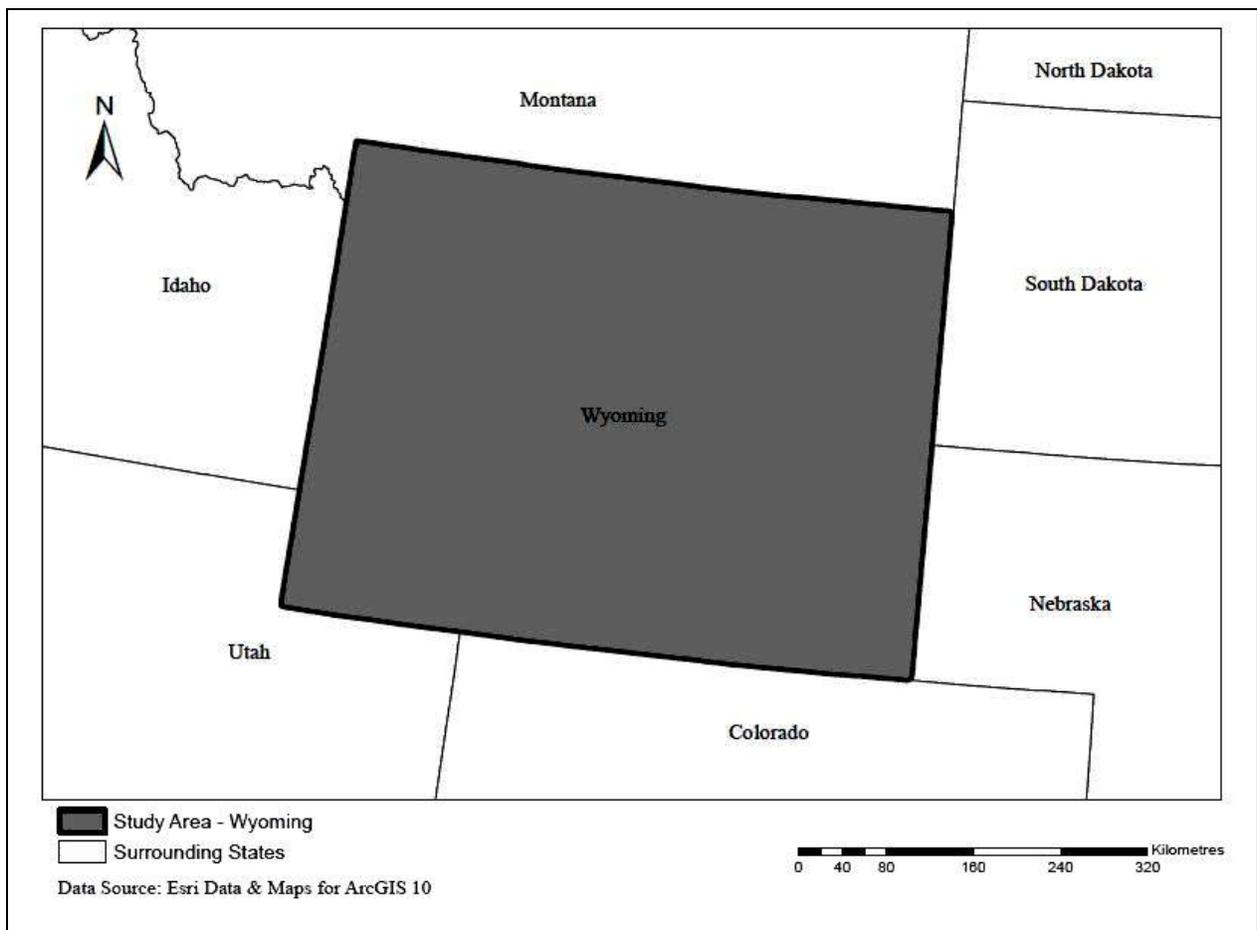


Figure 3.1-1. Map of Study Site

The study site, Wyoming, USA is highlighted in grey.

The highest point of Wyoming is Gannette Peak at 13,804 feet above sea level and the lowest point is the Belle Fourche River at the northeast corner of Wyoming at 3,099 feet above sea level. With a mean elevation of 6,700 feet above sea level, Wyoming is the second highest state after Colorado. The Continental Divide goes through the northwest to the south central border of the state – cutting through Yellowstone National Park continuing down into Colorado. The rivers located on the east side of the divide drain into the Missouri River Basin and then into the Atlantic Ocean, while the rivers to the west of the divide drain into the Columbia or Colorado River Basins and into the Pacific Ocean. The Yellowstone, Platte, Big Horn and Wind rivers are the major eastern rivers, whereas the Green River and Snake River are the major western rivers in Wyoming.

3.2 Climate Conditions

As the state with the second highest elevation, Wyoming normally has relatively cool and dry climate conditions and it is one of the windiest states in the United States. Overall, the state is known to having a semi-arid and continental climate along with mild springs followed by hot summers and cold winters. Temperatures reach around -6° Fahrenheit (-21° Celsius) in the winters, and rise to around 90° Fahrenheit (32° Celsius) in the summers with 15 to 152 centimetres of rain and snow annually - with the majority of annual rainfall occurring in the mountains – especially the Grand Tetons (Kummer, 2003). The mountains act as an effective barrier standing perpendicular to the westerly winds and forces the air currents from the Pacific Ocean to leave much of the moisture down the western slopes (Wyoming State Climate Office, n.d.). Since elevation has a major influence on precipitation, areas in Wyoming with lower elevations such as in the Big Horn Basin are nearly a desert, while areas on the eastern plains and the north are of semi-arid conditions.

While the majority of the precipitation occurs during the late spring and early summer, snow can fall across the entire state during the winter (Kummer, 2003) with heavy snowfall in the mountains. According to the Wyoming State Climate Office, freezing is experienced early in the fall and late in the spring, resulting in long winters. Generally, January is considered to be the coldest month. Snow usually falls from November to May, and blizzards or near blizzard conditions are caused with high winds and low temperatures which can last 1-2 days (Wyoming State Climate Office, n.d.). Furthermore, rapid changes between mild and cold spells can be expected as a frequent winter characteristic, with most of the cold waves moving to the south on the eastern side of the Continental Divide (Wyoming State Climate Office, n.d.). Mountain ranges prevent wind from stirring the air which causes the colder heavier air to settle into the valleys. Therefore, temperatures in the valleys (e.g. Big Piney in the Green River Valley) are usually significantly lower than in the mountains (Wyoming State Climate Office, n.d.). Furthermore, sometimes as the cold air moves eastward over the plains, only the northeast areas of Wyoming are affected; however, the majority of the cold waves do not include enough snow to result in severe conditions (Wyoming State Climate Office, n.d.).

3.3 Vegetation

Areas consisting of semi-arid climate conditions are dominated by short or scrubby vegetation consisting primarily of grasses or shrubs. As summer precipitation reaches below 282 mm, shrub-dominated communities tend to occur more than grass-dominated communities in Wyoming with soils of a coarse-texture favouring shrubs more (Knight, 1994; Driese et al., 1997). Sagebrush (*Artemisia* spp.) is believed to be the most widespread type of vegetation in the state for the past 8000 years (Beiswenger, 1991). In addition, there are a wide range of plants in Wyoming that are known to thrive amongst sagebrush, such as: sego lily (*Calochortus nuttallii*),

larkspur (*Delphinium nuttallianum*), bitterroot (*Lewisia rediviva*) and the prickly pear cactus (*Opuntia polyacantha*) (U.S. Department of the Interior, 2014). However, sagebrush shrublands are not homogeneous as they are often sparsely distributed which overall could add up to low a total of plant coverage over wide areas (Driese et al., 1997). The three most dominant vegetation covers in Wyoming are: 34% Wyoming big sagebrush (*Artemisia tridentate* ssp. *Wyomingensis*), 17.5% mixed grass prairie and 6.5% lodgepole pine (*Pinus contorta*) forest (Driese et al., 1997). There is a shift in dominance of vegetation from grasses to shrubs from the eastern plains to the basins of the west indicating an important phytogeographic transition in the state (Driese et al., 1997) – which could be explained in relation to the amount of precipitation received during the summer months (West, 1988). Furthermore, Wyoming mountain ranges are mostly covered by coniferous forests while the rest of the state is made up of mostly riparian vegetation distributed down drainages and various kinds of taller shrub-dominated plants featured in the foothills (Driese et al., 1997).

3.4 Land-Use and Resources

Wyoming has a total land area of 97,105 square miles and 714 square miles of water coverage – in which cities and towns cover only 77 square miles altogether (U.S. Census Bureau, 2012). Land use in this state is dominated by agriculture, livestock grazing, logging and mineral extractions (Driese et al., 1997). It is sparsely populated, and humans are outnumbered by livestock in addition to being outnumbered by bison, elk and antelope at a ratio of 2:1 (Knight, 1994; Driese et al., 1997). The state or the federal government owns more than half of the state (54% - increasing from east to west) including national forests, national parks, grasslands, and forests; while 43% of Wyoming is privately owned land in which 93% is for agricultural use (Taylor, 2003; Hulme et al., 2009). The publicly owned land is used for activities such as:

grazing, timber harvest, mining and recreation - mainly under the management of the U.S. Bureau of Land Management, National Park Service and U.S. Forest Service - with the majority of development limited to recreation infrastructure and resource extraction (Hamerlinck et al., 2013). According to the 2012 Census of Agriculture State Data, an estimated 30.3 million acres of land were farms (11,736 farms), with Laramie, Campbell and Sheridan counties experiencing the largest increase. Large areas of Wyoming are being used for grazing and the majority of agricultural land is located on the riparian zones as well as the eastern plains (Driese et al., 1997).

Government mineral rights and federal land ownership influences how land use is controlled in major areas of the state of Wyoming, and is an increasing federal interest in the production of domestic energy, which includes: coal, oil, gas, wind and solar (Hamerlinck et al., 2013). Mineral extraction occurs in many of the basins and to a lesser degree in the mountains on which logging is the primary form of resource extraction (Driese et al., 1997). Wyoming produces approximately 40% of the nation's coal and Wyoming is the leading state in coal production since 1986. The top 10 coal mines are situated in the Powder River Basin (Bureau of Land Management Wyoming, 2014). With over 2 million pounds of uranium produced for electricity in 2014, it is also the nation's leader in uranium production with 12 authorized sites and five Plans of Operations still pending (Bureau of Land Management Wyoming, 2014). Wyoming is ranked number one in federal gas production and two in oil production. Furthermore, it is also largely known for its wind resources – mainly in the southern region of the state - and already home to one of the nation's largest wind farms, located in Uinta county. According to the 2012 Census of Agriculture State Data, 768 farms in Wyoming have implemented renewable energy systems – mainly wind turbines and solar panels.

3.5 Additional Information

Over the last two decades, outdoor recreation, tourism, the development of rural residential areas and the natural resource industry have gradually intensified throughout Wyoming (Hamerlinck et al., 2013) resulting in significant habitat loss and fragmentation. These changes along with land management practices have altered the landscape and natural distribution of wildlife and vegetation across the state. The sage-steppe is currently undergoing a dramatic decline (Knick, 1999; Miller and Eddleman, 2000; Bunting et al., 2002; Connelly et al., 2004). While increasing development, invasive species and historic disturbances of fire have had a large impact on Wyoming's sagebrush landscape, according to recent studies, researchers suggest that the changes in the climate may present the greatest risk to sagebrush habitat and obligate species (Neilson et al., 2005; Bradley, 2010; Schlaepfer et al., 2012a; Schlaepfer et al., 2012b; United States Geological Survey, 2015; Homer et al., 2015). While attempting to coexist with increasing development and related disturbances, sagebrush and obligate species (i.e., the largest grouse in North America, the greater sage-grouse (*Centrocercus urophasianus*) - currently a species of great conservation concern), will be required to cope with the rising temperatures and reduced precipitation which increases sagebrush vulnerability to fires, invasive species and disease. The historic alteration and reduction of sagebrush ecosystems has had a great impact on many sagebrush dependent species – most significantly the sage-grouse (Connelly et al., 2004; Garton et al., 2011; Homer et al., 2015). Currently the state and affiliated land and wildlife management agencies have strategic plans underway in order to facilitate coexistence of wildlife and human civilization while keeping up with natural environmental and climate changes. The state implemented a core area policy for the conservation of sage-grouse (Sage-Grouse Core Protection Strategy), which restricts development in a set of core areas

identified based on breeding biology. These breeding-based core areas are tailored for multiple land-use purposes and have a high influence on Wyoming's land-use decisions. In order to improve conservation outcomes, Doherty et al., (2011) and Fedy et al., (2012) have recommended broadening the sage-grouse core areas concept to include multiple seasonal habitats.

Chapter 4 A Quantitative Spatial Prioritization for Combining Multiple Seasons: An Example Using the Greater Sage-Grouse in Wyoming, USA

Abstract

Habitat loss caused by human disturbances and widespread land-use changes is widely recognized as the primary cause of global declines in biodiversity (Menon et al., 2001). As a consequence wildlife species must persist on landscapes that are greatly modified and fragmented (Moilanen et al., 2005). Identifying conservation priority areas that are essential for protecting species and ecosystems is an important step in wildlife conservation planning. Thus, in order to achieve long term conservation success amid increasing developments and environmental degradation, we must utilize comprehensive approaches that take multiple biological and ecological factors into consideration when defining conservation priority areas. Traditionally, wildlife conservation efforts have focused mainly on one season – the breeding season. However, different seasonal habitats are typically required for a species to persist with seasonal environmental changes. The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a gallinaceous bird species limited to semi-arid sagebrush (*Artemisia sp.*) in North America. Here, I developed a state-wide annual habitat prioritization for sage-grouse by using a quantitative spatial prioritization method implemented in Zonation Version 3.1 (Moilanen et al., 2012) to combine habitat selection models for nesting, summer, and winter seasons across the sage-grouse distribution in Wyoming, USA. In western North America, nearly 50% of the original range of sage-grouse has been extirpated and the state of Wyoming is considered to be a stronghold for the species (Knick et al., 2003). The annual (multi-seasonal) habitat prioritization developed in this study identified areas of low to high conservation value simultaneously across all life stages. To examine how it compared to a single-season approach, the top 5, 10, 15 and 25 percent quantiles of the annual habitat were compared to the top

quantiles of each individual seasonal habitat. Furthermore, I assessed the capacity of Wyoming's current protected areas for sage grouse conservation – core management areas (i.e., Core Area Protection Strategy) – for capturing priority areas across the full annual cycle by examining how well the protected areas captured the top quantiles of the annual habitat. While the annual habitat prioritized substantial as well as very similar fractions of the best habitat from each individual season, results indicated that Wyoming's core management areas did not include 52% of the top 25% of best annual habitat. As expected, the individual seasonal analysis confirmed that the protected areas contain more nesting priority habitat than summer and winter. My research explicitly integrated across all seasonal habitats supporting a multi-seasonal approach over a single-season approach for identifying priority areas in order to protect sage-grouse from human and climate induced disturbances across the full annual cycle. The ability to combine multiple large-scale seasons of habitat selection data in an ecologically meaningful way to prioritize the landscape is highly beneficial for any species of conservation concern. A multi-seasonal approach aims to study the full range of the species distributed across the study area over the annual cycle, which is important for species such as sage-grouse competing with increasing anthropogenic and climatic stressors.

4.1 Introduction

Many wildlife populations –especially avian populations – are known to have seasonal movements placing them in various environmental conditions across seasons (Marra et al., 2011; Hostetler et al., 2015). The importance of conserving seasonal habitats has been addressed extensively for long-distance migrants. However, regardless of whether populations move long or short-distances or simply have local seasonal movements, they typically have different seasonal requirements (Rappole, 2013) to persist through seasonal environmental changes – especially with the added effects of anthropogenic stressors, climate change and other unpredictable catastrophic events, such as wildfire (Bilcke, 1984; Morrison et al., 1986; Keller and Yahner, 2007; Carey, 2009; McClure et al., 2013). Traditionally, conservation efforts for birds have focused mainly on a single season – the breeding season (e.g., Chandler et al., 2009, King et al., 2009, Schlossberg et al., 2010; McClure et al., 2013; Rodewald, 2015). However, demographic occurrences and other factors such as climate change and density dependency in one season can have a significant and unpredictable affect on subsequent seasons altering seasonal ranges, reproduction, behaviour, habitat requirements and interseasonal movements (Silllett et al., 2000; Webster and Marra, 2005; Calvert et al., 2009; Marra et al., 2011; Fedy et al., 2012). Although generally resident species are not expected to have widely separated seasonal habitats, dramatic shifts in habitat use between seasons have been known to occur for many species (Carey, 2009; McClure et al., 2013). Therefore, for a complete understanding of habitat requirements, a multi-seasonal approach is required.

Incorporating multiple sources of biologically relevant data increases the biological meticulousness, thus increasing the potential to be more effective overall when prioritizing land (Doherty et al., 2011; Fedy et al., 2012). However, incorporating multiple factors and sources of

data is dependent upon the availability of data and computer-processing limitations. Over the years, there have been major advances in technology, increasing numbers of individual studies, and increasing efforts and improvements in large scale habitat prioritizations with the use of remote sensing and Geographic Information Systems (GIS) (Fedy et al., 2014). Thus, with the availability of novel methods and advanced technologies, wildlife conservation and management efforts should ideally aim to incorporate multiple seasons of data and study the full annual cycle when possible in order to protect species against threats encountered across all life stages.

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a gallinaceous bird species limited to semi-arid sagebrush (*Artemisia sp.*) in North America. Sagebrush ecosystems and associated species are significantly affected by the loss and degradation of much of the native vegetation (Knick, 1999; Miller and Eddleman, 2000; Bunting et al., 2002; Knick et al., 2003; Connelly et al., 2004; Davies et al., 2011; Fedy et al., 2012; Homer et al., 2015). In western North America, nearly 50% of the original population of sage-grouse has been extirpated (Figure 4.1-1), primarily due to habitat loss (Schroeder et al., 2004). The state of Wyoming is considered to be a stronghold for populations of sage-grouse (Knick et al., 2003) and an estimated 37% of the range wide population is found in Wyoming (Doherty et al., 2011). Throughout their annual cycle, sage-grouse use seasonal habitats that generally group across three life stages: breeding (nesting), late-brood-rearing (summer), and winter (Connelly et al., 2011b). As sage-grouse seasonal habitat requirements differ in several ways across their life stages (Hagen et al., 2007), the persistence of sage-grouse populations require a sufficient amount of all seasonal habitats as well as a juxtaposition of seasonal habitats (Connelly et al., 2000; Fedy et al., 2012). Thus, identifying priority areas across all seasons is important for sage-grouse and other sagebrush associated species (Rowland et al., 2006; Hanser and Knick, 2011).

In order to evaluate options for the mitigation of development impacts on sage-grouse, Doherty et al., (2011) identified priority areas based on breeding biology and developed a set of core areas. These core areas (hereafter core biological areas (CBAs); Figure 4.2-1) were based on lek sites – locations where male sage-grouse perform displays of courtship during the breeding season – and breeding density buffered at 8.5 km to account for the delineation of nesting areas (Doherty et al., 2011). The CBAs identified locations of high- abundance population centres

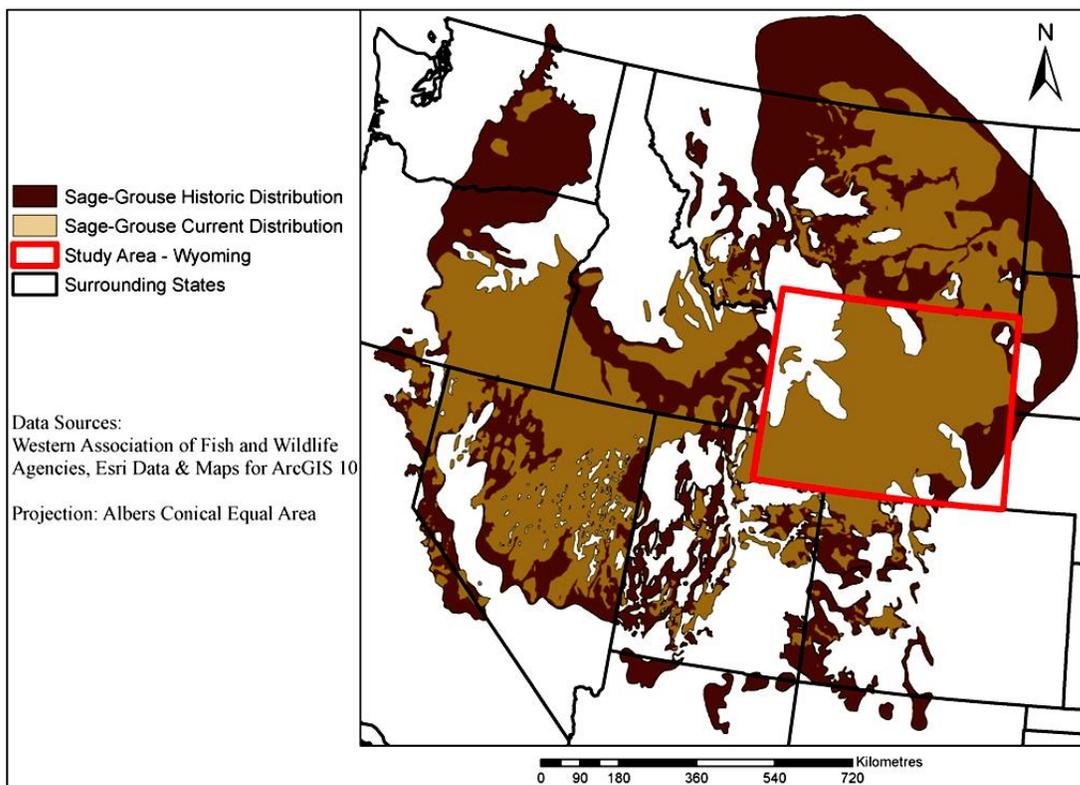


Figure 4.1-1. Historic and Current Sage-Grouse Distribution in Western North America. The historic distribution (dark brown) was developed based on sagebrush habitat. The current sage-grouse distribution (light brown) was derived from harvest, radio-telemetry, and survey (lek, brood, winter) data. Figure is based on data compiled by Schroeder et al., (2004).

containing 25%, 50%, 75% and 100% of the breeding population (Doherty et al., 2011). In the hopes of balancing habitat requirements with increasing energy developments, Wyoming implemented the sage-grouse Core Area Protection Strategy restricting development in a set of

priority areas (hereafter core management areas (CMAs); Figure 4.2-2). The CMAs are a modified version of the CBAs tailored for multiple land-use purposes and influence Wyoming's land-use decisions within these areas. Any developments on state and federal lands within the CMAs are guided by unique regulations to limit against disturbances (State of Wyoming Office of the Governor, 2011). As CBAs are based on lek counts and breeding biology, priority summer and winter habitats may not be protected from development impacts (Doherty et al., 2011). In order to improve conservation outcomes, Doherty et al., (2011) and Fedy et al., (2012) have recommended broadening the sage-grouse core areas concept to include multiple seasonal habitats.

Recently, there has been an increase in the development of seasonal habitat models for many species. Fedy et al., (2014) developed seasonally explicit habitat selection models to identify seasonal habitats for sage-grouse in Wyoming. These state-wide habitat selection models relied on biologically relevant data and presented nesting, summer and winter seasons separately (Fedy et al., 2014). My research explores an ecologically meaningful way to combine these separate seasonal models at a state-wide level in order to examine priority areas across the annual cycle. There are methods available for defining priority sites for the conservation of biodiversity worldwide (Bombi et al., 2011), and a relatively limited number of methods available for taking a multi-feature approach. Several quantitative habitat prioritization methods are designed for target-based planning, such as: MARXAN (Ball & Possingham, 2000), ConsNet (Ciarleglio et al., 2009), and C-Plan (Pressey et al., 2009). Furthermore, most multi-feature quantitative methods are used for biodiversity studies and require very detailed knowledge regarding the extent and distribution of species (Menon et al., 2013). Over the last decade, new spatial prioritization software have been developed for identifying conservation priority areas

and reserve design purposes, such as: Zonation Spatial Conservation Planning (Moilanen et al., 2012). Zonation is used to generate a ranked landscape based on the value of grid cells for conservation purposes. Although Zonation is also typically used for biodiversity analyses, it has the potential to combine multiple features in a meaningful way for conservation purposes accounting for long-term persistence of species based on habitat quality and richness of features. Therefore, I utilized Zonation to combine the individual seasonal models with similar considerations in order to generate an astute annual habitat prioritization.

The primary objective of this study was to quantify the importance of a multi-seasonal (i.e., annual) habitat prioritization. I addressed this by first developing a state-wide annual habitat prioritization for sage-grouse using the reverse iterative heuristic algorithm implemented in Zonation (Moilanen et al., 2012) to combine habitat selection models (relative probability of use) for nesting, summer, and winter seasons across the current sage-grouse distribution in Wyoming. Zonation has never been utilized in a multi-seasonal habitat prioritization before. Therefore, I used the annual habitat prioritization which was a hierarchical ranking of the landscape to examine 1) if the multi-seasonal approach captured the best habitat from each of the individual seasons equally. Then I examined 2) how much of the best combined habitat is contained within the core areas. I predicted that the core management areas strategy would not sufficiently capture priority areas of summer and winter habitats as they were only generated based on lek sites and breeding biology.

4.2 Methodology

The study area, Wyoming, has a total area of 253,000 km² and the current sage-grouse distribution encompasses approximately 68% of the state (Figure 4.1-1). This study utilizes the

models for the 75% CBAs (Figure 4.2-1) and the CMAs (Figure 4.2-2) to examine the capacity of both sets of core areas at capturing multi-seasonal priority areas within the current sage-grouse distribution in Wyoming. The 75% CBAs – which consist of 56 core areas - were chosen because they are known for being the population threshold used by managers in order to delineate priority areas for sage-grouse (Fedy et al., 2012) and were the basis for the development of the CMAs – which consist of 31 core areas.

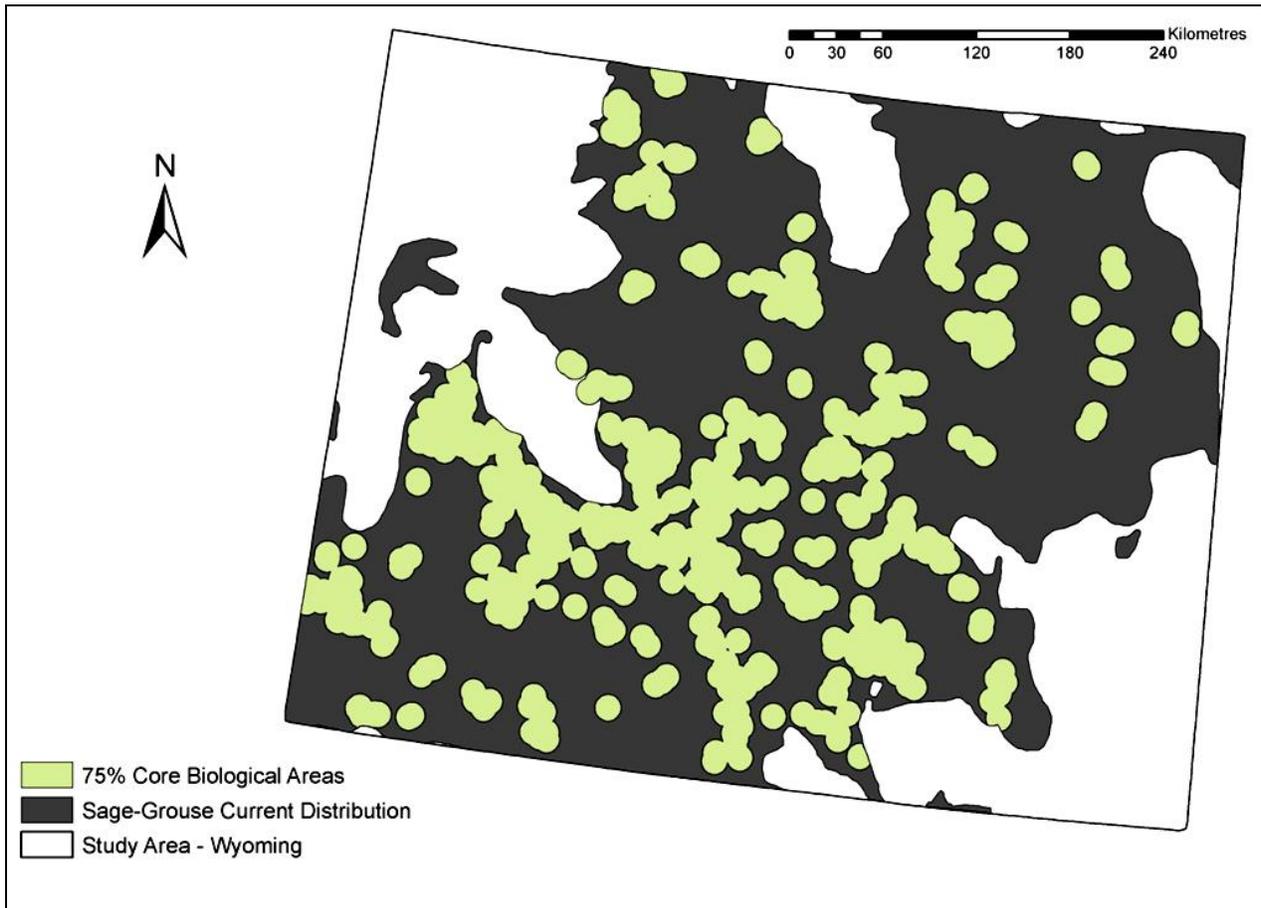


Figure 4.2-1. Core Biological Areas.

Developed by Doherty et al., (2011), the 75 percent CBAs consists of 56 core areas and are based on lek-count data and refined by breeding biology. The 75 percent CBAs are widely used by managers.

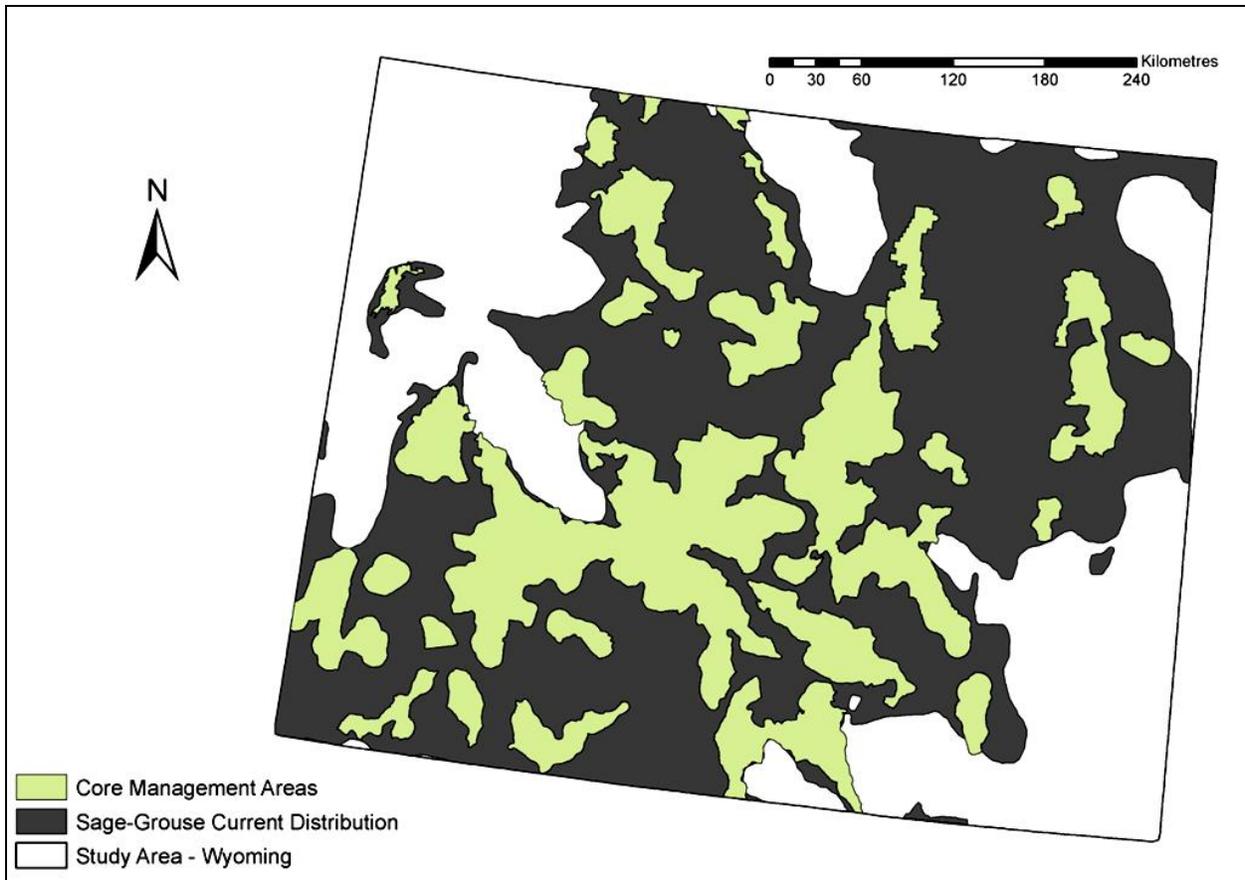


Figure 4.2-2. Wyoming Sage-Grouse Core Management Areas (Version 3).

The CMAs are an adapted version of the CBAs and consists 31 of core areas that highly influence land development decisions in Wyoming.

4.2.1 Data Acquisition and Preparation

Wildlife species use multiple spatial scales for habitat selection (e.g. Johnson, 1980; Kotliar and Wiens, 1990; Bergin, 1992; Ward and Saltz, 1994; Boyce et al., 2003; Boyce, 2006). Over the years, resource selection functions (RSF) have been widely used to analyze habitat use at multiple scales. As conservation and population dynamics can be influenced by large-scale patterns, it is also beneficial to implement management efforts across larger spatial extents (Fedy et al. 2014). For this study, I acquired raster (i.e., grid based) model predictions of seasonal habitat selection data (RSFs) developed in a recent large-scale study conducted by Fedy et al., (2014); from which I opted to use the state-wide landscape \times patch combined models for its

comprehensiveness over the regional models. Multiple (14) radio-telemetry studies and biologically relevant GIS data were used to develop the seasonal RSFs for sage-grouse in Wyoming. The development of the RSF models for nesting, summer and winter (Figure 4.2-3, Figure 4.2-4 and Figure 4.2-5) included the following variables for sage-grouse from 1994 – 2010: vegetation, roads, wells (oil and gas), agriculture, topography and climate. The three acquired nesting, summer and winter seasonal model-predicted raster layers represented a relative probability of use at a 30 m × 30 m cell size (i.e., spatial resolution). Details on model development can be found in Fedy et al., (2014).

By using the nearest neighbor assignment as the resampling algorithm, I resampled these layers to a 120 m resolution to reduce processing time while still representing a biologically meaningful and relevant scale. As this study focuses on broad-scale patterns of multi-seasonal habitat prioritization, the resampling to a coarser resolution did not negatively affect the study objectives. The spatial layer for the 75% CBAs was developed by Doherty et al., (2011) and acquired as a vector shapefile consisting 56 polygons, and the Wyoming sage-grouse CMAs (Version 3) spatial layer was acquired from the Wyoming Game and Fish Department also in the form of a vector shapefile consisting 31 polygons. The CMAs (Version 3) was developed by the Wyoming Governor’s Sage-Grouse Implementation Team and the Wyoming Game and Fish Department in cooperation with Wyoming Bureau of Land Management (BLM).

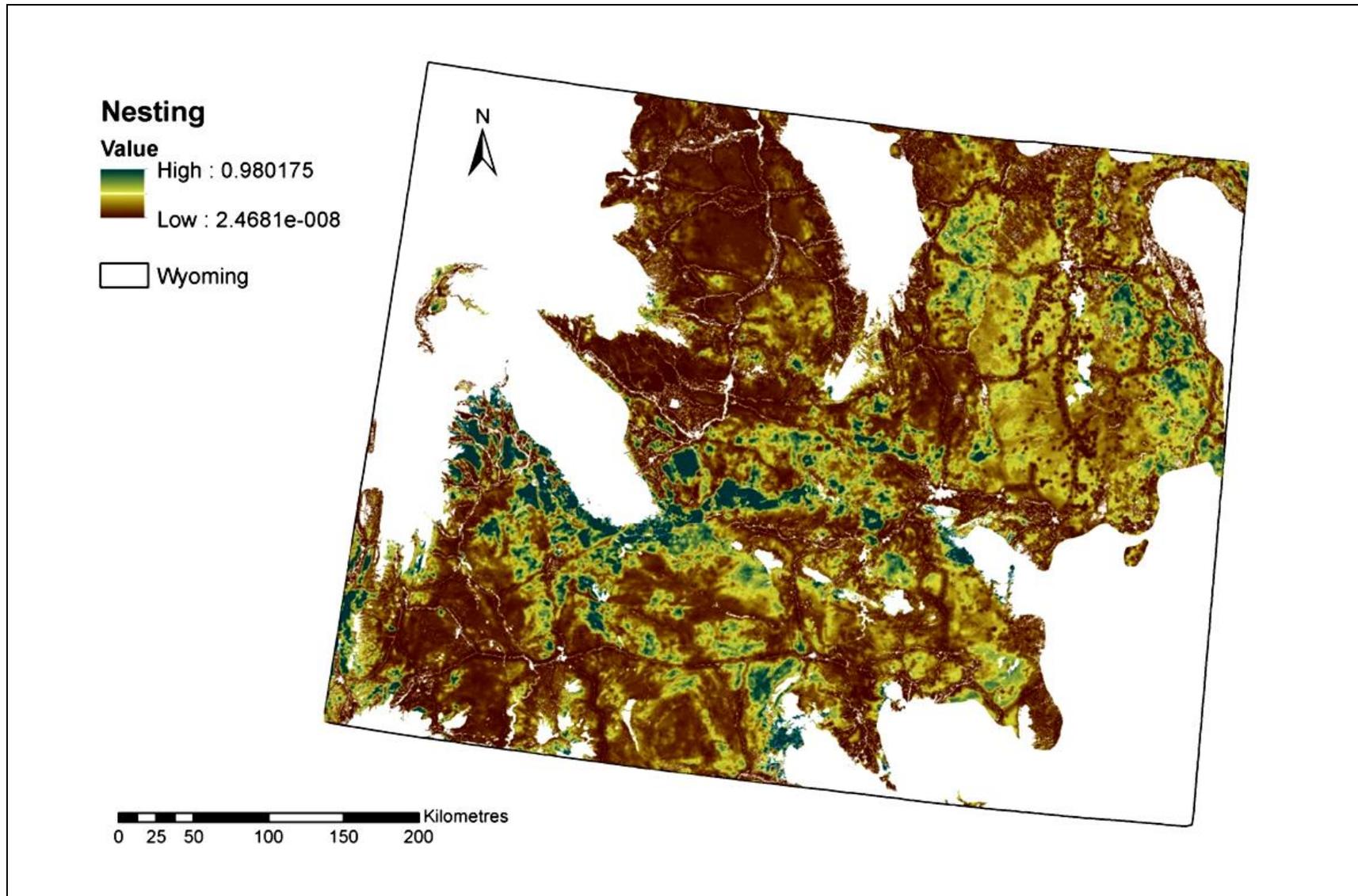


Figure 4.2-3. Nesting Habitat Selection Model.

The individual nesting habitat selection model (state-wide landscape \times patch combined RSF) developed by Fedy et al., (2014) representing low (dark brown) to high (dark green) habitat use at a 30 m spatial resolution. Projection: Albers Conical Equal Area.

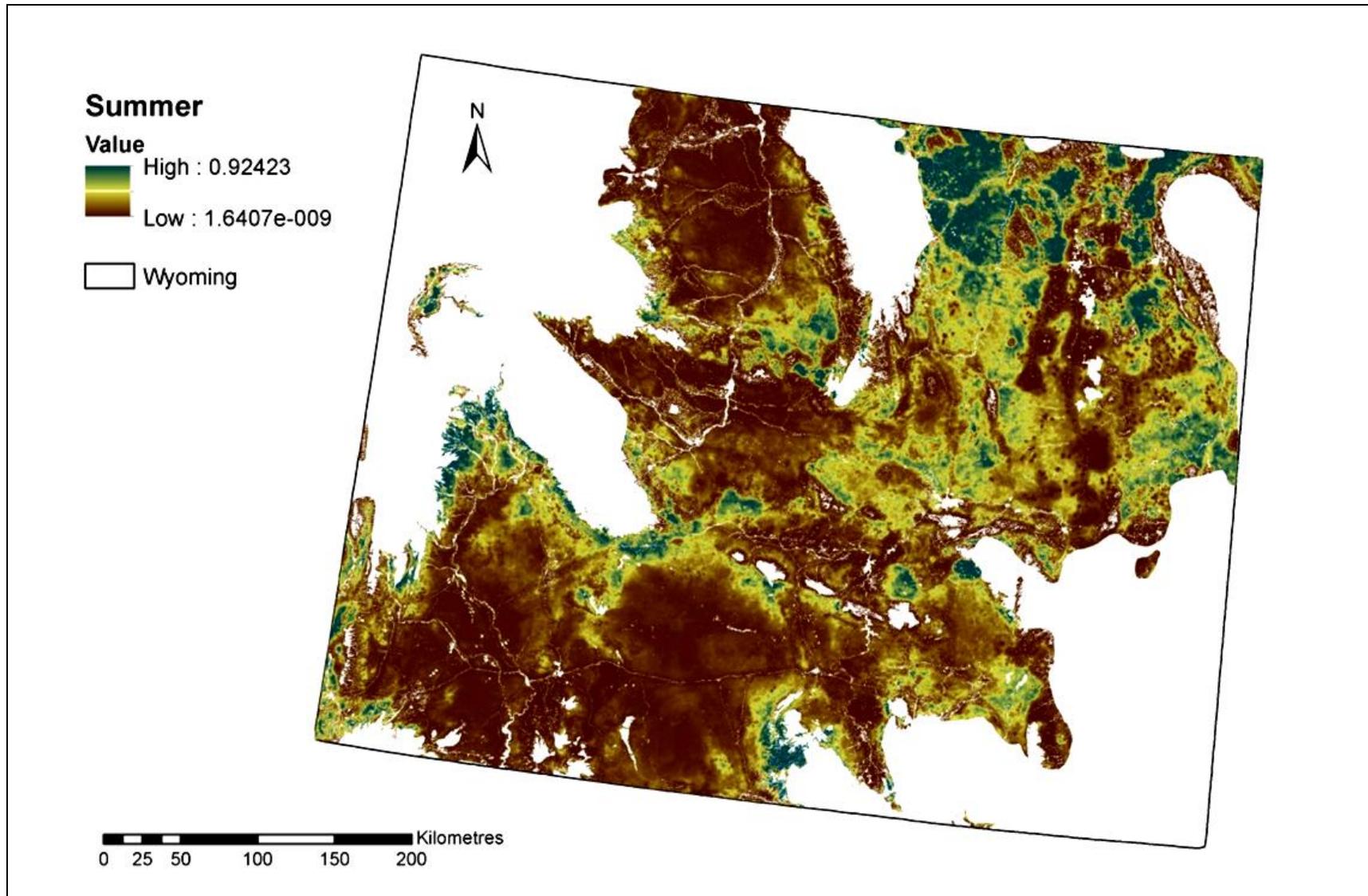


Figure 4.2-4. Summer Habitat Selection Model.

The individual summer (late-brood rearing) habitat selection model (state-wide landscape \times patch combined RSF) developed by Fedy et al., (2014) representing low (dark brown) to high (dark green) habitat use at a 30 m spatial resolution. Projection: Albers Conical Equal Area.

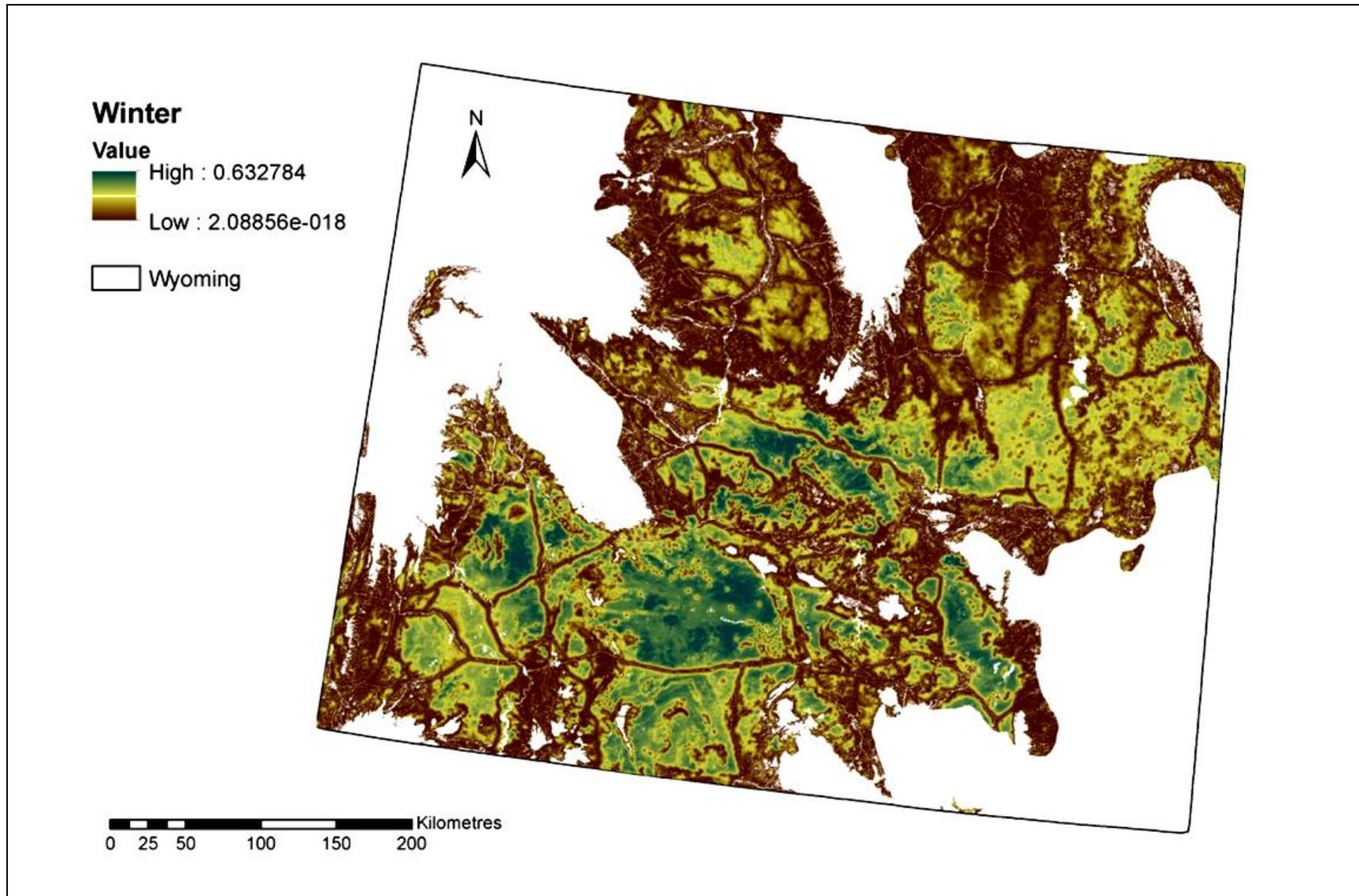


Figure 4.2-5. Winter Habitat Selection Model.

The individual winter habitat selection model (state-wide landscape \times patch combined RSF) developed by Fedy et al., (2014) representing low (dark brown) to high (dark green) habitat use at a 30 m spatial resolution. Projection: Albers Conical Equal Area.

4.2.2 Landscape Prioritization

I developed an annual habitat prioritization layer that combined seasonal habitats for sage-grouse across Wyoming using a reverse iterative heuristic algorithm as implemented in Zonation (Version 3.1; Moilanen et al., 2012) spatial conservation planning software. Zonation is designed for reserve selection purposes with the capacity for multi-feature analysis. Thus, it has the ability to generate a hierarchical prioritization of the landscape based on the “occurrence” levels of multiple features (Moilanen et al., 2012). The hierarchical process is a nested ranking of the landscape; therefore the most valuable 2% of the landscape is within the most valuable 5%, and the most valuable 5% within the most valuable 10%, and so on (Moilanen et al., 2012). The prioritization is generated using grid based data sets of predicted feature occurrences – in this case habitat quality represented by the seasonal habitat selection values (i.e., relative probability of use).

The Zonation methodology consists of two parts: 1) the Zonation meta-algorithm, and 2) the cell removal rule (Moilanen, et al., 2012). The Zonation meta-algorithm is the general underlying basis of the software for the hierarchical prioritization of the landscape based on conservation value. For the purpose of this study, conservation value of a grid cell is the multi-seasonal quality of usable habitat contained in the grid cell. The marginal loss (δ_i) determines the order of cell removal and the cell removal rule decides how the marginal loss is calculated for deciding which cells lead to the smallest amount of loss in value when considering all input raster models. With the analysis starting from a full landscape, Zonation uses minimization of the marginal loss as the criterion to iteratively remove cells beginning with the least valuable remaining cell, to produce the hierarchical ranking of the landscape while accounting for generalized complementarity (Moilanen et al., 2012). Complementarity can be defined as the

degree to which multi-seasonal value of a location contributes to the overall value of the landscape. Ranging from 0 to 1, the Zonation meta-algorithm assigns the lowest rankings (close to 0) to the least useful cells and the cells most valuable for biodiversity –or in this case multiple seasons are assigned the highest rankings (Lehtomäki and Moilanen, 2013).

In order to ensure that all seasons retained a balanced proportional representation as habitat was removed from the landscape, I assigned cell removal rule 1 which is the basic core-area Zonation algorithm. This method focuses on minimizing biological loss by selecting cell i which is the least valuable for the most valuable incidence across all seasons within the cells. Here, cell removal was done based on a removal index δ_i , which is defined as the minimum marginal loss of biological value. During the analysis, Zonation considers all cells in the input raster models in order to calculate and assign a value of δ_i based on the highest proportion of probability of “occurrence” left in a cell in the remaining landscape (Moilanen et al., 2012). A cell that has a high value of δ_i will have the highest biological value to be lost when that cell is removed. When cells are removed, the proportion located in each remaining cell increases (Moilanen et al., 2012) and features are then normalized based on the remaining range-size, thus increasing the relative significance of features due to increasing rarity at each iteration (Lehtomäki, 2014) . In other words, Zonation attempts to maintain core-areas of all seasons until the end of the analysis (end of cell removal) and the last cell to remain untouched would have the highest multi-seasonal value (Moilanen et al., 2005). Therefore, starting from the full study area which is formed by the input rasters featuring the individual seasonal habitats and the sage-grouse range, Zonation prioritizes the landscape by iteratively removing cells with the lowest conservation value by accounting for the seasonal habitat use in the cells and the remaining level of habitat use in each season across the whole study area (Lehtomäki, 2014). Overall, a Zonation

analysis starts and runs on the assumption that protecting everything would be best for conservation.

The number of cells that should be removed at once was defined by assigning a warp factor of 100. A low warp factor results in a finer prioritization but at the cost of increased running time. Assigning a warp factor of 100 has little influence on small-scale prioritizations compared to lower warp factors, while the runtime is significantly improved (Moilanen et al., 2012). I changed the default edge removal value to zero to indicate that the removal of cells can be from anywhere in the remaining landscape. Although this increased the running times for the large study area, this allowed the inclusion of available high-quality habitat at edges – important for maintaining fringe populations – thus maintaining areas possibly supporting connectivity to and from surrounding states which is important for genetic variability and population viability (Gilpin and Soule, 1986; Lacy, 1997).

Using the basic core-area Zonation multi-feature methodology, I combined the nesting, summer, and winter habitat selection models developed by Fedy et al., (2014) across the current sage-grouse range in Wyoming. I reclassified the resulting spatial layer to identify the top fractions of annual habitat across the sage-grouse distribution in the study area. After identifying the top 5, 10, 15 and 25 percent quantile areas across the full landscape prioritization, the annual cell values within each quantile area were extracted, and the same was done for each of the three individual seasonal models in order to quantify spatial overlaps of priority areas to test how well the multi-seasonal prioritization captured priority areas of each individual season. I also calculated correlation coefficients between the individual seasonal models, as well as between the annual habitat and individual seasons. The top 5% and the 25% quantile areas of the annual habitat and each seasonal habitat model were spatially analyzed to identify areas of seasonal

overlap as well as large expanses of continuous priority habitat across the landscape. Finally, I overlaid the 75% CBAs as well as the 31 CMAs on the annual prioritization layer and extracted the values within the CBA and CMA polygons in order to quantify how much of the annual habitat was contained within both sets of core areas. The CMAs were then ranked based on mean annual habitat values to determine how well each CMA performed across multiple seasons in comparison to the rest of the CMAs.

Furthermore, in order to examine the difference between the Zonation results and a simple overlay approach, I calculated the average between the nesting, summer and winter seasonal raster layers at a 120 m resolution using the raster calculator in ArcMap 10.1. Then using the rank function in the *base* R package, I ranked the cells of the resulting raster layer and rescaled to match the 0 to 1 range of the Zonation output layer to make both layers comparable. I then subtracted the ranked and rescaled overlay results from the Zonation results to produce a histogram and a map representing the difference between the layers.

All statistical analyses were performed in R statistical software version 3.1.2 (R Foundation for Statistical Computing, Vienna, Austria) and all spatial analysis, pre-processing and post-processing were carried out in ArcMap 10.1 (Environment Systems Research Institute, Redlands, California). Throughout the study, all analyses and maps were based on the Albers Conical Equal Area projection (Datum: WGS 1984).

4.3 Results

The hierarchical ranking of the landscape generated in this study prioritized each season equally as intended and produced an annual habitat layer which ranked areas across multiple life-stages at a 120 m spatial resolution (Figure 4.3-1). The overlay approach produced a habitat model (Figure 4.3-2) representing low to high average multi-seasonal habitat suitability across the landscape also at a 120 m spatial resolution. The ranked and rescaled overlay results confirmed that a simple averaging of seasons produce a substantially different habitat model compared to the Zonation algorithm used for the hierarchical ranking of the landscape (Figure 4.3-3 and Appendix A). The annual habitat model produced by Zonation prioritized areas that consisted of high-quality usable habitat suited for multiple seasons, resulting in more than half of the top 25% of each individual seasonal habitat captured within the top 25% of the annual habitat prioritization (Table 4.3-2).

Based on an analysis of the highest ranked (top 5% quantile) annual habitat, the largest (by area) clusters of high-quality multi-seasonal sites (clusters of cells $\geq 50 \text{ km}^2$ within the top 5 percent quantile) were located across 13 out of the 23 counties (Table 4.3-1 and Figure 4.3-4) spatially distributed mostly across the southwestern region of Wyoming. The CMAs contain 63% of these sites. Overall, the highest quality multi-seasonal habitat (top 5%) was distributed dominantly across the Sublette, Sweetwater, Fremont and Natrona counties and up across Johnson, Sheridan, Campbell and Crook counties (Figure 4.3-4). Furthermore, by observing the hierarchical ranking of the annual habitat prioritization (Figure 4.3-1), a high spatial concentration of large quantities of low-quality multi-seasonal habitat was seen in the northwestern region of Wyoming, falling (approximately) within: Hot Springs, Washakie, Park and Big Horn counties (Figure 3.3-1).

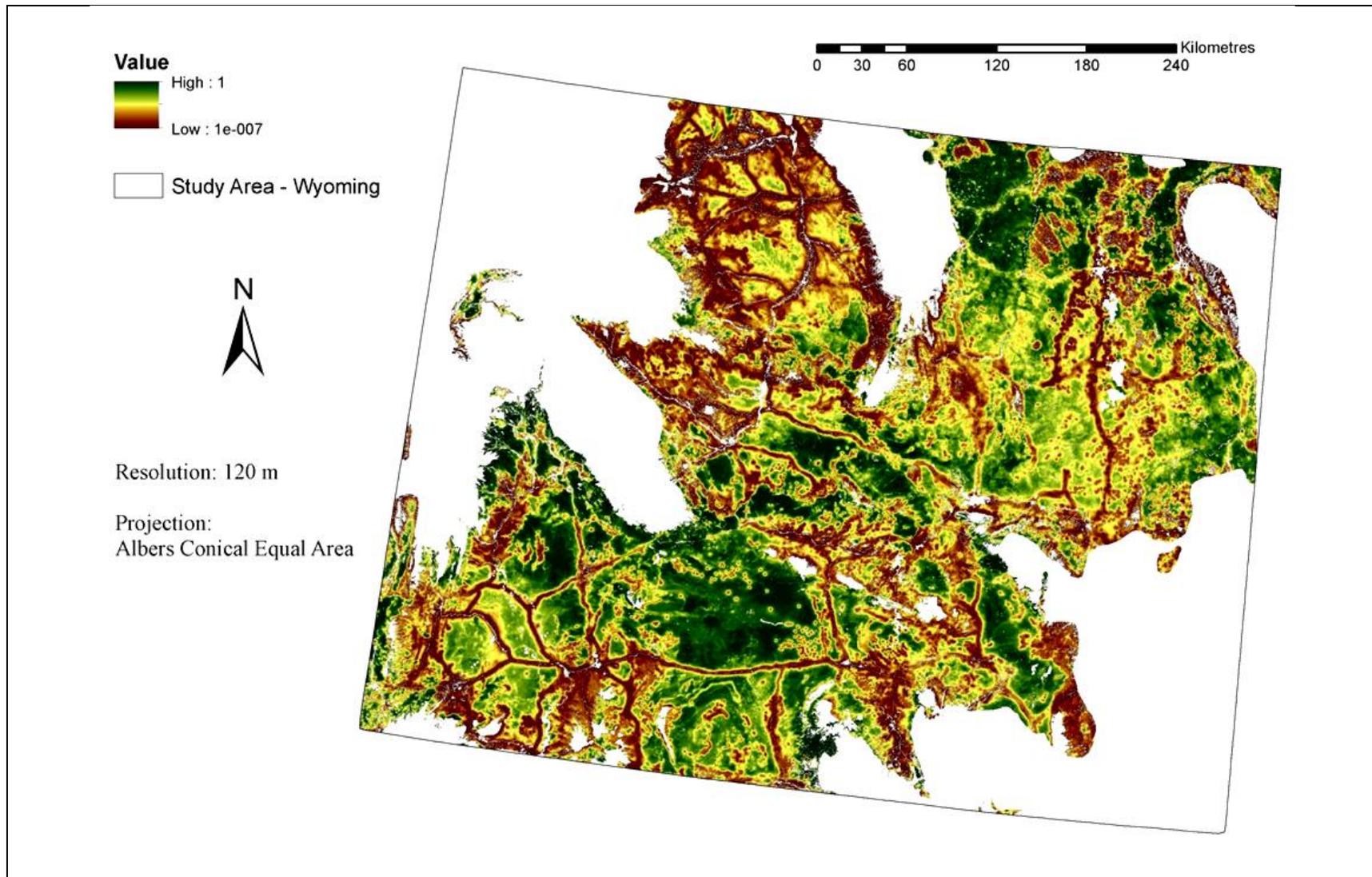


Figure 4.3-1. Sage-Grouse Annual Habitat across Wyoming

The multi-seasonal (annual) landscape prioritization produced by Zonation V3.1 with an improved visual contrast by applying a stretch (type = standard deviation, $n = 2.5$) using ArcMap 10.1 and classified to represent least (brown) to best (green) annual habitat suitability within the sage-grouse distribution in Wyoming.

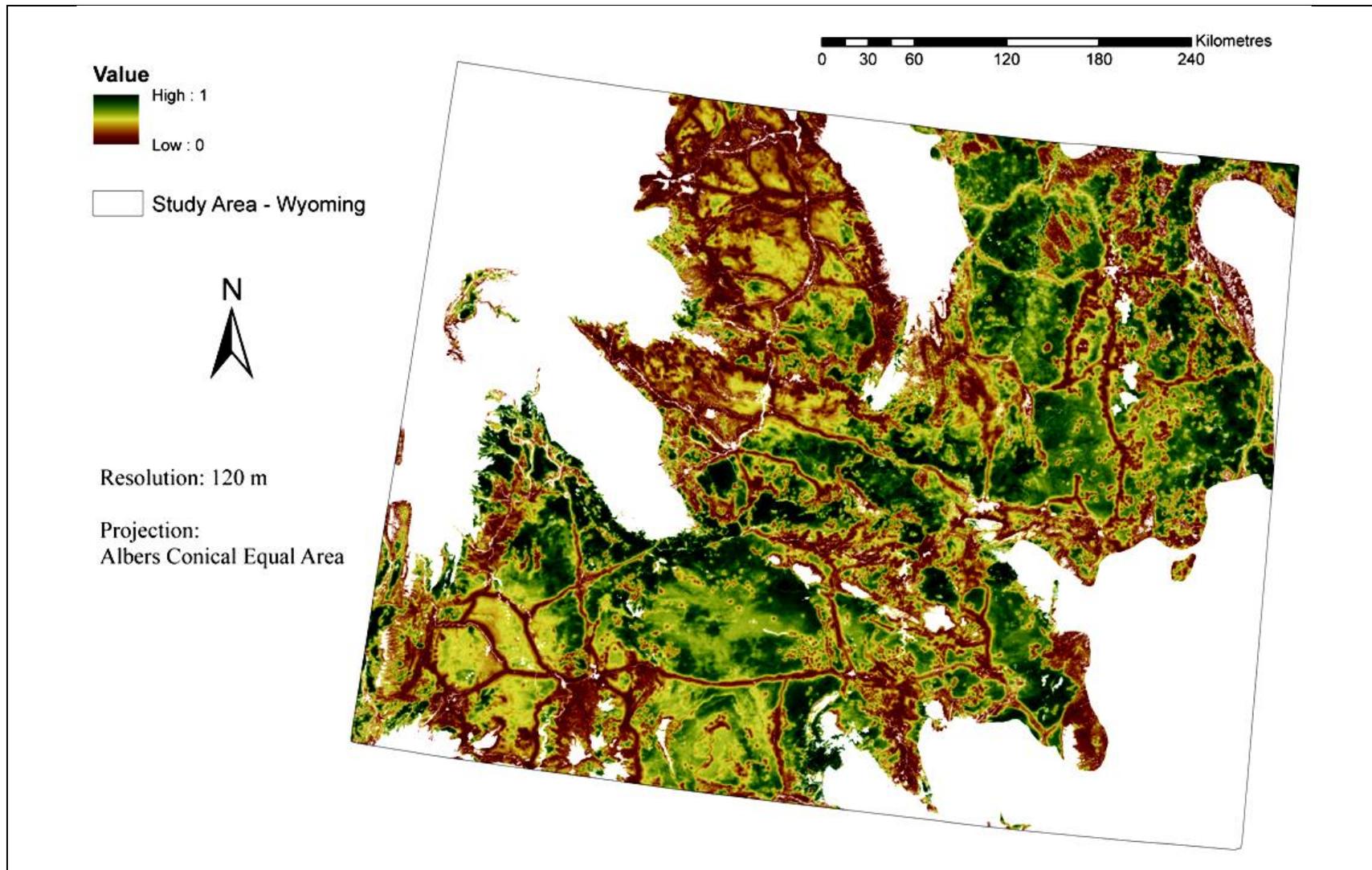


Figure 4.3-2. A Simple Overlay Averaging of Seasons

The averaging of seasons was done using the raster calculator in ArcMap 10.1. Raster cells ranked and rescaled in R and the visual contrast improved by applying a stretch (type = standard deviation, $n = 2.5$) in ArcMap; classified to represent low (brown) to high (green) average multi-seasonal habitat suitability within the sage-grouse distribution in Wyoming.

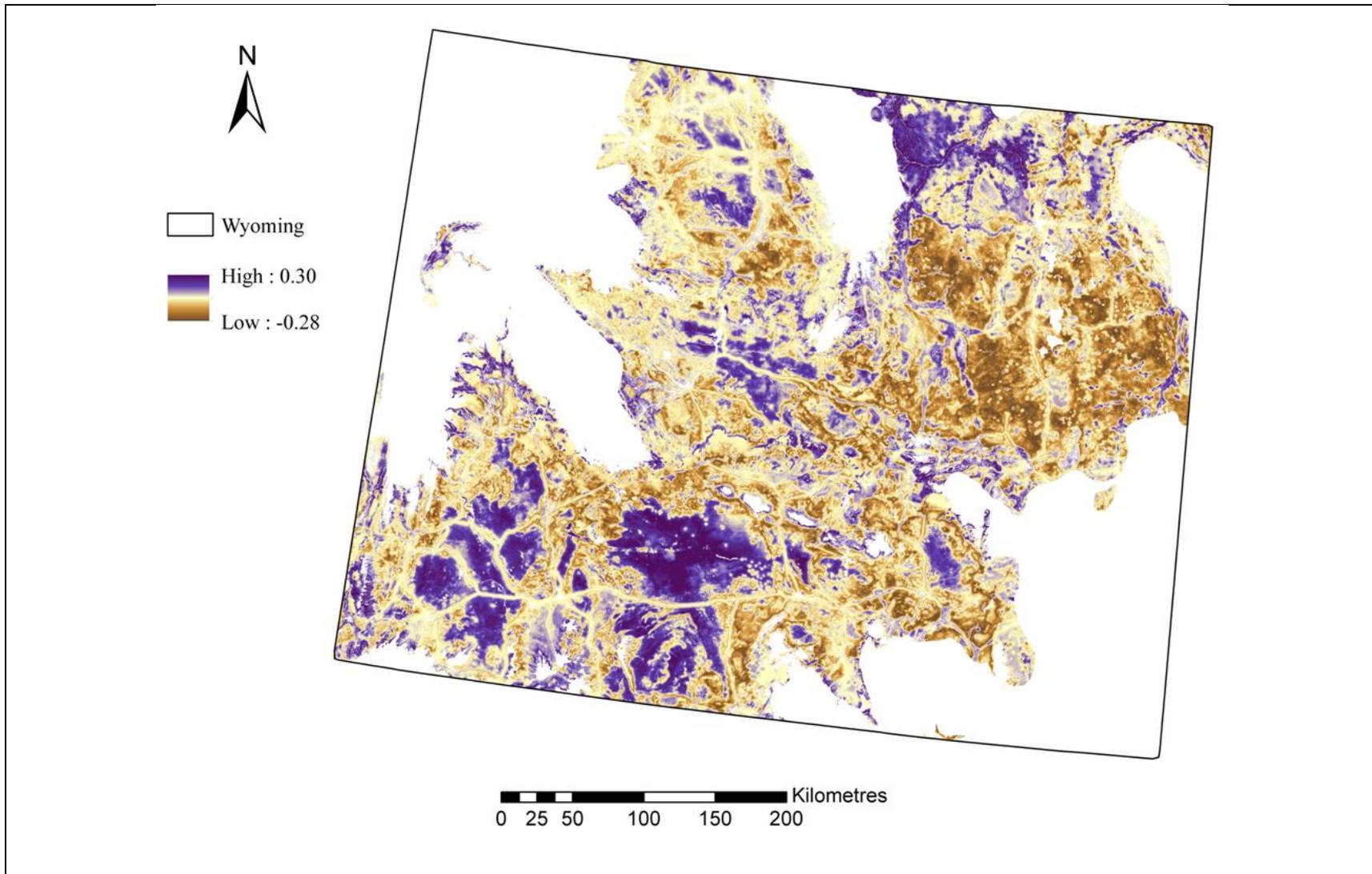


Figure 4.3-3. The Difference between Zonation Results and a Simple Overlay Averaging of Seasons

A representation of the rescaled overlay results subtracted from the Zonation results. Visual contrast improved by applying a stretch (type = standard deviation, $n = 2.5$) in ArcMap 10.1. Negative (overlay values higher) to positive (Zonation values higher) values are represented from dark brown to dark purple. Resolution: 120 m.

Table 4.3-1. Counties capturing clusters of grid cells with a spatial area ≥ 50 km² from the highest quality (top 5%) annual habitat for sage-grouse across Wyoming using an Albers Conical Equal Area projection.

Name of County	Largest clusters (km ²) from the top 5% annual quantile
Sweetwater	1473
Sublette	973
Fremont	828
Crook	418
Carbon	319
Natrona	276
Sheridan	226
Campbell	197
Johnson	157
Lincoln	90
Weston	51
Converse	26
Albany	11

When each individual seasonal habitat selection model was compared, the top 25% quantile areas of each season covered a combined area of 76984 km² across the landscape in which all 3 seasons overlapped across an area of 8505 km², while the top 5% quantile area of each season covered a combined area of 20617 km² across the landscape in which all 3 seasons overlapped across 179 km². Therefore, an overlap of 11% was observed between the best 25% combined quantile area of all seasons, while a 0.9% overlap was observed between the best 5% combined quantile area of all seasons across Wyoming. Furthermore, the top 25% quantile of the annual habitat prioritization contained a 17% overlap of all 3 seasons, while the top 5% annual quantile contained a 2.2% overlap of all seasons.

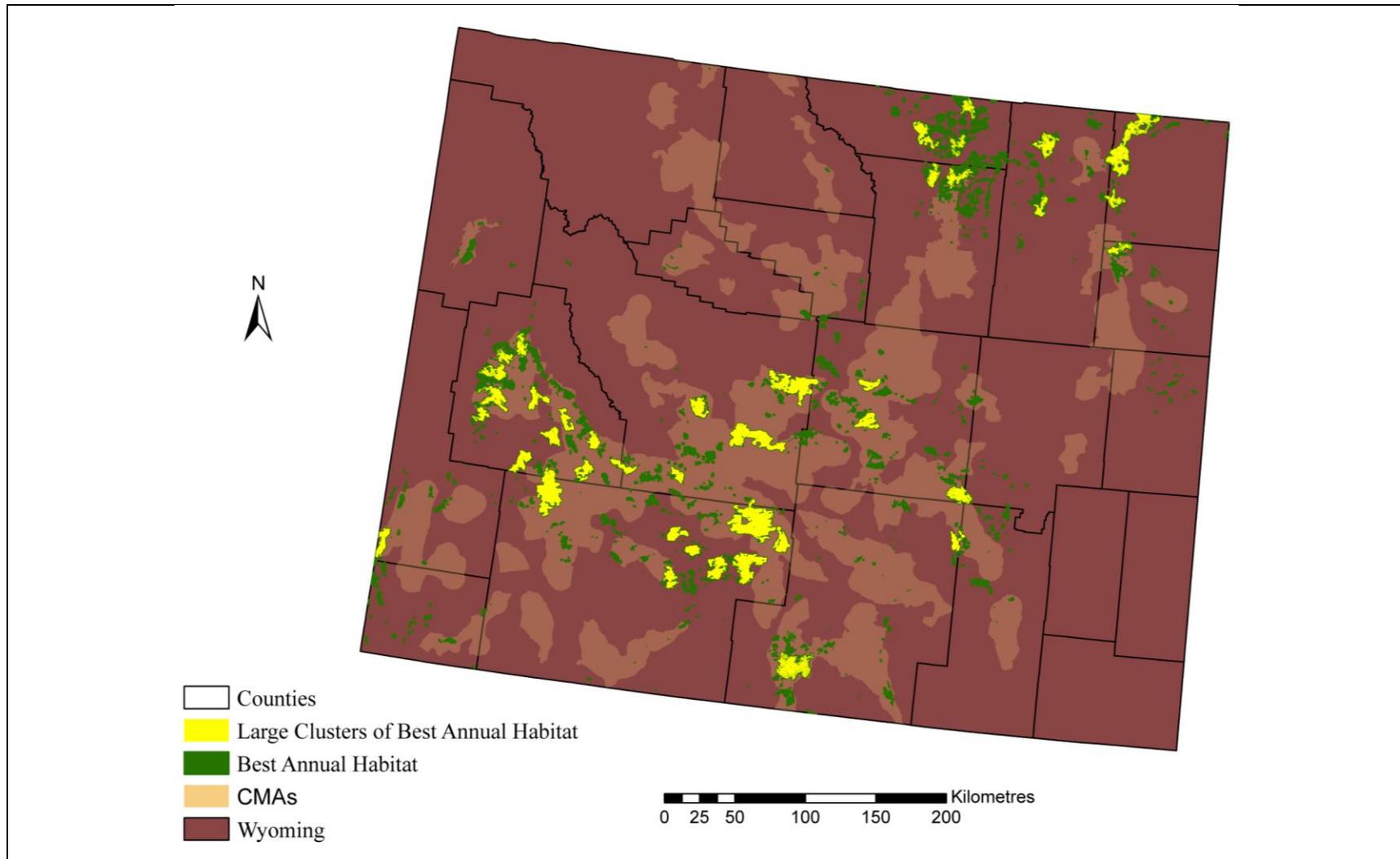


Figure 4.3-4. Best Annual Habitat

Best annual habitat (top 5% quantile) shown in green. Continuous clusters of grid cells with a spatial area ≥ 50 km² from the top 5% annual habitat shown in yellow. CMAAs shown in light brown and 63% of the ≥ 50 km² sites are contained within the CMAAs.

Table 4.3-2. The percentages of the top quantiles of each individual seasonal habitat captured within the top quantiles of the annual habitat. The quantiles are a nested sequence, where the top 5% is within the top 10%, the top 10% is within the top 15%, and the top 15% is within the top 25%. Similar percentages of each individual seasonal quantile are captured within each annual habitat quantile.

Individual Seasonal Habitats (Top 25% Quantile)	Captured Within Annual Habitat (Top 25% Quantile)	Individual Seasonal Habitats (Top 15% Quantile)	Captured Within Annual Habitat (Top 15% Quantile)
Summer	56.75%	Summer	50.59%
Winter	56.98%	Winter	49.97%
Nesting	60.45%	Nesting	51.54%
Individual Seasonal Habitats (Top 10% Quantile)	Captured Within Annual Habitat (Top 10% Quantile)	Individual Seasonal Habitats (Top 5% Quantile)	Captured Within Annual Habitat (Top 5% Quantile)
Summer	47.70%	Summer	43.24%
Winter	46.48%	Winter	43.08%
Nesting	45.82%	Nesting	40.74%

Significant fractions of the top quantiles of each individual season were captured relatively well within the top quantiles of the annual habitat - with less than 5% difference across seasons (e.g., top 25 percent annual quantile: 56.75% summer, 56.98% winter, 60.45% nesting; Table 4.3-2). In addition to prioritizing areas with significant amounts of high-quality multi-seasonal habitat use, results also indicated that relatively similar percentages of each season were prioritized across the landscape (Table 4.3-2); thus demonstrating an equal seasonal consideration. Furthermore, the correlation coefficients also indicated that the annual habitat correlated equally well with each individual season (nesting: 0.67, summer: 0.64, winter: 0.69;

Figure 4.3-5) as intended; thus further confirming that in addition to capturing substantial amounts of high quality habitat from each individual season, multiple seasons were given equal importance in the development of the annual habitat prioritization.

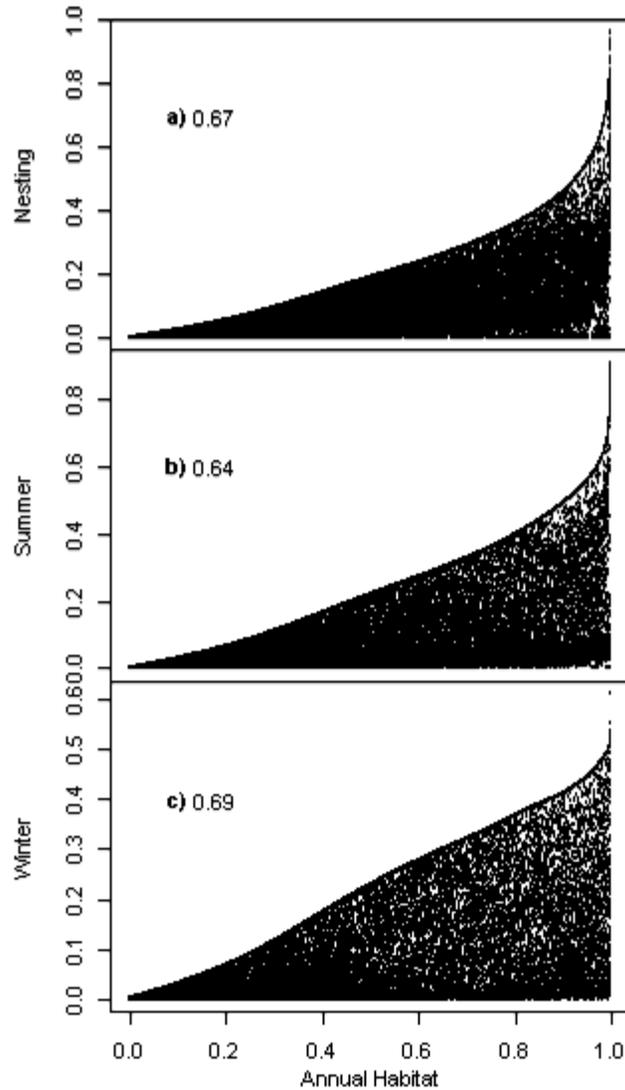


Figure 4.3-5. The Correlation of Single Seasons across the Annual Habitat.

The x-axis represents annual habitat prioritization values, and the y-axis represents individual seasonal habitat use values. The correlation between nesting and the annual habitat is represented by **a) 0.67**, the correlation between summer and the annual habitat represented by **b) 0.64**, and the correlation between winter and the annual habitat represented by **c) 0.69**. The correlation values indicate an equal correlation across the three seasons in the annual habitat prioritization.

As predicted, the CBAs and CMAs captured a greater percentage of the high quality nesting habitat than summer and winter habitat (Table 4.3-3). The multi-seasonal landscape

prioritization indicated that 52.45% of the top 25% best annual habitat was not captured by the CBAs and 51.7% was not captured by the CMAs. Furthermore, from an overlay of the CMAs on the multi-seasonal prioritization, it is clear there is a wide variation in overall prioritization values with the median values ranging from 0.09 to 0.81 (Figure 4.3-9). Finally, ranking the CMAs based on mean values indicated that CMA 21 is best suited to protect habitat across all 3 seasons, while the following CMAs are ranked relatively low: 3, 26, 28, 6, 2, 9 and 7 across the annual habitat (Figure 4.3-9 and Figure 4.3-10).

Table 4.3-3. The percentages of the top annual and seasonal quantiles captured within the core biological areas (CBAs) and the core management areas (CMAs).

Season		% captured by CBAs	% captured by CMAs
Summer	Top 25%	39.43%	41.60%
	Top 15%	38.35%	39.12%
	Top 10%	37.24%	37.16%
	Top 5%	33.96%	35.86%
Winter	Top 25%	45.34%	48.89%
	Top 15%	52.15%	54.23%
	Top 10%	56.59%	56.38%
	Top 5%	64.53%	62.39%
Nesting	Top 25%	51.65%	52.40%
	Top 15%	58.14%	59.44%
	Top 10%	63.06%	65.46%
	Top 5%	70.15%	73.87%
Annual Habitat (combined seasons)	Top 25%	47.55%	48.30%
	Top 15%	51.96%	51.41%
	Top 10%	54.79%	54.88%
	Top 5%	58.93%	59.89%

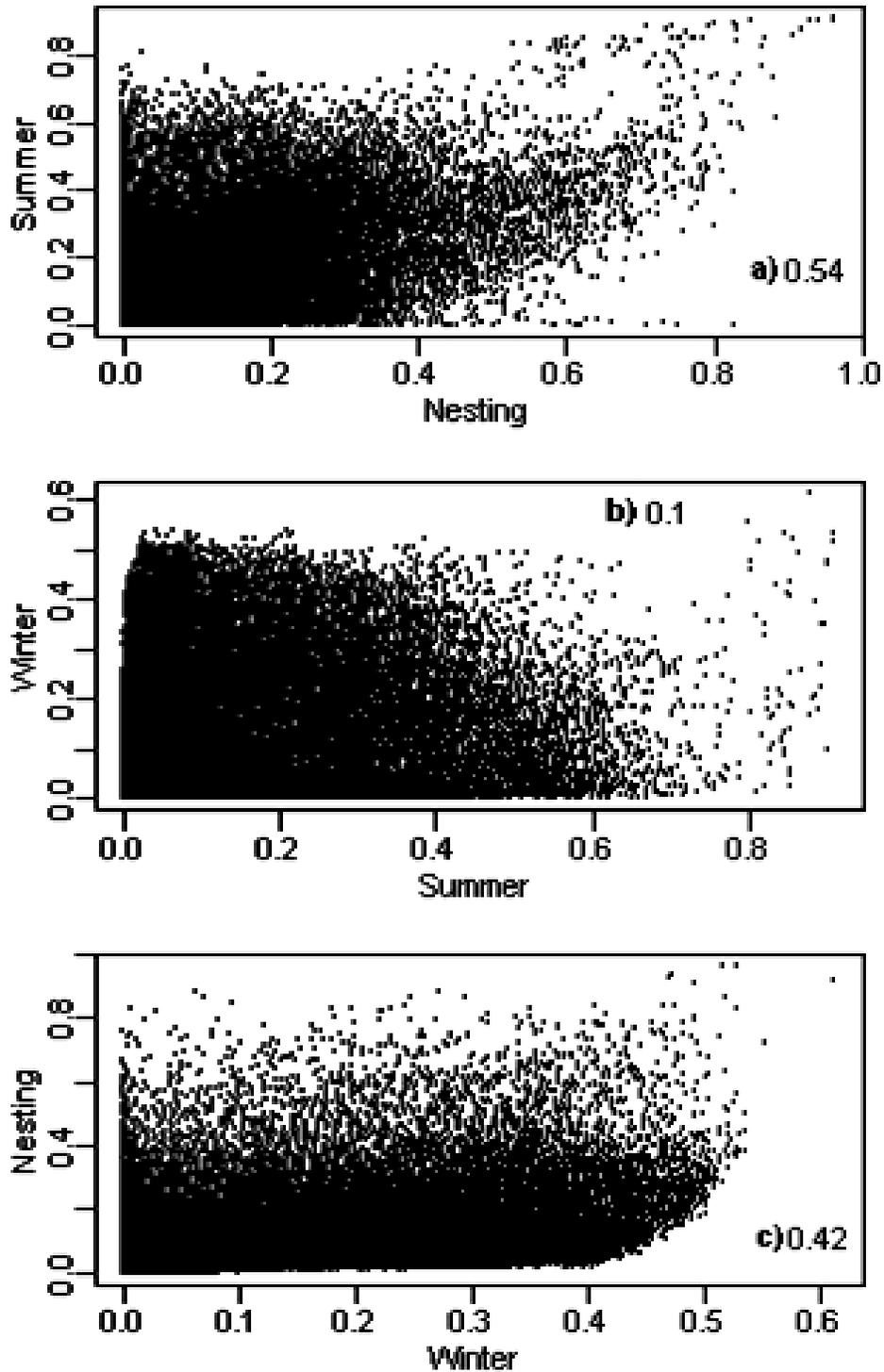


Figure 4.3-6. The Correlation between Seasons across Wyoming.

The correlation between summer and nesting habitat is represented by **a) 0.54**, the correlation between winter and summer by **b) 0.1**, and the correlation between nesting and winter by **c) 0.42**. The x-axis and y-axis represent seasonal habitat use (cell values).



Figure 4.3-7. The CBAs Overlaying the Top Quantiles of the Annual Habitat Prioritization.

The top 5, 10, 15 and 25 percent quantiles (green) across the annual habitat prioritization were extracted. The overlaying red polygons are sage-grouse CBAs – Wyoming’s core area strategy. This figure visually illustrates how well the CBAs capture high quality usable habitat across multi-seasons.

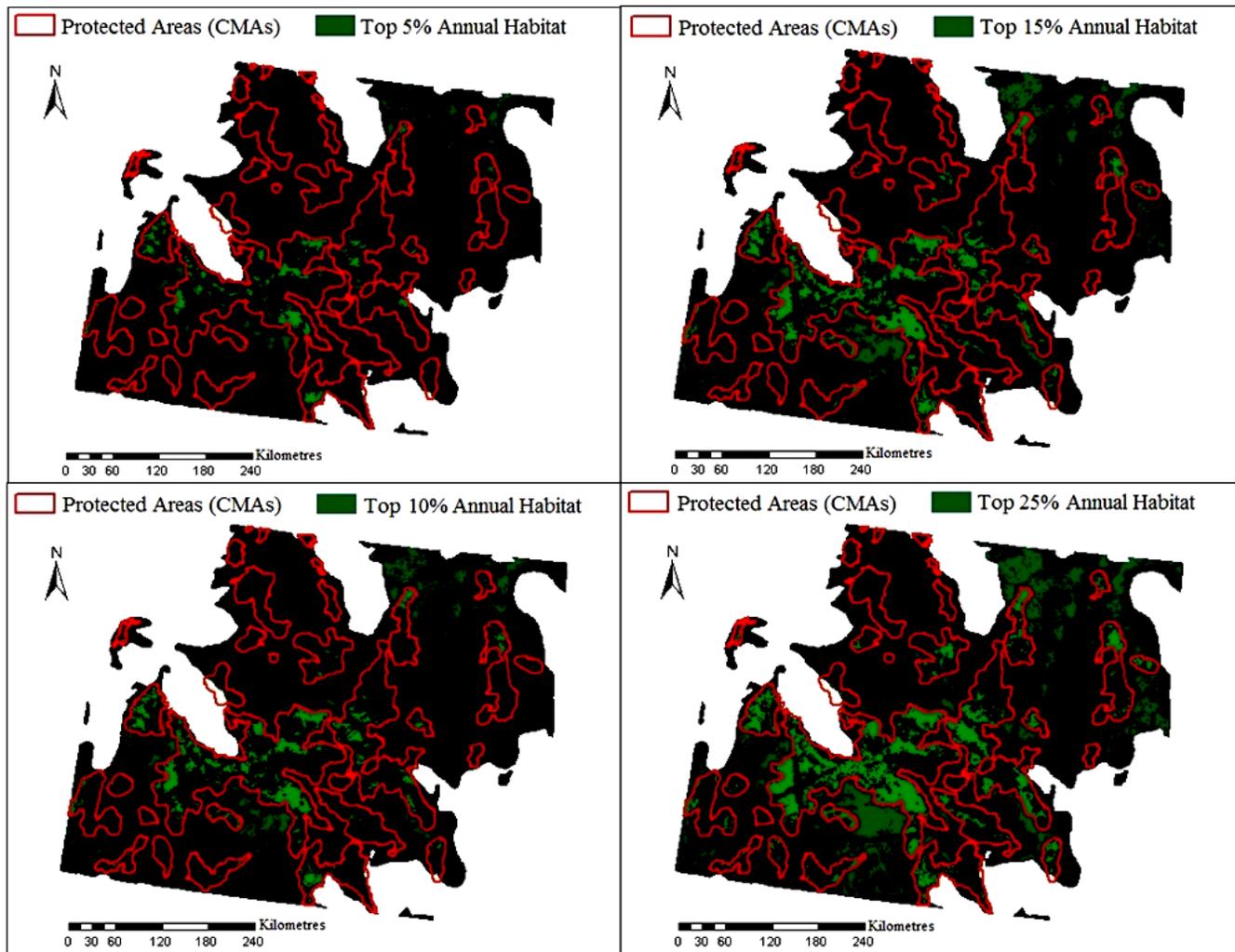


Figure 4.3-8. CMAs Overlaying the Top Quantiles of the Annual Habitat Prioritization.

The top 5, 10, 15 and 25 percent quantiles (green) across the annual habitat prioritization were extracted. The overlaying red polygons are sage-grouse CMAs – Wyoming’s core area strategy. This figure visually illustrates how well the CMAs capture high quality usable habitat across multi-seasons.

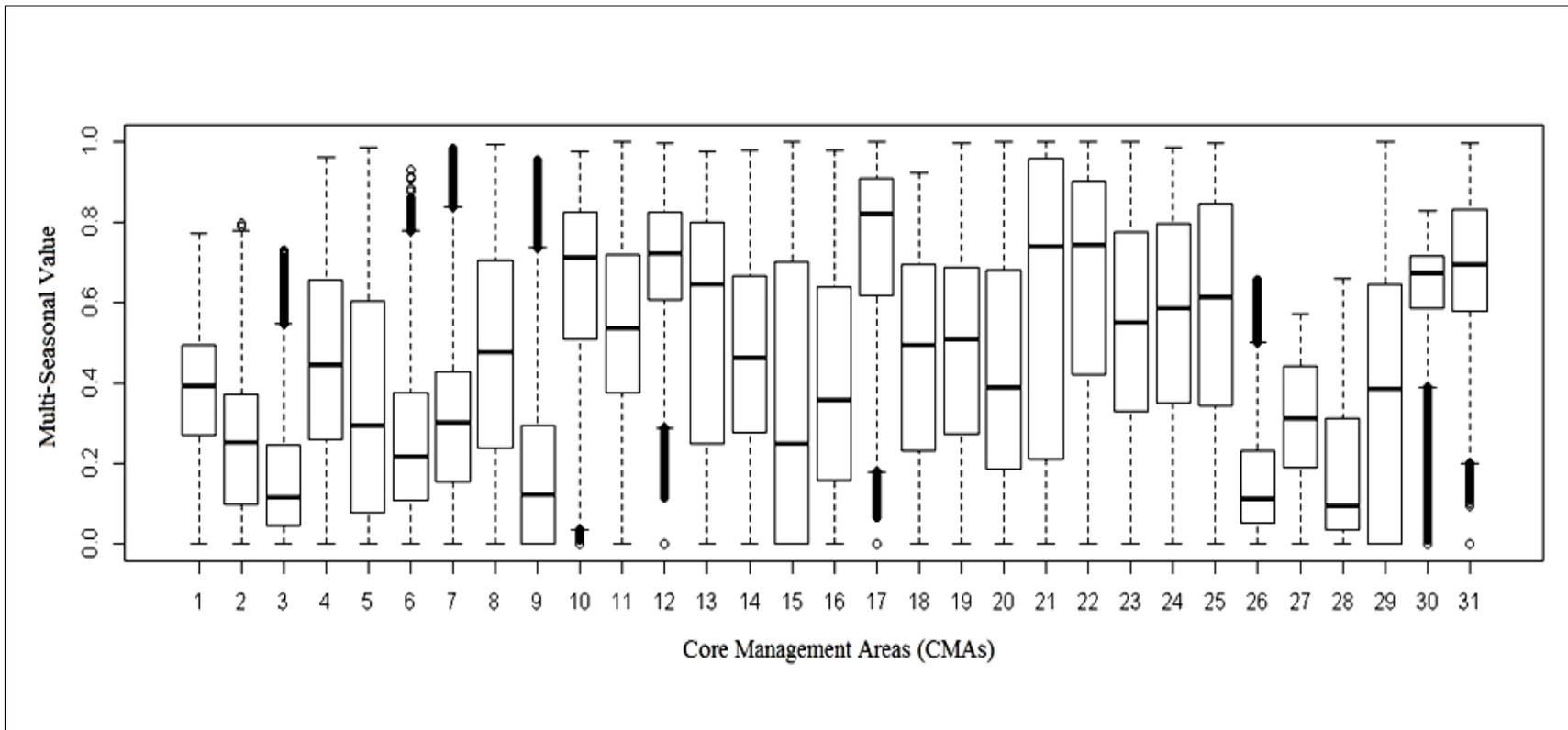


Figure 4.3-9. The Multi-Seasonal Value of CMAs.

This boxplot represents the annual habitat cell values falling within each of the CMAs. The cell values were extracted by applying the nearest neighbour resampling method using a CMA raster as a mask. The CMA raster mask was created by converting the CMA polygons to a raster with an equal cell size (120 m) and cell centre as the cell assignment method.

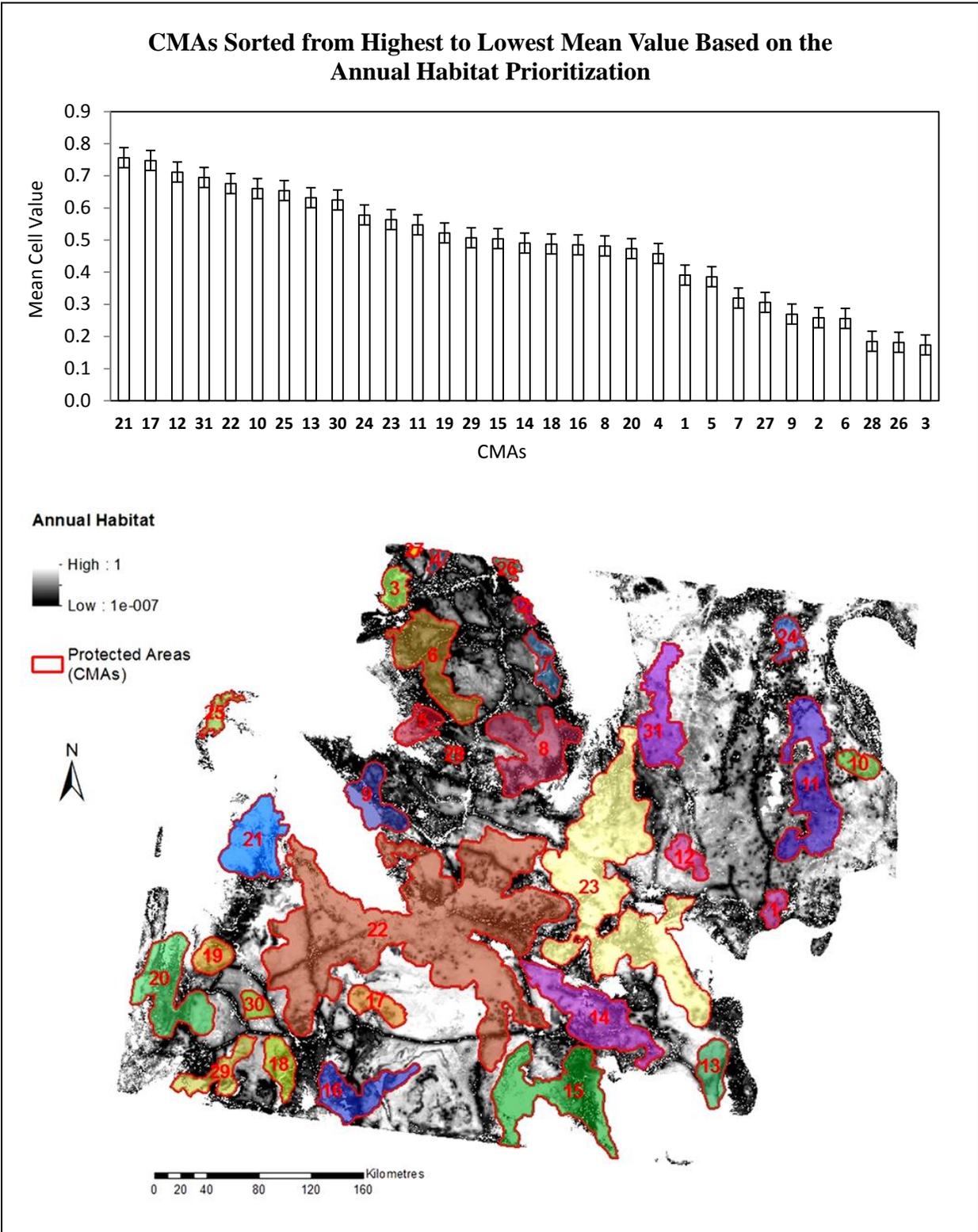


Figure 4.3-10. CMAs Ranked by Multi-Seasonal Suitability
 The CMAs are sorted from highest to lowest multi-seasonal suitability based on the average cell values extracted from the annual habitat prioritization. Error bars displayed using Standard Error.

4.4 Discussion

An annual habitat prioritization drawing from seasonally-explicit habitat selection models addresses the full annual cycle of sage-grouse and aims to inform conservation plans and management decisions to account for habitat across multiple life stages. This study explored the use of a quantitative spatial prioritization method – Zonation – to combine multiple state-wide seasonal habitats in an ecologically meaningful way and examined how it compared to a single-season approach. When the multi-seasonal habitat prioritization produced using Zonation was compared to the habitat model produced by the separate overlay approach, Zonation proved to prioritize the landscape differently than a simple overlay with some areas receiving higher prioritization and vice versa (e.g., southwestern region; Figure 4.3-3). I compared the Zonation habitat prioritization model to the individual seasonal habitats and assessed the capacity of Wyoming’s breeding-based core area concept to capture priority areas across the full annual cycle.

Sage-grouse are known to exhibit a variety of migratory patterns across the annual cycle (Beck, 1975; Hulet, 1983; Fischer, 1994), and are documented to move extensively between large home ranges (Dalke et al., 1960; Berry and Eng, 1985; Connelly et al., 1988; Connelly et al., 2011a) with non-migratory populations exhibiting well-integrated seasonal habitats (Connelly et al., 2000). Connelly et al., (2011a) categorized the movements of sage-grouse into four different types: 1) dispersal between hatching to breeding, 2) movements within a season, 3) migration between widely separated seasonal ranges, and 4) home ranges summing up all seasonal or annual movement types. These categories are known to share significant overlap particularly for seasonal or annual home ranges (Connelly et al., 2011a). In general, for resident and short-distant migrant populations, wintering, breeding and summer habitats usually do not

take place in widely separated locations; hence significant overlap is expected across seasonal habitats. For this reason, it is typically studies on migratory birds in the literature predominantly emphasize the need for multiple seasonal requirements. My research presents the largest ecologically meaningful annual habitat prioritization conducted to date for sage-grouse combining multiple large-scale comprehensive seasonal habitats, and can be utilized for a more robust delineation of sage-grouse core areas across the annual cycle.

For sage-grouse populations in Wyoming, the correlation between each individual seasonal habitat indicated that the sage-grouse relative probability of habitat use does not correlate well across seasons (Figure 3.4-1). A study conducted by Fedy et al., (2012) based on radio-telemetry data also reported high variation observed in the amount of overlap between sage-grouse breeding core areas and non-breeding locations in Wyoming. Some individuals moved more than 50 km in between life stages; therefore, indicating that conservation efforts focussing solely on prioritizing breeding habitat for sage-grouse is likely not adequate to capture all requirements across the full annual cycle. The correlation coefficients indicated a higher correlation between nesting and summer habitat ($r = 0.54$) and the lowest correlation between summer and winter habitat ($r = 0.1$). Consistent with this, Berry and Eng (1985) reported that nesting and summer habitats were relatively close while winter habitat was more distant for sage-grouse in Wyoming. Fedy et al., (2012) reported an average of 8.1 km movement distance from nest sites to summer locations, while an average of 14.4 km was reported from nest sites to winter locations, and an average of 17.3 km from summer to winter locations. These findings suggest that sage-grouse use different strategies across seasons (Fedy et al., 2012); thus resulting in high variation in habitat use across the annual cycle. I concur with Fedy et al., (2012) that it is

inappropriate to address sage-grouse populations in Wyoming as non-migratory; therefore, it is neither efficient nor suitable to rely on a single seasonal approach.

In terms of weighting the individual seasonal habitats, Fedy et al., (2014) warned against the application and use of the winter habitat selection models as there were some concerns regarding the predictions of snow cover and its accumulation and redistribution affected by high winds. Sage-grouse winter habitat strongly depends on the availability of food which is essentially based on snow depth and shrub height (Remington and Braun, 1985; Homer et al., 1993; Schroeder et al., 1999; Connelly et al., 2000; Crawford et al., 2004; Fedy et al., 2014), but the accumulation of snow had been difficult to predict and the snow data was not able to capture local variability (Fedy et al., 2014). Therefore, Fedy et al., (2014) were uncertain that the winter seasonal models would be accurate. However, a recent study conducted by Row et al., (2015) using the same seasonal habitat selection models demonstrated that while the functional connectivity was associated between nesting and summer, it was more important between nesting and winter seasons. Thus, an equal consideration of the winter seasonal habitat selection model was retained and my hierarchical ranking of the landscape was aimed to conserve all seasonal habitats equally while prioritizing areas of seasonal diversity (i.e., seasonal richness). Furthermore, the correlation coefficients generated between the annual habitat and individual seasonal habitat models confirmed that the annual habitat prioritization contains an equal correlation ($r = 0.6$) across the three seasons (Figure 4.3-5).

Although, the majority of ecological studies in the past have mainly focussed on a single season and prioritized species' breeding requirements (e.g., Morrison et al., 2006; Chandler et al., 2009, King et al., 2009, Schlossberg et al., 2010; McClure et al., 2013; Rodewald, 2015) – due to the key role reproduction plays in the maintenance of a species (e.g., Hoekman et al.,

2002), non-breeding areas as well as areas of movement to and from seasonal centres are also important for the conservation of a species (Morrison et al., 2006; Aldridge and Boyce, 2007; Reudink et al., 2009; Carpenter et al., 2010; Fuller, 2012; McClure et al., 2013; Morrison and Mathewson, 2015; Rodewald, 2015). For example, as habitat tends to be more limited during the winter season than other seasons, failing to protect and maintain habitat and areas of movement (e.g. interseasonal movements) during the winter season could for instance lead to significant population declines, if not extinction (Beck, 1977; Remington and Braun, 1985; Swenson et al., 1987; Hanf et al., 1994; Morrison et al., 2006; Doherty et al., 2008). Therefore, it was necessary to consider all seasons with equal importance in order to address annual sage-grouse needs.

Based on the annual habitat prioritization, 56-60% of the top 25% of each individual season was captured within the top 25% of the annual habitat (Table 4.3-2). None of the individual seasons dramatically surpassed other seasons in the annual prioritization as a result of equal weighting and Zonation's built-in repeated range-size normalization, where features with narrow-ranges possessed a relatively high influence on the prioritization; thus giving high priority to cells with the best quality habitat as well as the smallest seasonal range remaining across the distribution as cells were prioritized (Moilanen et al., 2011; Kareksela et al., 2013). This method therefore prioritized cells that contained the highest possible habitat suitability for all seasons with the smallest possible aggregate marginal loss in seasonal richness. As grid cells with high rankings suggest high probability of multi-feature loss if not prioritized (Moilanen et al., 2012), locations with high annual habitat values indicate high conservation value for the full annual cycle and areas on the low-priority end exhibit low ecological value thus, high potential for other land uses (e.g., Kareksela et al., 2013). This method of quantitative spatial prioritization is not simply additive –in which areas of higher seasonal richness generally would have been prioritized; instead it is a prioritization of areas that exhibited the highest possible habitat

suitability for all seasons simultaneously while aiming to conserve seasons equally under the assumption that protecting habitat across all seasons is best for conservation.

According to the quantile analysis, the highest quality annual habitat (5% quantile area) contained less than 50 percent of each of the highest quality individual seasonal habitat (summer: 43.24%, winter: 43.08%, nesting: 40.74%; Table 4.3-2). Increasing fractions of all seasonal quantiles were prioritized within the larger quantile areas across the annual habitat (Table 4.3-2) – which is likely due to the increasing probability of seasonal overlap with increasing ground coverage. Based on the quantile analysis, it is also evident that different levels of habitat use were contained within each of the top seasonal quantiles that made up the annual quantiles. Thus, a landscape prioritization based solely on the high priority areas of a single season would not cover requisite areas across other seasons unless a significant amount of seasonal overlap existed across the landscape. For example, knowing only where the best nesting areas are located is not sufficient to identify areas best suitable for all seasons. Furthermore, the best 25% of the annual habitat only contained a 17% spatial overlap of all three seasons, while an even lower 2.2% seasonal spatial overlap was contained within the best 5% of the annual habitat. When the individual seasonal habitat selection models were compared to each other, an overlap of 11% was observed between the best 25% of all seasons, while a 0.9% overlap was observed between the best 5% of all seasons. Thus, sage-grouse relative probability of habitat use does not have large areas of spatial overlap across priority nesting, summer and winter habitats in Wyoming, indicating that a single season is not sufficient to act as a surrogate to spatially account for all annual sage-grouse needs.

Protecting essential habitat is one of the most effective ways to conserve the majority of animal populations (Noss, 1994). For species of conservation concern, a principal challenge and

an urgent management concern is the identification of those specific areas that are critical for the long-term persistence or recovery of a species' population (Heinrichs et al., 2010; Fedy et al., 2014). My individual seasonal analysis of CBAs and CMAs indicate that these protected areas capture more nesting priority areas than the other seasonal components. Although the nesting habitat consisted of the highest percent captured within the lek-based protected areas compared to winter and summer habitats; it is important to note that only 52.4% of the top 25% nesting habitat was actually captured. Furthermore, the protected areas also did not capture large amounts of the annual (multi-seasonal) priority areas as expected – only 48% of the top 25% annual habitat was captured within the CMAs. When the CMAs were ranked based on how well they would facilitate across multiple seasons, the two largest CMAs (22 and 23) were ranked in 5th and 11th place; based on this, I point out that even the largest breeding-based areas are not as highly suited to protect important habitat across the annual cycle.

As part of the Sage-Grouse Core Area Protection Strategy, a separate set of connectivity zones have been identified in order to maintain and improve the population connectivity between Montana and both North and South Dakota (Wyoming's Sage-Grouse Conservation Strategy, 2014). These connectivity zones are identified as routes most likely of dispersal connecting to known populations of neighbouring states in order to reduce populations within Wyoming from isolating – particularly across the state boundaries (State of Wyoming Office of the Governor, 2015). As connectivity areas limit development and anthropogenic stressors, the protected habitat should facilitate the natural flow of movement required for the maintenance of genetic variability and the loss of genetic variation is known to affect population viability (Gilpin and Soule, 1986; Lacy, 1997). However, these connectivity zones are not part of the protected core areas (CMAs) (State of Wyoming Office of the Governor, 2011); instead the delineation of

CMA is influenced by the connectivity zones to facilitate movement between sage-grouse populations in Wyoming and neighbouring states. Based on the annual habitat, CMAs such as 3, 26, 6, 2, and 27 have low rankings, but these core areas likely form a critical connection to populations in Montana. With a large intact sage-grouse core area located in the southeastern corner of Montana (Taylor et al., 2010; Foster et al., 2013), CMA 24 and 31 are also important, and are aligned with connectivity zones leading up to the southeastern corner of Montana. Thus, the CMA ranking in this study is not built to advocate the dismissal of low ranked core areas; instead it is aimed to highlight the significance and efficacy of a multi-seasonal approach. The annual habitat model can however refine sage-grouse protected areas for improved long term conservation outcomes as it represents a balanced coverage of all seasons.

Across Wyoming, Montana, Colorado, Utah, and both North and South Dakota, Wyoming holds the greatest risk from oil and gas and wind energy developments (Doherty et al., 2011). For the BLM, identifying and prioritizing areas exhibiting low disturbances is critical in order to continue conserving while also allowing developments in the region (i.e., multiple use mandate - Federal Land Policy and Management Act 1976; Taylor et al., 2010). Protecting large, intact areas that continue to maintain and support biological functions and natural resources is the best way to prevent further declines of animal populations (Kiesecker et al., 2010) from habitat loss and fragmentation. Therefore, the management challenge is to direct future developments away from large expanses of undisturbed priority habitats best suitable for survival (Taylor et al., 2010). Based on an analysis of the highest quality (top 5% quantile) annual habitat, the largest expanses ($\geq 50^2$ km) of high-quality multi-seasonal sites were located across 13 counties (Table 4.3-1) spatially distributed mostly across the southwestern region of Wyoming. While southwestern Wyoming includes some of the highest sage-grouse densities and a

substantial amount of remaining sagebrush landscapes in North America (Connelly et al., 2004), it is also one of the areas experiencing rapid developments (Doherty et al., 2011); therefore is a potential area of conflict between development and needs for sage-grouse populations. The CMAs currently provide protection to 59.89% of the top 5% annual habitat in which 76.55% of the large expanses ($\geq 50 \text{ km}^2$) of spatially continuous high quality (top 5%) annual habitat are captured; thus protected under the core area strategy.

Overall, my research explicitly integrates across all seasonal habitats supporting a multi-seasonal approach over a single-season approach for identifying priority areas in order to guide management and limit human disturbances. The annual habitat prioritization captured substantial fractions of the best habitat from each individual season, thus indicating this quantitative method of spatial conservation prioritization was capable of combining three seasonal habitats with equal importance accounting for multi-seasonal habitat suitability (based on relative probability of use). This state-wide annual habitat prioritization developed for sage-grouse in Wyoming identified areas of high to low conservation value across all life stages, making it possible to direct conservation efforts to areas of best quality usable habitat for multiple life stages, while the low-priority end of the annual habitat prioritization represented comparatively low ecological and conservation value thus exhibiting high potential for other land uses (e.g., Kareksela et al., 2013). In addition, when attempting to conserve a species of conservation concern, time is of the essence, and with the use of seasonally explicit state-wide comprehensive data including multiple biological factors, we can expect more biological rigour (Fedy et al., 2012) resulting in optimal conservation efforts.

While some could argue that a nesting-based prioritization is sufficient for the short-distant migrant bird populations, a fragmented landscape along with climatic changes may pose

conditions limiting even a resident population who have different seasonal requirements within a rapidly developing region. With increasing environmental changes, events occurring across winter and summer habitats could affect behaviour and population sizes which will ultimately influence breeding success and overall survival as a result of carryover effects from previous seasonal locations (Morrison and Mathewson, 2015). As seasonally explicit state-wide habitat information is now available (Fedy et al., 2014) along with advanced technologies and less computational limitations, a multi-seasonal approach is more achievable – and promising – and the use of comprehensive data proves to capture more biologically valuable priority areas. The ability to combine large grids representing multiple seasons of comprehensive habitat selection data in an ecologically meaningful way to prioritize the landscape is highly beneficial – not only for the conservation of sage-grouse but also advantageous for all sagebrush obligate species. As developments increase, structural connectivity is often limited with increasing habitat fragmentation preventing natural ecological processes and meta-population dynamics. Thus, future work requires a landscape-scale analysis of structural connectivity across Wyoming.

Chapter 5 An Analysis of Structural Connectivity for the Conservation of Greater Sage-Grouse in Wyoming, USA

Abstract

Habitat loss and landscape fragmentation are widely recognized as two of the primary sources of global declines in biodiversity. Disruptions occurring in the structural connectivity of the landscape can impede ecological flows of energy and nutrients through ecosystems and the dispersal of species across the landscape. Corridors facilitate the movement of species between habitat patches and can maintain natural ecological processes and meta-population dynamics. Thus, identifying areas promoting high structural connectivity between habitats is of great conservation interest for wildlife populations and species of conservation concern. Incorporating multiple biological factors when identifying connectivity could strengthen and improve conservation outcomes. Here I modeled structural connectivity by applying electric circuit theory on a comprehensive multi-seasonal habitat prioritization model for greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) in Wyoming. The connectivity model developed in this study identifies multiple corridors between breeding areas indicating regions with high structural connectivity between sage-grouse breeding hotspots across the full annual cycle. Structural connectivity is analyzed at lek locations – where male sage-grouse perform displays of courtship during breeding season – with a buffer of 12.86 km. Connectivity was not strongly correlated with the relative probability of habitat use (i.e., habitat selection models; $r = 0.3$); hence I tested if greater connectivity results in larger and more stable populations independent of habitat. With increasing connectivity, variability in lek counts decreased while population sizes (maximum counts) at leks increased. Thus, greater stability at breeding hotspots can be expected with increasing structural connectivity, signifying the importance of prioritizing areas of high structural connectivity in order to preserve density dependent dispersal at hotspots

throughout the full annual cycle. These trends in lek size and count variability stayed consistent during both population high (i.e., peaks) and low (i.e., trough) periods; highlighting that the structural connectivity of the landscape maintains a positive influence even during years of decline. Therefore, when prioritizing the landscape and identifying core areas for protection, considering areas of high structural connectivity in addition to good quality habitat would enhance overall conservation outcomes across the full annual cycle.

5.1 Introduction

Habitat corridors emphasize structural connectivity among populations with the expectation of maintaining and facilitating the functional connectivity of the landscape (With 1999). Regions with low functional connectivity may also result in increased demographic stochasticity, inbreeding depression and lower rescue opportunities resulting in relatively small, isolated populations of organisms with an increased risk of extinction (Richter-Dyn and Goel, 1972; Schippers et al., 1996; Koen et al., 2014). Therefore, when identifying priority areas, it is beneficial to prioritize multiple corridors for regions with high functional connectivity with greater potential to produce significant conservation benefits (Koen et al., 2014). However, the importance of structural connectivity in comparison to other prioritization approaches has been a controversial topic in conservation ecology (e.g., Doerr et al., 2011; Hodgson et al., 2009; Hodgson et al., 2011; Fuller, 2012). The most common concern is that it is difficult to measure the benefits of enhanced connectivity and that the evidence of the derived benefits is ambiguous (Fuller, 2012). There is much debate around whether investing in larger areas of high quality habitat is better than enhancing connectivity (Fuller, 2012). Furthermore, in addition to a lack of evidence testing the benefits of structural connectivity, usually information from only one life stage is quantified

Habitat loss and fragmentation can seriously threaten the persistence of wildlife populations (Johnson et al., 1992; Schippers et al., 1996; Schumaker, 1996; Koen et al., 2014). Habitat fragmentation results in spatial separations reducing population connectivity which interferes with critical ecological processes required for the preservation of biodiversity and the health of wildlife populations, consequently compromising the functional integrity of landscapes (With, 1999; Koen et al., 2014). Disruptions in the structural connectivity of the landscape can

impede ecological flows of energy through ecosystems, nutrients and the dispersal of organisms (Gardner et al., 1993). Thus, landscape fragmentation can reduce dispersal success (Gibbs, 1998), increase mortality (Fahrig et al., 1995), reduce genetic diversity (Reh and Seitz, 1990; Wilson and Provan, 2003) and lead to population declines. With increasing developments, wildlife populations become relatively isolated, and if these populations are small and with few individuals, there is a high probability of local extinctions (Richter-Dyn and Goel, 1972; Schippers et al., 1996). Therefore, connectivity between habitats must be maintained to facilitate meta-population dispersal (Levins, 1970; Verboom et al., 1993; Schippers et al., 1996). Furthermore, an organism's ability to move across landscapes will likely also influence its capacity to respond to changing climates, thus increasing the probability of survival (Heller and Zavaleta, 2009; Zeller and Rabinowitz, 2011; Cushman et al., 2013). Ever increasing human developments will continue to decrease and fragment available habitat. Thus, conservation plans should consider how to maintain and improve population connectivity for wildlife in complex landscapes in order to potentially mitigate impacts of increasing fragmentation and habitat loss.

For species with varying habitat requirements across life stages, wildlife conservation and management efforts should ideally incorporate habitat requirements across multiple seasons to identify and maintain connectivity throughout all life stages. Often the habitat requirements of a species vary seasonally, but the majority of ecological studies have focused on a species' breeding habitat (Chandler et al., 2009; King et al., 2009; Schlossberg et al., 2010; McClure et al., 2013) due to the important role of reproduction in maintaining populations (Morrison et al., 2006). However, the functional connectivity of populations may be related to habitats other than those preferred for breeding (Row et al., 2015). Hence, non-breeding areas such as wintering sites and migratory (both short and long distance) routes may also be important for maintaining

populations and preventing local extirpations (Morrison et al., 2006). Thus, protecting and maintaining multi-seasonal structural connectivity across the landscape is a step towards safeguarding species' adaptability to threats and changing environments. Furthermore, with changing densities in local populations, the structural connectivity of the landscape is also important for meta-population dynamics. Therefore, analyzing connectivity across the full annual cycle has many benefits.

It is usually assumed that necessary areas of connectivity are captured when defining a species' habitat – especially when it comes to resident species with short-distant movements. However, while this may be partially true in some cases (e.g., species-specific), understanding the relationship between habitat and structural connectivity and examining its independent contribution is particularly important when prioritizing the landscape across multiple seasons amid increasing disturbances – especially for species at risk. Spatial models of dispersal (e.g., meta-population and island biogeography models; MacArthur and Wilson, 1967; Levins, 1969; Hanski, 1999) predict that movement amongst patches will result in increased population size and persistence (Moilanen and Hanski, 2006). There have been an increasing number of studies exploring how corridors affect movement between habitat patches supporting the notion that population viability will be enhanced and stochastic temporal variation will be reduced in local and regional population sizes increasing the rates of movement from high-density to low-density areas (Haddad and Tewksbury, 2006). Thus, corridors are expected to cause declines in local extinctions while maintaining stable population dynamics (Brown and Kodric-Brown, 1977; Gonzalez and Chaneton, 2002; Haddad and Tewksbury, 2006). Hence prioritizing habitats alone without explicit consideration of connectivity may not be sufficient for the long-term survival of a species. Furthermore, in order to appropriately allocate conservation efforts, it is important to

study the relationship between structural connectivity and population dynamics. However, the identification of habitat corridors among habitat patches is difficult, particularly when considering across multiple life stages. This process requires time and cost-effective methods to identify multiple high priority habitat corridors that account for multiple seasons in order to analyze connectivity across all life stages of a species.

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) is a bird species limited to semi-arid landscapes of sagebrush (*Artemisia* spp.). Due to habitat loss, nearly 50% of the historic range of sage-grouse is currently extirpated in western North America (Schroeder et al., 2004). Anthropogenic stressors such as agricultural conversion (Connelly et al., 2004), energy extraction and exploration (Holloran et al., 2005; Aldridge and Boyce, 2007; Doherty et al., 2008), and invasive plant species (Knick et al., 2003) have altered the sagebrush ecosystems and significantly threatened populations of sage-grouse (Knick, 1999; Miller and Eddleman, 2000; Bunting et al., 2002; Knick et al., 2003; Connelly et al., 2004; Davies et al., 2011; Fedy et al., 2012; Homer et al., 2015). Wyoming, United States is currently considered as a stronghold for sage-grouse containing an estimated 37% of its range-wide population (Knick et al., 2003; Doherty et al., 2011). During the sage-grouse annual cycle, multiple seasonal habitats are used that are generally grouped into three life stages: breeding (i.e., nesting and early brood-rearing), late brood-rearing (i.e., summer), and winter (Connelly et al., 2011b). To ensure the persistence of populations, sage-grouse require sufficient amount of all seasonal habitat requirements and a juxtaposition of seasonal habitats – including areas of connectivity required to maintain movement across all seasonal habitats (Connelly et al., 2000; Fedy et al., 2012).

In this study, I investigated the relative influence of structural connectivity and habitat suitability on lek size and stability of sage-grouse across Wyoming. First, a multi-seasonal

connectivity model was developed by using electric circuit theory to quantify the connectivity across an annual-habitat prioritization. Circuit theory is an effective means of modelling habitat connectivity and dispersal (e.g. Howey, 2011; Gimona et al., 2012; Walpole et al., 2012; Pelletier et al., 2014) as it is capable of integrating variable probabilities of connectivity throughout the whole landscape (Koen et al., 2014). Sage-grouse leks are locations where male sage-grouse perform displays of courtship during the breeding season. With the use of Circuitscape (McRae and Shah, 2011) – a software that applies electric circuit theory, I quantify structural connectivity for sage-grouse across their current distribution in Wyoming based on lek locations interpreted as “hotspots”. Researchers focus on the disappearance of active leks and annual changes in the number of males counted at a lek to determine declines in sage-grouse populations (Hess and Beck, 2012). Using sage-grouse male lek counts I examine the relationship between connectivity and lek size and variability, as well as habitat dependency across the last 15 years. Over the years, male lek count data have been useful for the assessment of change, used extensively for lekking species and known to relate to estimates of annual abundance of males (Connelly et al., 2004; Alonso et al., 2005; Warren and Baines, 2008; Fedy and Doherty, 2011; Broms et al., 2010; Fedy and Aldridge, 2011). Traditionally, peak (maximum) male counts have been used as the population index. A cyclic population can be defined as consisting repeated fluctuations in population numbers or oscillation in density across regular periods of ≥ 3 years (Berryman, 2002). A study conducted by Fedy and Doherty (2011) revealed that the sage-grouse male lek attendance in Wyoming possessed a cyclic nature with 6-9 years of regular periodicity consisting periods of population peaks and troughs. It is therefore beneficial to examine across both sage-grouse peak years and trough years in order to reduce declines and revive the sage-grouse populations in Wyoming.

5.2 Methodology

The current sage-grouse distribution in Wyoming covers approximately 68% of the state's total 253,000 km². I used a statewide annual-habitat model (Chapter 4) prioritizing the landscape across the current sage-grouse distribution in Wyoming along with sage-grouse lek locations to model structural connectivity of the landscape among leks. Male lek count data were used to examine the relationships between population size and structural connectivity. In addition to the annual-habitat model, I also used a statewide nesting habitat selection GIS model to test the dependence between habitat and structural connectivity for sage-grouse in Wyoming.

5.2.1 Data Acquisition and Preparation

The annual-habitat model used for this study has been acquired from a recent large-scale habitat prioritization (Chapter 4); in which, an annual (i.e., multi-seasonal) hierarchical prioritization of the landscape was produced for sage-grouse in Wyoming by combining three seasons of comprehensive habitat selection models – nesting, summer, and winter – developed in Fedy et al., (2014). The annual-habitat model consisted of a prioritization of the landscape ranging from 0 to 1 representing conservation value (i.e., habitat quality or suitability) at a 120 m spatial resolution acquired as a raster (grid based) model. Sage-grouse lek data were acquired from the Wyoming Game and Fish Department, and the individual nesting habitat selection model predictions were acquired from Fedy et al., (2014). Specific details on the development of the annual and the nesting habitat models can be found in Chapter 4 of this thesis and Fedy et al., (2014) respectively.

The annual-habitat model was a spatially continuous (raster grid) ranking of the landscape representing low to high (i.e., worst to best) conservation value based on habitat suitability (Moilanen et al., 2012). In order to assess structural connectivity throughout the

landscape, a resistance surface which represented low to high resistance (i.e., cost) was required instead of low to high suitability. Using raster math, I created a resistance grid by subtracting the annual-habitat model from its maximum cell value, so that it represents low to high resistance instead of suitability. The resulting resistance surface was then prepared as a TIFF raster file with a 250 m spatial resolution. The reason the resistance surface was resampled to a 250×250 m cell size was due to processing constraints and the computational limitations (memory, speed and landscape size) of the software; which limited solvable landscapes to < 6 million cells.

I quantified structural connectivity between a set of leks based on several criteria (population size, stability, quality of data) that were designed to select the largest leks that were consistently counted over the last 15 years (2000 - 2014). This was a sufficient timeframe to capture two complete population cycles (Fedy and Doherty, 2011, Fedy et al., in press). The criteria for the selection of leks were as follows: 1) leks with counts of males across more than 50 percent of the selected years (i.e., 2000 - 2014), 2) leks in which < 50 percent of these counted years observed zero individuals, and 3) leks in which the mean number of individuals counted between these years is > 10 . A set of 763 leks were identified which met these criteria across the sage-grouse distribution in Wyoming to use as connectivity nodes.

The annual habitat model was also resampled to match the 250 m resolution of the resistance surface and of the resulting connectivity model in order to calculate the correlation between connectivity and habitat. Similarly, as the lek-based nodes are directly associated with the nesting season, the individual nesting habitat model was also resampled to match the 250 m resolution to calculate the correlation between connectivity and nesting habitat. Both connectivity and habitat (annual and nesting) data were standardized using the R package *arm* (Gelman et al., 2011) during all statistical modeling in order to measure at the same numerical

scale. Furthermore, all nodes falling outside of the final connectivity distribution and in areas of no data were excluded; thus focussing only on 726 leks in the statistical analysis.

5.2.2 Structural Connectivity

Circuitscape 4.0 (McRae et al., 2013) identifies areas consisting of relatively high probability of use for movement corridors by applying electric circuit theory (Koen et al., 2014). This method highlights connectivity across a resistance surface (i.e., cost surface) similar to how an electric current moves through a circuit board (McRae et al., 2008; Koen et al., 2012). Rather than identifying single corridors between source and destination sites as in a least cost path analysis, this method considers all possible pathways between multiple defined points or polygons (i.e., nodes) with current flow analogous to random walkers on the landscape (McRae, 2006; McRae and Beier, 2007; McRae et al., 2008; Koen et al., 2012; Koen et al., 2014) . Circuitscape converts raster grids to electrical networks where each cell is a node, and resistors are used to connect adjacent cells to their immediate neighbors. In this study, the cell connection scheme was set to eight neighbors in order to connect all cells to their cardinal neighbors and their 4 diagonally adjacent cells across the resistance surface. I used the 763 lek locations as nodes – current sources – to model structural connectivity between these breeding hotspots. The one-to-all mode was selected which iterated across all 763 chosen leks before generating the final cumulative current map (i.e., connectivity model) as a continuous grid to calculate connectivity between nodes. During this mode, one lek location is connected to a 1-amp current source, while the remaining lek locations are grounded.

In order to quantify areas of high structural connectivity across the sage-grouse distribution, first the cumulative current map – the additive current map file generated in Circuitscape - was binned into 10 quantiles. I estimated the area used by the majority of sage-

grouse to be the sum of the mean distance from leks to nests (4.79 km) and the mean distance from nests to summer areas (8.07 km) (Holloran and Anderson, 2005; Fedy et al., 2012). Therefore, I calculated the average current based on a 12.86 km buffer at each node as a measure of connectedness of a lek. Similarly, I extracted the mean values within a 12.86 km buffer at each node location for the annual-habitat model and the individual nesting-habitat model. The approach used in this study for developing a predictive map for sage-grouse annual structural connectivity across Wyoming did not require separate connectivity models for each season and was not based on pairs of points. This methodology models current cumulatively across the sage-grouse distribution based on defined points with a one-to-all perspective across a multi-seasonal resistance surface using lek locations as sage-grouse origins of dispersal to test the influence of structural connectivity across breeding hotspots.

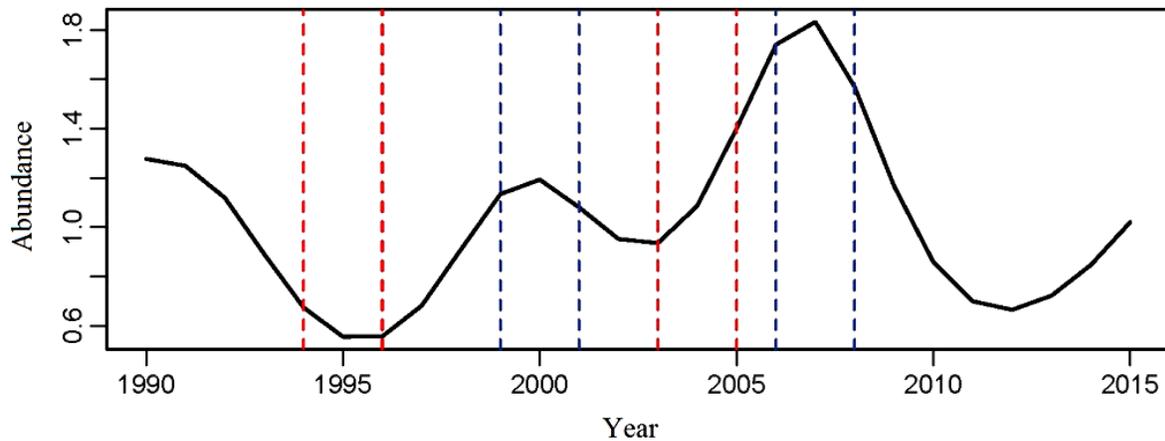


Figure 5.2-1 Sage-Grouse Population Abundance
 The red dashed lines highlight the two population trough periods (1994-1996 and 2003-2005) and blue lines highlight the population peak periods (1999-2001 and 2006-2008).

I summarized mean connectivity values across the binned current model and mean habitat values across both the annual and nesting models for the 726 buffered sites for three different time periods. The entire time series of interest from 2000 – 2014 was covered first, the second

time period represented known peak population years (1999 – 2001 and 2006 – 2008), and the third time period represented trough years (1994 – 1996 and 2003 – 2005; Fedy and Aldridge, 2011). First, the correlation between the connectivity model and habitat models (annual and nesting) were calculated. Then the relationship between structural connectivity and lek size (i.e., maximum male count at lek), and the relationship between structural connectivity and the coefficient of variation (relative standard deviation – a measure of heterogeneity or variation in counts) were examined by applying a linear model; in which annual and nesting models were also included as we control for habitat. A poisson generalized linear model was used to quantify the influence of mean current (binned) plus the mean habitat value on peak (i.e., maximum) male counts at each of the buffered lek locations (hereafter: sites or hotspots). The coefficient of variation of counts were calculated at each site and a generalized linear model was applied to the coefficient of variation as a function of mean current (binned) plus the mean habitat value within each site.

Furthermore, I tested for evidence that indicate the need to account for a spatial correlation by plotting the model residuals using the spatial coordinates for the entire time series of interest (2000 – 2014) with lek size as the response variable. To plot residuals, I applied a bubble plot – which presents a qualitative way of determining spatial correlation – using the *sp* R package. For a more quantitative approach, I applied the variogram function in the *gstat* R package to test semivariance – which presents a measure of spatial correlation at different distances. All statistical analyses were performed in R statistical software version 3.1.2 (R Foundation for Statistical Computing, Vienna, Austria) and all spatial analysis, pre-processing and post-processing were carried out in ArcMap 10.1 (Environment Systems Research Institute, Redlands, California).

5.3 Results

The structural connectivity model developed in this study (Figure 5.3-1) parsed the study area into regions of high and low connectivity (i.e., current) by assigning each pixel a value representing the amount of current flow ranging from 0 – 1 (low to high connectivity). Current flow was not strongly correlated with annual habitat quality ($r = 0.33$; see Figure 5.3-2) or nesting habitat quality ($r = 0.31$; Figure 5.3-2). It was evident from the bubble plot and variance estimates (see Appendix B and C) that a strong spatial correlation structure did not exist in the data. Therefore, a spatial autocorrelation was not conducted.

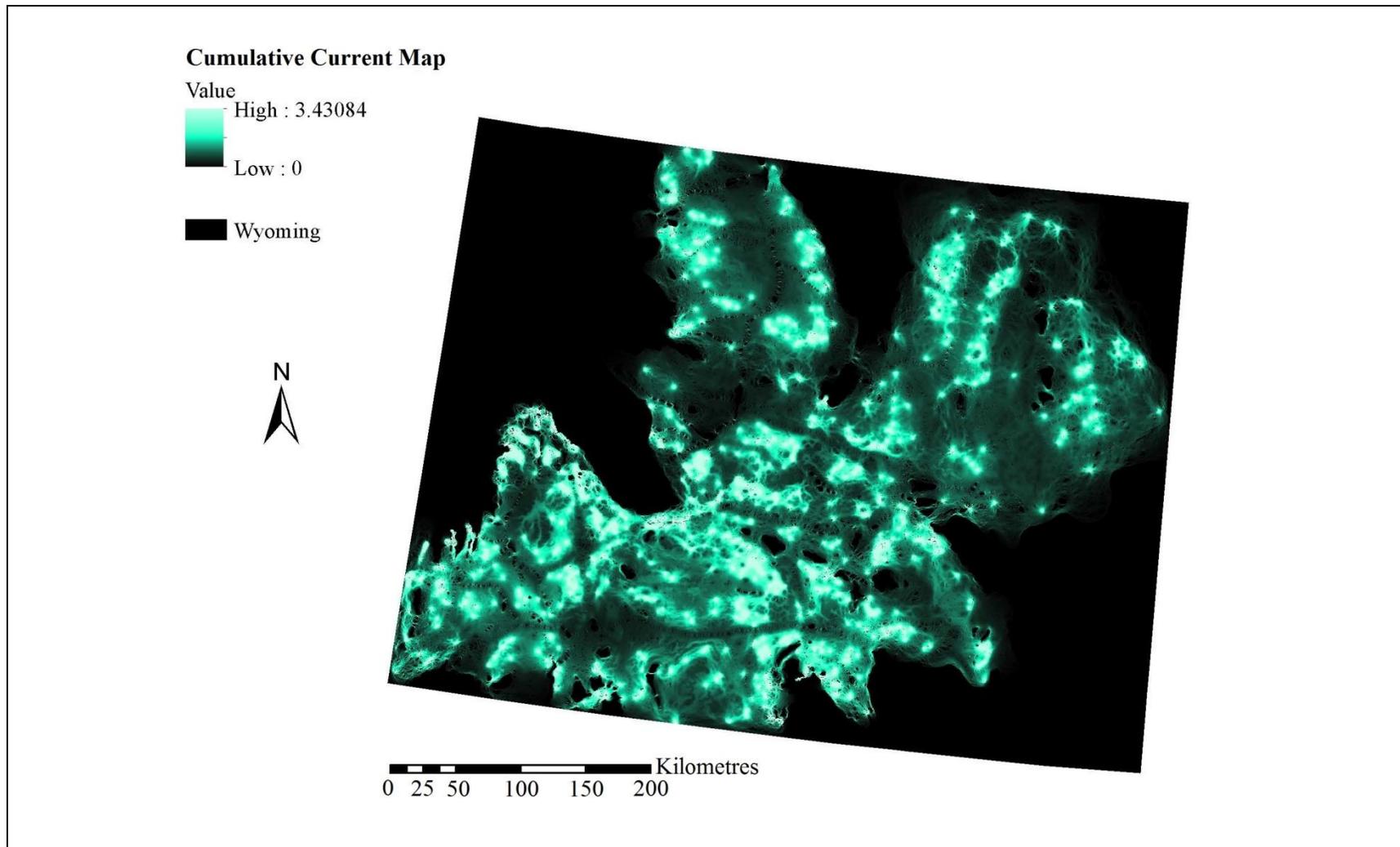


Figure 5.3-1. Wyoming Sage-Grouse Structural Connectivity

Cumulative current map produced by applying electric circuit theory on the multi-seasonal habitat resistance surface. Low to high structural connectivity is represented by low to high cell values across the current sage-grouse distribution in Wyoming at a 250 m spatial resolution using an Albers Conical Equal Area Projection. In order to visualize the currents distribution better, the nodes are masked and the visual contrast is improved by applying a stretch (type = standard deviation; $n = 2.5$) using ArcMap 10.1 and classified with a colour ramp representing low to high structural connectivity across the continuous grid.

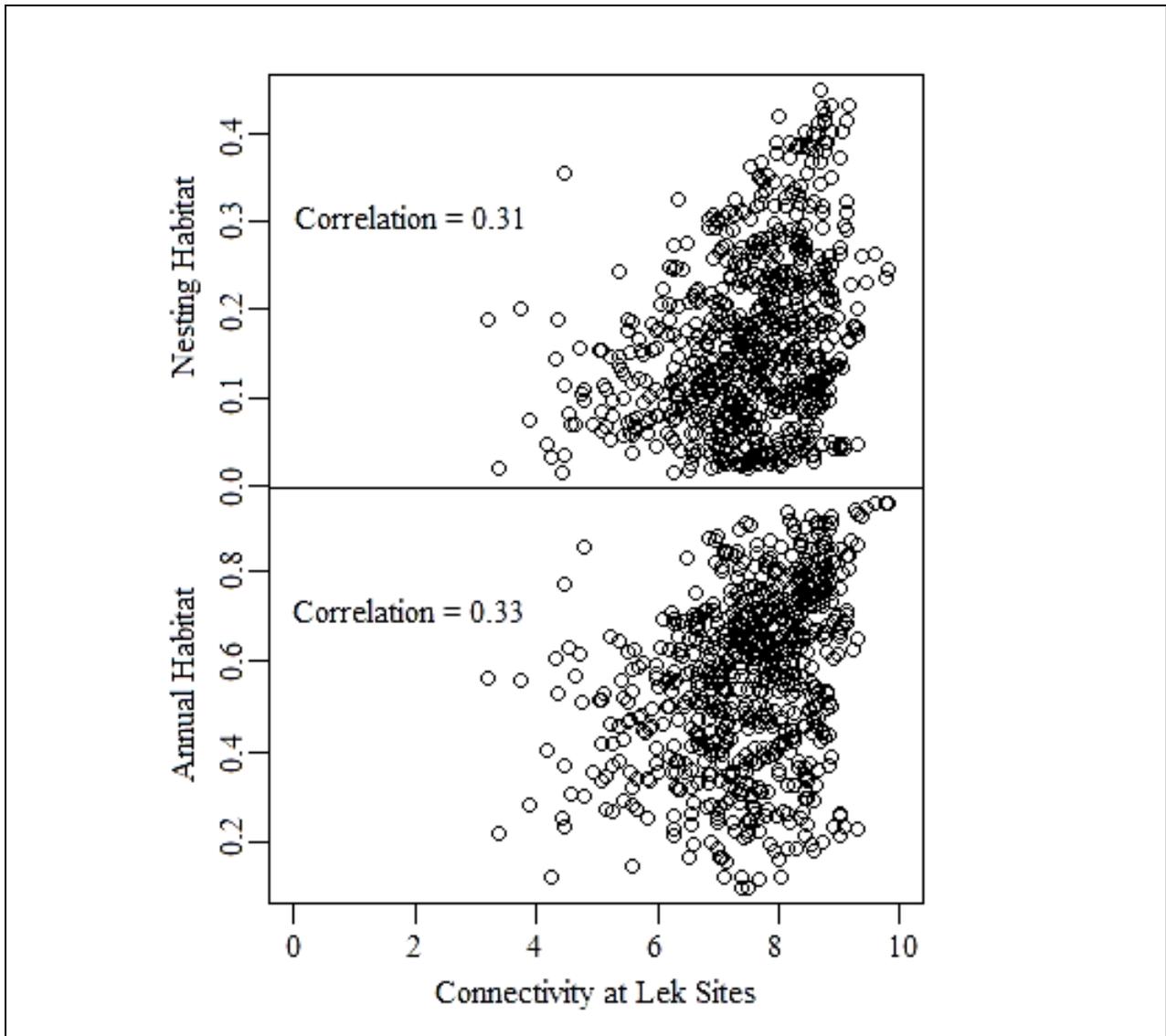


Figure 5.3-2. Correlation between Structural Connectivity and Habitat

The x-axis represents the mean structural connectivity values extracted from the binned cumulative current grid at a 12.86 km buffer and the y-axis represents the mean annual and nesting habitat values at each of the 726 buffered lek sites. Similarly weak correlations exist between both connectivity and annual habitat (0.33), and connectivity and nesting habitat (0.31).

Increasing connectivity is associated with decreasing variability in lek counts and increasing abundance at lek sites when lek counts were summarized over the whole time period (2000 and 2014; Table 5.3-1 and Table 5.3-2) while controlling for both annual and nesting habitat quality. Furthermore, when examining the influence of structural connectivity on lek size

Table 5.3-1. Coefficient Estimates for Connectivity and Maximum Counts.

Coefficient estimates produced by applying a generalized linear model. The response variable is peak male counts (maximum count) at each lek site from 2000 – 2014 (all years). Peak period 1 and 2 represent 1999 to 2001 and 2006 to 2008 respectively. Trough period 1 and 2 represent 1994 to 1996 and 2003 to 2005 respectively. The predictor variable is connectivity. Table includes both annual and nesting habitat models.

Year	Model	Connectivity			Habitat		
		Coefficient	SE*	Pr (> t)*	Coefficient	SE*	Pr (> t)*
All Years	Annual	0.103	0.010	< 0.001	0.407	0.010	< 0.001
Peak Period 1	Annual	0.090	0.014	< 0.001	0.294	0.014	< 0.001
Peak Period 2	Annual	0.147	0.011	< 0.001	0.439	0.010	< 0.001
Trough Period 1	Annual	0.065	0.027	0.016	0.280	0.026	< 0.001
Trough Period 2	Annual	0.125	0.012	< 0.001	0.352	0.012	< 0.001
All Years	Nesting	0.071	0.010	< 0.001	0.501	0.009	< 0.001
Peak Period 1	Nesting	0.090	0.014	< 0.001	0.317	0.013	< 0.001
Peak Period 2	Nesting	0.107	0.010	< 0.001	0.551	0.009	< 0.001
Trough Period 1	Nesting	0.108	0.026	< 0.001	0.219	0.024	< 0.001
Trough Period 2	Nesting	0.070	0.012	< 0.001	0.513	0.011	< 0.001

SE* standard error

Pr (>|t|)* p-value

Table 5.3-2. Coefficient Estimates for Connectivity and the Coefficient of Variation.

Coefficient estimates produced by applying a generalized linear model. The response variable is the coefficient of variation at each lek site from 2000 – 2014 (all years). Peak period 1 and 2 represent 1999 to 2001 and 2006 to 2008 respectively. Trough period 1 and 2 represent 1994 to 1996 and 2003 to 2005 respectively. The predictor variable is connectivity. Table includes both annual and nesting habitat models.

Year	Model	Connectivity			Habitat		
		Coefficient	SE*	Pr (> t)*	Coefficient	SE*	Pr (> t)*
All Years	Annual	-6.870	2.255	0.002	5.440	2.255	0.016
Peak Period 1	Annual	-15.131	4.840	0.002	8.700	4.840	0.073
Peak Period 2	Annual	-12.182	2.862	< 0.001	1.626	2.862	0.570
Trough Period 1	Annual	-8.133	5.993	0.176	-20.978	5.993	0.001
Trough Period 2	Annual	-12.604	4.079	0.002	8.819	4.079	0.031
All Years	Nesting	-4.869	2.243	0.030	-0.622	2.243	0.782
Peak Period 1	Nesting	-14.322	4.793	0.003	6.794	4.793	0.157
Peak Period 2	Nesting	-11.620	2.838	< 0.001	-0.083	2.838	0.977
Trough Period 1	Nesting	-14.429	5.895	0.015	-5.611	5.895	0.342
Trough Period 2	Nesting	-9.487	4.051	0.02	-0.716	4.051	0.86

SE* standard error

Pr (>|t|)* p-value

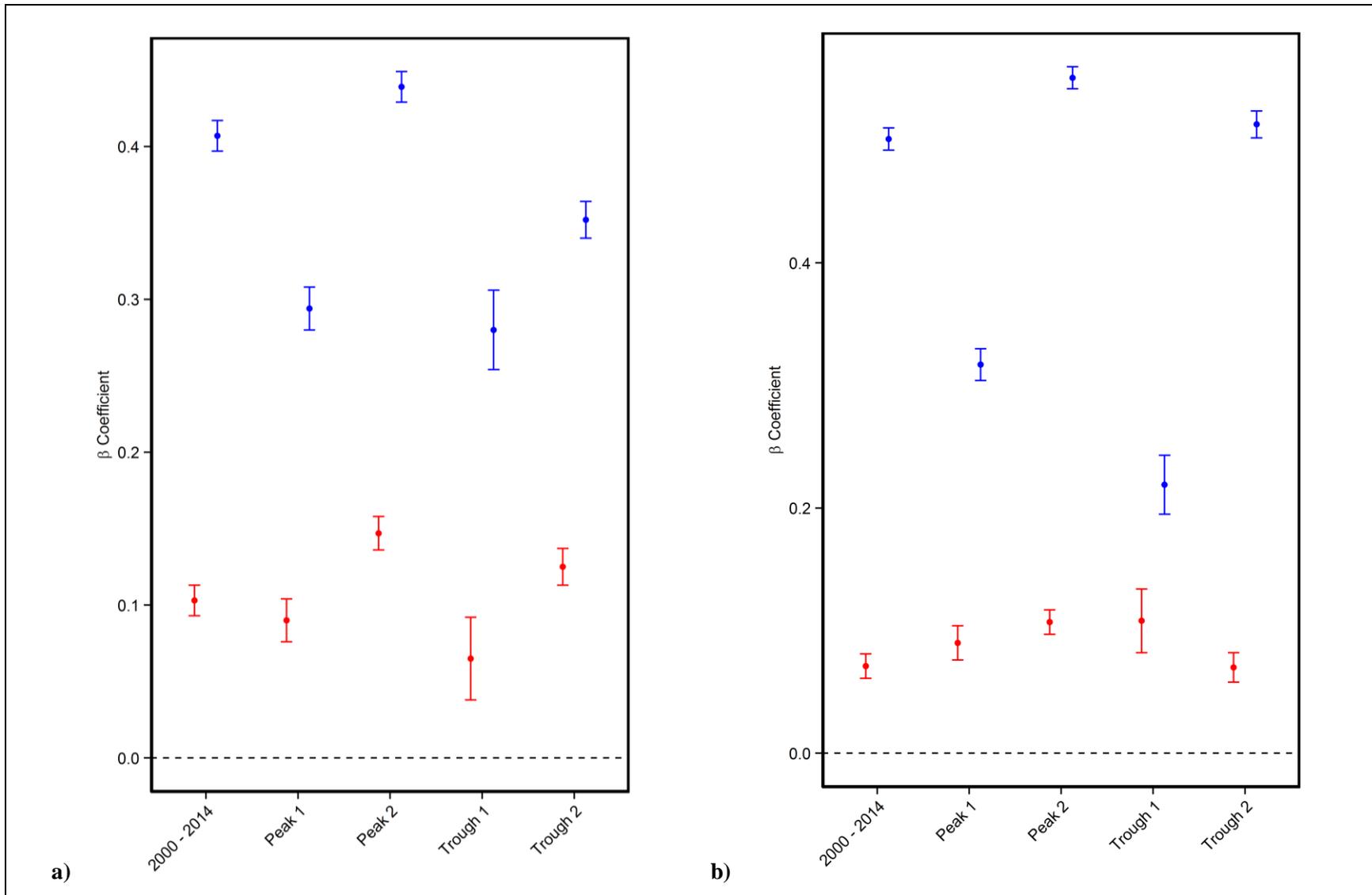


Figure 5.3-3. Coefficient Estimates. Standardized coefficient estimates and standard errors for all time periods. Plot **a)** focuses on the annual model, and plot **b)** focuses on the nesting model. Connectivity estimates are in (red) and habitat in (blue). Both plots represent maximum male counts. Peak 1 and 2 represent 1999 to 2001 and 2006 to 2008 respectively. Trough 1 and 2 represent 1994 to 1996 and 2003 to 2005 respectively.

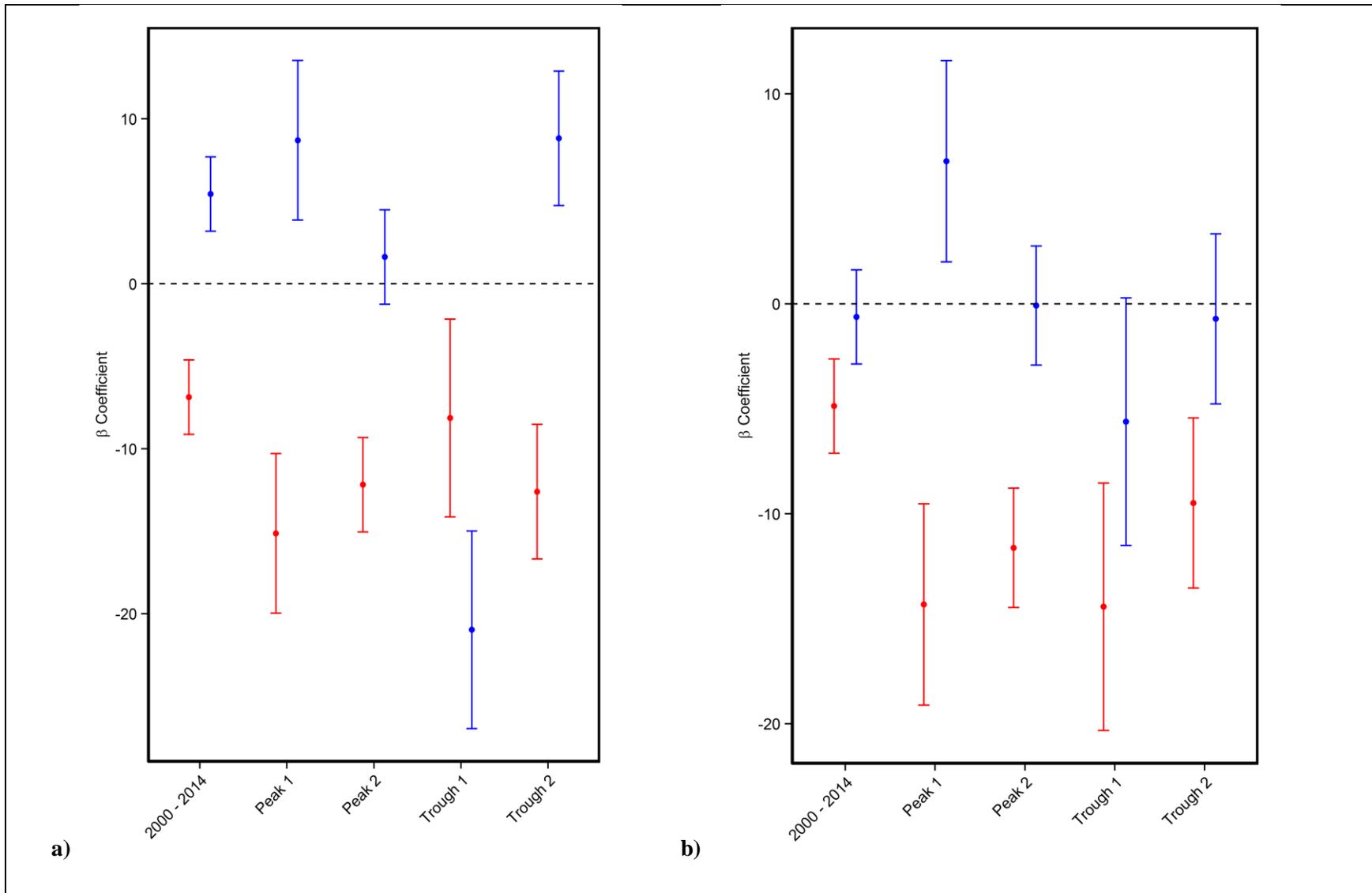


Figure 5.3-4. Coefficient Estimates. Standardized coefficient estimates and standard errors across all time periods. Plot **a)** focuses on the annual model, and plot **b)** the nesting model. Connectivity estimates are in (red) and habitat in (blue). Both plots represent coefficient of variation at leks. Peak 1 and 2 represent 1999 to 2001 and 2006 to 2008 respectively. Trough 1 and 2 represent 1994 to 1996 and 2003 to 2005 respectively.

and variation for sage-grouse peak years (1999 – 2001 and 2006 - 2008) and trough years (1994 - 1996 and 2003 - 2005) in Wyoming, the model results were consistent with those across the full time series (2000 – 2014; Table 5.3-1 and Table 5.3-2). Based on the model coefficients, for peak and trough years, positive estimates were observed for maximum counts, and negative estimates were observed for the variation in counts (Table 5.3-1, Table 5.3-2, Figure 5.3-3 and Figure 5.3-4). Overall, while lek size and count variation consist a level of dependence on the individual nesting habitat model as well as the annual habitat model across all examined years, the p-values suggest significance in structural connectivity for maximum counts and variation of counts across all sites during all examined time periods. Thus, lek sites with greater connectivity exhibited larger and more stable populations independent of habitat.

5.4 Discussion

This study developed a structural connectivity model and tested the importance of structural connectivity for population abundance and variability at breeding hotspots (i.e., lek sites). Connectivity demonstrated a low correlation with annual ($r = 0.33$) and nesting habitat ($r = 0.31$). Current flow was observed to have an impact on sage-grouse lek size and variability. Therefore, I found that the structural connectivity of the landscape is beyond simple summarization of habitat availability.

While habitat quality is a main factor influencing species persistence, species dispersal across the landscape is beneficial for numerous ecological reasons, such as for survival during local catastrophes (Olivieri et al., 1995; Parvinen et al., 2003; Kun and Scheuring, 2006), climate change (Heller and Zavaleta, 2009), dealing with predation, competition (Perrin and Goudet, 2001) and demand for resources (Cushman et al., 2013). This study – based on multiple seasons – indicated that increasing sage-grouse structural connectivity is associated with increased

abundance (maximum male counts at leks), and a decrease in variability in lek counts; thus signifying greater population stability at sites of high structural connectivity. Therefore, the trends and model coefficients produced in this study support past research studies that have indicated the potential of corridors to enhance population viability and reduce stochastic temporal variation in local population sizes with the ability to cause stable population dynamics and declines in local extinctions (Brown and Kodric-Brown, 1977; Gonzalez and Chaneton, 2002; Haddad and Tewksbury, 2006).

Animal populations fluctuate through time particularly for cyclic species, and sage-grouse populations in Wyoming demonstrate cyclic population cycles (Fedy and Doherty, 2011). Model results indicated that the relationship between structural connectivity and maximum counts as well as variation in counts at lek sites similarly extended through all examined years. Even across years of decline, areas of higher density exhibited high levels of connectedness and low variability in counts. These results are indicative of positive density dependent dispersal for sage-grouse in Wyoming. Overall in this study, connectivity is observed to maintain a positive influence during both peak and trough years highlighting the significance of structural connectivity across the landscape at all times. Although the structural connectivity will not always increase dispersal (Haddad, 2009) presumably connectivity would be more important when there is more dispersal. For example, under the assumption that rates of dispersal are not consistent throughout a cycle, I would expect changes in the importance of connectivity across the years. Unfortunately not much data are currently available with regards to sage-grouse dispersal and the majority of available studies focus mostly on dispersal and migratory movements in relatively small areas across its range on small numbers of individuals (Connelly et al., 1988; Connelly et al., 2011a). Information regarding sage-grouse temporal changes in

dispersal – rates of dispersal across population peaks and troughs to be more specific – would allow for a better elucidation of structural connectivity and dispersion on cyclic population dynamics. In any case, another study conducted by Knick and Hanser (2011) also found that larger and more connected leks with lower levels of disturbance persisted during population declines in the Columbia Basin sage-grouse management zone from 1965-1979 to 1998-2007. Thus, structural connectivity is an essential factor contributing to the persistence of sage-grouse populations overall, and should be considered in conservation plans to strive for optimal conservation results amid disturbances in complex landscapes.

My results indicate that connectivity is important for both high as well as low densities, and this is of interest as the influence of connectivity across multiple densities is seldom assessed. In the most typical cases in conservation, smaller populations possess rare dispersal and lower population growth rates, where corridors are expected to facilitate higher numbers of organisms at patches maintaining stability in population dynamics and reducing local extinctions (Brown and Kodric-Brown, 1977; Gonzalez and Chaneton, 2002; Haddad and Tewksbury, 2006). Many populations of sage-grouse have exhibited patterns of density dependent fluctuations (Garton et al., 2011; Stevens et al., 2012). According to numerous theoretical studies, the rate of dispersal is a decreasing function of dispersal cost (Travis et al., 1999; Poethke and Hovestadt, 2002; Cadet et al., 2003; Parvinen et al., 2003; Poethke et al., 2003; Kun and Scheuring, 2006). In some cases, organisms tend to disperse when they reach a certain threshold in local population density. However, with increasing dispersal costs, the threshold value is also known to increase (Poethke and Hovestadt 2002; Kun and Scheuring 2006). Therefore, enhancing structural connectivity can reduce dispersal costs and prevent density thresholds from increasing, which could have a significant affect during years of population

declines by increasing movements from high to low density areas and maintaining active leks; thus preventing local extinctions.

Connectivity has often been equated to the spatial contagion of habitat and typically measured with an analysis of physical structure without any significant reference to species movement or habitat processes associated across the landscape (Crooks and Sanjayan, 2006). In contrast, while this study does not directly use species movement data to generate connectivity, a multi-seasonal habitat model was used as the underlying basis for the resistance surface; thus incorporating a multitude of habitat information covering the full annual cycle. My model results indicated sage-grouse maximum male counts and variability in lek size differed between the relative probability of habitat use and structural connectivity across the landscape – with higher coefficients (Table 5.3-1, Table 5.3-2, Figure 5.3-3, Figure 5.3-4) in habitat for both annual and nesting habitat models. This indicated that larger lek sizes are consistently occurring in areas of high habitat use across all time periods, and high population densities may lead to competition for resources and high quality habitat; therefore may result in dispersal of individuals. Prioritizing structural connectivity can increase the rates of movement from high-density to lower-density, thereby reducing stochastic temporal variation in population sizes (Haddad and Tewksbury, 2006).

My results for the coefficient of variation across all models were not consistent – particularly for habitat use, coefficients were not all negative. Therefore a high variation existed in the coefficient estimates for variability of counts. According to the literature, populations exhibiting high variability are more prone to extinction compared to populations showing low variability (Pimm, 1991, Belovsky et al., 1999, Vucetich et al., 2000). With increasing levels of habitat use, variability of lek counts was observed to increase across the annual habitat model.

This is likely due to the representation of individuals across the combination of different seasons (i.e., multi-seasonal model; Chapter 4). Furthermore, the same trends of coefficient of variation were not seen across the individual nesting habitat model. This is likely due to the fact that the nesting habitat model is more of a direct representation of lek locations; thus spatially corresponding with lekking sites better than the annual habitat model which is a combination of nesting, summer and winter seasonal habitat models representing an equally balanced coverage of all seasons (Chapter 4). However, an analysis across a multi-seasonal model (i.e., annual habitat) is likely more important for functional connectivity over the traditional single season approach focusing on the nesting habitat. For example, Row et al., (2015) found both the nesting and winter habitat to be important for functional connectivity as they drove effective dispersal patterns for sage-grouse in Wyoming. Furthermore, the nesting habitat selection model was tested in Fedy et al., (2014) by using the lek sites and telemetry data as a proxy to assess nesting model performance, where the predicted nesting habitat model corresponded with the lek locations and captured a substantial number of leks. Therefore, this justifies the importance of assessing structural connectivity across both annual and nesting habitat models in this study. Based on this, structural connectivity has a more positive influence on lek size and variability overall than habitat. Thus, the inclusion of areas of high structural connectivity in landscape prioritizations will likely lead to increased stability at leks. However, it is also important to note that the nesting habitat model is a RSF model while the annual habitat model is a hierarchical ranking of the landscape ranging from 0 (low) to 1 (high) multi-seasonal suitability. Therefore, these models were not directly comparable and were standardized and centred around the mean in order to measure at the same numerical scale so that the interactions between the variables were more interpretable (Gelman, 2008).

Prioritizing structural connectivity could result in restored lek sizes causing higher, more stable rates of population abundance during years of decline and possibly improve rates of abundance across the full cycle. As a landscape prioritization based only on habitat would not directly capture significant areas of connectivity in the process, conservation plans prioritizing critical areas for sage-grouse must identify and incorporate areas of high structural connectivity in addition to good quality usable habitat in order to ensure meta-population connectedness is accounted for. Facilitating structural connectivity in an area with increasing developments and fragmentation has the potential to mitigate impacts of disturbances and reduce declines. In areas of high density, the protection and maintenance of connectivity facilitating dispersal is critical for providing relief of pressure over resources (e.g., sagebrush). When prioritizing seasonal habitats, managing for annual connectivity is necessary in order to spatially define all seasonal area requirements to effectively manage across all life stages. Therefore, identifying and analyzing structural connectivity across the annual cycle is highly beneficial for sage-grouse and other sagebrush associated species. Based on the model coefficients, the structural connectivity of the landscape is significant and more consistent across all years while the role of habitat influencing the variability of lek counts was equivocal across all years and models. Prioritizing areas of high structural connectivity is consistently beneficial all the time as it has revealed a significant positive influence on population abundance and stability at lek sites over both peak periods and periods of decline. Thus, I conclude that the structural connectedness of the landscape exhibits value beyond habitat quality and needs to be considered in conservation plans to strive for optimal conservation results amid disturbances in complex landscapes. It would be highly beneficial to identify and incorporate areas of high structural connectivity in sage-grouse

habitat prioritizations when identifying core areas for management in order to protect and revive populations of sage-grouse in Wyoming.

Chapter 6 Summary and Conclusions

6.1 Chapter 4 Summary of Findings

- The correlation coefficient indicated that relative probability of habitat use does not correlate well across seasons, although a higher correlation was found between nesting and summer habitat and the lowest correlation was between summer and winter.
- Based on the annual habitat prioritization, none of the individual seasons dramatically surpassed other seasons as a result of equal weighting and Zonation's built-in repeated range-size normalization. Approximately 56-60% of the top 25% of each individual season was captured within the top 25% of the annual habitat.
- The highest quality annual habitat (5% quantile area) contained less than 50 % of each of the highest quality individual seasonal habitat, and increasing fractions of all seasonal quantiles were contained within the larger quantile areas across the annual habitat; which was likely due to the increasing probability of seasonal overlap with increasing ground coverage.
- Different levels of habitat use were contained within each of the top seasonal quantiles that made up the annual quantiles; thus, a habitat prioritization based solely on the high priority areas of a single season would not cover requisite areas across other seasons unless a significant amount of seasonal overlap existed across the landscape.
- Based on the low levels of spatial overlap detected between seasons and within the annual priority areas, it is further evident that a single season approach would not be sufficient to act as a surrogate to spatially account for all annual sage-grouse needs.
- The CBAs and CMAs capture more nesting priority areas than the other seasonal components in addition to failing to capture large amounts of the annual (multi-seasonal)

priority areas. Therefore, Wyoming's current core area strategy leaves out a considerable amount of the best habitat from individual seasons.

- The ranking of the CMAs revealed that even the largest breeding-based areas are not as highly suited to protect important habitat across the annual cycle.
- The CMAs currently provide protection to 59.89% of the top 5% annual habitat in which 76.55% of the large expanses of spatially continuous annual habitat are captured; therefore protected under the core area strategy.
- The CMA ranking in this study does not advocate the dismissal of low ranked core areas; instead it is aimed to highlight the significance and efficacy of a multi-seasonal approach.

6.2 Chapter 5 Summary of Findings

- Increasing connectivity was associated with increasing abundance and decreasing count variability at leks signifying population stability at areas of high structural connectivity.
- Trends between structural connectivity and maximum counts as well as variation in counts extended similarly across all years, maintaining a positive influence during both peak and trough years; thus highlighting the significance of structural connectivity at all times.
- Sage-grouse maximum male counts and variability in counts exhibited higher coefficients in habitat use – than for connectivity – for both annual and nesting habitat models.
- The coefficient of variation was not consistent across all models; particularly for habitat use, the variability was not all negative across the annual model – likely due to the combination of multiple seasons integrated in the annual model.
- The nesting habitat is a RSF model while the annual habitat model is a hierarchical ranking of the landscape from 0 to 1. Therefore, these models were not directly comparable.

- Structural connectivity is significant and more consistent across all years while habitat influencing the variability of lek counts was equivocal across all years and models.
- The structural connectedness of the landscape therefore exhibits value beyond habitat quality and must be considered in conservation plans to strive for optimal conservation results amid disturbances in complex landscapes.
- Prioritizing structural connectivity could result in restored leks and larger, more stable lek sizes during years of decline; possibly improving population growth rates across the full cycle.

6.3 Overall Conclusion and Recommendations

Wyoming's breeding-based protected areas for the conservation of sage-grouse captured more nesting priority areas than the other seasonal components while the annual habitat model prioritized substantial fractions of each season with equal consideration; thus demonstrating the significance and efficacy of a multi-seasonal approach over a single season approach when identifying conservation priority areas. While the state-identified protected areas attempt to balance between developments and the needs for sage-grouse conservation, a considerable amount of the best habitat from individual seasons were left out. The state-wide annual habitat prioritization represents a hierarchical ranking of the landscape identifying areas of low to high conservation value across all life stages; thus making it possible to direct conservation efforts to areas of best habitat for multiple life stages, while areas of low-priority across the annual habitat indicates high potential for other land uses. The quantitative method of spatial conservation prioritization I used to develop the annual habitat model clearly demonstrated that it was capable of combining multiple seasonal habitats with equal importance; simultaneously accounting for

areas of multi-seasonal suitability. The ability of multi-seasonal core areas to better safeguard and prevent further declines of a species by protecting habitats best suitable for persistence across all seasons will undoubtedly hinge habitat prioritization and core area implementation.

Furthermore, my research indicates that the structural connectivity across the landscape exhibits value beyond habitat quality; therefore areas of high structural connectivity should be included in landscape prioritizations in order to enhance density dependent dispersal needs and strive for optimal conservation results amid disturbances across complex landscapes. Structural connectivity has a positive influence on population stability as it is associated with increasing abundance and decreasing variability in counts across years of high population as well as years of population declines. Therefore, my research supports existing studies that have indicated the potential of corridors to enhance population viability and reduce stochastic temporal variation; thus signifying the importance of prioritizing areas of high structural connectivity for reviving and conserving sage-grouse in Wyoming.

Overall, my research presents one of the largest annual habitat prioritizations and landscape-level analysis of connectivity conducted to date for sage-grouse by combining multiple state-wide comprehensive seasonal habitats in an ecologically meaningful way, which can be utilized for a more robust delineation of sage-grouse core areas across the annual cycle. With the use of seasonally explicit state-wide data including multiple biological factors, we can expect more biological rigour resulting in optimal conservation efforts.

6.4 Recommendations for Future Research and Conservation Efforts

While the current sage-grouse management strategy in Wyoming captures and protects considerable amounts of seasonal habitats with the resources that were available, my results found that the protected areas have room for improvement and can be refined significantly by

using a comprehensive multi-seasonal habitat prioritization to serve as the underlying surface for protected area delineation. In addition to delineating core areas for protection across multiple seasons, it would be highly beneficial to also identify and incorporate areas of high structural connectivity in sage-grouse habitat prioritizations when identifying core areas for management in order to protect and revive populations of sage-grouse in Wyoming. Next steps would be to model structural connectivity between protected areas (i.e., core areas) and perhaps also across state boundaries connecting to core areas in neighboring states. With advanced technologies, modeling techniques and less computational limitations, a multi-seasonal approach is now more achievable; therefore conservation efforts should strive to account for species' requirements across its full annual cycle. Future research should also focus on the temporal changes in dispersal across a full cycle to obtain dispersal patterns for peak years as well as years of decline, so that a better understanding of structural connectivity and dispersion on cyclic population dynamics could be achieved.

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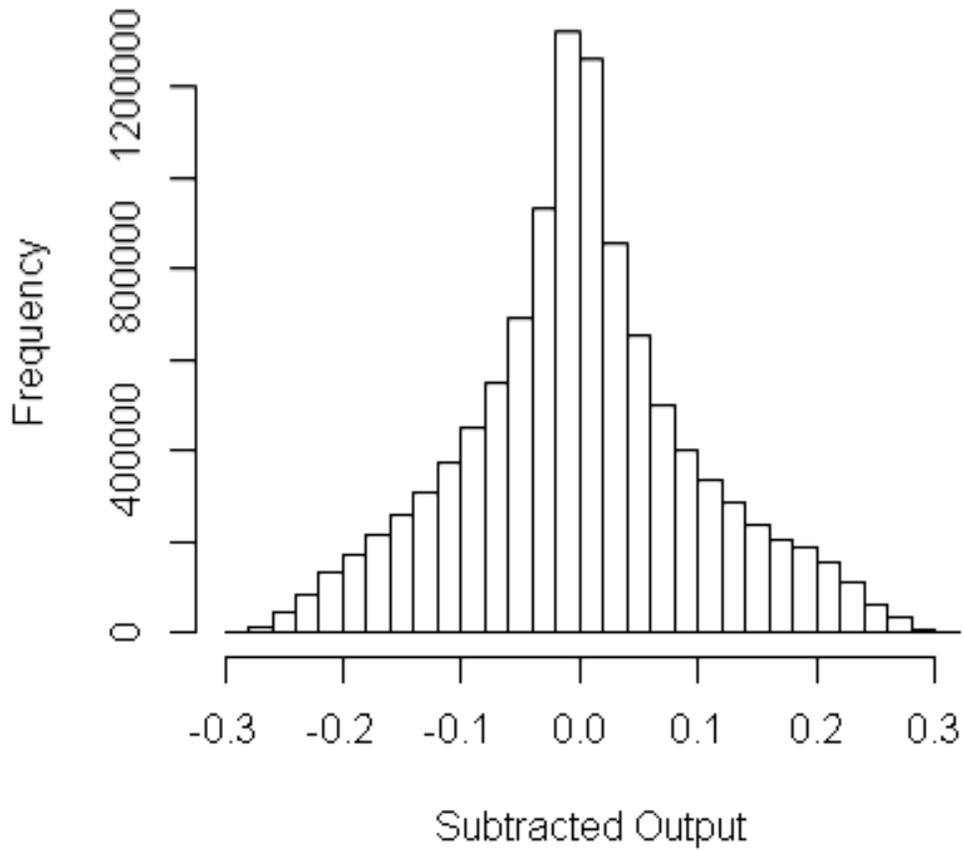
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Appendix A

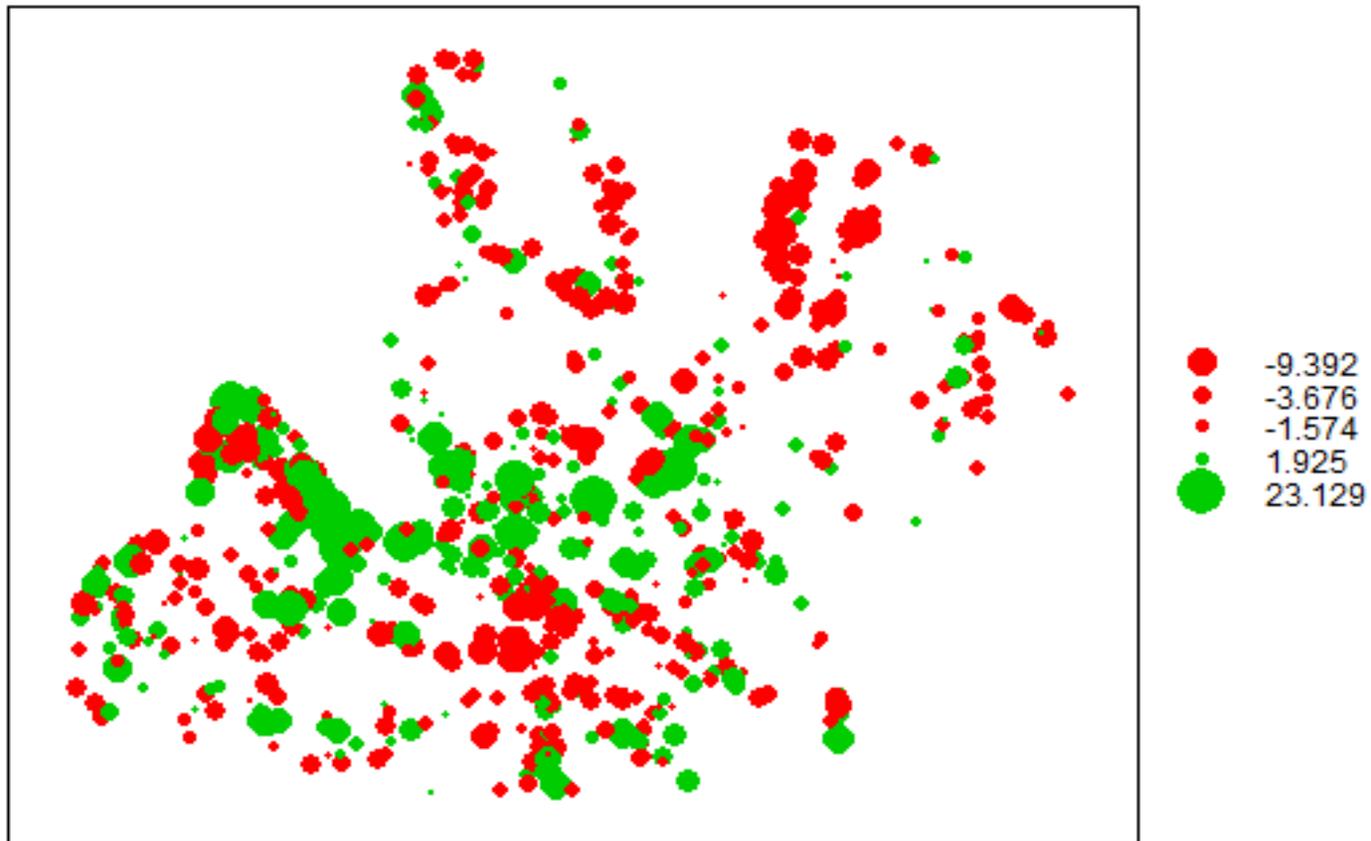
Histogram of the ranked and rescaled overlay grid cell values subtracted from the Zonation output grid cell values.



Appendix B

The model residuals for the full time series (2000 – 2014) plotted by their spatial coordinates using the bubble function in the R package *sp*.

Residuals



Appendix C

An estimate of semivariance by applying the variogram function (R package *gstat*) on the model residuals for the full time series (2000 – 2014) plotted by their spatial coordinates.

